

## **A word from the editor**

The book series “MARINE ECOLOGY – A Comprehensive Treatise on Life in Oceans and Coastal Waters” (organized and edited by Otto Kinne and contributed to by numerous outstanding experts over years) is now freely available with online Open Access.

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The technical problems involved in the re-publication of the Treatise were mastered by Konstantin Kambach (Inter-Research). Unavoidably, the print quality of the final product is somewhat inferior to the original.

Otto Kinne

Oldendorf/Luhe  
29.04.2008



# MARINE ECOLOGY

A Comprehensive, Integrated Treatise on Life in Oceans  
and Coastal Waters

Editor

OTTO KINNE

*Biologische Anstalt Helgoland  
Hamburg, West Germany*

VOLUME I

Environmental Factors

Part 2

1971

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# INTRODUCTION

## to the

## TREATISE

No words can introduce a Treatise on Marine Ecology more adequately than those by JOHANN WOLFGANG VON GOETHE<sup>1</sup> (1749–1832). I am quoting here the German text, as well as a favourite English translation by JOHN ANSTER:

<p>'Alles ist aus dem Wasser entsprungen!!          Alles wird durch das Wasser erhalten!          Ozean, gönn uns dein ewiges Walten.          Wann du nicht Wolken sendetest,          Nicht reiche Bäche spendetest,          Hin und her nicht Flüsse wendetest,          Die Ströme nicht vollendetest,          Was wären Gebirge, was Ebenen und Welt?          Du bist's, der das frischeste Leben erhält.'</p>	<p>'In Water all hath had its primal source;          And Water still keeps all things in their course.          Ocean, still round us let thy billows proud          Roll in their strength—still send up mist and cloud.          If the rich rivers thou didst cease to spread—          If floods no more were from thy bounty fed—          And the thin brooklet died in its dry bed—          Where then were mountains—valleys? Where would be          The world itself? Oh! thou dost still, great Sea,          Sustain alone the fresh life of all things.'</p>
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To modern science, the field of ecology comprises studies of organisms in relation to their environment, abiotic and biotic. Marine ecology is a branch of ecology dealing with the vast multiplicity of organisms living in oceans and coastal waters. The present treatise attempts to cover all major aspects of marine ecology. It consists of several volumes which, for convenience, in some cases have been subdivided into parts. At present 5 volumes are envisaged:

- Volume I —Environmental Factors
- Volume II —Physiological Mechanisms
- Volume III—Cultivation
- Volume IV —Dynamics
- Volume V —Ocean Management

Environmental Factors is introduced on the following pages (Foreword). Volumes II to V are presently being organized and are scheduled to be published in the next few years.

Physiological Mechanisms will deal with support mechanisms, such as photosynthesis, respiration, reproduction; timing mechanisms, e.g. biological clocks, rhythms; orientation mechanisms; regulatory mechanisms, e.g. volume-, ion-, turgor-, osmo- and thermo-regulation; mechanisms of adaption; and communication mechanisms, such as sound production and perception, as well as visual and chemical communications.

Cultivation will be concerned with maintaining, raising, rearing and breeding marine and brackish-water organisms in laboratories, ponds, under-sea farms, restricted sea areas, etc., both for scientific and economic purposes; this volume will also include sections on technical aspects and diseases.

<sup>1</sup> Werke (Hamburger Ausg., 4th ed.) Vol. 3. Faust. Part 2, p. 255. Wegner, Hamburg, 1959.

Dynamics will focus on production, transformation and decomposition of organic matter in the marine environment; population dynamics; food-chain relations; nutritional requirements; as well as on flow and balance of energy and matter.

Ocean Management—a rather ambitious term for a young and virgin aspect of marine ecological research—will present a brief synopsis of important taxonomic groups, zonations, organismic assemblages; sea-water pollution (sources, biological consequences, avoidance, control, conventions); organic resources of the seas (distribution, use, control, conservation); and a general discussion concerning possible ways and means for management of important sea areas.

A comprehensive, integrated treatise on life in oceans and coastal waters cannot be written by a single author; it must draw from a multitude of talents and sources, and hence requires interdisciplinary and international co-operation. Neither a compendium nor an encyclopaedia, the treatise is intended to be an exhaustive systematic exposition summarizing and evaluating information obtained thus far on living systems in the seas and littoral areas. It has been conceived with the growing number of individuals in mind who are professionally concerned with life in the marine environment, especially investigators, engineers, teachers, students, administrators and businessmen. Although, for the benefit of the reader, integrated into a methodically arranged general concept, each contribution is intended to represent a detailed, authentic critical account in its own right; all contributors are free in choice of material and emphasis.

The first tentative outline of the treatise was circulated among several hundred marine ecologists in November, 1965. The warm response received from the international scientific community and the stimulating support from the publishers have encouraged me to proceed with my plans. Criticism, advice and assistance of numerous colleagues have greatly affected and improved the first proposal. I gratefully acknowledge all this support. It is not possible to list here the names of even the most active supporters; they will be mentioned in the forewords to the respective volumes.

A treatise such as this needs continued criticism and advice. Any comments—especially on outline, coverage and new points of view—will be most welcome.

O. KINNE

FOREWORD  
to  
VOLUME I: ENVIRONMENTAL FACTORS

'Environmental Factors' summarizes and evaluates all important information available to date on the responses of ocean and coastal-water living organisms to intensity variations of the major abiotic and biotic ecological factors. It is subdivided into 3 parts which contain the following chapters:

Part 1

- Chapter 1 : Oceans and Coastal Waters  
                  as Life-supporting Environments
- Chapter 2 : Light
- Chapter 3 : Temperature

Part 2

- Chapter 4 : Salinity
- Chapter 5 : Water Movement
- Chapter 6 : Turbidity

Part 3

- Chapter 7 : Substratum
- Chapter 8 : Pressure
- Chapter 9 : Dissolved Gases
- Chapter 10: Organic Substances
- Chapter 11: Ionizing Radiation
- Chapter 12: Factor Combinations

Chapter 1 considers oceans and coastal waters as life-supporting environments. It describes briefly the ocean basins, their principal water masses and circulation, the sea-land boundary, the properties of sea water and the chemical cycles in the seas.

Chapters 2 to 11 deal with responses to environmental factors. Of course, only factors about which enough information is available can be treated. Each chapter begins with a general introduction informing the reader about (1) general aspects of the environmental factor concerned, (2) methods of measuring its intensities, and (3) its intensity patterns in oceans and coastal waters. The chapter outline, suggested to all contributors, distinguishes between functional and structural responses. Functional responses are subdivided into tolerance, metabolism and activity, reproduction, and distribution; structural responses are dealt with under the subheadings size (body length, width, volume), external structures (shape, differentiation, etc. of external body parts) and internal

structures (organs, tissues, cells or parts thereof). The monofactorial approach used in Chapters 2 to 11 has been chosen because of the insufficient amount of information at hand on multifactorial relationships, and because organisms—whether bacteria, plants or animals—frequently exhibit comparable responses to intensity variations of environmental entities such as light, temperature or salinity. A monofactorial (univariable) design facilitates comparison, evaluation and generalization of reactions to a given environmental factor by members of different taxa. It is realized, of course, that in natural habitats organisms respond to their total environment rather than to single factors (selected by man for methodological, conceptual or historical reasons). Factor interactions, known or expected to be of special importance, are therefore referred to briefly in each chapter.

Chapter 12 presents a special, detailed account on organismic responses to factor combinations. There can be no doubt: investigation of responses to intensity variations of environmental factors acting in concert must be given priority if man wants to understand ecological dynamics and to achieve forecasting and controlling capacities in regard to life in the marine environment. There is great need for (i) conducting large-scale research projects based on multivariable designs and including all life-history stages of important food-web representatives, (ii) developing appropriate analyzing and evaluating techniques (computation, mathematical models and concepts of abstraction, formalization and generalization). Chapter 12 represents a pioneer effort to stimulate progress in this modern branch of ecological research.

Our intention to provide the reader with a well-organized source of information which enables him to find and compare facts and problems of interest to him quickly and easily created several difficulties. The first difficulty was to achieve general agreement in regard to gross taxonomic subdivisions. The subdivisions 'bacteria, fungi and blue-green algae', 'plants', and 'animals' have been adopted after long discussions; they are the result of a compromise between the need to keep the number of taxa as small as possible and to choose groups of organisms which can be conveniently treated by single authors; whenever necessary these groups are subdivided further, e.g. 'animals' into 'invertebrates' and 'fishes'. The second difficulty concerned the treatment of 'nutrition'. In bacteria, nutrients and substratum (Chapter 7) are hardly separable; in plants, nutrients overlap to a certain degree with salinity (Chapter 4), in animals with organic substances (Chapter 10). While some aspects of nutrition have been considered under various headings, nutritional aspects will be treated in detail in Volumes III and IV. The third difficulty was created by differences in thematic emphasis and in the usage of certain scientific terms in the fields of marine microbiology, botany or zoology. An example is the connotation of the term 'growth', which means increase in individual numbers in microbiology, but increase in organic matter of individuals in botany and zoology. Such terminological problems were solved by providing definitions or explanations.

The policy of placing the conceptual grid of the chapter outlines on the body of knowledge available and reviewing the material found near each 'point of intersection' (rather than following, as usual, the meandering path along which information happens to have accumulated) made us aware that many important areas of marine ecological research have hardly been touched upon, while others have

attracted unparalleled attention; such disproportions are reflected in the lengths of the respective contributions. The Chapter 'Water Movement: Bacteria, Fungi and Blue-green Algae' had to remain unwritten because of insufficient knowledge available.

Lack of information also created a serious gap in regard to biotic factors (e.g. behavioural and biochemical interactions between organisms of a given ecosystem) which may affect, or even govern, intra- and interspecific patterns of organismic co-existence. Little pertinent information is at hand on marine mammals and birds; their responses to environmental stress often depend on homeostatic mechanisms.

'Environmental Factors' concentrates on responses of intact organisms. However, if considered relevant, information obtained at the individual level is complemented by findings at the sub- or supra-individual levels. Functional and structural responses are primarily considered under the aspect of quantitative variability, i.e. in terms of changes in rates or intensities of performance. The physiological mechanisms involved will be dealt with in Volume II. General trends that have become apparent are documented by referring to one or a few well worked out examples rather than by presenting a long list of parallel findings. All literature cited appears in alphabetical order at the end of each chapter; it is hoped that such a procedure will help to strengthen interdisciplinary contacts between the fields of marine microbiology, botany and zoology and to facilitate a fast and convenient survey of important pertinent literature.

While an effort has been made to concentrate on marine and brackish-water organisms, in some instances information obtained on limnic forms has been included, especially in situations where knowledge on salt-water living organisms is scarce, or in which it appears safe to assume that both groups of aquatic organisms would exhibit comparable responses.

Much of our present knowledge on responses of marine and coastal-water living organisms to environmental stress has been obtained during casual observation or in insufficiently equipped and staffed laboratories. More complete studies require modern scientific dimensions: more space, better facilities and teams of scientists and technicians.

I am deeply indebted to all contributors for their patience, dedication and willingness to co-operate far beyond the usual demands; despite technical difficulties it was possible in most cases to adhere closely to the outlines proposed. The publishers have supported me wholeheartedly and considerably reduced the many problems by not imposing any space or time limits; I am grateful for this confidence and for excellent co-operation. It is a pleasure to acknowledge support, advice and criticism received by many colleagues, especially by D. F. ALDERDICE, J. R. BRETT, A. W. COLLIER, M. GILLBRICHT, E. HAGMEIER, M. HOPPENHEIT, H. W. JANNASCH, R. I. SMITH, R. W. TAYLOR and B. P. USHAKOV. During the years of organizing and preparing Volume I, Mrs. J. M. CHRISTIAN, Miss V. J. CLARK and Miss F. W. CROUSE have served as reliable and highly capable editorial secretaries and assistants. Mr. J. MARSCHALL has given generously of his time and talent in altering or improving illustrations and Mr. W. MEISS was an indispensable and conscientious helper in all matters related to bibliographical problems. It is with a deep sense of gratitude that I acknowledge all this assistance.

O. KINNE



CONTENTS  
of  
VOLUME I, PART 2

Chapter 4 Salinity

4.0 General Introduction . . . . .	<i>K. Kalle</i>	683
4.1 Bacteria, Fungi and Blue-green Algae . . . . .	<i>R. A. MacLeod</i>	689
4.2 Plants . . . . .	<i>F. Gessner and W. Schramm</i>	705
4.3 Animals		
4.31 Invertebrates . . . . .	<i>O. Kinne</i>	821
4.32 Fishes . . . . .	<i>F. G. T. Holliday</i>	997

Chapter 5 Water Movement

5.0 General Introduction . . . . .	<i>R. Riedl</i>	1085
5.1 Bacteria, Fungi and Blue-green Algae . . . . .		1089
5.2 Plants . . . . .	<i>H. Schwenke</i>	1091
5.3 Animals . . . . .	<i>R. Riedl</i>	1123

Chapter 6 Turbidity

6.0 General Introduction . . . . .	<i>C. G. Wilber</i>	1157
6.1 Bacteria, Fungi and Blue-green Algae . . . . .	<i>G. Rheinheimer</i>	1167
6.2 Plants . . . . .	<i>E. Hagmeier</i>	1177
6.3 Animals . . . . .	<i>C. G. Wilber</i>	1181

Author Index . . . . .	1195
------------------------	------

Taxonomic Index . . . . .	1209
---------------------------	------

Subject Index . . . . .	1225
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## ENVIRONMENTAL FACTORS



# 4. SALINITY

## 4.0 GENERAL INTRODUCTION

K. KALLE

### (1) General Aspects of Salinity

In view of the water cycles on earth we may expect that all chemical elements found in nature are also present in the oceans. This point of view is also supported if one applies the principle of the 'omnipresence' of elements in minerals (NODDACK, 1936) to the situation in the sea. Of the 89 elements occurring in nature, up till now 74 have been clearly determined analytically in sea water; it is to be expected that the remaining 15 elements are also present; probably they have not yet been detected because their concentrations are too small for our present analytical techniques. A superficial consideration of the distribution of the different elements in sea water reveals no direct relation to their position in the periodic system. The regularities, which have given rise, during geological development, to the existing property and distribution of individual elements in the sea, can be understood only on the basis of geochemical and chemical considerations (KALLE, 1945).

Purely for reasons of convenience, we distinguish between the major components of sea salt and the trace elements. The dividing line between the two groups is the quantity of about 1 mg/l, with the exception that silicon as a biologically limiting substance is included with the trace elements.

Table 4-1 lists the abundance of the major elements of sea water of 35‰ salinity, subdivided into 5 cations and 6 anions (in which form the salts are predominantly present in the sea water in solution); together with the hydrogen and oxygen of the water, there are 13 major elements.

Table 4-2 presents a survey, according to orders of magnitude, of the remaining 61 minor elements, which—apart from helium, neon, argon, krypton, xenon, and radon—exist mostly in combination as salts. Our knowledge of the nature, concentration and distribution of the trace elements in the sea is still very incomplete (RICHARDS, 1956; GOLDBERG, 1963; JOHNSTON, 1965).

The physical properties of sea water depend, in general, on the three factors temperature, salinity and pressure. Since the salts cause alterations of physical properties primarily through their total amount, trace elements (which constitute less than 0.2% of the total salt content, Table 4-2) may be neglected in this respect. The most important physical properties of sea water which are subject to quantitative modification due to changes in the salt content are: density, osmotic pressure, and vapour pressure (and consequently boiling and freezing points as well as the density maximum); density and osmotic pressure increase, vapour pressure decreases, with increasing salinity. These changes in the physical properties of sea water cause, in turn, a whole series of important biological and climatological consequences and significantly influence the large scale mixing processes in the

Table 4-1

Composition of sea water of 35‰ salinity. Major elements (Original)

Elements	g/kg	Millimole/kg	Milli-equivalent/kg
Cations			
Sodium	10.752	467.56	467.56
Potassium	0.395	10.10	10.10
Magnesium	1.295	53.25	106.50
Calcium	0.416	10.38	20.76
Strontium	0.008	0.09	0.18
			<u>605.10</u>
Anions			
Chlorine	19.345	545.59	545.59
Bromine	0.066	0.83	0.83
Fluorine	0.0013	0.07	0.07
Sulphate	2.701	28.12	56.23
Bicarbonate	0.145	2.38	—
Boric acid	0.027	0.44	—
			<u>602.72</u>

Surplus of cations over strong anions (alkalinity): 2.38

Table 4-2

Composition of sea water of 35‰ salinity. Minor elements (trace elements) (After GOLDBERG, 1965)

Element	mg/l	Element	mg/l	Element	mg/l
Si	3.0	Sb	0.0005	La	0.000012
A	0.6	Cs	0.0005	Nd	0.0000092
N	0.5	Se	0.0004	Ce	0.0000052
Li	0.17	Y	0.0003	He	0.000005
Rb	0.12	Kr	0.0003	Au	0.000004
P	0.07	Cd	0.00011	Dy	0.0000029
J	0.06	X	0.0001	Pr	0.0000026
Ba	0.03	W	0.0001	Gd	0.0000024
In	<0.02	Co	0.0001	Er	0.0000024
Fe	0.01	Ne	0.0001	Yb	0.0000020
Al	0.01	Ge	0.00006	Sm	0.0000017
Zn	0.01	Cr	0.00005	Ho	0.00000088
Mo	0.01	Th	0.00005	B <sup>e</sup>	0.0000006
As	0.003	Ag	0.00004	Tm	0.00000052
Cu	0.003	Sc	0.00004	Lu	0.00000048
U	0.003	Ga	0.00003	Eu	0.00000046
Mn	0.002	Hg	0.00003	Pa	$2 \times 10^{-8}$
Ni	0.002	Pb	0.00003	Ra	$1.0 \times 10^{-10}$
V	0.002	Bi	0.00002	Rn	$0.6 \times 10^{-15}$
Ti	0.001	Nb	0.00001		
Sn	0.0008	Tl	<0.00001		

oceans (KALLE, 1945). The complex influences of temperature and salinity on different physical properties of the sea water are illustrated in Fig. 4-1; it presents lines of equal density, equal light refraction, equal electrical conductivity, and equal speed of sound.

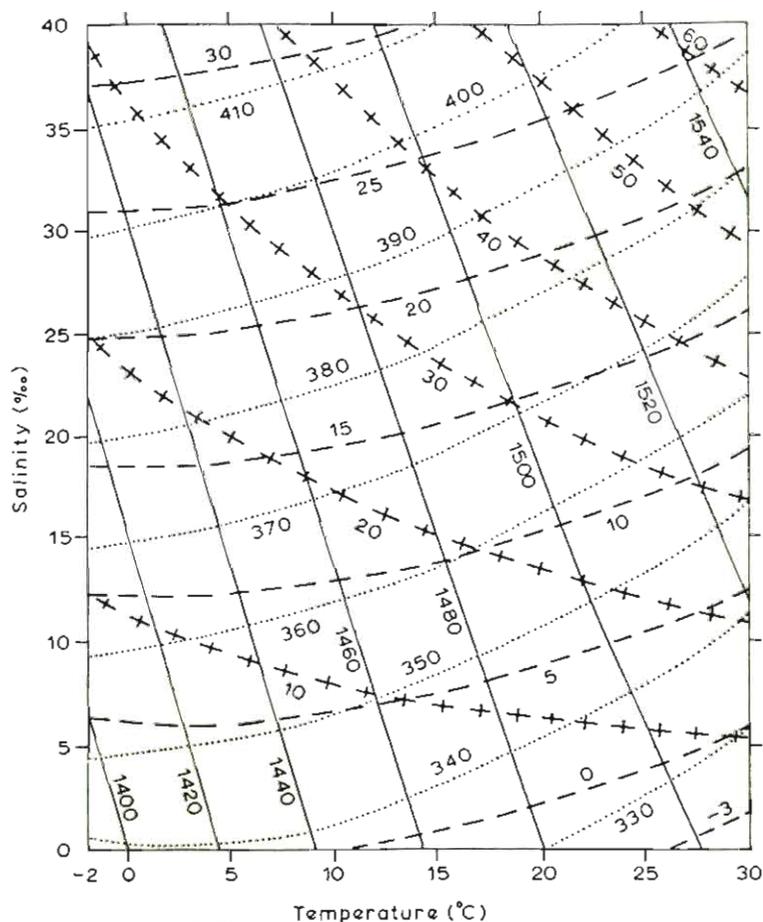


Fig. 4-1: Some important properties of sea water as a function of salinity and temperature. Density - - - ; light refraction ... (place 1.3 before the numbers given); electrical conductivity (reciprocal ohms times 1000) + + + ; and speed of sound (m/sec)——. (Original.)

In regard to the chemical properties, sea water differs from a simple NaCl solution in an essential point. The equivalent amounts of cations and anions are not balanced against each other; the cations exceed the 'strong' anions by 2.38 milli-equivalents (Table 4-1). This state of affairs is expressed in practice in the 'alkalinity' of sea water. The result is that sea water is not neutral but weakly alkaline (normal pH = 8.0 to 8.3) and shows a strong buffering capacity, which is of great significance biologically. A further peculiarity of sea water is the constant ratio, within quite wide limits of total salinity, of the major salt components, so that we can speak of a 'constancy of the composition of sea salt'. The largest

relative variations occur, as a result of biological metabolic processes, in the calcium-carbonate content. In the oceans, these variations may attain a maximum of some hundredths of milli-equivalents. Coastal waters represent an exception to this rule, as do largely enclosed secondary seas, for example the Baltic Sea, in which the oceanic salt content is considerably diminished by strong inflows of fresh water.

In contrast to the major components of sea water, trace elements—especially when they are strongly affected by the biological turnover—can show very marked fluctuations. This is especially true of the biologically limiting elements phosphorus, nitrogen and silicon.

## (2) Measuring Salinity: Methods

In measuring salinity, one must distinguish principally between two fundamentally different methods. One is concerned with the 'total salt content' characterizing water masses and their physical properties. The other is concerned with the determination of individual chemical components, whereby, in general, problems of biological or chemical transformations in oceans and coastal waters are involved.

In the determination of the total salinity, the simplest and most obvious method would be to evaporate carefully a sea-water sample of known volume and to determine its saline residue by weighing. Unfortunately, this method is not suitable in practice because invariably in this procedure uncontrollable proportions of volatile hydrochloric acid are given off to the atmosphere.

In view of the great importance of reliable and uniform total salt-content values, a standard method for the determination of salinity had already been worked out on an international basis more than 60 years ago (KNUDSEN and co-authors, 1902). This method makes use of the constancy of the relative abundance of elements in sea water; it is based on chemical titration of the chlorine ion content (chlorine-titration). On the basis of the relation:  $S = 1.805 Cl + 0.030$ , in which  $S$  is the total salt content and  $Cl$  the chlorine ion content, both in parts per thousand (ppt or ‰), the corresponding salt-content value may be derived with the aid of the 'Knudsen-tables' (OXNER, 1920; BARNES 1959; DIETRICH and KALLE, 1963). The accuracy of this method for a normal salinity of 35‰ $S$  is  $\pm 0.02$ ‰ $S$ , which indicates at the same time the lower limit at which the law of the 'constancy of the elements' is still valid. By comparison of the measured value with that of 'normal sea water' with an exactly established chlorine ion content, obtainable from the International Council in Copenhagen, an accurate correlation of all measured values on a world-wide basis is guaranteed. In the last decade, additional standard methods have been developed which estimate salinity on the basis of measurements of the density or of the electrical conductivity of sea water.

Because of the special conditions in the standard determination, there is a small difference between the total salinity '‰ $S$ ' according to definition and the true total salt content as the sum of the individual saline components dissolved in sea water. According to definition, we understand by '‰ $S$ ' the total amount of dissolved substances present in a kilogram of sea water, on the assumption that all carbonates are converted into oxides, the bromides and iodides into chloride, and the total organic matter is oxidized. Generally, the value of salt content is

referred to the unit of 1 kg of sea water. This value is denoted by the expression 'chlorinity', in contrast to the term 'chlorosity' in which the value of the salt content is referred to 1 l of sea water at 20°C.

From the composition of the salts in sea water as set down in Table 4-1, one is in a position to prepare artificial sea water for experimental purposes (see also PROVASOLI and co-authors, 1957). The following tested recipe gives a sea water of 35‰S. Two separate solutions, A and B are prepared by dissolving salts as listed in Table 4-3. Solution B is added in a thin stream to solution A while constantly stirring the mixture. After standing for a day, the mixture is filtered through as fine-pored a filter as possible for the removal of the small quantity of cloudy material formed (see also HORNE, 1969; CONOVER, 1970).

Table 4-3

Recipe for the preparation of artificial sea water of 35‰ salinity (After DIETRICH and KALLE, 1963)

Solution A		Solution B	
NaCl	239.0 g	Na <sub>2</sub> SO <sub>4</sub> 10H <sub>2</sub> O	90.6 g
MgCl <sub>2</sub> 6H <sub>2</sub> O	108.3 g	NaHCO <sub>3</sub>	0.20 g
CaCl <sub>2</sub> , anhydrous	11.5 g	NaF	0.003 g
SrCl <sub>2</sub> 6H <sub>2</sub> O	0.040 g	H <sub>3</sub> BO <sub>3</sub>	0.027 g
KCl	6.82 g	Distilled water	1,000 ml
KBr	0.99 g		
Distilled water	8,560 ml		

When it is necessary to determine the content in sea water of the individual trace elements, special analytical methods must be used. Because of their high analytical sensitivity, until recently, practically only colorimetric methods—in which one estimates the concentration level of the substance to be determined from the strength of a colour reaction—were used for this purpose. In recent years, other, still more sensitive, methods have been developed, which seem to promise a deeper understanding of the economy of trace substances in the sea: neutron-activation analysis (RONA and co-authors, 1962; SCHUTZ and TUREKIAN, 1965), atomic absorption spectroscopy (ANGINO and BILLINGS, 1965), mass spectrometric determinations (CHOW and GOLDBERG, 1962), and complex chemical separation methods (BAYER, 1964).

### (3) Salinity in Oceans and Coastal Waters

In the open oceans, the surface salt content varies between 32‰ and 38‰S; one can take the mean value as 35‰S. With the inclusion of the secondary seas, the breadth of fluctuation extends between 0‰ and 41‰S. In oceans and secondary seas, the regions of maximum and minimum salt contents are distributed as indicated in Table 4-4.

The considerable differences in surface salinities are caused by variations in the extent of evaporation, the quantity of rain and the inflow of freshwater rivers,

and—in the polar regions—also by the melting of ice. In vertical direction, the variations in salinity in the open ocean are considerably less, being of the order of only a few parts per thousand. These minute differences are, nevertheless, of high significance for the deep oceanic circulation; together with temperature changes they affect fundamentally the density of the oceanic water masses and hence their circulation. Since water layers with more than 35‰S are not very thick, one can place the mean salinity value for all water masses of the oceans at about 34.85‰S. If one imagines the whole of the ocean water removed from the ocean basins by evaporation, the sea floor would remain covered with a layer of salt some 62 m in depth.

Table 4-4

Distribution of areas with maximum and minimum salt contents in oceans and secondary seas (Original)

Oceans	Regions of maximum salt content	Regions of minimum salt content
Atlantic Ocean	Northern horse latitudes: more than 37.5‰S 15°—20°S latitude, off the Brazilian coast: over 37‰S	Northern Polar Sea: 32‰ to below 20‰S
Indian Ocean	Arabian Sea: over 36.5‰S 30° S latitude, west of Australia: 36‰S	In the Northeast (Gulf of Bengal): below 34‰S
Pacific Ocean	West and southwest of the Hawaiian Islands: over 35.5‰S 20° S, in the middle ocean: over 36.5‰S	In the Northeast: below 33‰S
Antarctic Sea region		Below 34‰S
<b>Secondary seas</b>		
European Mediterranean Sea	Eastern area: over 39‰S	
Northern Red Sea	Gulf of Suez: over 41‰S*	
Persian Gulf	Over 40‰S	
Baltic Sea		Middle part: 7‰S Northern Gulf of Bothnia: below 2‰S
Black Sea		Below 19‰S; in the Northwest: 10‰S

\* See also Chapter 4.31, p. 821.

## 4. SALINITY

### 4.1 BACTERIA, FUNGI AND BLUE-GREEN ALGAE

R. A. MACLEOD

#### (1) Introduction

Many of the micro-organisms isolated from marine habitats will grow in laboratory media only if suitable concentrations of sea water, or salt solutions providing at least some of the ions of sea water, are included. Such organisms are usually considered to be obligately marine. Some of these organisms are capable of withstanding very high salinities while others survive at salinities which are no higher than those permitting the growth of their terrestrial counterparts. Also in the sea are micro-organisms which will grow at very low salinities, even in media prepared with distilled water. Although such organisms may not be considered to be obligately marine, in some cases they constitute an important part of the marine flora. Organisms representative of each of these groups in their response to salinity are found among the bacteria, fungi and blue-green algae isolated from the sea or from marine materials.

#### (2) Functional Responses

##### (a) *Tolerance*

##### *Bacteria*

FISCHER (1894) observed that the highest bacterial counts on sea-water samples or marine materials were obtained if the plating medium was prepared with sea water or 3% NaCl. This finding was subsequently confirmed by a number of other workers (see ZOBELL, 1946). TYLER and co-authors (1960) tested 96 bacterial isolates from the sea, all Gram-negative rod or spiral forms, and found that all required added NaCl for good growth. HIDAKA (1965) examined 275 cultures isolated from sea water in the northern part of the North Pacific Ocean and the Bering Sea. He divided the cultures into three types on the basis of their capacity to grow in media prepared with either fresh water, 0.5% NaCl, 3.0% NaCl, dilute or normal strength sea water. Terrestrial types were considered to be those which could grow in all five media. Halophilic types were judged to be ones lacking the capacity to grow in media prepared with fresh water or containing up to 0.5% NaCl, while marine bacteria were defined as those able to grow in the two media prepared with sea water. On this basis, 32% of the isolates were classified marine, 5% terrestrial and 18% halophilic. Of the isolates tested, 49% were Gram-positive rods or cocci and 75% of these fell into the terrestrial category. The high proportion of Gram-positive isolates in this study is not representative of their distribution in the sea, as HIDAKA himself pointed out. Most surveys indicate that 95% of the bacteria in the sea, capable of growing on laboratory media, are Gram-negative (ZOBELL, 1946).

The findings to date indicate that most Gram-negative bacteria in the sea require sea water or NaCl in the medium for growth, at least on initial isolation. Though Gram-positive bacteria in the sea are few in number, most of these appear able to grow in media prepared with fresh water.

The upper limits of salt tolerance of marine bacteria examined are lower than those of many terrestrial species (MACLEOD, 1965). The Na<sup>+</sup> level in normal sea water expressed as NaCl is 2.6%. Growth of three marine bacteria investigated by MACLEOD and ONOFREY (1957) was inhibited by 4.8% NaCl. TYLER and co-authors (1960) examined 15 marine bacteria and found that all grew in 4.7% NaCl, 9 grew in 8.2% NaCl and none grew in 15.2% NaCl. By comparison, many terrestrial species tolerate 20 to 25% NaCl (LARSEN, 1962).

The adaptability of marine bacteria to establish populations in media prepared with fresh water is a matter of some controversy. ZOBELL and MICHENER (1938) found that nine of twelve cultures requiring sea water in the medium on initial isolation grew in the same medium prepared with fresh water after the cultures had been held 5 months without transfer. On the other hand, attempts to adapt the organisms to grow in media of reduced sea water concentration met with only limited success. Subsequently, 56 of 60 species of marine bacteria were reported to have developed a capacity for population growth in freshwater media (ZOBELL, 1946). In contrast, KORINEK (1927) stated that after a year's cultivation on laboratory media, original differences in salinity requirements between freshwater and marine bacteria were not eliminated. STANIER (1941) was unable to adapt marine agar digesting bacteria to grow at appreciably lowered sea water or salt concentrations.

As in the case of some marine yeasts and Phycomycetes (p. 692) there is evidence that the nutrient composition of the medium can affect the salt tolerance of some marine bacteria. MACLEOD and ONOFREY (1963) serially streaked plates of Trypticase medium containing progressively lower concentrations of NaCl with a culture of a marine pseudomonad requiring initially 0.2M Na<sup>+</sup> for optimum growth. A culture was eventually obtained which was able to grow readily on the Trypticase medium without added NaCl. The medium contained 0.028M Na<sup>+</sup> as a contaminant. When the adapted organism was tested on a simple chemically defined medium it was found still to require 0.2M Na<sup>+</sup> for optimum growth. MERKEL and co-authors (1964) reported that, upon prolonged cultivation in the laboratory, the marine bacterium *Aeromonas proteolytica* was able to grow at a greatly reduced salt concentration, provided relatively large amounts of peptone were supplied in the medium.

As in the case of certain species of fungi, both marine and terrestrial (p. 692), there appears to be an interrelation between temperature and salt concentration for the growth of some marine bacteria. GRAHAM (1966) found that the addition of 1M NaCl to the medium raised the upper limit of temperature for growth of the lobster pathogen *Gaffkya homari* from 42° to 45 C. Neither other chlorides nor other sodium salts could act in this capacity. STANLEY and MORITA (1967) reported that the maximal growth temperature of *Vibrio marinus*, an obligate psychrophile, was markedly affected by the concentration of salts in the medium. At the lowest level of NaCl at which growth would take place (0.15M), the maximum growth temperature was 11.6°C. A further increase in the NaCl level in the medium

resulted in a progressive elevation of the maximal growth temperature to 19.8°C at 0.35 to 0.45M NaCl.

### Fungi

Marine fungi can be divided into two major groups on the basis of their response to salinity (VISHNIAC, 1955a). One group consists of the higher fungi which, in the case of the marine flora, refer to Ascomycetes and Fungi Imperfecti, and includes marine yeasts; most members of this group grow over a wide range of salinities including media prepared with fresh water. The other group consists of the primitive marine fungi, the Phycomycetes and of the marine Labyrinthulales, which are not true fungi, but which nevertheless are usually included in discussions of marine fungi (JOHNSON and SPARROW, 1961). This second group grows over a much narrower range of salinities and will not grow in media prepared with fresh water. Because members of this group fail to grow unless the medium contains sea water or a solution of salts supplying the major ions of sea water at approximately the concentrations found in sea water, they are considered obligately marine.

The pioneer work on the relation of higher marine fungi to salinity was carried out by BARGHOORN and LINDER (1944). Pure cultures of six species were grown on media prepared with fresh water, normal filtered sea water and sea water evaporated to one-third its original volume. Two species, *Amphisphaeria maritima* and *Ceriosporopsis halima*, developed more rapidly in fresh water than in sea water. The other four species, *Helicoma salinum*, *Peritrichospora integra*, *Halophiobolus opaca* and *Halophiobolus salina*, grew more rapidly in sea water at its normal concentration. All six species grew in concentrated sea water but less rapidly than in normal sea water.

GUSTAFSSON and FRIES (1956) studied the nutritional requirements of ten species of marine Ascomycetes and Fungi Imperfecti. Most species proved to be almost indifferent to the salts contained in sea water, producing the same or almost the same amount of growth in media prepared with distilled water. Only *Halophiobolus opaca* failed to grow without sea water. Further tests indicated that *H. opaca* produced good growth if sea water was replaced by a solution containing appropriate concentrations of CaCl<sub>2</sub>, NaCl, MgCl<sub>2</sub> and Na<sub>2</sub>SO<sub>4</sub>. *Ceriosporopsis maritima*, on the other hand, grew much better in distilled water than in sea water medium.

SLEPMANN (1957, 1959) found that higher fungi collected from basin sediments in an estuary, and which were normally considered to be terrestrial, had maximum tolerance limits ranging from 10 to 25% salt. A supposedly marine fungus, *Pythium salinum*, on the other hand, had a maximum tolerance limit of only 3% salt.

PHAFF and co-authors (1952) obtained 35 isolates of yeasts from shrimp. Some were obtained from the surface washings of freshly caught shrimps and were presumably marine. Others were isolated from the surface washings obtained during processing. The origin of the latter is open to question. The isolates belonged to the genera *Rhodotorula*, *Trichosporon*, *Torulopsis*, *Pullularia*, *Candida* and *Hansenula*. The yeasts were tested for salinity tolerance using 10% wort agar slants containing NaCl ranging in concentration from 8 to 16%. Sixteen of the isolates tolerated 16% salt, another nine tolerated the 9.8% level, three did not grow above 8.3% and one failed to grow at 8.3% salt.

BHAT and co-authors (1955) tested the salt tolerance of 37 marine yeasts

isolated from the Indian Ocean and compared it with that of terrestrial strains. The marine group grew well at 14 to 16% salt, which was about twice the salt concentration tolerated by the terrestrial forms. Several of the marine yeasts tolerated 21% NaCl.

ROSS and MORRIS (1962) studied strains of yeasts isolated from newly caught fish in the Clyde estuary and in the River Dee (Scotland). All strains of *Debaromyces* grew best in the presence of 1 to 3% NaCl. The rest, comprising species of the genera *Torulopsis*, *Pichia*, *Rhodotorula* and *Candida*, grew best in the absence of NaCl. The maximum tolerance exhibited by the *Debaromyces* strains varied from 18 to 23% w/v\* NaCl. The rest tolerated from 9 to 18% NaCl. Strains of *Debaromyces kloecckeri* accounted for the largest single group of yeasts isolated from marine sources by these workers. Since the salt concentration found optimum for this group was of the same order as that found in the sea, it would be easy to suggest that these strains were true marine yeasts. ROSS and MORRIS point out, however, that it is difficult to uphold this contention because terrestrial strains having no previous history of contact with salt behave in a similar manner.

In all of the studies involving the higher fungi of marine origin, only one species, *Halophiobolus apaca*, has been found to require sea water in the medium for growth. In contrast, the lower marine fungi, the Phycomycetes and the Labyrinthulales for the most part fail to grow without sea water or suitable concentrations of NaCl in the medium. VISHNIAC (1960) examined 49 isolates of marine Phycomycetes and found that only 1 grew at 6% NaCl, all grew well at 2.5% NaCl, 22 grew well at 1% NaCl and only 2 grew well at 0.5% NaCl, the lowest NaCl concentration tested. Two of the isolates studied in detail showed sharp optima at 2% with little growth in the absence of added NaCl or in the presence of 6% NaCl. The salt response of these organisms was similar to that of another marine phycomycete, *Sirolopidium zoophthorum*, which parasitizes clam and oyster larvae (VISHNIAC, 1955c). The optimum NaCl requirement for growth of all Phycomycetes examined by VISHNIAC was at the concentration characteristic of sea water rather than of either fresh water or brine pools. She concluded that these non-filamentous fungi were a distinct ecological group physiologically specialized for growth in sea water.

VISHNIAC (1955b) also showed that three strains of *Labyrinthula* failed to grow in the absence of NaCl. For these strains, 2 to 3% was optimum and 4% inhibitory.

Two factors, temperature and medium composition, may affect the salt-tolerance limits of some marine fungi. RITCHIE (1957) found in the case of a species of *Phoma* isolated from pine panels submerged in the sea, that the salinity optimum increases as the temperature increases. At 16°C, the lowest temperature tested, the salinity optimum is 2.0% while at 37°C it is 4.7%. The *Phoma* pattern occurs in modified form in species of *Aspergillus* not obtained from the sea, but it is not a universal phenomenon either in marine or terrestrial species (RITCHIE, 1959). According to JOHNSON (1960), the marine phycomycete *Lagenidium chthamalo-philum* becomes more tolerant of higher salinities as the temperature increases. VISHNIAC (1960) reported that the salinity optima of the marine Phycomycetes which she examined are not affected by temperature.

The nutrient composition of the medium, in some cases, affects the salinity

\* w/v is weight/volume, i.e. % expressed as g solute per 100 ml of solvent.

range over which a marine fungus can grow. JOHNSON (1960) working with the marine phycomycete *Lagenidium chthamalophilum* observed that growth occurs on high-salinity agar provided a rich nutrient source is available. According to ROSS and MORRIS (1962), the ability of strains of the yeast *Debaromyces* to tolerate NaCl is affected by the nature of the nitrogen source in the medium. Fish extract causes a significant increase in tolerance from that found with  $(\text{NH}_4)_2\text{SO}_4$ , whereas urea causes a decrease in tolerance.

Information on the adaptability of marine fungi to salinity changes is very limited. The salinity optima of the Phycomycetes examined are not affected by serially subculturing the organisms at salinities appreciably different from the optimum (VISHNIAC, 1960).

#### *Blue-green algae*

Concentrations of NaCl greater than 3% or less than 1.5% decrease the growth of the red-pigmented marine blue-green alga *Phormidium persicinum* (PINTNER and PROVASOLI, 1958). NaCl concentrations approaching that in sea water are necessary for optimum growth of blue-green algae isolated from inshore marine environments (VAN BAALEN, 1962). Three isolates examined grew much more poorly when the NaCl concentration of the medium was raised to 5%. STEWART (1964) studied the salinity requirements for growth and nitrogen fixation of the two blue-green algae *Calothrix scopulorum* and *Nostoc entophyta* isolated from the sea. Data on growth in nitrogen-free medium indicate that nitrogen fixation occurs over wide salinity ranges. No well-defined optimum salinity level was detected for either species. Growth of *Calothrix scopulorum* was not significantly different in salinities of 0.1 to 4.5% (w/v) although there was evidence of slightly better growth at salinities between 1 and 3.5%. At 6%, growth was significantly poorer than at lower salinities. Growth rates of *Nostoc entophyta* were similar at 1.0 to 3.5% but appreciably lower at 4.5%. It was concluded that the salinity levels occurring in nature should not markedly affect growth and nitrogen fixation by these organisms. The strain of *Calothrix scopulorum* examined appears to be one of the most euryhaline algae isolated in pure culture. Extrapolation of the *Nostoc* data indicates that the organism studied should grow in freshwater habitats. STEWART (1964) suggested that the ability of certain blue-green algae to fix nitrogen both in marine and freshwater environments is probably a more common phenomenon than generally realized. In this connection, it has been reported that freshwater blue-green algae *Anabaena cylindrica*, *Calothrix parietina* and various *Nostoc* species fix nitrogen at salinities approaching those of natural sea water (ALLEN, 1958). *Chlorogloea fritschii*, which occurs in paddy soils and elsewhere, grows in sea water or in 1.5% NaCl (FAY and FOGO, 1962).

#### (b) *Metabolism and Activity*

##### *Bacteria*

Marine luminous bacteria fail to luminesce when the sea water in which they are suspended is too greatly diluted with fresh water (HARVEY, 1915). This effect has been ascribed to cytolysis caused by lowered osmotic pressure, since luminescence is maintained if the sea water is replaced by a 1 M sucrose solution.

These and subsequent observations by HILL (1929) led to the general belief that the requirement of marine bacteria for sea water or NaCl in the medium reflects a requirement of these organisms for a medium of suitable osmotic pressure to maintain cell integrity. The first indication that there might be a specific function for the ions of sea water in the growth of marine bacteria was provided by RICHTER (1928). By using low concentrations of peptone and taking precautions to avoid introducing Na as a contaminant into his medium, he was able to show that a marine luminous bacterium has a specific requirement for Na for growth and luminescence. MUDRAK (1933) lowered the level of contaminating Na in the medium still further by replacing peptone with asparagine or aspartic acid. As a result, ten more strains of marine luminous bacteria could be shown to require Na. BUKATSCH (1936) found that luminous bacteria from the sea required K in addition to Na. Na salts are needed by a number of marine isolates for growth and cannot be replaced by equimolar concentrations of K salts (DIANOVA and VOROSHILOVA, 1935). Six marine bacterial isolates, consisting of 3 pseudomonads, 2 *Vibrio* and a *Cytophaga*, grow best if the sea water employed as diluent in an otherwise chemically defined medium is supplemented with iron and used at half-strength (MACLEOD and ONOFREY, 1956). Equally good growth is obtained if the sea water is replaced by artificial sea water, a solution containing a mixture of salts approximating the composition of sea water. Tests to determine which of the ions in artificial sea water are required for growth revealed that all of the organisms need Na, K, Mg, PO<sub>4</sub> and SO<sub>4</sub>, two also require Ca and three fail to grow without added Cl.

Studies on the quantitative requirements of marine bacteria for Na revealed that the amount of this ion in the medium affects the rate as well as the extent of growth of the organisms (MACLEOD and ONOFREY, 1957). Maximum rate and extent of growth is obtained with 0.2 to 0.3M Na, which is approximately the level of Na in half-strength sea water. Below 0.2M Na, the rate of growth is reduced in proportion to the amount of Na present. On sufficiently long incubation, growth occurs in media prepared with only 0.03M Na but never in the absence of the ion. It was not possible to train these organisms to grow without Na by serial subcultures into media of progressively lower Na concentration (MACLEOD and ONOFREY, 1963). Efforts to replace Na by Li, K, Rb, Cs or sucrose for two marine pseudomonads and a *Cytophaga* tested were unsuccessful. K and sucrose had only a limited capacity to spare the Na requirement (MACLEOD and ONOFREY, 1957). These findings indicate that, at least for the organisms examined, the effect of Na is not primarily osmotic. PAYNE (1958) came to a similar conclusion as a result of studies with another marine pseudomonad, *Pseudomonas natriegens*. PRATT and AUSTIN (1963), on the other hand, found that a number of salts and sucrose could greatly reduce but not replace completely the requirement for Na of a marine *Vibrio* species. Further studies by PRATT (1963) indicate that approximately half the bacteria in sea-water samples which he plated grow in media in which a substantial replacement of NaCl by sucrose or KCl has been made. Different marine bacteria seem thus to differ in the extent to which non-specific solutes can replace Na for growth. In all cases examined, however, bacteria which have been found to require sea water in the medium for growth on initial isolation, have a specific requirement for at least minimum amounts of Na.

HIDAKA (1965) observed that 75% of the Gram-positive and 27% of the Gram-negative cultures isolated from the sea grow on freshwater media. Since these cultures were grown on chemically undefined media, from which contaminating traces of Na had not been removed, it would be of interest to know if any of these cultures have detectable requirements for Na. Studies on the mineral requirements of *Gaffkya homari*, a Gram-positive coccus causing septicemia in lobsters, have revealed that this organism can grow without sea water or NaCl in a chemically defined medium which was shown by flame photometric analysis to contain not more than  $1.36 \times 10^{-4}$ M Na present as a contaminant (GRAHAM, 1966). Two Gram-negative bacteria of marine origin, which grew on initial isolation in a peptone medium prepared with fresh water, require small amounts of Na for growth when grown on a chemically defined medium containing only  $3 \times 10^{-6}$ M Na as a contaminant (MACLEOD and ONOFREY, unpublished). Both require 0.005M Na for optimum growth. These findings indicate that, although most marine bacteria examined need sea water or Na at or near normal sea water concentrations for optimum growth, there are members of the marine bacterial flora that can grow optimally at greatly reduced sea-water or Na concentrations and some, like *Gaffkya homari*, in the absence of Na.

Three Gram-negative marine bacteria which require 0.2 to 0.3M Na for optimum growth also require Cl at a similar concentration. Three others with a similar requirement for Na grow without added Cl in the medium but are stimulated by its addition (MACLEOD and ONOFREY, 1956).

Like all other living cells, with the possible exception of some blue-green algae (ALLEN, 1952), marine bacteria require K for growth (BUKATSCH, 1936; MACLEOD and ONOFREY, 1957; PAYNE, 1960; TYLER and co-authors, 1960). The level of K in sea water, about 10mM, is more than adequate for optimum growth of those marine bacteria whose quantitative requirements for K have been determined (MACLEOD and ONOFREY, 1956).

All marine bacteria so far examined require Mg for growth and some also require Ca (MACLEOD and ONOFREY, 1956). As in the case of marine fungi (p. 697) and blue-green algae (p. 699) considerable Mg Ca interaction occurs in the growth of marine bacteria. At low levels of Ca, a marked sparing action of Ca on the Mg requirement is evident. At higher Ca concentrations antagonism between Ca and Mg exists.

Of the ions in sea water essential for growth of marine bacteria, Na is the one usually required in greatest amount and the one most likely first to become limiting if in an isolation medium the sea water concentration were to be progressively lowered. Knowledge of the role played by Na in the physiology and biochemistry of marine bacteria is, therefore, essential for an understanding of the dependence of these organisms on the presence of sea water for survival in nature.

Na is required for the oxidation of exogenous substrates by cell suspensions of a marine pseudomonad (MACLEOD and co-authors, 1958). When cell-free extracts of the organism were examined, none of the enzymes of the tricarboxylic-acid cycle could be shown to require Na specifically for activity (MACLEOD and co-authors, 1958; MACLEOD and HORN, 1960). Cell suspensions of a marine *Vibrio* species require Na for the production of indole from tryptophan but cell-free extracts of the organism do not (PARR and HAROLD, 1960).

That the requirement for Na by intact marine bacteria might represent a Na requirement for the transport of metabolites into the cells was first indicated by DRAPEAU and MACLEOD (1963). They showed that the active transport of the non-metabolizable amino-acid analogue *a*-amino-isobutyric acid (AIB) is Na dependent in the case of the marine pseudomonad previously examined and in *Photobacterium fischeri*. More detailed studies with the marine pseudomonad revealed that the amount of Na required for transport varies with the compound transported and corresponds to the Na requirement for oxidation by whole cells of the corresponding metabolizable analogue (DRAPEAU and co-authors, 1966). This indicates that the Na requirement for oxidation represents a Na requirement for transport.

The Na requirement for growth is quantitatively similar to the Na requirement for oxidation and transport when an amino acid is the sole source of carbon and energy in the medium but not when an oxidizable sugar, galactose, is used. In the latter case, less Na is needed for oxidation and transport than for growth. The additional requirement for Na for growth with galactose could be supplied as well by K, suggesting that there is a minimal specific requirement for Na for transport and, superimposed upon this, a non-specific requirement for a medium of suitable ionic strength for growth (DRAPEAU and co-authors, 1966). More recent studies (WONG and MACLEOD, unpublished) have shown that the uptake of inorganic orthophosphate by the marine pseudomonad is also Na dependent and that the amount of Na required for the transport of phosphate ion is similar to the Na requirement of the organism for growth. Since phosphate is an essential metabolite, its requirement for Na for transport into the cell could well establish the minimum amount of Na required for growth by the organism. It is of interest that a marine phycomycete requiring Na for growth also requires Na for the transport of phosphate into the cells.

In the course of the above studies, observations were made which may have a bearing on the specific role of Na in transport in marine bacterial cells. Cells of the marine pseudomonad which had been allowed to accumulate AIB-<sup>14</sup>C were centrifuged from the incubation medium and resuspended in various salt solutions. In some salt solutions, radio-activity was retained by the cells, in others it was released into the medium (DRAPEAU and MACLEOD, 1965). Maximum retention was achieved when Na was present at the concentration required for optimum rate of transport by the cells both of the marine pseudomonad previously investigated and *Photobacterium fischeri* (WONG and co-authors, 1969; SRIVASTAVA and MACLEOD, unpublished). Above and below these concentrations of Na, leakage of radio-activity occurred. Plate counts on the suspensions showed that, at Na concentrations at which leakage of AIB-<sup>14</sup>C occurred, the cells rapidly became non-viable. In these experiments, sufficient Mg was included in the suspending solution to prevent lysis of the cells. Tests showed that under conditions permitting the release of AIB-<sup>14</sup>C, K and phosphate ions also are lost from the cells (MATULA and co-authors, 1970; WONG and MACLEOD, unpublished). These findings are consistent with the conclusion that above and below a certain optimum range of Na concentration, key intracellular solutes are lost from the cells, causing the cells to die. This conclusion provides an explanation for both the upper and the lower limit of salt tolerance (p. 690) of these organisms. The observations so far obtained are also consistent with the conclusion that Na is

required to maintain cytoplasmic membrane proteins in the proper conformation to permit tight packing of membrane subunits, thereby preventing leakage of intracellular solutes. This function can also be performed, though much less efficiently, by some other monovalent cations, particularly Li. The specific requirement for Na for transport can be attributed to the need for Na not only to permit the closest packing of membrane subunits but also to enable transport proteins to acquire the conformation necessary to function as transport particles. No other ion seems able to replace Na for this latter purpose.

RHODES and PAYNE (1962) noted that an elevated concentration of K (0.26M) increases the rate of penetration into the marine bacterium *Pseudomonas natriegens* of two non-ionizing substrates, mannitol and L-arabinose, but not an ionizing compound, glucuronate. Since the incubation medium used contained phosphate buffer added as the Na salt, uptake is not in fact taking place in the absence of Na. The amount of Na contributed by the buffer (0.04M) would have been sufficient to permit the uptake of D-fucose by another marine pseudomonad at a near optimum rate (DRAPEAU and co-authors, 1966).

Induction of a penetration mechanism for mannitol occurs in *Pseudomonas natriegens* if the cells are pre-incubated with the substrate either in the presence of 0.25M Na and 0.01M K or 0.26M K (plus 0.04M Na supplied by the buffer) but not in the presence of Na alone (RHODES and PAYNE 1966). Since the cells failed to grow in a medium containing K in place of Na, these authors concluded that Na plays a specific role for the induction of a penetration mechanism in these cells which is separate from a role for Na in transport. The medium used in the growth experiments, however, did not contain the amount of Na supplied by the buffer used in the penetration studies. Furthermore, if Na is required for the transport of phosphate ion into cells of this pseudomonad, as it is into the pseudomonad studied by WONG and MACLEOD (unpublished), failure to obtain growth in the absence of Na could be due to failure of the cells to take up phosphate ion. The authors also concluded that in the presence of elevated K, substrates must get into the cells by diffusion. They report, however, that 0.01  $\mu$ moles of 2, 4 dinitrophenol completely suppresses uptake of the substrate by the cells in a medium containing elevated levels of K. It is difficult to understand how such an inhibitor could prevent the entry of a substrate if it is in fact entering by diffusion.

### Fungi

Except for one species of the higher fungi so far examined only the primitive fungi, the Phycomycetes and the Labyrinthulales from the sea are obligately marine. Efforts to define the determinants of the stenohaline niche in the ocean occupied by marine Phycomycetes and Labyrinthulales have been made by studying the mineral requirements of the organisms in a mineral-base defined medium (VISHNIAC, 1955a,b). The results obtained suggest that the niche is determined by the requirements of the organisms for NaCl, K, Mg and Ca in the concentrations of these components found in sea water having a salinity of 19‰ (VISHNIAC, 1955a). By varying the various ions and salts independently and in combination it was found that for the three *Labyrinthula* strains examined, 2 to 3% NaCl is optimum; small amounts of K, in addition to those provided by the phosphate buffer, are needed for two of the strains, while high absolute requirements for Ca and

Mg are indicated. Ca and Mg were also found to be interchangeable to some extent for all isolates.

Studies by GOLDSTEIN and his associates have been directed toward defining more specifically the requirement for NaCl. Neither KCl nor  $\text{CaCl}_2$  could substitute for NaCl in the growth of a species of *Thraustochytrium* (GOLDSTEIN, 1963). KCl did not decrease the inhibitory effect of high concentrations of NaCl for the organism. Similar results were obtained with another species of non-filamentous fungus, *Schizochytrium aggregatum* (GOLDSTEIN and BELSKY, 1964).

In the obligately marine, non-filamentous phycomycete *Thraustochytrium roseum* exists a specific requirement for Na for the uptake of phosphate (SIEGENTHALER and co-authors, 1967). Phosphate uptake varies linearly with an increase in NaCl concentration to 200 mM with no further increase in uptake between 200 and 400 mM. Above the latter concentration, phosphate uptake decreases. The decline is attributed to unfavourable osmotic conditions since sucrose at concentrations giving comparable osmotic pressures is also inhibitory.  $\text{MgCl}_2$  also enhances phosphate uptake but maximal enhancement is only 30% of that achieved with NaCl. Sucrose and  $\text{MgCl}_2$  at equal osmolarities give the same response suggesting that the action of  $\text{MgCl}_2$  is primarily osmotic and pointing further to the functional specificity of NaCl for phosphate uptake. The stimulatory effect of NaCl is due to Na since various Na salts are effective. The nutritional requirement for Na could be viewed, at least in part, as a consequence of its role in facilitating ion transport. Although NaCl always stimulates endogenous respiration, this effect could be duplicated by a variety of other substances that do not stimulate phosphate uptake. This indicates that there is no necessary direct relation between enhancement of respiration and phosphate uptake. These findings are of particular interest since the specific requirement of marine bacteria for Na for growth has been shown to represent a dependence on Na for the transport of a number of substances, including phosphate ion.

#### *Blue-green algae*

A number of blue-green algae have a specific requirement for Na for metabolism and growth. Most of the observations have been made with organisms of either unstated or freshwater origin. Cultures of a species of *Chroococcus* obtained from C. B. VAN NIEL failed to grow if Na or Ca was omitted from the medium (EMERSON and LEWIS, 1942). *Anabaena cylindrica* requires 5 ppm or more Na for optimal growth (ALLEN and ARNON, 1955). Neither K, Li, Rb nor Cs can substitute for Na. The culture studied had been isolated originally by FOGG (1942) from a freshwater pond. *Anabaena variabilis* and *Anacystis nidulans* require both Na and K (KRATZ and MYERS, 1955). Na is required for respiration and photosynthesis by cell suspensions of a *Chroococcus* (EMERSON and LEWIS, 1942). Similar observations were made by ALLEN (1952) for *Synechococcus cedrorum*. In all the above cases, only traces of Na are required for growth and metabolism.

Studies to determine if blue-green algae of marine origin have specific requirements for Na are extremely limited. NaCl requirement of *Phormidium persicinum* for optimum growth cannot be substituted even partly by pentaerythritol (PINTNER and PROVASOLI, 1958). Since the latter compound is toxic for the organism at a concentration of 0.05%, it is not possible to say whether the need for NaCl is

specific. One of three isolates of blue-green algae obtained from the sea failed to grow in a chemically defined medium in the absence of added NaCl (VAN BAALEN, 1962). The other two grew poorly under the same conditions. In the case of the organism which failed to grow without NaCl,  $\text{Na}_2\text{SO}_4$  could replace NaCl for growth but neither KCl nor glycerol were able to do so. These data suggested to VAN BAALEN that levels of NaCl approaching those in sea water are necessary for the growth of blue-green algae from marine environments. The observations of STEWART (1964) indicate, however, that this might not apply to some of the more euryhaline marine blue-green algae. The results obtained by VAN BAALEN (1962) with one organism indicate that, as in the case of some marine bacteria and fungi, the requirement for sea water represents a requirement for Na. The concentration of Na required by the marine organism was much higher than the traces needed by the freshwater strains examined.

PROVASOLI and co-authors (1957) and PROVASOLI (1958) have developed artificial media for the growth of a number of marine algal species including representatives of the Cyanophyta. In the course of these studies, evidence was obtained of a wide interchangeability of Mg and Ca for these organisms. A small amount of Ca has the capacity to substitute for a quite large amount of Mg. These findings supplement the observations of VOLLENWEIDER (1950) who considered the interaction of Ca and Mg in a wide range of concentrations for *Oscillatoria rubescens* and *Ankistrodesmus falcatus*. He found that Ca stimulates growth and cell division. This effect becomes less evident on longer incubation, and the density of final growth depends upon the Mg concentration. With Mg at suboptimal levels, added Ca enhances growth and vice versa. This same interchangeability of Ca and Mg at suboptimal levels has been observed in strains of marine *Labyrinthula* (p. 698) and in several species of marine bacteria (p. 695).

### (c) Reproduction

In bacteria and blue-green algae, reproduction is synonymous with cell division and is measured by the increase in cell numbers or cell mass. In the case of these organisms the effects of salinity on growth can be interpreted as effects on reproduction.

The fungi, on the other hand, can reproduce by spore formation. So far as the author is aware, there are no published reports on the effects of salinity on the sporulation of marine fungi.

### (d) Distribution

#### *Bacteria*

BERKELEY (1919) isolated bacteria from coastal waters where the density of the water indicated a considerable degree of dilution by fresh water. None of his isolates was able to grow in media prepared with fresh water. LIPMAN (1926) plated inshore waters on agar medium prepared with various dilutions of sea water. The highest plate counts were obtained on medium prepared with undiluted sea water. The counts decreased from 960,000 per ml in undiluted sea-water medium to 640,000 per ml when 50% sea water was used; in 25% sea water, no further

decrease occurred. Sea-water samples obtained a mile from shore, when plated on undiluted sea-water medium, contained only 100 to 200 bacteria per ml. The high counts in inshore waters were ascribed to terrigenous contamination. It is evident, however, that very much higher numbers of bacteria requiring undiluted sea water for growth were present in inshore than in open sea waters, presumably because of a higher concentration of organic nutrients.

ZOBELL (1941) obtained the highest bacterial counts on mud and water from Mission Bay and San Diego Bay (USA) when the medium used was prepared with 10 to 25% sea water. GRAY (1963) studied the bacteria of a salt marsh at the mouth of a river. The areas tested were covered at various times by high tides. Highest bacterial counts on samples from the marsh were obtained with media of the salinity of sea water.

### *Fungi*

GOLD (1959) reported that the distribution pattern of Ascomycetes in an estuary is influenced by the combined effect of salinity and temperature. Certain fungi could be collected at low temperatures only in low salinities but when the temperature approached 25°C they were found in salinities of 30‰ or more. These findings in the natural environment would seem to be reflections of the temperature-salinity relations observed with certain species of fungi '*in vitro*'.

RITCHIE (1954) has pointed out that there is an active fungus flora in the sea and that, although some species are halophiles, many are able to thrive and reproduce in salt water or out of it and have been found previously on land or in fresh water. The conclusion of some authors that the latter types are not in fact truly marine he considers, with justification, to be invalid. They are as much a part of the marine flora as those which are obligately marine.

VISHNIAC (1960), working with obligately marine Phycomycetes, failed to select by serial subculture mutants of these forms with salinity optima different from those of the group and concluded that this argues against their ready interconvertibility with freshwater counterparts. She decided that the obligately marine Phycomycetes are a distinct ecological group, physiologically specialized for growth in sea water.

### *Blue-green algae*

ERCEGOVIĆ (1930) studied the distribution of species and genera of blue-green algae on rocks along the coast of Dalmatia. In a region where the salinity remained normal, a rich flora containing some 60 species of Cyanophyceae was found. At a point where a river entered the sea and rapid desalinization of the sea water occurred, the population of cyanophytes was much reduced. Certain genera were absent. The ones present were very euryhaline. In depressions in rocks where sea water was trapped and able to evaporate, salinities up to 284‰ developed. After rain these same depressions contained water of salinity close to zero. The blue-green algal flora found in these pools was composed of only a few genera. Except for *Scopulonema*, the organisms located here were seldom, if ever, found in areas of normal salinity. The genera *Solentia* and *Hormathonema* appeared exclusively in these areas of variable and elevated salinity.

### (3) Structural Responses

#### (a) *Lysis*

##### *Bacteria*

HARVEY (1915) and HILL (1929) observed that marine luminous bacteria lysed when suspended in distilled water and concluded that the salts of sea water prevent lysis of the cells by providing a medium capable of balancing the intracellular osmotic pressure. According to TYLER and co-authors (1960), suspensions in fresh water of most of the 96 Gram-negative marine bacterial isolates they examined show a reduced optical density when compared with suspensions of the same organisms in sea water. MACLEOD and MATULA (1962) reported that Gram-negative marine bacteria vary in their susceptibility to lysis at low salt concentration. Some lyse completely, others only partially when suspended in fresh water. A Gram-positive marine bacterium, *Gaffkya homuri*, shows no tendency to lyse in fresh water (GRAHAM, 1966). NaCl and LiCl are more effective than KCl and  $\text{NH}_4\text{Cl}$  in preventing lysis of marine bacteria (PRATT and RILEY, 1955). This fact is confirmed by studies which revealed that divalent cations are much more effective than monovalent cations in preventing cell lysis (MACLEOD and MATULA, 1962).

Since different salts vary in their capacity to prevent lysis, the hypothesis that salts prevent lysis primarily through their osmotic effects seems invalid. This conclusion is further supported because NaCl, which at an appropriate concentration was able to prevent lysis of a marine pseudomonad, actually equilibrates across the cytoplasmic membrane, quickly reaching the same concentration inside as outside the cells (TAKACS and co-authors, 1964).

Suspensions of isolated envelopes of a marine pseudomonad in a dilute phosphate buffer reveal a decrease in optical density with time which coincides with the release of soluble material into the suspending medium (BROWN, 1961, 1962). The material released could be divided into a dialysable and a non-dialysable fraction. The latter is a complex substance which after hydrolysis contains hexosamine, muramic acid, and the usual amino acids present in proteins. Since the dialysable fraction contains a number of peptides, BROWN concluded that the release of soluble material from the envelope results from the action of a lytic enzyme which is proteolytic in nature. He suggested that salts serve to maintain cell-wall proteins in a conformation which is not attacked by the lytic enzyme.

Cell envelopes of another marine pseudomonad release a complex non-dialysable hexosamine containing material when the salt solution used to suspend the envelopes is diluted sufficiently with water (BUCKMIRE and MACLEOD, 1965). Very little dialysable material could be detected. The non-dialysable substance is similar in composition to the corresponding fraction reported by BROWN (1961, 1962). Cell envelopes which had been heated release as much non-dialysable hexosamine-containing material into solution at low salt concentration as do unheated preparations, suggesting that the release is not due to the action of a lytic enzyme. Studies on the interrelationship between temperature and salt concentration in governing the release of material from cell envelopes, together

with the effect on the pH of the suspending medium when the salt concentration of the latter was reduced, suggest that the material released consists of electro-negative units which maintain close proximity in the envelope through the screening action of the cations of salts. The material released contains muramic and diaminopimelic acid; hence, it apparently arises from a mucopeptide layer requiring salts to maintain it intact. More recent evidence (FORSBERG and co-authors, unpublished) indicates that the muramic and diaminopimelic acid present in the material released is probably a contaminant arising from a separate underlying mucopeptide layer. The non-dialysable hexosamine-containing material appears to be associated with a lipoprotein lipopolysaccharide outer layer, but chemically distinguishable from it. Evidence has been obtained indicating that all layers of the cell envelope of this marine pseudomonad interact with salts and require the presence of salts to maintain them intact.

### *Fungi*

No published reports on lysis in marine fungi exposed to sea water sufficiently diluted with fresh water have come to the reviewer's attention. Since all except one of the higher marine fungi examined are able to grow in media prepared with fresh water, one must assume that most of this group maintains its mycelial integrity at low salt concentrations. The primitive marine fungi which have been studied, however, will not grow in media prepared with fresh water. Whether any of these organisms lose their cell integrity at low salt concentration has not, so far as we are aware, been reported.

### *Blue-green algae*

A brackish-water form of blue-green alga, *Oscillatoria peneta ad int.*, was still actively motile after suspension in distilled water for 40 days (PERNAUER, 1958). This blue-green alga, at least, maintains its cell integrity at very low salt concentrations. Whether other marine blue-green algae behave similarly has, to our knowledge, not been investigated.

### (b) *Cytorrhysis*

#### *Bacteria*

BUCKMIRE and MACLEOD (1970) compared the capacity of glycerol, sucrose and inulin to penetrate cells of a marine pseudomonad. The data obtained indicate that (i) the cells are freely permeable to glycerol, (ii) sucrose penetrates to the cytoplasmic membrane of the cells, and (iii) inulin does not get past the outer wall. When the sucrose concentration increases, the sucrose space and the inulin space in the packed cell preparation increase proportionally. This observation indicates shrinkage of the whole cell rather than plasmolysis. Such a phenomenon is referred to as 'cytorrhysis.'

MATULA and MACLEOD (1969) found that when cells of a marine pseudomonad are suspended at elevated NaCl concentrations, the cells also shrink. The cytorrhysis occurring with NaCl, unlike that produced by sucrose, cannot be due to osmotic effects since NaCl freely diffuses across the cytoplasmic membrane of this organism. Studies with isolated envelopes of the marine pseudomonad

have shown that NaCl interacts with components of the cell wall and the cytoplasmic membrane, thereby causing shrinkage of the cell.

Studies by THOMPSON and co-authors (1970) show that when cells of a marine pseudomonad are washed with a  $MgSO_4$  solution they become plasmolyzed. Plasmolysis has been shown to be due to the loss of K from the cells, which occurs when the medium used to suspend the cells contains no Na. Deplasmolysis of the cells occurs when the latter are incubated in the presence of Na and K. Under these conditions, the internal K concentration is restored.

### *Fungi*

No evidence of cytorrhysis in marine fungi has been reported.

### *Blue-green algae*

Cells of blue-green algae in hypertonic solutions do not usually exhibit typical plasmolysis but instead undergo cytorrhysis, that is, shrinkage of the whole cell rather than withdrawal of the cytoplasmic membrane from the wall (STADELMANN, 1962). The brackish-water *Oscillatoria peneta ad int.* plasmolyzes when placed in concentrated sea water (PERNAUER, 1958). The concentration at which plasmolysis and deplasmolysis of the cells occurs depends on the salinity of the solution used to suspend the cells prior to their transfer into the test solution. Cells suspended in distilled water plasmolyze in only 30% sea water. Cells suspended in waters from their natural habitat require 160% sea water for plasmolysis. Conversely, cells suspended in 400% sea water deplasmolyze when suspended in 300% sea water. PERNAUER concluded that this organism has a marked osmotic regulatory capacity. PERNAUER also noted that the organism seems insensitive to extremes of tonicity. Cells exposed to 200% sea water, though plasmolyzed, are still motile. If exposed to 280% sea water motility ceases but is restored again after the cells deplasmolyze. Cells suspended in distilled water for 40 days are still actively motile.

Since K has been shown to have such a marked osmoregulatory effect on a marine pseudomonad (THOMPSON and co-authors, 1970), it would be of great interest to know whether the observations of PERNAUER (1958) on the effect of prior treatment of *Oscillatoria peneta ad int.* with the sea-water concentration at which plasmolysis takes place can be related to the internal K concentration of the cells.

## (4) Conclusions

Among the sea-water living bacteria, fungi and blue-green algae are organisms which are obligately marine in the sense that they depend on the salts of sea water for their survival. Other bacteria, fungi and blue-green algae from the sea are not obligately marine; they can grow without sea water or its major salts. Both groups are part of the marine flora, and any attempt to label one group as being more truly marine than the other is futile. Nevertheless, obligately marine microorganisms are unique and, as evidence obtained with marine bacteria and Phycomyces indicates, appear to share a Na requirement for transport of metabolites into the cells.



# 4. SALINITY

## 4.2 PLANTS

F. GESSNER and W. SCHRAMM\*

### (1) Introduction

The term 'salinity' has a special meaning for marine ecologists (Chapter 4.0; see also introduction to Chapter 4.31). This factor has several aspects—such as total osmoconcentration, ion composition, and density—which must be differentially analyzed if we are to obtain a sufficiently complete picture of the ways in which salinity affects biological systems. In addition, several other environmental factors are a function of salinity, changing automatically in their intensity if the salinity varies. Hence a multitude of factor intercorrelations can affect the relationships between salinity and plants.

Due to differences in salinity, the marine vegetation is completely different from the vegetation inhabiting the various types of fresh water. The term salinity barrier ('Salzschranke') is often used to point out the importance of salinity as ecological master factor (see also Chapter 4.31). Indeed, there are no other environmental factors which divide the earth's aquatic media into such different habitats as are the seas and the fresh waters.

In spite of such differences, several plant phyla have representatives in sea, brackish and fresh water (Table 4-5). While diatoms and dinoflagellates occur both in sea and fresh water, no single species is abundant in both habitats. The higher plants have many species, belonging to numerous families, in freshwater lakes, ponds or rivers; but only 50 species of truly marine vascular plants are known;

Table 4-5

Occurrence of plant phyla in sea water, brackish water and fresh water (Original)

Plant phyla	Sea water	Brackish water	Fresh water
Cyanophyta (blue-green algae)	++	+	+++
Chrysophyta (mainly diatoms)	+++	+	+++
Phaeophyta (brown algae)	+++	+	(+)
Euglenophyta	+	+	+++
Pyrrhophyta (dinoflagellates)	+++	+	+
Rhodophyta (red algae)	+++	++	+
Chlorophyta (green algae)	+++	++	+++
Vascular plants	+	+	+++

(+++ : large, ++ : intermediate, + : small number of species)

\* W. SCHRAMM has contributed the sections on desiccation.

they belong to the two families Potamogetonaceae and Hydrocharitaceae. While some animals (salmon, eel, wool-handed crab, etc.) spend certain periods of their life cycle alternating between marine and limnic conditions, comparable cases are not known in autotrophic organisms. The salinity barrier between marine and limnic habitats is, therefore, more pronounced in plants than in animals.

Benthic marine plants, which occupy the sea-land boundary, are frequently subject to temporary emergence, i.e. exposure to air during low water. Air exposure results in considerable changes of environmental aspects: temperature, light, osmotic gradients, etc., attain quite different intensities and fluctuation patterns than in the sea. Among these aspects, changes in osmotic conditions, as a result of rain or water loss, are of considerable ecological importance. Responses of intertidal plants to water loss during emergence, therefore, will be considered separately under the subheading desiccation.

The basic importance of the salinity factor for historical and present-day aspects of plant ecology necessitates some further general remarks. It is part of the fundamental phenomenon of the specialization of physiological processes that progressive adjustments to specific environmental circumstances are correlated with a loss of the ability to perform optimally under other circumstances. A plant which develops non-genetically or genetically towards a shade plant, frequently loses, at the same time, the ability to make optimum use of high light intensities. An organism which adapts to low temperatures becomes, simultaneously, more sensitive to high temperatures; and organisms which—as is mostly the case—are adapted to medium temperature ranges are hardly capable of tolerating extreme temperature intensities. In the last analysis, all these changes are based on the principle of enzyme adaptation, since—according to the old conceptions of WILHELM ROUX—a fight of the parts of the organisms takes place in which non-active enzymes tend to become replaced by active ones (GESSNER, 1955, p. 95).

We may expect that the phenomenon of adaptive specialization reveals itself even more clearly in regard to the factor salinity than to other environmental entities. On Earth, light and temperature possess their most frequently exhibited intensities in the middle parts of their ranges, i.e. their intensity abundance follows a one-maximum GAUSS-curve. In contrast, salinity distributions on earth reveal two major plateaus, one in sea-water, the other in freshwater habitats; transitional areas, i.e. brackish waters, are much rarer and, in terms of the geological time scale, ephemeral habitats.

The protoplasm of aquatic organisms had to adjust in its function and structure either to sea water or to fresh water, thereby creating the basis for the distributional salinity barrier already referred to. Interestingly, euryhaline species (which thrive both in sea and fresh water) are much rarer among plants than among animals; plants depend on plasmatic adaptation, while animals have a multiplicity of additional mechanisms of adaptation at their disposal.

It is easier for marine organisms to immigrate to brackish waters than for limnic forms. This is a well-known fact. Reductions in ion concentration can be compensated for more easily than augmentations. Brackish waters of half or one-third of the salinity of sea water are still occupied purely by marine plants; a few originally marine plants have even succeeded in conquering pure freshwater habitats. The diatom *Hydrosera triquetra*, which belongs to the Biddulphiaceae,

lives—as epiphyte on *Bostrychia* sp.—in marine waters (SIMONSEN, 1965); however, it occupies also rivulets and water falls of the Sunda Isles (HUSTEDT, 1938). Also the red alga *Caloglossa ogasawaraensis*, which thrives in small rivulets of the Sunda Isles, has migrated—like other red algae—into fresh water from sea; all its close relatives still live in the ocean.

Examples exist for the reverse case also, the population of the sea by freshwater plants. Typical freshwater algae, such as species of *Chlorella*, *Chlamydomonas*, *Ulothrix* and *Dinobryon*, have marine representatives. For a long time, it was assumed also that the marine angiosperms provide examples of such reverse migrations, since their closest relatives of the families Potamogetonaceae and Hydrocharitaceae exhibit their greatest species diversity in fresh water (ARBER, 1920). However, recent information (DEN HARTOG, 1970) suggests—on the basis of fossil evidence—that sea-grasses already populated, from land, marine as well as limnic habitats during the Cretaceous Age, i.e., at the time of the phylogenetical development of the phanerogams.

Different ontogenetic developmental stages of marine plants sometimes respond differently to changes in salinity. Thus the gametophytes of the Laminariales appear to be more sensitive to reduced salinities than the sporophytes, while on the other hand, the *Conchocelis* phase (which represents the sporophyte) of the red algae genus *Porphyra*, tolerates salinity variations less well than the planar thallus. Detailed investigations into these interesting relationships are highly desirable.

## (2) Functional Responses

### (a) Tolerance

#### *Tolerance to variations in total ambient osmoconcentration*

BIEBL (1937) investigated the question whether there exist relations between the habitat of marine algae and their ability to withstand decreased or increased concentrations of sea water, pointing out that fluctuations in osmotic values within the range of the tidal zone may exert a selective influence on the protoplasmatic features of the cell. Some results of his experiments are listed in Table 4-6. BIEBL interprets the results of his experiments as follows:

'Surface-algae generally show a higher osmotic resistance range than deep-water algae. Above all, they prove to be much more resistant against concentrated sea-water. While red algae occurring mainly in deep water already reach their viability limit at an average concentration of 1.4 sea-water\* and show deadly injury at 1.5, the algae located near the ebb-line and in the tidal zone tolerate an average concentration of 2.0 sea-water and even more without undergoing injury. The range of resistance to diluted sea-water is not so different in surface-algae and deep-water algae. In algae generally located in deep water, it may be assumed an average resistance-range of 0.5 and in algae living quite near the ebb-line or in tide-pools it may be about 0.4.'

In fact, some particularly resistant euryhaline species exist among algae occurring near the low-water level, e.g. *Antithamnion cruciatum*, *Callithamnion tetragonum*

\* 1.4 sea water refers to a salinity 1.4 times that of normal sea water (35‰S).

var. *brachiatum* or *Polysiphonia urceolata*, which tolerate dilutions down to 0.2 or 0.3 sea water for 24 hrs, as well as some very stenohaline algae, such as *Nitophyllum punctatum*, which live preferably in deep waters; most of the stenohaline marine algae die even in 0.8 sea water.

Table 4.6

Salinity tolerances of marine algae from the English coast. Exposure time to test salinities: 24 hrs (After BIEBL, 1937; modified)

Species	Locality	Tolerance to reduced and increased salinities, expressed in concentrations of sea water (1 $\cong$ 35‰ S)
<i>Polysiphonia urceolata</i>	ebb-line	0.3-2.0
<i>Membranoptera alata</i>	ebb-line	0.4-1.9
<i>Ptilota plumosa</i>	ebb-line	0.4-2.2
<i>Ceramium ciliatum</i>	ebb-line	0.4-2.2
<i>Heterosiphonia plumosa</i>	8-10 m water depth	0.6-1.3
<i>Cryptopleura ramosum</i>	8-10 m „ „	0.5-1.4
<i>Brongniartella byssoides</i>	8-10 m „ „	0.4-1.4
<i>Phycodrys rubens</i>	8-10 m „ „	0.6-2.0

Despite such pronounced differences in salinity tolerance, most algal species from the regions mentioned exhibit less marked divergencies in their tolerance to diluted sea water than to concentrated sea water. The assumption that tolerance ranges are related to habitat localities is supported by numerous observations. We often find *Polysiphonia urceolata* and *Callithamnion tetragonum* var. *brachiatum* above the deep-water level, and frequently exposed to air during low tides (HÖFLER, 1931). Species of *Elachista* and *Polysiphonia* resist heavy rain falls even though, as a rule, air-exposed algae are seriously endangered if their surface film of salt water is washed off. Thus air-exposed *Nitophyllum punctatum* were killed by heavy rain (TECHET, 1904; OLTMANN, 1923).

In addition to variations in salinity *per se*, the duration of exposure to reduced or increased salt concentrations, and the speed with which a given change is effected, are of ecological importance. Estuarine algae, which are subject to regular salinity variations, do not seem to suffer from such tidal effects. It is also assumed that algae which grow just above the ebb tide line and are regularly exposed to air for not more than 1 to 3 hrs at a time, are not seriously affected. According to numerous experiments, diluted as well as concentrated sea water exerts damaging effects only after several hours. In soft-bodied algae, capillary-bound sea water or, perhaps, a thin slime film containing sea water, appears to prevent excessive, detrimental salt loss or water uptake due to rainfalls. This might explain why surface and deep-water algae are generally more tolerant to subnormal than to supranormal salinities.

A useful criterion for assessing salinity tolerances and salinity-caused injuries in algae is the process of plasmolysis (Fig. 4-2). HÖFLER (1930, 1931) points out that in red algae the plasma sticks tightly to the cell wall and consequently

plasmolysis causes extreme injuries. He considers such responses a significant protoplasmic characteristic of the Rhodophyceae. However, the studies on plasmatic features in red algae do not support this view (see also WEBER, 1931).

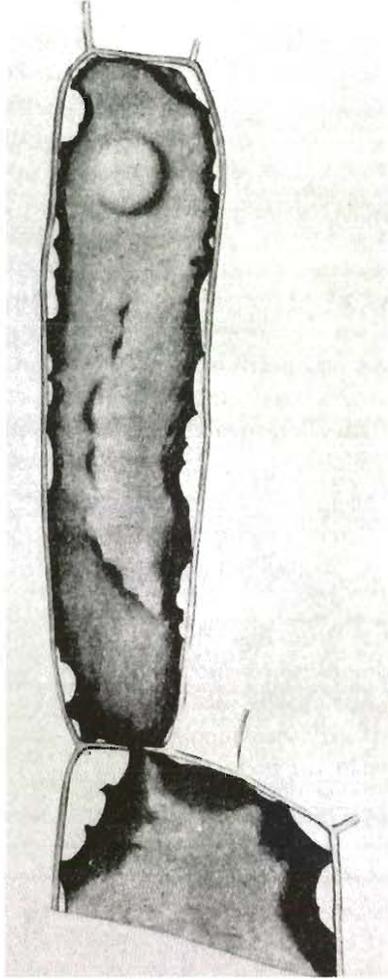


Fig. 4-2: Plasmolysis in *Griffithsia opuntiooides* exposed to 1.8 sea water (1.8 times the salinity of normal sea water). (After HÖFLER, 1930.)

In red algae showing plasmolysis, it is verified that—after the plasma has detached from the cell wall—the various projections of the protoplast which do not retract (as in *Heterosiphonia plumosa*) or wrinkle (as in *Ceramium ciliatum*) stick tightly to the cell walls and appear to be rather viscous. Wrinkle formations have also been described as a frequently occurring characteristic feature in the plasmolysis of siphonocladial algae. HÖFLER (1930) ascribes these plasmatic properties partly to the fact that the embedding chromatophore apparatus resists

a contraction of the plasma, and partly to a high degree of friction in the cytoplasm.

Only in a few cases, the plasma detaches easily from the cell wall and plasmolysis is harmless. This happens frequently in temporarily air-exposed species such as *Polysiphonia urceolata*, *Ceramium ciliatum* and *Callithamnion tetragonum* var. *brachiatum*. Plasmolysis is indicative of changes in the steady-state balance of water and salt exchanges between plant and environment. Distortion of the steady-state balance is followed by a new equilibrium, which manifests itself in the form of deplasmolysis occurring within several hours after the initial salinity change. These algae also tolerate deplasmolysis caused by salinity increase. Other red algae (provided they show plasmolysis at all), are in most cases killed immediately. It may be taken as a general rule that salinities which cause plasmolysis also kill the cells of red algae occurring along the ebb line and in the tidal zone.

In red algae susceptible to plasmolysis, but with the plasma sticking so firmly to the cell membrane that it scarcely detaches in hyperosmotic water, the lowest deadly salinity may be regarded to cause the 'incipient plasmolysis' which serves to determine the critical osmotic value (e.g. in *Heterosiphonia plumosa*).

How are algae, which tolerate salinity increases up to 2.0 sea water and more, protected against injuries due to plasmolysis? Membrane imbibition can only be considered a conditional protection, since it scarcely occurs as a general factor in hyperosmotic salinities. Immediately before the incipient plasmolysis is reached, the detachment of the protoplast of some algae (e.g. *Griffithsia flocculosa*) may be somewhat delayed when the membrane starts swelling. Comparative experiments revealed that red algae, endangered by plasmolysis in their respective localities, possess a far more efficient and simpler means of avoiding plasmolysis, namely, their high natural osmotic value. While incipient plasmolysis in algae living at different water depths of the sea occurs on an average at a salinity equivalent to that of 1.5 sea water, this value usually rises to about 2.0 sea water in algae inhabiting tide pools or ebb tide lines. Although the cells of these algae are killed by salinities causing plasmolysis (or slightly higher ones), the danger of lethal damage is considerably reduced by their high internal osmoconcentration.

An exception among temporarily air-exposed algae is *Ceramium ciliatum*; while it tolerates salinities equivalent to those of 2.2 sea water and higher, incipient plasmolysis occurs at 1.5 sea water. *C. ciliatum* is the only red alga known to tolerate plasmolysis in salinities which exceed the internal osmoconcentration to such an extent. *Polysiphonia urceolata* from Tromsø (Norway), which plasmolyzed in 1.9 sea water and remained vital and intact in 2.0 sea water after natural deplasmolysis for a period of 3 days, died after 24 hrs in 2.2 sea water. *C. ciliatum* is the only red alga in which natural plasmolysis has been observed in the natural habitat (HÖFLER, 1931, p. 68).

It is of interest to compare salinity effects on plasmolysis and vitality of red algae to those of the green alga *Cladophora* sp. which occurs in tide pools (BIEBL, 1937). Individuals of *Cladophora* sp. turned out to be perfectly healthy and intact after a 24-hr exposure to ambient concentrations ranging from 0.3 to 2.0 sea water. The effects of intermediate salinities, equivalent to 2.0 to 3.0 sea water, were not tested, but in 3.0 sea water, only part of the cells was killed. Thus the upper lethal salinity lies above 2.0 sea water and may extend to 2.2 sea water. Incipient plasmolysis occurs in 1.3 sea water.

It seems quite possible that in some temporarily air-exposed red and green algae, which tolerate plasmolysis for a certain time, plasmolysis never occurs even in the smallest tide pools because of fast deplasmolysis (penetration of salts from the ambient medium into the cell sap); the penetrating salts may increase the internal osmoconcentration of the respective alga parallel to the rate of increase in salinity.

The responses of brown algae, which plasmolyze quite readily but never deplasmolyze, have not yet been studied.

The highest salinity tolerances ever found in marine plants have been reported for mangrove algae (BIEBL, 1962a). *Caloglossa leprieurii*, *Catenella repens*, *Bostrychia tenella*, *Murayella pericladus*, and others can survive 24 hrs in salinities ranging from that of fresh water to that of 4 times sea water. Submerged algae of the same locality, such as *Dasya mollis*, *Wrangelia bicuspadata*, *Hypnea musciformis*, *Centroceras clavulatum*, *Spyridia filamentosa* and others can tolerate salinities equivalent to the range 0.4 to 1.8 sea water. The salinity tolerances of the mangrove algae mentioned are not significant in regard to their natural distribution, because equilibrium with the ambient medium is by no means reached within 24 hrs. Continuous exposure of mangrove algae to pure fresh water or to 4 times the salinity of sea water will certainly lead to irreversible damage and, hence, death. Exposure times of 1 month instead of 24 hrs would result in different values for the salinity range tolerated. Carefully conducted long-term experiments are urgently needed for a more complete assessment of tolerances to salinity variations in marine algae.

On the basis of pertinent experimental information, our present knowledge concerning multicellular algae may be summarized as follows: The maximum osmotic tolerance range of macroscopic algae inhabiting tide pools and ebb lines amounts to about 0.3 to 2.2 sea water. This range pertains especially to red and green algae which inhabit the higher vegetation zones of temperate sea coasts. The internal osmoconcentration (cell fluids) of marine algae generally ranges from 1.3 to 1.5 sea water. Red and green algae (experiments on brown algae are lacking) which tolerate plasmolysis without injury maintain these low osmoconcentrations even in temporarily exposed habitats. Algae, subject to habitat salinity variations which could bring about lethal plasmolysis, are characterized by fast osmotic adjustments; they increase rapidly the osmoconcentration of their cells to a level corresponding to the hyperosmotic stress imposed by their environment (BIEBL, 1937).

Among unicellular algae, the flagellate *Amphidinium hofleri* shows a very high osmotic tolerance (HÖFLER and co-authors, 1956). The cells preserve their normal motility between 0.3 and 2.4 sea water, even if transferred directly into the different test concentrations. Still higher is the salinity tolerance of the nearly colourless dinoflagellate *Oxyrrhis marina* from the same locality (Lagoon of Venice, Italy), which remains motile for several days between 0.1 and 3.0 sea water.

Lower salinity tolerances, especially to higher salinities have been reported by NAKANISHI and MONSI (1965) from Japanese estuarine phytoplankton forms. The values are summarized in Table 4-7. It is obvious that survival is observed more frequently in reduced salinities than in salinities above those of normal sea water. Possibly, the specific estuarine locality has exerted selective influences on the tolerance ranges observed.

Table 4-7

Tolerated and optimum salinities of estuarine phytoplankton forms (After NAKANISHI and MONSI, 1965; modified)

Phytoplankton forms	Tolerance (‰S)	Optimum (‰S)
<b>Diatoms</b>		
<i>Cerataulina pelagica</i>	6-45	
<i>Chaetoceros radians</i>	4-48	15
<i>Leptocylindrus danicus</i>	6-45	
<i>Thalassiosira decipiens</i>	5-45	
<i>Skeletonema costatum</i>	12.5-50	
<i>Thalassiosira decipiens</i>	15-	
<i>Cyclotella</i> sp.	2.5-35	
<i>Chaetoceros elmorei</i>		10-30
<b>Flagellates</b>		
<i>Ceratium furca</i>	15-40	17-32
<i>Ceratium fusus</i>	15-40	20-25
<i>Hymenomonas carterae</i>	5-45	25-35
<i>Peridinium triquetrum</i>	5-40	10-30
<i>Syracosphaera carterae</i>	5-45	15-45
<i>Amphidinium</i> sp.	5-45	15-35
<i>Exuviaella</i> sp.	5-40	10-40
<i>Cryptomonas</i> sp.	10-35	15-20
<i>Platymonas</i> sp.	2.5-35	15-35
<i>Monochrysis lutheri</i>	2.5-	
<i>Olithodiscus</i> sp.	15-35	20-35

#### *Tolerance to variations in ambient ionic composition*

SCHWENKE (1958a) showed that red algae tolerate hypo-osmotic salinities better if tap water rather than distilled water is used as dilutant; he suggested that the higher survival rates in fresh water are due to the presence of calcium ions. This suggestion was later put to critical examination (SCHWENKE, 1958b) and found to be correct; some results, obtained on three species of red algae of the western Baltic Sea, are listed in Table 4-8.

In further experiments, tolerance to media without K, Mg and Ca was examined (Table 4-9). Among the three cations omitted in the ionic composition of the artificial sea water employed, the absence of Ca causes the highest degree of cell damage. Damage increases with increasing exposure time. Tolerance to absence of Ca differs in the four species tested; it is lowest in *Delesseria sanguinea* and *Membranoptera alata*, higher in *Ceramium rubrum* and highest in *Ceramium diaphanum*. In view of the fairly constant ionic composition of natural sea waters, the ecological importance of these findings is quite limited.

Transfer into distilled or brackish water is followed by plasmatic exosmosis. It has been well known for a long time, that Ca ions reduce the plasmatic permeability

Table 4-8

Tolerance of macroscopic marine red algae to hypo-osmotic artificial sea water. Dilutant: distilled water with and without Ca; exposure time: 24 hrs; temperature: 10° C. The degree of damage is expressed in percentages of dead cells per individual; + : 100% of the cells dead (After SCHWENKE, 1958b; modified)

Medium	Algae	Salinity (‰)					
		1	2	3	4	5	6
Artificial sea water	<i>Delesseria sanguinea</i>	50	10	10	1	1	1
	<i>Membranoptera alata</i>	25	10	10	10	10	1
	<i>Phycodrys sinuosa</i>	25	25	10	10	1	1
Artificial sea water without Ca	<i>Delesseria sanguinea</i>	90	90	90	90	90	90
	<i>Membranoptera alata</i>	+	+	90	90	+	90
	<i>Phycodrys sinuosa</i>	+	+	+	90	90	+

Table 4-9

Tolerance of four red algae to artificial sea waters (asw) of different ionic composition. Table body: degree of damage expressed in percentages of dead cells per individual. Salinity: 20‰; temperature: 10° C. + : 100% of the cells dead (After SCHWENKE, 1958b; modified)

Exposure time (days)	<i>Delesseria sanguinea</i>				<i>Membranoptera alata</i>			
	asw	asw without		Ca	asw	asw without		Ca
		K	Mg			K	Mg	
1	1	1	1	+	1	1	1	+
2	1	1	10		1	1	1	
4	1	1	10		10	1	50	
7	1	10	25		10	10	50	
10	1	25	50		10	10	+	
Exposure time (days)	<i>Ceramium rubrum</i>				<i>Ceramium diaphanum</i>			
	asw	asw without		Ca	asw	asw without		Ca
		K	Mg			K	Mg	
1	1	50	1	50	1	25	1	25
2	1	+	1	+	1	90	1	90
4	1		25		1	+	25	+
7	1	2	25		1		50	
10	1		75		1		90	

for other ions and molecules. This fact accounts for a delay, and possibly a reduction, of damaging effects under hypo-osmotic conditions in the presence of Ca.

The importance of Ca was also demonstrated by EPPLEY and CYRUS (1960) in *Porphyra* species. Lack of Ca in rain water results in rapid loss of K and weight; these losses are accelerated during osmotic stress. In the absence of Ca, *Porphyra* sp. may survive up to 30 hrs in 100% sea water, but only 6 to 8 hrs in 30% sea water. The presence of Ca, K and Na (and probably also of Mg) is required for the normal functioning of cellular processes including ion transport (EPPLEY and CYRUS, 1960).

The physiological mechanisms of ion uptake, ion loss and ion transport are largely unknown. They must be analyzed in physicochemical experiments. Our pertinent knowledge has been summarized by GUTKNECHT (1966); it will be documented in Volume II of the present Treatise. Ionic relations have up to now been examined primarily in multicellular plants. In such cases, responses of identical cells to different ionic conditions can be studied. In unicellular algae, assessments of tolerance to variations in ionic composition are more difficult. Differences between cells, and cell generations, as well as long-term modifications, may considerably complicate the situation.

#### *Salinity and heat tolerance*

In *Chaetomorpha cannabina*, salinity affects the degree of heat tolerance (BIEBL, 1969). Subsequent to a 48-hr pretreatment in diluted sea water, heat tolerance becomes markedly reduced. Pretreatment in 0.1 sea water (in this case, 1 sea water is equivalent to 13.42‰S) kills 90% of the cells during a 30-min exposure to 36°C; pretreatment in 0.3 sea water kills 50%, pretreatment in 0.5 sea water only 2% of the cells; after pretreatment in 0.7 sea water all cells survive. Increase of salinity beyond the normal level leads to further increases in heat tolerance. Following pretreatment (also 48 hrs) in 4 sea water (53.6‰S), all cells survive, even in a test temperature of 39°C. Supranormal salinities have also been shown to increase heat tolerance of animals (Chapters 3.3, 4.3). Interestingly, *C. cannabina* exhibits also changes in heat tolerance as a function of the tidal rhythm. Such rhythmic tolerance changes could be observed by BIEBL for at least 2 days after the algae had been removed from their natural habitat.

BIEBL (1970) compared the salinity and heat tolerances of algae inhabiting the west coast of the USA. Salinity and heat tolerances decrease more or less parallel to each other (Tables 4-10, 4-11). This finding is hardly surprising since in littoral areas both salinity and temperature exert comparable stresses and selection pressures.

#### *Tolerance to desiccation*

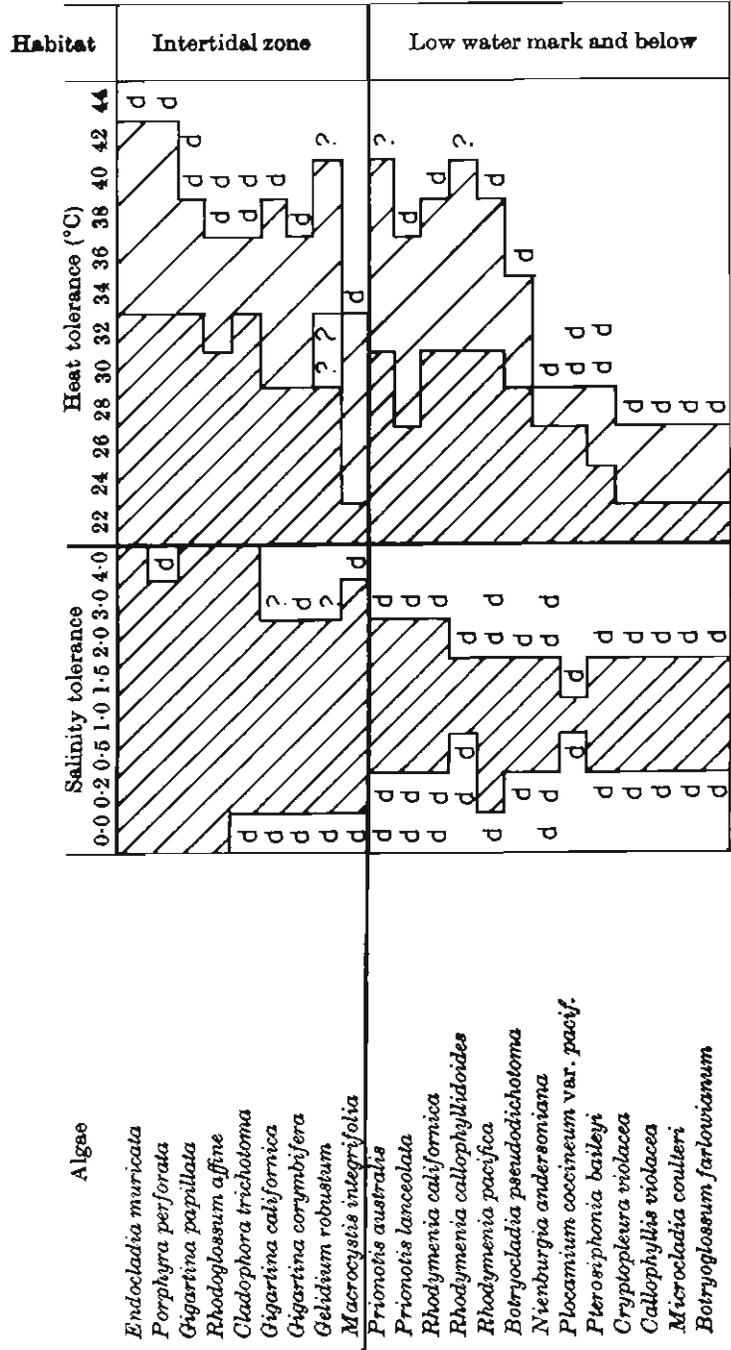
As has been pointed out in the introduction to this chapter, littoral benthonic algae are frequently subject to temporary air exposure leading to increased environmental stress and, especially, to water loss. Desiccation tends to affect the water and salt balance of the plants concerned and therefore may be conveniently considered along with salinity effects.

Although the ecological importance of water loss during exposure has been stressed by many authors, the information available on responses of plants to



Table 4-11

Comparative salinity and heat tolerances in algae inhabiting the west coast of the USA near Pacific Grove, California. For details consult legend to Table 4-10 (After BREBL, 1970; modified)



desiccation is quite restricted. Only a few critical studies have been conducted on marine algae (e.g. GESSNER, 1971); practically nothing is known about responses to desiccation in marine phanerogams and lichens.

Marine plants subject to desiccation employ two groups of adjustments to counteract detrimental effects of water loss: (i) Avoidance (retardation) of desiccation, or promotion of water uptake via structural properties of single cells, whole plants or even the whole vegetation. Compared to many terrestrial plants such adjustments are, in most cases, only imperfectly developed in marine forms. (ii) Ability to tolerate the water loss by 'physiological' compensations, i.e. increased resistance to desiccation.

Both avoidance of and resistance to desiccation are considered here to be aspects of tolerance. In the botanical literature, these terms frequently have different meanings (STOCKER, 1956; LEVITT, 1958; BIEBL, 1962b). Many authors follow LEVITT (1958) who uses the terms avoidance and tolerance as subdivisions of the term resistance.

*Lethal limits of desiccation.* Hardly any detailed studies on lethal limits of desiccation stress have been conducted. There exists, however, a number of pertinent observations. BERTHOLD (1882) mentions the ability of the Mediterranean red algae *Bangia fuscopurpurea*, *Porphyra leucosticta* and *Nemalion lubricum* to tolerate heavy desiccation. He reports that *Bangia fuscopurpurea*, which on the coasts of the European Mediterranean occasionally remains out of the water for more than 15 consecutive days (FELDMANN, 1937), survives emersion periods of several days in sunlight and even weeks in shade. BIEBL (1939) found representatives of this alga from the Gulf of Naples (Italy) undamaged after 21 days of air exposure (room temperature, diffuse daylight). Re-immersed in sea water, the previously exposed individuals did not reveal any differences relative to untreated specimens. Among the brown algae, *Pelvetia canaliculata* is known for its considerable tolerance to desiccation. According to MONTFORT (1937) and RIED (1969), this alga can tolerate a period of about 2 weeks in an air dry condition without injury.

In general, the degree of desiccation tolerance attained in marine plants is not as high as in a number of terrestrial thallophytes (e.g. LANGE, 1953; BIEBL, 1962b). POST (1963) claimed that it was possible to cultivate tetrasporoclings of the West Indian red algae *Caloglossa adnata* and *Caloglossa leprieurii* from material kept for 28 years in a herbarium. This unusually extreme degree of desiccation tolerance is surprising, since marine benthic algae characteristically lack typical resting stages (OLTMANN, 1923). Vegetative thallus parts of members of the red alga genus *Bostrychia*—which contains exceedingly drought-resistant species—can survive air dryness for hardly more than a few weeks. GESSNER (*in*: POST, 1963) states that algae of a *Bostrychietum* from the Amazon estuary still consumed oxygen after a desiccation period of 2 months. Own measurements on a sample of a *Bostrychietum*, collected in October 1965 in Venezuela, and brought in an air dry condition to Germany, however, revealed lack of photosynthesis after 14 days, when re-immersed in sea water.

In this connection, it is noteworthy that a number of algae of the supralittoral, such as *Bangia fuscopurpurea* from the Mediterranean Sea or *Urospora penicil-*



*iformis* from the North Sea, seem specifically to require periodic desiccation in their respective habitats (BIEBL, 1962b). Investigations on *Fucus vesiculosus* from the Baltic Sea and on *Porphyra umbilicalis* from the North Sea (OGATA and SCHRAMM, 1971) reveal that moderate periodic desiccation has positive effects on the rate of photosynthesis, as well as on the general condition of the algae.

A critical assessment of lethal desiccation conditions is particularly difficult in view of the fact that most authors employed different survival criteria and that the information available on other simultaneously effective environmental factors is insufficient.

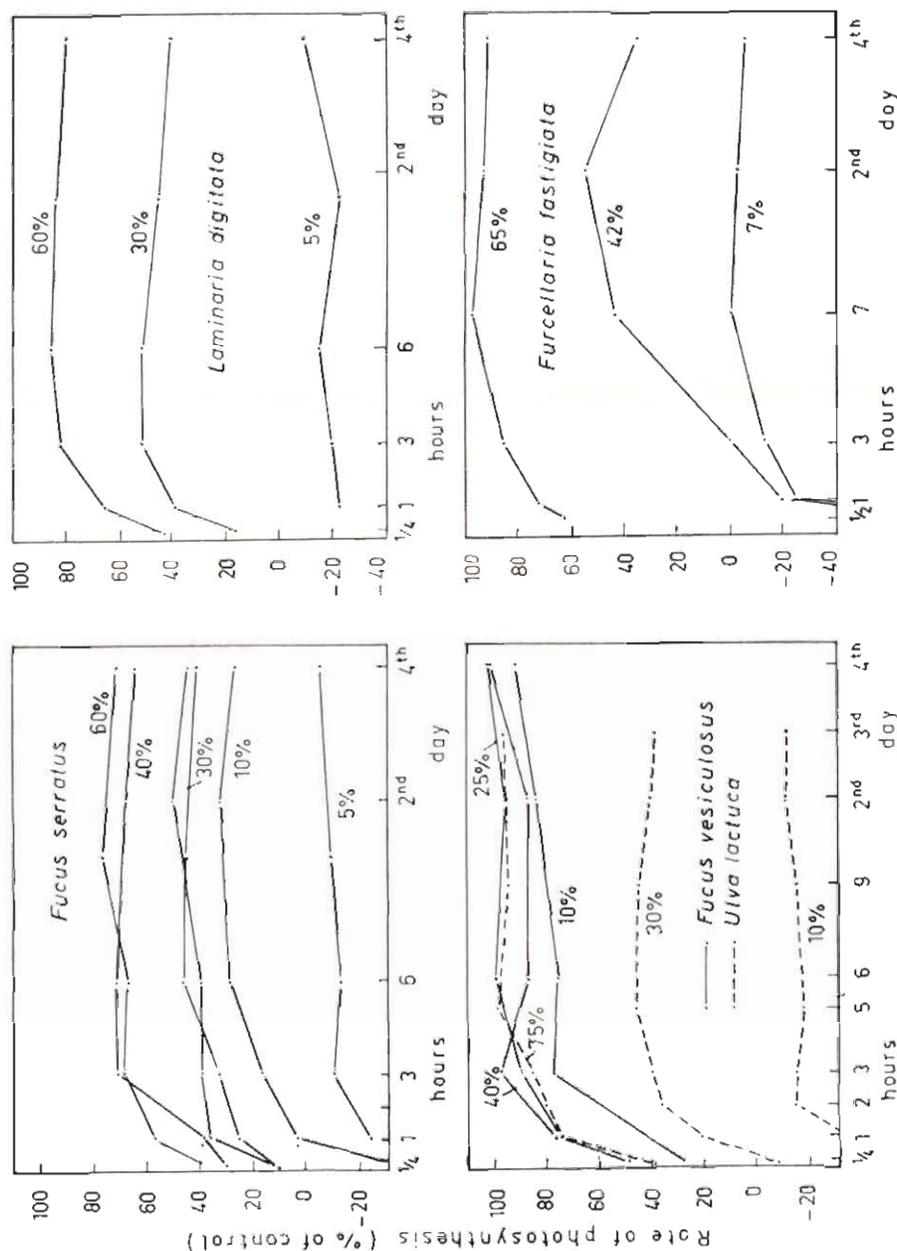
BIEBL (1938) studied desiccation tolerance of marine algae under more defined experimental conditions. He placed his objects for periods of 14 hrs at room temperature over salt solutions with different vapour pressure, retransferred them into sea water and evaluated the degree of injury suffered on the basis of microscopical inspection of the cells (Table 4-12). His experiments showed that algae from habitats subject to regular air exposure reveal a higher degree of desiccation tolerance than those maintained under permanently submerged conditions. In other experiments, the algae were exposed to free air at 18° to 20°C and 72 to 74% relative humidity. Under these conditions, sublittoral species such as *Trilliella intricata* or *Plocamium coccineum* were partly damaged after 15 secs, the whole individuals died after 4 to 5 mins. It seems quite possible that in these cases emersion damage is not only caused by water loss but also by other factors associated with air exposure.

*Porphyra laciniata* is considerably more tolerant. On Helgoland (southern North Sea) it grows together with the green alga *Urospora penicilliformis* at the highest algal habitats above the sea level. BIEBL (1938) found this alga alive even after 4 days of air exposure. *Porphyra perforata* from the coast of California (USA) tolerated 14 hrs at 66.6% relative humidity, but died at 48.3% relative humidity (BIEBL, 1956a).

It is a disadvantage that the experimental techniques employed by BIEBL and others give no information on the state of protoplasmic water, which, ultimately, is the most important parameter determining the degree of desiccation damage. Even under constant desiccation conditions, one must expect different hydration values and time courses of desiccation, depending on species-specific differences in plasma colloids, initial water content and desiccation avoidance.

The simplest way of determining the degree of water loss is by weighing. MONTFORT (1937), KALTWASSER (1938) and others have used this method and assessed the biological consequences on the basis of post-exposure damage to oxygen exchange processes of marine algae. KALTWASSER investigated *Ulva lactuca*, *Fucus vesiculosus*, *Fucus serratus*, *Laminaria digitata* and *Furcellaria fastigiata* from the Baltic Sea.

The lowest degree of desiccation tolerance is exhibited by *Laminaria digitata* and *Furcellaria fastigiata*, which, in the Baltic Sea, live permanently submerged (Fig. 4-3). In contrast, *Fucus vesiculosus*, which is often exposed to air, even after desiccation to 5 to 7% body water content, still shows positive photosynthesis values after re-transfer to sea water. Re-activation after such intensive desiccation is, however, only incomplete and restricted to a short period of time (SCHRAMM, 1968).



Time after re-transfer to sea water

Fig. 4-3: Time course of recovery of photosynthesis following different degrees of water loss in Baltic Sea algae. Percentage values indicate the degree of prior desiccation expressed in percent maximum water content. Desiccation in open air at room temperature. Photosynthesis measured in Baltic Sea water of 17‰ S at 10° to 11°C. Light source: 300 W bulb; distance 12 cm. (After KALTWASSER, 1938; modified.)

Up to now, almost nothing is known about the biological consequences of desiccation speed. It seems that—in contrast to the findings of ILJIN (1930, 1953) on higher terrestrial plants—in algae, the speed of water loss does not affect the degree of desiccation damage. Thus *Ulva lactuca* from the Baltic Sea showed no differences in desiccation damage, when desiccated to the same degree of water loss within different periods of time (KALTWASSER, 1938). Also in *Fucus vesiculosus* from the Baltic Sea, desiccated at room temperature to 30% of its saturation weight in periods ranging from 5 to 28 hrs, speed of water loss was unimportant with regard to the rate of photosynthesis obtained after re-immersion (SCHRAMM, 1967).

In addition to the degree of water loss, the duration of a given desiccated state greatly affects the degree of damage incurred. Desiccation intensities which may be tolerated over short periods of time may become critical if the duration of the desiccated state is prolonged. The relation between desiccation damage, as indicated by O<sub>2</sub> output after re-immersion, and the duration of the desiccated state is illustrated in Figs 4-4 and 4-5. Rate of photosynthesis as assessed by O<sub>2</sub> output clearly decreases as a function of the length of the desiccation period. *Fucus vesiculosus*, immediately re-immersed after reaching desiccation degrees equivalent to 10 to 12% body water content, shows only short-lasting after-effects; after 2

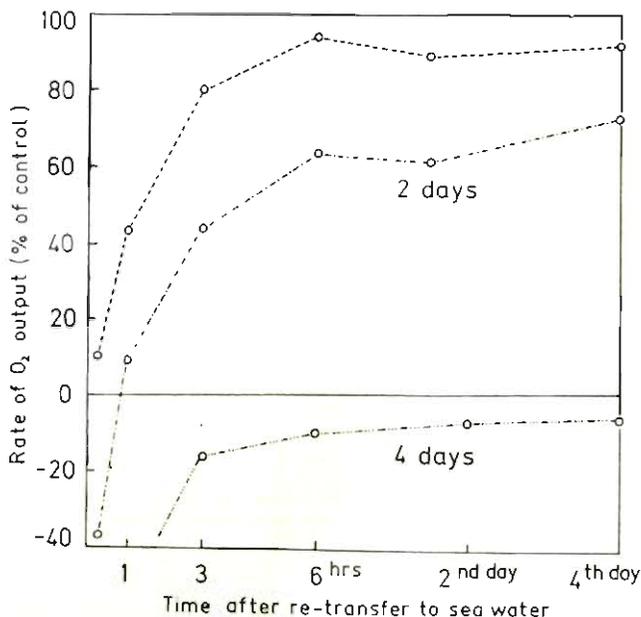


Fig. 4-4: *Fucus vesiculosus* (Baltic Sea). Time course of recovery of photosynthesis following different periods of maintenance in dehydrated state (10 to 12% body water content). Upper curve: rate of photosynthesis of a thallus re-immersed immediately after reaching a desiccation degree of 10 to 12%; middle and lower curves: dehydration periods of 2 and 4 days, respectively. Desiccation conditions and photosynthesis measurements as in legend to Fig. 4-3. (After KALTWASSER, 1938; modified.)

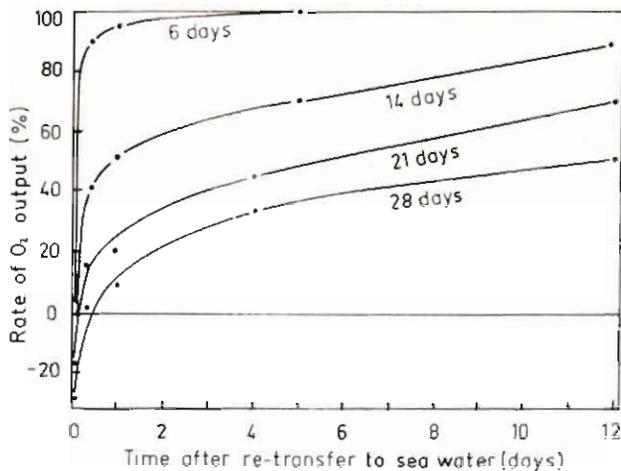


Fig. 4-5: *Pelvetia canaliculata*. Time course of recovery of photosynthesis following different periods (6, 14, 21, 28 days) of maintenance in dehydrated state. Material kept at 14° C and 40% relative humidity. Rate of O<sub>2</sub> output expressed in per cent of photosynthetic activity measured before desiccation. Photosynthesis measured in 34‰S at 14° C; 4000 lux. (After RIED, 1969; modified.)

days in this desiccated state, thallus parts are moderately damaged; after 4 days, they show no O<sub>2</sub> output at all. Considerably more resistance to water loss is exhibited by the brown alga *Pelvetia canaliculata* (Fig. 4-5).

The relationship between different desiccation levels and the length of time spent at these levels has been investigated by SCHRAMM (1968) in terms of the resulting changes in O<sub>2</sub> output after re-immersion (Fig. 4-6). Damage due to the different levels of desiccation and to the different periods of time spent at these levels occurs much faster at low body water contents. At 60%, rate of photosynthesis after re-immersion in sea water decreases from about 90% to 45% within about 6 days; at 25%, a corresponding 50% decrease occurs within 1/2 to 1 day.

The tolerance limits of individuals to different conditions of desiccation are of considerable importance for assessing intraspecific and interspecific differences of intertidal plants to desiccation stress. However, under natural conditions in the field, the tolerance limits of individuals are of lesser importance than those of populations. Whereas, at the individual level the criterion for tolerance is death, at the population level the criterion for tolerance is the critical reduction of reproductive activities or of the competitive potential of the population as a whole.

Unfortunately, no experiments have been conducted yet to assess critical desiccation conditions for populations of marine plants. These, of course, would be important prerequisites for the understanding of distributional ranges of marine plants (p. 810). One of the major differences between a single plant and a whole vegetation is the fact that a vegetation may significantly influence the microclimate of its own habitat. In emerged populations of *Enteromorpha* sp., for example, one can often observe that only the peripheral plants or parts of them are imme-

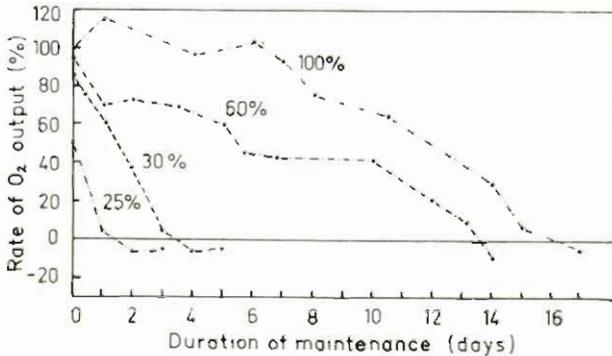


Fig. 4-6: *Fucus vesiculosus* (Baltic Sea). Rate of photosynthesis following different periods of maintenance at different body water contents (25, 30, 60, 100% of saturation weight). Ordinate: Rate of O<sub>2</sub> output 24 hrs after re-transfer into sea water, expressed in % of photosynthetic activity before desiccation. Desiccation and maintenance at ca 20° C; O<sub>2</sub> output measured in Baltic Sea water of 15‰S at 15° C and 10 klux. November; individual data. (After SCHRAMM, 1968, modified.)

diately subjected to the full impact of detrimental emersion conditions. The outermost plant parts frequently become heavily dehydrated and exposed to intensive heat; consequently they often die during summer. In contrast, the deeper layers of the majority of the population remain protected by the peripheral layers against excessive water loss, radiation, heat, etc. In model experiments, SCHRAMM (1968) has attempted to demonstrate such a situation also in *Fucus vesiculosus*. In early spring and summer, several hundred individuals from the *Fucus vesiculosus* belt of the western Baltic Sea, which were attached to stones of from fist to head size, were removed from the water and placed on the beach at the niveau of the upper swash mark. Whereas MUENSCHER (1917), conducting similar experiments, made sure that the thalli did not overlap, in order to assure equal exposure conditions for all individuals and parts, in SCHRAMM's experiments the algae were arranged for natural overlapping. Throughout several subsequent days, the progressive water loss and its effects on photosynthesis rates were recorded. The peripheral thallus parts dried fast, especially during the summer experiment, and consequently revealed heavy damage (Fig. 4-7, curves 1 and 3). During the early spring experiment these changes were comparable but less pronounced (Fig. 4-8, curves 1 and 3). In the main mass of the deeper lying plant parts, water loss proceeded significantly slower and so did the time course of damage suffered (Figs 4-7 and 4-8, curves 2 and 4). The major environmental factors governing these processes are, next to water loss, temperature and relative humidity (rain): during rain periods (Fig. 4-8, r) only the peripheral plant layers are affected and become damaged due to critical freshwater influence.

Modifications of microclimate by plant populations also tend to reduce environmental stress on early ontogenetic life-cycle stages under conditions of air exposure. Germination and early development may, for example, proceed successfully in

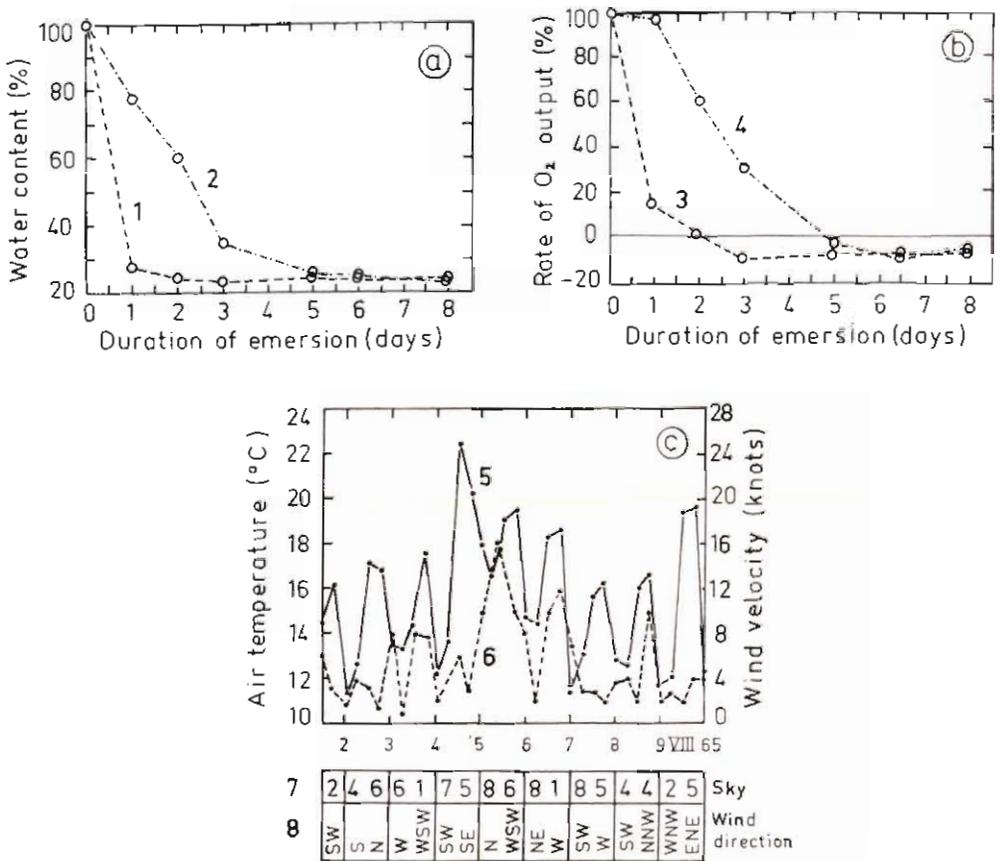


Fig. 4-7: *Fucus vesiculosus* (Baltic Sea). After-effects of emersion under field conditions on photosynthesis. Summer conditions. (a) Time course of water loss in five thallus parts: 1: most heavily desiccated peripheral thallus parts; 2: least desiccated thallus parts (from middle and lower layers). Water loss expressed as percentage of average saturation weight, determined at the beginning of the experiment. (b) Average rate of O<sub>2</sub> output 24 hrs after re-transfer of thallus parts to Baltic Sea water of 15‰S, expressed in percent of the mean values determined at beginning of experiment. 15°C; 10 klux. Curves 3 and 4 correspond to 1 and 2 in (a). (c) Emersion conditions during experiment; 5: air temperature close to plants; 6: wind velocity; 7: cloud covering of sky in 8/8; 8: wind direction at 0700 and 1900 hours. (After SCHRAMM, 1968; modified.)

the deeper layers of emersed *Fucus vesiculosus* vegetations under desiccation stress which would, in single plants, lead to irreversible damage (p. 815). These examples illustrate clearly that intertidal macro-algae vegetations can modify the lethal desiccation limits of individuals. Plants of a vegetation provide some degree of mutual protection against critical water loss, radiation and extreme temperatures and hence allow the populations to survive environmental stresses which would be lethal to single, separately growing individuals. For this reason, BERTHOLD (1882, p. 404) pointed out that the distributional limits of various littoral plants can only be appreciated fully when considering the integration of the species into the local vegetation as a whole.

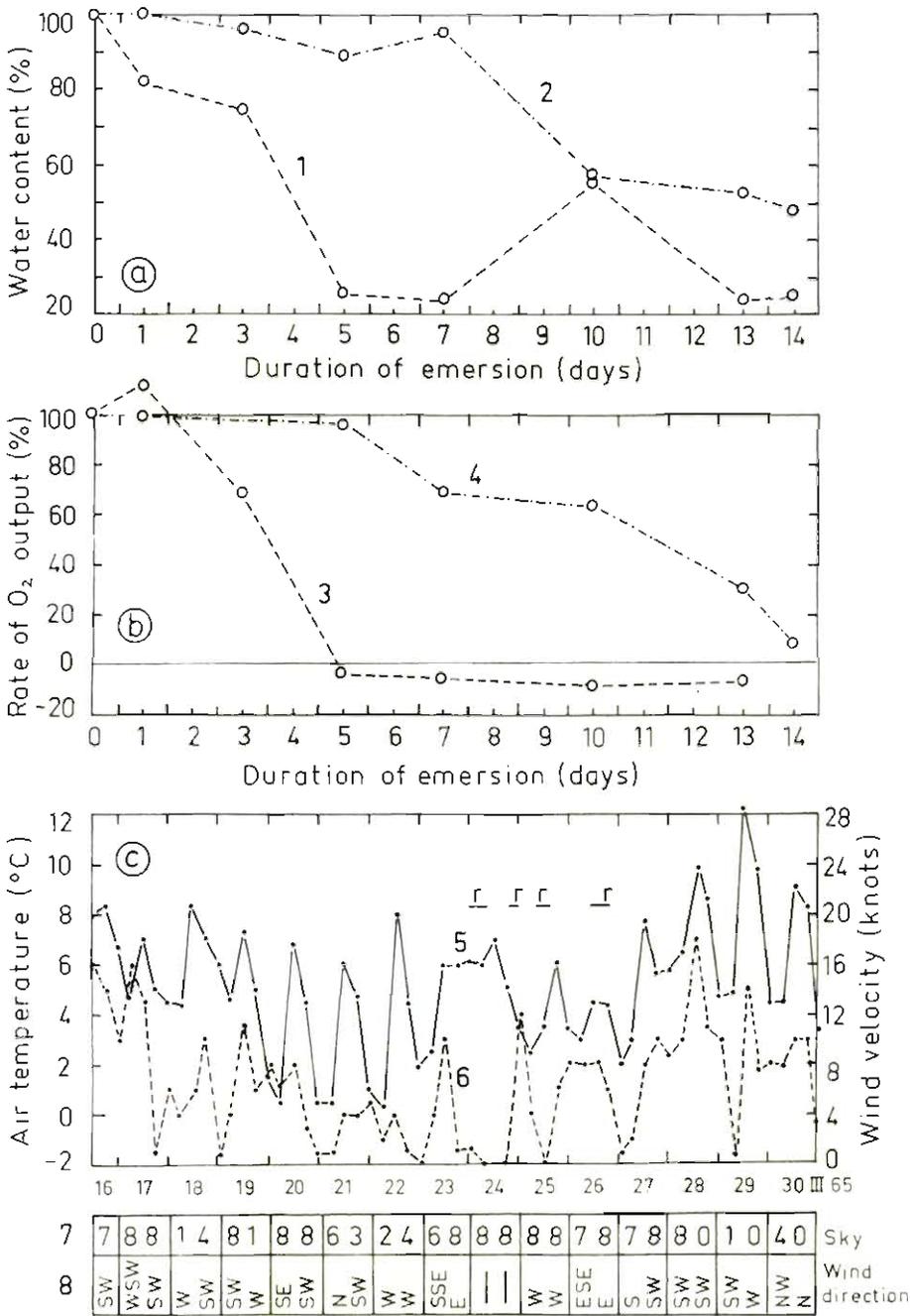


Fig. 4-8: *Fucus vesiculosus* (Baltic Sea). Details as in legend to Fig. 4-7. Early spring conditions. r: rain. (After SCHRAMM, 1968; modified.)

Practically nothing is known about seasonal differences in the degree of desiccation tolerance of intertidal plants. The same is true in regard to possible variations in desiccation tolerance as a function of life-cycle stage or age. In general, the delicate young stages of marine plants exhibit less avoidance of water loss than the older life-cycle stages (e.g. CHAPMAN, 1966; KRISTENSEN, 1968; Fig. 4-9).

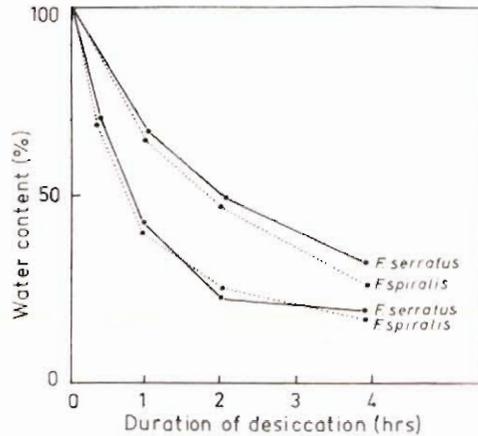


Fig. 4-9: Water loss during desiccation in adult and juvenile individuals of *Fucus serratus* and *Fucus spiralis* (northern French Atlantic coast). Upper two curves: adults; lower curves: juveniles. (After KRISTENSEN, 1968; modified.)

These differences may possibly also play a role in regard to SAITO's (1960) investigations on desiccation tolerance of various developmental stages of *Undaria pinnatifida*. Young gametophytes of various growing stages, resting zoospores and young sporophytes of this alga were exposed to air of various humidities (45, 60·7, 84 and 100%) for various durations (15 to 180 mins) and at different air temperatures. After retransfer to sea water, the plants were cultivated for 2 or 4 days. Their survival rate, growth rate and health condition were estimated. The general results were: Resting zoospores are less tolerant to desiccation than gametophytes and young sporophytes. Gametophytes which grow actively are more sensitive than those in the resting stage. It is not possible to deduce from SAITO's results whether they are based on differences in resistance to water loss, i.e. in the ability to tolerate drying, since no data on the degree of water loss are presented.

Variations in drought resistance could, however, be established by RIED (1969) on thallus parts of different age. Thus, young thallus tips of *Fucus vesiculosus* were more sensitive to water loss than older thallus parts. In contrast, younger thallus parts seem to be less sensitive than older ones in the red alga *Polyides rotundus* (Fig. 4-10) or in the brown alga *Fucus distichus*. RIED's observation that changes in temperature resistance may be almost opposite to changes in desiccation resistance illustrates the difficulty in regard to pinpointing ecological effects of single environmental factors.

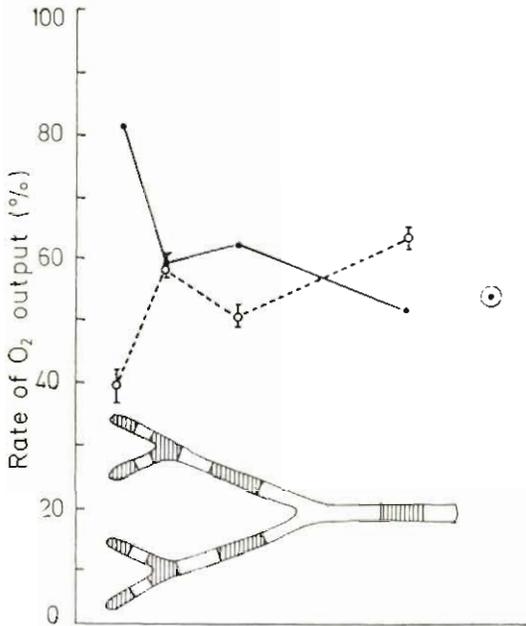


Fig. 4-10: *Polyides rotundus*. Differences in local desiccation and heat tolerance. The marked regions of the thallus were desiccated to about 52% maximum water content or exposed to sea water of 15‰S and 34°C for 90 mins. The curves show the rate of O<sub>2</sub> output 11 days after retransfer into 15‰S, measured at 14°C. Solid line: O<sub>2</sub> output of desiccated thallus parts; broken line: O<sub>2</sub> output of heated thallus pieces; large circle: O<sub>2</sub> output of heated undivided thallus. (After RIED, 1969; modified.)

During the emersion period, marine plants are subject not only to water loss, but also to, often extreme, modifications of environmental factor intensities, particularly of light, temperature and osmotic climate. The degree to which these factors may influence desiccation tolerance of plants has hardly been investigated as yet. In regard to light, no pertinent information has come to the reviewer's attention.

There is also little definite information available on the influence of temperature on desiccation tolerance; however, it may be generally assumed that temperature plays an important role in desiccation tolerance: up to now we do not know how water loss affects the organisms, but in general it can be presumed that responses of plants following water loss depend on variations in plasmatic state and metabolic conditions. Thus desiccation tolerance depends ultimately on physical states and chemical processes which are temperature dependent (BUNNING, 1948; PRECHT and co-authors, 1955; Chapter 3).

First, tentative experiments on temperature effects on desiccation tolerance have been conducted by SCHRAMM (1968) on *Fucus vesiculosus* from the Baltic Sea (Fig. 4-11). Under comparable conditions (at 18°C over sulphuric acid), thallus parts of equal size (from one individual plant) were adjusted to different water

contents (100, 60, 30% saturation weight) and exposed to different constant temperatures for 24 hrs. Thereafter, saturation weight was, under identical conditions, further reduced to 30%. The degree of desiccation damage was then assessed on the basis of photosynthetic rates 24 hrs after retransfer into sea water. Fig. 4-11 shows that the rate of metabolic performance ( $O_2$  output) varies with exposure

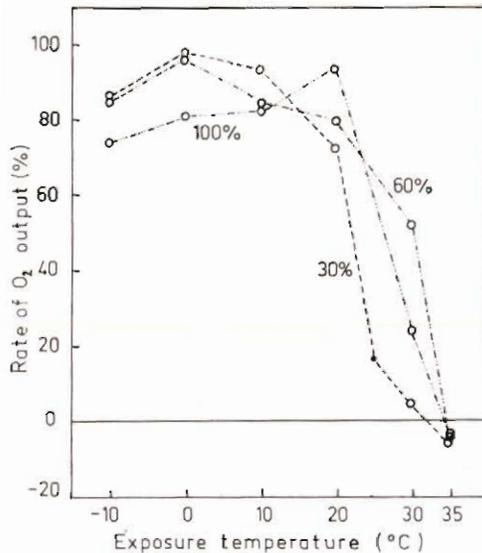


Fig. 4-11: *Fucus vesiculosus* (Baltic Sea). Rate of  $O_2$  output (% of initial values measured at 15°C) following 24-hr exposure to temperatures ranging from -10° to 35°C at different body water contents (100, 60, 30% saturation weight) and subsequent desiccation to 30% saturation weight.  $O_2$  output measured in 15‰S at 15°C and 10 Klux. April; mean values. (After SCHRAMM, 1968; modified.)

temperature. The amount of damage suffered by the differentially dehydrated thallus parts during exposure to the different temperature levels may perhaps be interpreted as being due to a summation of temperature and dehydration damage, or to changes in the degree of inhibition of metabolic reactions, possibly by progressive reduction of energetic gradients with increasing temperatures. OHNO (1969) investigated the influence of desiccation at different temperatures on survival rates of spores of various marine algae. All species tested show a tendency for their desiccation tolerance to decrease with rising temperatures (Table 4-13).

The osmotic climate may affect desiccation tolerance in various ways. In regard to terrestrial plants, FITTING (1911), MAXIMOV (1929), PARKER (1956), and others presented a number of hypotheses. In intertidal marine plants, the immediate osmotic climate is of particular importance; water loss during air exposure progressively increases the salt concentration of the adhering sea water, whereas

Table 4-13  
 Survival times (hrs) of spores of marine algae as a function of desiccation and temperature conditions, r.h.: %  
 relative humidity (After OHNO, 1969; modified)

Algae (spores)	40 r.h.			60 r.h.			80 r.h.		
	3°C	10°C	30°C	3°C	10°C	30°C	3°C	10°C	30°C
<i>Ulva pertusa</i>	4	4	2	10	12	2	30	22	4
<i>Monostroma nitidum</i>	8	6	4	16	18	4	26	22	4
<i>Porphyra tenera</i>	4	2	0	22	22	0	32	28	0
<i>Gelidium amansii</i>	2	1	1	2	1	1	2	4	0
<i>Scytosiphon lomentaria</i>	4	2	0	14	10	2	24	22	2
<i>Eisenia bicyclis</i>	1	0	0	2	3	1	5	4	1

extensive rain causes salt loss and water imbibition. Such extreme changes in osmotic conditions must significantly affect the osmoconcentration of the cell fluids. BIEBL (1938, 1962b) discusses the possible consequences of this situation for algae which exhibit plasmolysis. Removal of water from water-rich cells via evaporation may hinder the protoplasm withdrawing properly from the cell wall, i.e., the cells do not plasmolyze (HOLLE, 1915). ILJIN (1927, 1930, 1933, 1953) assumes that drying damage of the protoplast is largely caused by mechanical forces; if the protoplast fails to detach from the rigid cell wall during dehydration, intraplasmatic tension and, finally, rupture may result. In fact, ILJIN was able to increase considerably drought tolerance of higher plant tissues, when protoplast detachment was supported prior to dehydration by employing a plasmolyticum. The same effect could possibly prevail in some algae under habitat conditions, due to progressive salt concentration in the adhering sea-water film (BIEBL, 1938). The ability of marine algae to plasmolyze in their normal habitat has been observed by HÖFLER (1931) on the British coast in *Ceramium ciliatum* and a species of *Cladophora*.

*Resistance adaptation to desiccation stress.* Resistance adaptation (Chapter 3.31, p. 438) refers to changes in organismic tolerance to extreme intensities of environmental factors. Detailed studies on resistance adaptation of marine plants to desiccation stress have not yet been conducted. However, there is some pertinent information available.

Non-genetic resistance adaptation may have been involved in some experiments conducted by SCHRAMM (1968) on *Fucus vesiculosus*. Samples of adult algae obtained in the Baltic Sea were exposed to 15°C and ca 1000 lux (14 hrs light, 10 hrs darkness) and submersed for 30 days in water of 15‰S; other, comparable, samples were dehydrated (60 to 30% saturation weight) and rehydrated in irregular intervals of 1 to 3 days over the 30-day period. A comparison of the tolerances of the two groups was made 48 hrs after the end of the conditioning period (criterion: after-effects of dehydration to 30% saturation weight on photosynthesis rate). The comparison revealed a higher desiccation tolerance of the group conditioned to dehydration-rehydration treatment.

Intraspecific differences in resistance to desiccation of plants from different habitats have been documented in a few cases. *Hormosira banksii*, a member of the Fucales, occurs on the coast of New Zealand in several, morphologically clearly different forms (BERGQUIST, 1959). Depending on their habitat, these forms are subject to varying periods of air exposure. Measuring the photosynthesis during exposure under conditions of high humidity (80% relative humidity), photosynthesis of the emerging forms (maximum exposure time from 6.5 to 4.5 hrs daily) continued several hours. However, when a permanently submersed form of *Hormosira banksii* is used, very little or no net photosynthesis occurs when emersed, and respiratory output of CO<sub>2</sub> is the only gas exchange phenomenon observed (CHAPMAN, 1966). *Fucus vesiculosus* grows in the western Baltic Sea (in contrast to the situation on most of the tidal coasts) not only in the upper littoral, but also at all other water depths between mean high water level and a depth of 8 to 10 m. The 'surface form' is frequently distinguishable from the 'depth form' on the basis of external features (MÜLLER-STOLL and KÜNZENBACH,

1956; OVERBECK, 1956). These forms show, according to MONTFORT (1937), a sequence of desiccation tolerance similar to that established in interspecific comparisons among the *Fucus* species and *Pelvetia canaliculata* occurring at different depths of tidal coasts. The degree of tolerance increases with habitat height relative to the mean high water level. The lower tolerance of the deeper forms manifests itself both in a more pronounced increase of respiration or depression of photosynthesis surplus at the beginning of rehydration, and in the degree of reversibility of gas exchange after 1 or 2 days.

In contrast to MONTFORT's (1937) observations, similar studies on *Fucus vesiculosus* from different water depths of the 'Kieler Förde' (western Baltic Sea) did not reveal significant differences in dehydration tolerance (SCHRAMM, 1968). However, in this case, the algae, which were collected at 2 to 3 m depth and from just below the water surface (and externally characterized by depth-form and surface-form features, respectively) were examined after 3 weeks of maintenance under constant conditions (Baltic Sea water of 15‰S, 15° C, 14 hrs 1000 lux: 10 hrs darkness). Hence only long-term, persisting differences in tolerance could have been recorded.

Genetic resistance adaptation to desiccation is witnessed by interspecific differences of intertidal algae which are correlated to habitat exposure. Such interspecific differences are often very pronounced and are referred to in this chapter on various occasions.

#### (b) *Metabolism and Activity*

The study of salinity effects on metabolism and activity of plants is a matter of considerable complexity. For the oceanographer, salinity represents an entity which effects the dynamics of water masses, primarily via variations in density. The marine ecologist, too, may consider salinity as a single environmental aspect as far as the total osmoconcentration of the medium (the sum of the dissolved constituents) is concerned. However, sea water influences biological processes also through specific effects of its numerous ions. Ultimately, the biological consequences of salinity variations are based on ionic or molecular exchanges between plant and ambient medium.

Since metabolic processes of living systems are closely interrelated, each type of ion or molecule may interfere in a multitude of ways, providing they can enter the outer protoplasmic borders. This state of affairs makes it clear that a detailed causal analysis of biological salt effects is not possible without considering quantitative and qualitative parameters of permeability. The phenomenon of permeability, however, is an aspect of life which is particularly complex and most difficult to analyze.

Only in cases where it is possible to study ion effects on biological subprocesses, e.g. of photosynthesis in isolated chloroplasts under *in vitro* conditions, will it be possible to neglect the importance of the permeability barrier. Since such cases are rare, it will be appreciated that all attempts to explain how salinity variations influence the metabolism of marine plants must remain rather superficial. Only specific biochemical research appears adequate to analyze further the governing causal forces. A comprehensive treatment of permeability and active transport,

including the physiological and biochemical mechanisms involved, will be presented in Volume II of the present Treatise.

*Water economy and internal osmoconcentration*

In terrestrial plants, water economy and internal (cellular) osmoconcentration are closely related (WALTER, 1931). Usually, the plant roots have to obtain water against the capillary retaining forces of the soil and the hygroscopic gradients. Scarcity of water results in increased cellular osmoconcentration. This situation is, of course, quite different in marine plants which are surrounded by their aquatic medium; the frequently mentioned 'turgor pressure deficit' is an artefact.

Since osmotic conditions—except in brackish-water and littoral habitats—are practically the same for all truly marine plants, one might expect that cellular osmoconcentrations also are more or less identical in the various species. As will be documented later, this is, however, by no means the case; the differences in osmotic pressures of internal and external media range between zero and about 20 atm. Since these differences apparently have no ecological significance in regard to water uptake, it must be concluded that they represent criteria for genetic (phylogenetic) divergencies, and, indeed, closely related plants often exhibit very similar internal osmotic pressures. While submerged freshwater plants live in aquatic environments exerting osmotic pressures of close to 0 atm, their marine counterparts are confronted with ambient osmotic pressures of about 23 to 25 atm. These considerable differences in the respective osmotic climates of limnic and marine algae constitute striking divergencies in regard to water and salt exchanges between plant and environment.

As pointed out by KOTTE (1915), determinations of incipient plasmolysis values (generally applied in higher plants for assessing their internal osmotic pressures) cannot be employed in many algae; the main reasons are: intensive membrane imbibition, strong turgor expansion, high plasmatic permeability for dissolved substances, plasmolytic responses to a variety of external factors (BÜNNING, 1934) and, above all, the poor plasmolyzing abilities of many algae, which have been demonstrated especially in red algae (HÖFLER, 1930; p. 709, 710).

In hyperosmotic ambient media, the protoplast of many marine algae neither detaches smoothly from the cell wall, nor acquires a round form as in most phanerogams; but it exhibits forms of spasmodic plasmolysis (Fig. 4-2) indicative of strong adhesive forces which bind the plasma to the cell wall. Consequently, all internal osmoconcentrations determined in marine algae by means of incipient plasmolysis must be viewed with critical reservation; it cannot be excluded, without further qualification, that the rapid salt permeation in hyperosmotic salinities produces values far beyond those indicative of cells exposed to normal sea water. Thus TRAMER (1957), employing incipient plasmolysis, obtained values in three marine algae which are about 23 atm higher than the osmotic pressure of sea water: *Chaetomorpha aerea* 45.6 atm, *Chaetomorpha tortuosa* 46.5 atm, *Griffithsia opuntioides* 45.3 atm. One can only agree with MOSEBACH's (1936) opinion that osmotic values obtained by plasmolytic methods are too high, and with his warning against using such values as indicators of normal cellular osmoconcentrations. In view of this situation, MOSEBACH attempted to apply the cryoscopic

method, used in terrestrial plants, to osmotic studies on marine algae also. The main difficulty was to remove the water adhering to the outer surface areas of algae without loss of cellular water. MOSEBACH solved this problem by centrifuging his test objects; he obtained the values listed in Table 4-14; the values correspond to normal cellular osmotic pressures.

Table 4-14

Determinations of cellular osmotic pressures in marine algae after removal of adhering water via centrifuging. Temperature: 20° C  
(After MOSEBACH, 1936; modified)

Species	Osmotic pressure (atm)		
	Cells	Sea water	Difference
<i>Cystoseira barbata</i> (shoots)	30.2	25.2	5.0
<i>Sargassum linifolium</i> (blades)	31.8	25.1	6.7
<i>Sargassum linifolium</i> (floating vesicles)	31.7	25.1	6.6
<i>Rytiphylaea tinctoria</i> (main boughs)	29.6	25.0	4.6
<i>Spyridia filamentosa</i> (main boughs)	29.0	25.2	3.8
<i>Valonia macrophysa</i> (cell sap)	27.2	26.2	1.0
<i>Valonia utricularis</i> (cell sap)	27.3	26.2	1.1

Since cryoscopic determinations are conducted on cell saps pressed out of freshly killed thalli, it is unknown whether the values obtained are identical with those in living tissues. Besides, the method of pressing out cell saps produces only average values for the plant part used; it does not allow for differentiations between individual cells or regions of the thallus piece tested.

Employing a microcryoscopic technique, KESSELER (1958) succeeded in collecting saps from individual cells and in determining their osmoconcentration. However, such a procedure is restricted to algae with large cells. KESSELER found the values listed in Table 4-15. These values are far below those reported by TRAMER (1957) but exceed those obtained by MOSEBACH (1936).

Table 4-15

Microcryoscopically determined osmoconcentrations of cell sap of marine algae from the Baltic Sea (After KESSELER, 1958; modified)

Species	Osmoconcentrations		
	Cell sap (atm)	Sea water (atm)	Difference (atm)
<i>Bryopsis hypnoides</i>	11.25	9.05	2.2
<i>Chaetomorpha linum</i>	27.5	11.5	16.0
<i>Chara baltica</i>	15.7	11.05	4.65

Cellular osmoconcentrations of marine algae are not always higher than those of the surrounding sea water. HÖFLER (1963) documented that cell saps of certain planktonic centric diatoms are isosmotic to the ambient sea water. Considering the osmotic pressure of normal sea water to be 1, diatoms investigated by HÖFLER (*Lauderia borealis*, *Rhizosolenia alata*, *Guinardia staccida*, *Hemiaulis sinensis*, and others) plasmolyze already in sea water of 1.01. In *Ditylum brightwellii*, osmotic relations are extremely complicated and influenced greatly by variations in pH values (GROSS, 1940).

Extensive investigations on cellular osmoconcentrations of marine algae from the Venetian coasts (Mediterranean Sea) have been made by PIGNATTI (1962). He obtained cell sap by compression, after killing the thalli with chloroform. Table 4-16 demonstrates the extent to which the cellular osmoconcentrations in some

Table 4-16

Osmotic pressures of marine algae from the Lagoon of Venice (Italy). Mean values of differences between internal and external osmoconcentrations (After PIGNATTI, 1962; modified)

Algae	Osmotic pressure differences (atm)	Algae	Osmotic pressure differences (atm)
<i>Fucus virsoides</i>	4.87	<i>Cystoseira barbata</i>	6.03
<i>Ceramium ciliatum</i>	3.06	<i>Bryopsis duplex</i>	1.79
<i>Ulva lactuca</i>	3.24	<i>Dictyota dichotoma</i>	3.16

of the algae exceed those of the ambient sea water. Individual values fluctuate considerably. The fluctuations are caused possibly by considerable variations in cellular osmotic pressures occurring during the course of 1 day. Osmoconcentrations also vary appreciably in emerged and submerged algae (Table 4-17). Emersion values are in all cases higher, probably because of water loss during air exposure. Annual fluctuations were not observed by PIGNATTI and, according to the present author, daily differences are too irregular to establish relations to photosynthesis such as have been reported in lower and higher freshwater plants.

Table 4-17

Osmotic pressures (atm) of algae from the Lagoon of Venice (Italy) during emersion and submersion (After PIGNATTI, 1962; modified)

Algae	Emersion	Submersion	Difference
<i>Fucus virsoides</i>	34.36	27.56	6.80
<i>Ulva lactuca</i>	34.92	26.77	8.15
<i>Ceramium ciliatum</i>	27.84	26.19	1.65
<i>Enteromorpha compressa</i>	27.92	24.16	3.76

It is surprising that—except for the papers by HÖFLER (1930, 1963), GROSS (1940) and KESSELER (1967)—no information is available on osmotic values on unicellular phytoplankton algae. Technically, it should not be very difficult to determine the internal osmoconcentration in marine dinoflagellates and diatoms.

#### *Rate of respiration*

In marine algae, relations between respiratory rates and salinity variations have been dealt with in only a few papers. Today, most of the older contributions are hardly of more than historical interest. Such papers and those concerned with freshwater algae (species of the genus *Chlorella*) will not be treated here.

The results obtained on marine algae by different authors reveal, up to date, little agreement. This is not surprising. The rate of respiration is a very labile parameter which depends largely on the physiological state of the alga. Hence salinity can also be expected to cause different responses in plant individuals subject to different physiological conditions. In addition, the different algal species may respond quite differently. It is, therefore, rather difficult to draw general conclusions.

HOFFMANN (1929) distinguished two groups of algae on the basis of their responses to salinity variations: the first group shows no significant changes in respiration rate upon salinity changes, whereas the second group reveals considerably increased intensities of respiration with decreasing salinity. The first group is represented, for example, by *Enteromorpha* species, *Fucus vesiculosus* and *Porphyra laciniata*, the second by *Fucus serratus* and *Laminaria digitata*. According to HOFFMANN, increased respiratory rates due to reduced salinities cause a reduction in final body size (p. 815) and in the number of species per habitat (p. 790). Higher respiratory rates lead to augmented losses of organic matter produced by photosynthesis; consequently, the existence of marine algae in brackish water appears to be limited by some kind of starvation.

The findings of OGATA (1963) on *Porphyra tenera* are similar to those obtained by HOFFMANN (1929). However, respiration rates of *P. tenera* decrease in both very low and very high salinities. OGATA and TAKADA (1968) report the same responses for *Ulva pertusa*, *Ceramium* sp. (Fig. 4-12), *Sargassum thunbergii*, *Gloiopeltis furcata*, *G. tenax*, *Undaria pinnatifida* and *Gracilaria verrucosa* (Fig. 4-13). Further experiments proved that not only the level of salinity but also the time span of exposure to different salinity levels affects the responses observed (Fig. 4-14). In other experiments, OGATA and TAKADA studied the after-effects in normal sea water after 24-hr exposures to different salinities (Figs 4-15 to 4-18). The curves obtained are quite different. It is difficult to appreciate why OGATA made the final determinations in normal sea water and not in the test salinities to which the algae were previously exposed for 24 hrs. With some reservation, it may be concluded that the respiratory rates tend to increase in somewhat diluted sea water, whereas both extreme low and extreme high salinities tend to cause damages, indicated by reduced intensities of respiration.

New clues have been provided by NATH (1967). He confirmed the findings of GESSNER and PANNIER (1958) that respiratory rates of aquatic plants decrease with a reduction in ambient oxygen supply. It may be assumed, therefore, that the salinity influence on respiration is, at least in part, indirect (see also KINNE

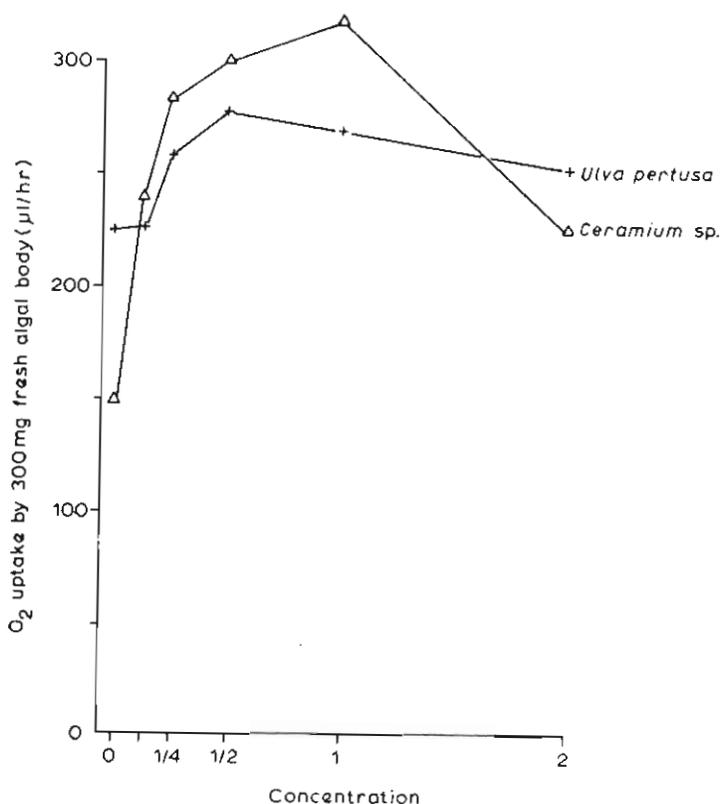


Fig. 4-12: Respiratory rates of marine algae as a function of salinity (concentration 1 = 19.79‰ chlorinity). (After OGATA and TAKADA, 1968; modified.)

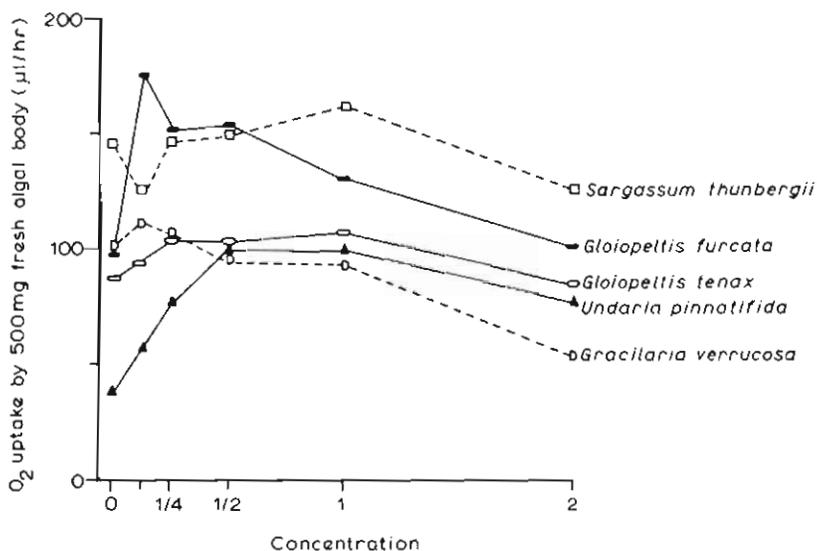


Fig. 4-13: Respiratory rates of marine algae as a function of salinity (concentration 1 = 19.79‰ chlorinity). (After OGATA and TAKADA, 1968; modified.)

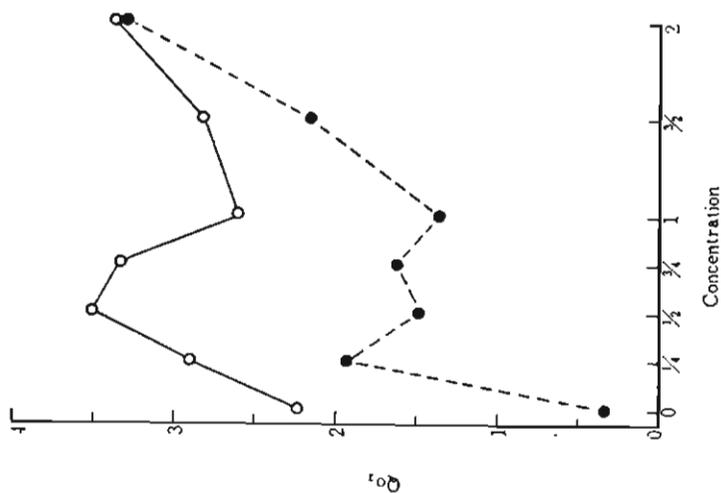


Fig. 4.15:  $Q_{O_2}$  values of *Ulva pertusa*. Open circles: after 24-hr exposures to the different salinities indicated (concentration 1 = 19.79‰ chlorinity); closed circles: after re-transfer into normal sea water. (After OGATA and TAKADA, 1968; re-drawn.)

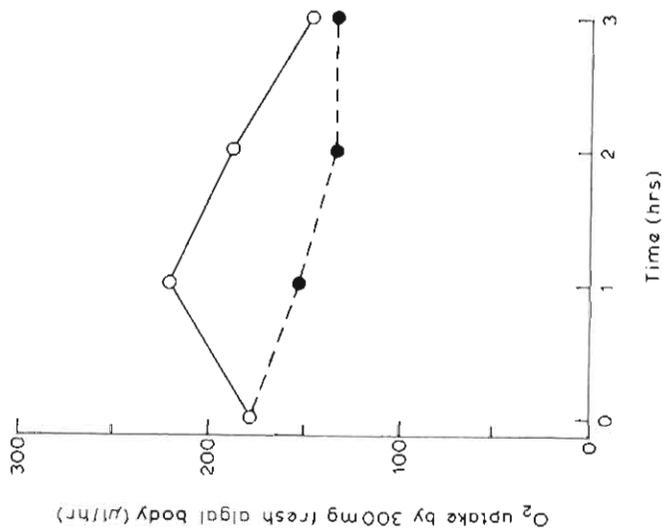


Fig. 4.14: Time course of respiratory rates in *Polysiphonia urceolata* after immersion in hypo- or hyperosmotic sea water. Open circles: 0.5 sea water; closed circles: 2.0 sea water. (After OGATA and TAKADA, 1968; modified.)

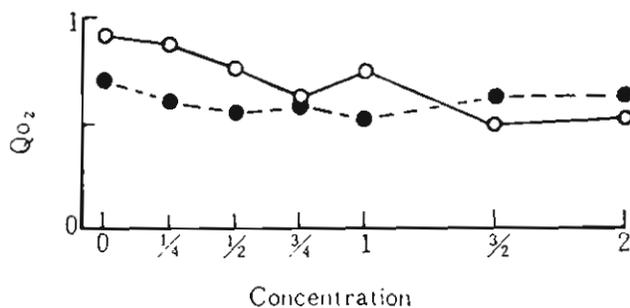


Fig. 4-16: QO<sub>2</sub> values of *Ishige okamurai*. Details as in legend to Fig. 4-15. (After OGATA and TAKADA, 1968; redrawn.)

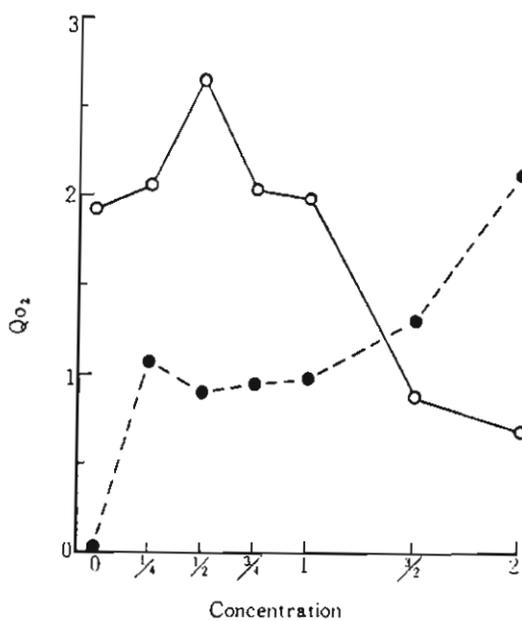


Fig. 4-17: QO<sub>2</sub> values of *Gelidium amansii*. Details as in legend to Fig. 4-15. (After OGATA and TAKADA, 1968; redrawn.)

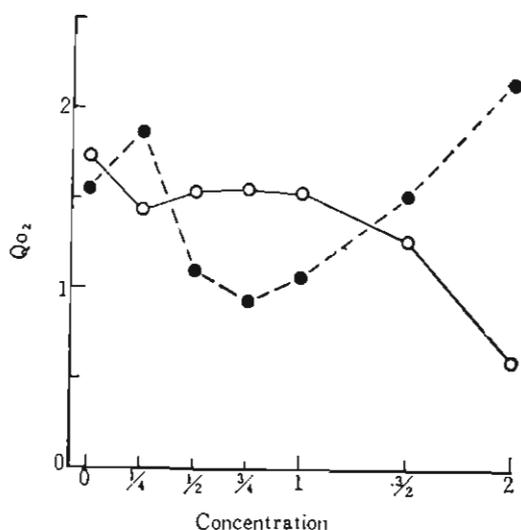


Fig. 4-18:  $QO_2$  values of *Zostera marina*. Details as in legend to Fig. 4-15. (After OGATA and TAKADA, 1968, redrawn.)

and KINNE, 1962a, b; Chapter 4.31). At 15°C, the saturation value for oxygen is 6.88 cm<sup>3</sup> O<sub>2</sub>/l in 5‰S, but 5.73 cm<sup>3</sup> O<sub>2</sub>/l in 35‰S. NATH tested the rates of respiration of brown and green algae at different O<sub>2</sub> saturations and in different salinities (Fig. 4-19). He found respiratory activities always to be proportional to the degree of O<sub>2</sub> saturation but not to salinity.

From these experiments it may be concluded that respiratory rates of marine algae are primarily affected by the oxygen supply. Only in extreme low or extreme high salinities may osmotic processes, according to OGATA (1963), interfere and influence directly the intensity of plant respiration.

Nothing seems to be known about salinity influences on respiratory rates of marine phytoplankton forms. Only freshwater plankton algae have been investigated in this respect (NAKANISHI and MONSI, 1965; see also p. 748). Both photosynthesis and respiration decrease with increasing salinity, but salinity affects photosynthesis more intensively than respiration. In both processes, responses on the first day are more pronounced than on the third day, indicating that adjustments (non-genetic adaptations) begin shortly after the initial exposure to experimental conditions.

Many papers deal with the biochemistry of respiration in algae (GIBBS *in*: LEWIN, 1962), but nothing seems to have been done to analyze salinity influences at the different steps of the respiratory pathway. Since it is obvious that salinity not only acts via total osmotic pressure but also affects the respiration system via ionic influences, experiments employing artificial sea water of different ionic composition may be expected to yield new and more detailed insights.

#### *Rate of photosynthesis*

In 1931 MONTFORT published two brief papers on assimilation and 'Stoffgewinn' of benthonic algae subjected to de-salinization and subsequent re-salinization.

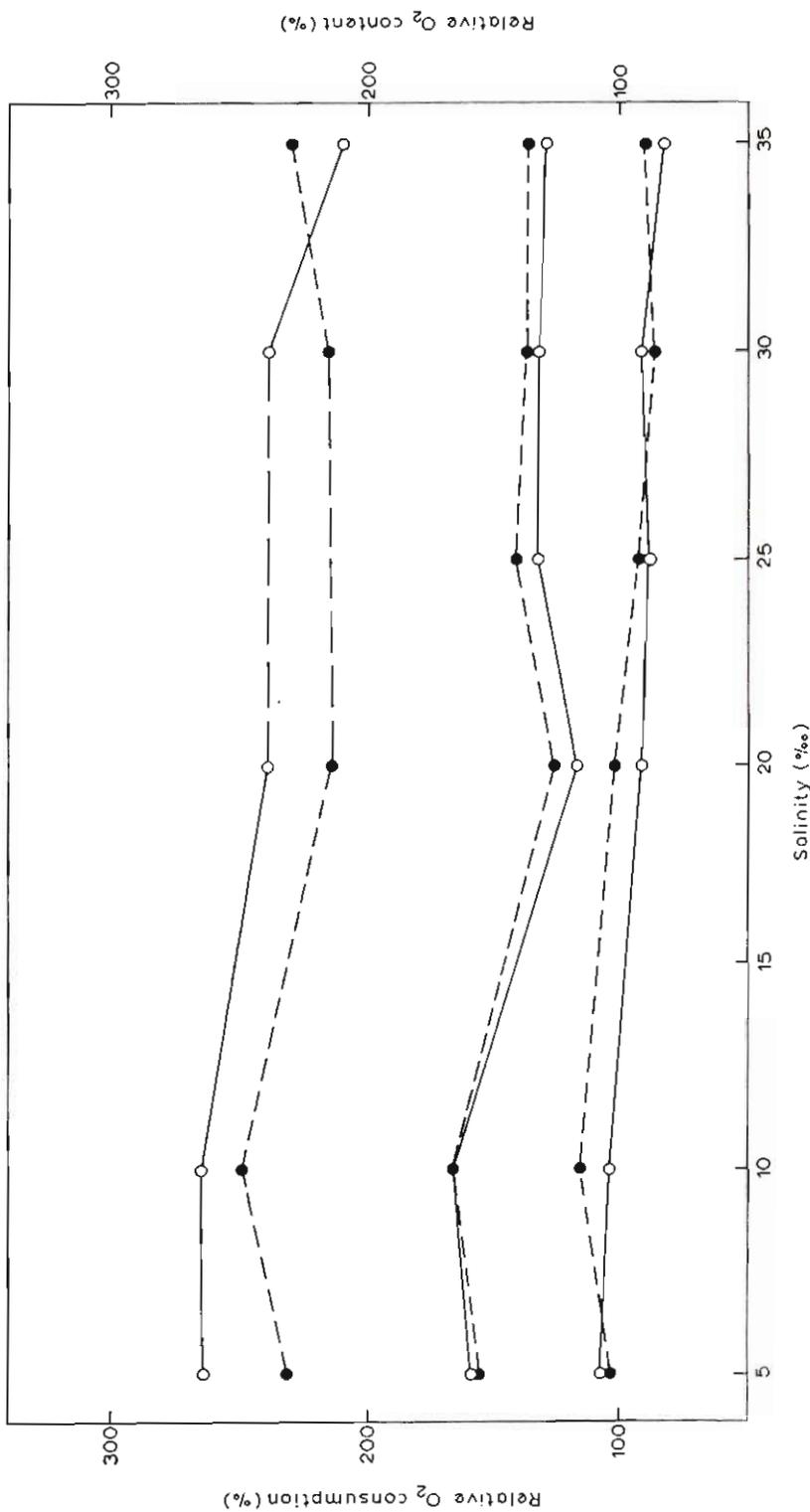


Fig. 4-19: *Fucus vesiculosus*. Relationship between respiratory rate and salinity in solutions of different O<sub>2</sub> content. Solid lines: relative O<sub>2</sub> consumption (left scale); 100%: 0.428 mg O<sub>2</sub>/g dry weight/hr; broken lines: relative O<sub>2</sub> content (right scale); 100%: 8.68 mg O<sub>2</sub>/l; 14.25‰ S). (After NARR, 1967; modified.)

He tested six species of brown algae and three species each of red and green algae from the North Sea and Baltic Sea. Representatives of these alga species were transferred successively into different dilutions of Baltic Sea water (obtained by adding river or tap water). In regard to the subsequent changes observed in photosynthesis rates, MONTFORT distinguished the following three types.

(i) A depression type which responds to decreased salinities with an irreversible depression in photosynthetic rate;

(ii) A stimulation-depression type which responds to decreased salinities at first with augmented rates of photosynthesis, later with an inhibition (it was possible to differentiate between fast and slow inhibitions, and to determine whether these were reversible or irreversible).

(iii) A resistant type which shows no decrease in photosynthesis rates following transfer from sea water into fresh water.

MONTFORT (1931) emphasized, however, that it is not possible to establish a definite relation between the photosynthetic intensities displayed by a given alga species and salinity since such a relation varies as a function of exposure time, resulting in an almost unlimited number of rate curves. This finding possibly illuminates the reason for the contradictory results reported by LEGENDRE (1921) and FROMAGEOT (1923). The diversity of MONTFORT's response types, the difficul-

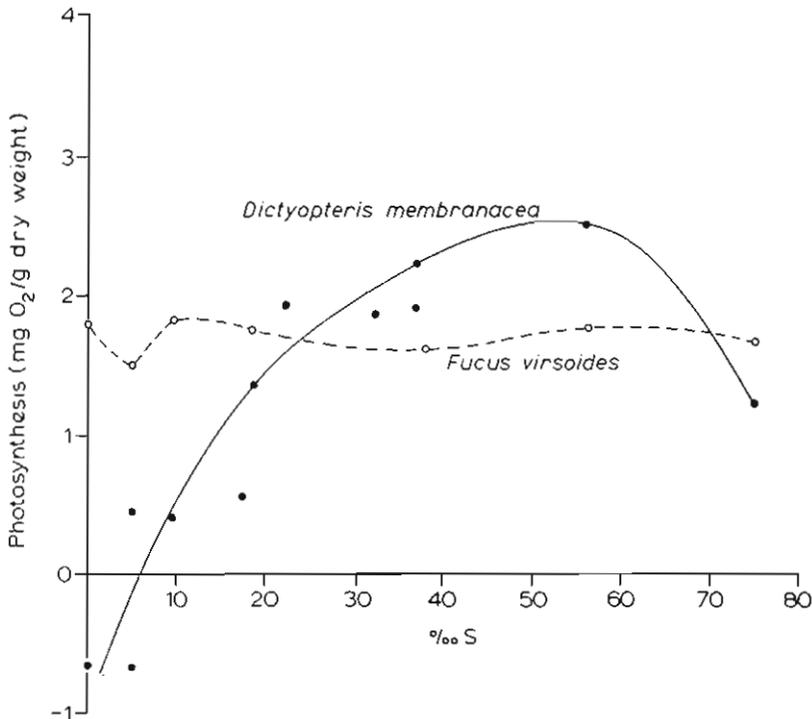


Fig. 4-20: Rates of photosynthesis in *Dictyopteris membranacea* and *Fucus virsoides* exposed to sea water after pretreatment at the different salinities indicated. Duration of pretreatment: in *D. membranacea* 30 mins, in *F. virsoides* 60 mins. (After GESSNER, 1969b; redrawn.)

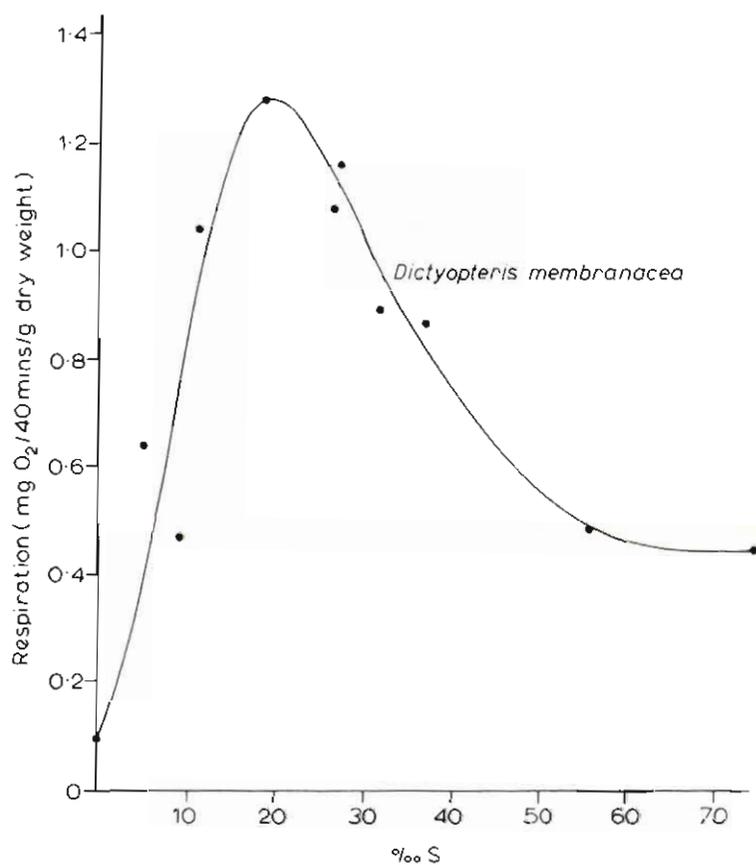


Fig. 4-21: Rate of respiration in *Dictyopteris membranacea* exposed to sea water after 30 mins pretreatment at the different salinities indicated. (After GESSNER, 1969b; redrawn.)

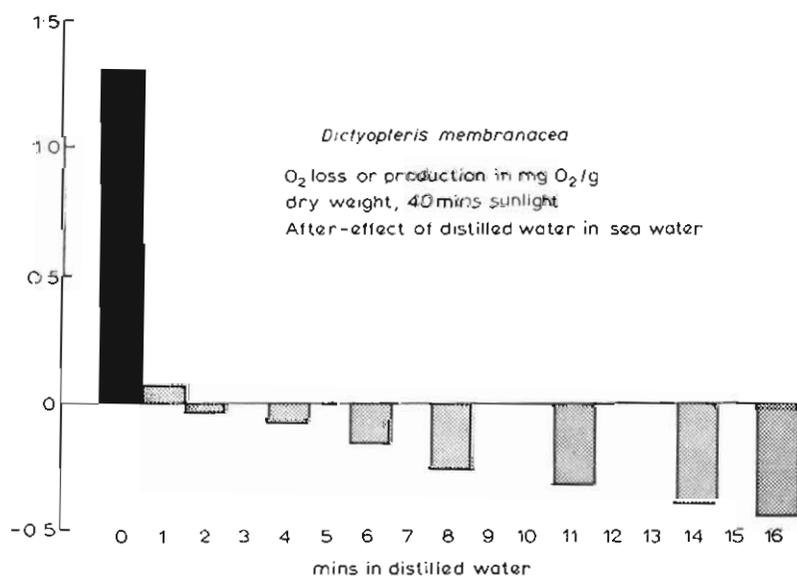


Fig. 4-22: Rate of photosynthesis in *Dictyopteris membranacea* exposed to sea water after different periods of pretreatment in distilled water. (After GESSNER, 1969b; redrawn.)

ties of their interpretation due to his insufficiently defined experimental conditions, and the dominating influence of the time factor may have been the reasons why interest in such experiments has decreased; practically no further contributions have been made to these problems during the 30 years following MONTFORT's research, and MONTFORT himself did not continue his studies along these lines.

Only in the last 10 years have investigations concerned with the importance of salinity variations for photosynthetic activities of marine algae received new impetus. A number of authors have published contributions which, however, have not yet led to generally accepted conclusions. One reason for this slow progress is related to the fact that euryhaline and stenohaline algae respond, also in regard to their photosynthetic performances, very differently to changes in salinity. An extreme case of such different responses may exemplify this statement. In the northern Adriatic (Mediterranean Sea), the brown algae *Dictyopteris membranacea* and *Fucus virsoides* grow in a vertical distance of 30 cm; *F. virsoides* lives in the tidal zone, *D. membranacea* below it. *F. virsoides* thalli which had been exposed for 3 days to aerated distilled water exhibited no differences in photosynthetic performance after retransfer to sea water, while in *D. membranacea*, 2 mins exposure to distilled water sufficed to destroy irreversibly the photosynthetic mechanism (Figs 4-20 to 4-22). It could be demonstrated that this destruction coincides with a very rapid loss of ions in distilled water and that there are probably causal connections between these two processes (GESSNER, 1969b).

In the red alga *Halymenia floresia* also, the photosynthetic system is irreversibly destroyed in distilled water within 2 mins (GESSNER, 1971). Nevertheless, it could be documented that, in this case, it is not the ion loss but (due to the high osmotic gradient) the rapid water uptake which represents the initial damaging cause. Photosynthesis in *H. floresia* is not affected—at least not during the brief experimental period—when the alga is pretreated in 1 mole mannose solution isosmotic to sea water. The ion loss, due to the diffusion gradient, is the same, both in distilled water and in the, also ion free, mannose solution. *Dictyopteris membranacea* and *H. floresia* demonstrate the afore-mentioned importance of plasmatic permeability in the relations between salinity and photosynthesis.

OGATA and MATSUI (1965a, b) investigated photosynthesis rates of different Japanese marine algae, employing the manometric Warburg method. Their results are illustrated in Fig. 4-23. In nearly all cases, the maximum photosynthetic rate is found in normal habitat sea water. Photosynthetic depressions occur both in diluted and in concentrated sea water. The relation between photosynthesis and salinity appears to be simple, but it will be shown later that this is by no means the case, since many other factors may interfere.

NELLEN (1966) studied salinity influences on photosynthesis of *Delesseria sanguinea* and *Fucus serratus* from different habitats. She varied salinity and exposure time. Some of her results are shown in Figs 4-24 and 4-25. NELLEN attempts to generalize her findings in Fig. 4-26, postulating that every change in salinity causes a subsequent rise (stimulation) in performance, followed by a depression due to detrimental effects of the salinity change. Although certain algae follow such a response pattern, generalizations of this kind appear premature and do not adequately represent the multitude of possible reactions.

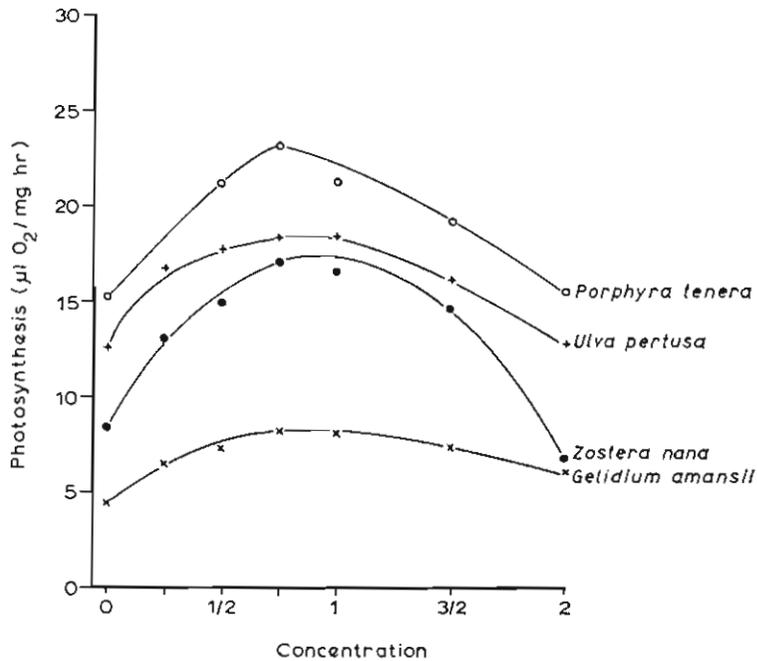


Fig. 4-23: Photosynthesis of marine plants in different salinities (concentration 1  $\approx$  18.4‰ chlorinity); based on fresh weight. (After OGATA and MATSUI, 1965b; modified.)

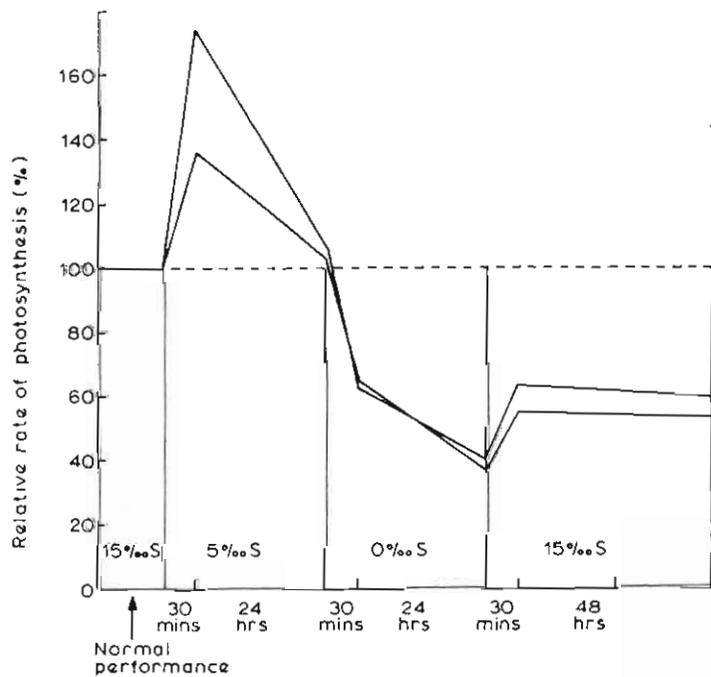


Fig. 4-24: Relative rates of photosynthesis in *Fucus serratus* (Baltic Sea form) during short (30 mins) and long (24 or 48 hrs) exposure to the salinities indicated. (After NELLEN, 1966; modified.)

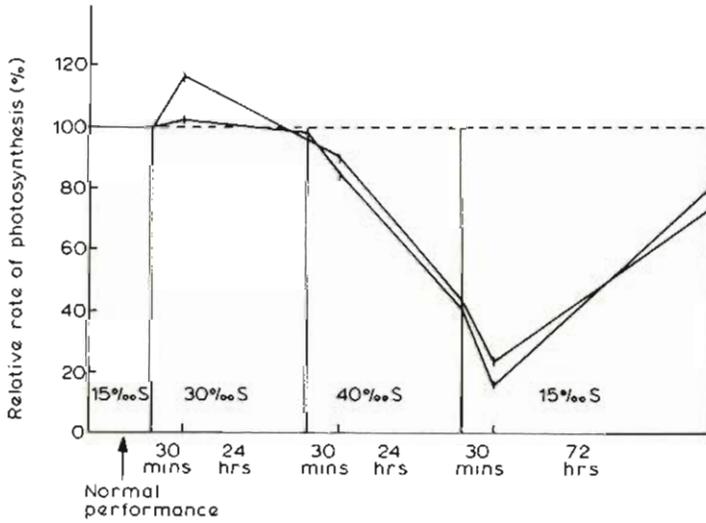


Fig. 4-25: Relative rates of photosynthesis in *Delesseria sanguinea* forma *lanceolata* during short (30 mins) and long (24 or 72 hrs) exposures to the salinities indicated. (After NELLEN, 1966; modified.)

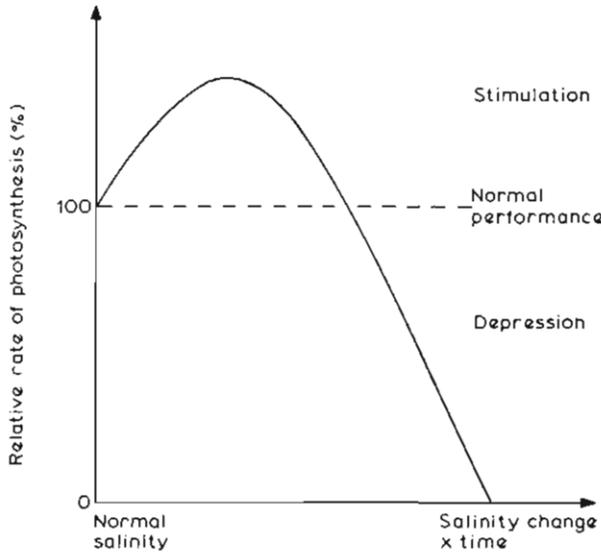


Fig. 4-26: Changes in relative rate of photosynthesis as a function of salinity. Schematic representation of typical responses. (After NELLEN, 1966; modified.)

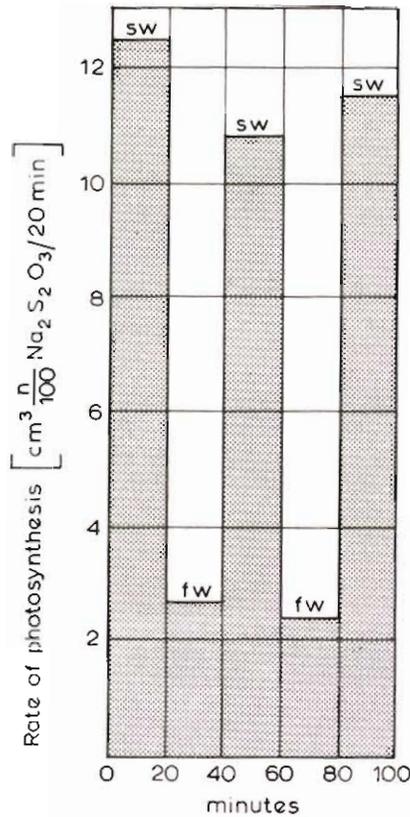


Fig. 4-27: *Ulva lactuca*. Photosynthesis of single thallus in sea water (sw) and fresh water (fw). (After GESSNER and HAMMER, 1960; modified.)

GESSNER and HAMMER (1960) published some striking results obtained on algae and higher marine plants. In a series of rapid transfers from sea to tap water, the authors observed a fast depression of photosynthesis rates in tap water and a quick recovery in sea water (Fig. 4-27). In her 1968 paper, HAMMER was able to explain this phenomenon. Marine plants, phanerogams as well as algae, show a proportional decrease in photosynthesis rate when the salinity is lowered by dilution with distilled water. If tap water is used instead, it is absolutely necessary to consider the carbon content. In natural fresh water with low alkalinity values, photosynthesis rates decrease; in fresh water with high bicarbonate content, photosynthesis rates are higher than in sea water. These results indicate that salinity may indirectly affect photosynthesis by causing differences in the carbon supply. Direct salinity effects are due to exosmosis in hypo-osmotic media; they are irreversible. HAMMER (1968) fully agrees with a statement made by OGATA and MATSUI (1965a):

'It may generally be said that the changes in salinity, osmotic pressure, pH, and also carbon dioxide supply, particularly in natural sea-water, are rather inseparably associated.'

Numerous papers deal with the action of specific ions on the photosynthetic system. However, none of these investigations has been carried out on marine plants. Primary processes of photosynthesis can be investigated in isolated chloroplasts. BOVE and co-authors (1963) found that chloride is essential for each of the photochemical reactions (including photoreduction of ATP, photophosphorylation, etc.) of chloroplasts in spinach leaves which produce oxygen. These results support the view that chloride is an essential cofactor for oxygen release during photosynthesis. Recent investigations by HIND and ISAWA (1968) emphasize the water-splitting role of the chloride ion and its role between photosystems I and II. It may be assumed that chloride plays a similar role in marine green algae; but

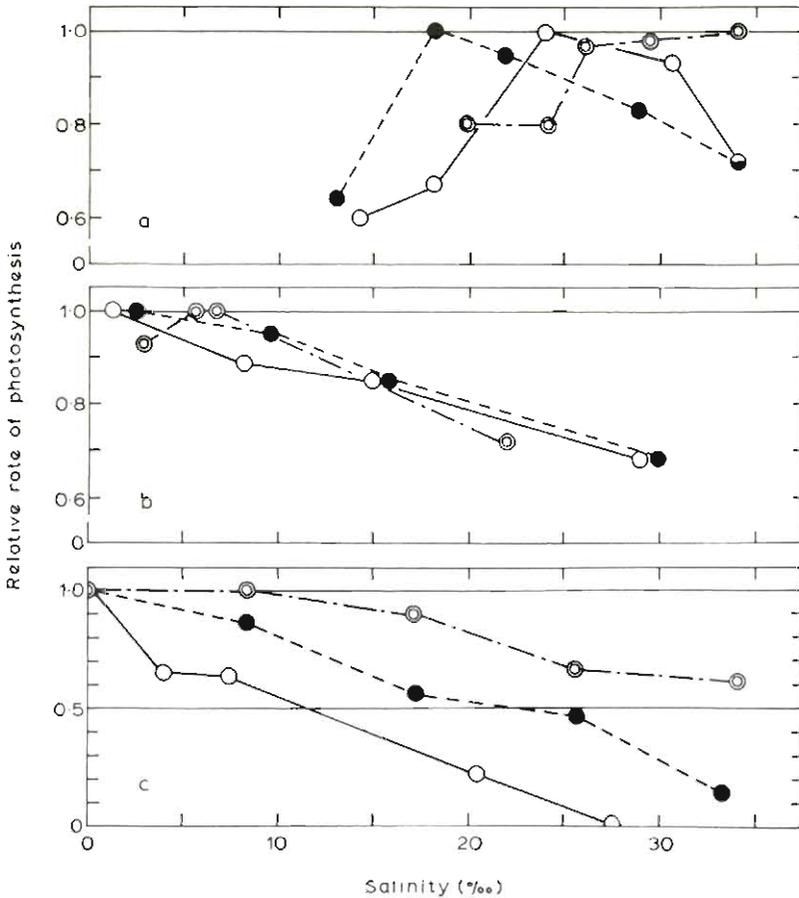


Fig. 4-28: Relative rate of photosynthesis of planktonic algae from Japanese waters with different salinities. (a) Plankton algae growing in waters with relatively high salinities: ○ plankton algae sampled from Tokyo Bay, ● *Skeletonema costatum*, ⊙ *Chaetoceros* sp.; (b) plankton algae from brackish-water lake Hinuma: ○ from station 2 (August 7), ● from Station 5 (August 7), ⊙ from Station 5 (September 7); (c) plankton algae from two freshwater ponds: ○ Shinjiike pond, ● Palace moat, ⊙ *Chlorella ellipsoidea*. (After NAKANISHI and MONSI, 1965; redrawn.)

nothing seems to be known about specific Cl-ion actions where phycobilines are involved in photosynthesis. The specific action of other ions is also unknown.

Information on the role of salinity in photosynthesis of phytoplankton is very scarce. NAKANISHI and MONSI (1965) studied these relations in plankton from Tokyo Bay, Lake Hinuma and two freshwater ponds. Their results are summarized in Fig. 4-28, demonstrating maximum performance of marine plankton in salinities above 20‰ and decreasing photosynthesis rates in phytoplankton from brackish and freshwater areas with increasing salinity. Other experiments by the same authors were carried out on *Chlorella ellipsoidea*, cultivated over 3 months in 17‰S and subsequently exposed to different salinities and light intensities; however, the results obtained are difficult to interpret. Experiments with non-identified freshwater plankton species yielded the results illustrated in Fig. 4-29. Net assimilation decreases progressively in higher salinities. The lower values obtained after 3 days (broken lines) cannot be attributed to salinity because they were also recorded in fresh water. Respiration, too, decreases with increasing salinity; the higher values obtained after 3 days suggest that some kind of salinity adaptation has taken place.

These few experiments do not suffice to discuss the metabolic responses of phytoplankton forms exposed to different salinities. This lack of information is unfortunate, since in estuaries, freshwater plankton is confronted with rapid

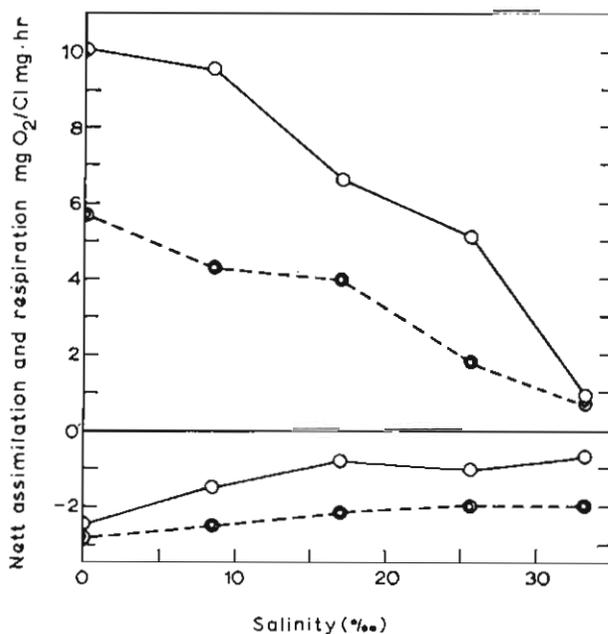


Fig. 4-29: Net assimilation and respiration of plankton algae as a function of salinity. The algae were collected from the moat of the Palace (Japan) on June 18, 1963. Solid lines: measurements taken on the 1st day, broken lines: on the 3rd day after transfer to test salinities. (23° C, 16 klux.) (After NAKANISHI and MONSI, 1965; redrawn.)

salinity changes. In the reviewer's opinion, it is still an open question whether the freshwater plankton in estuaries disappears seawards due to increasing salinity or to competition with marine plankton species.

*Salinity effects on chemical composition of algae*

Salinity also influences the chemical composition of algal thalli. Among the numerous papers dealing with such influences, the findings reported by MUNDA (1964, 1967) will be referred to in detail. She investigated the brackish-water species *Fucus ceranoides* and *Fucus vesiculosus* in different localities of the River Gaula estuary near Trondheim (Norway). Temperature, salinity and the Ca + Mg content of the sample localities are given in Table 4-18.

Table 4-18

Temperature, salinity and Ca + Mg (meq./l) at various sample localities in the River Gaula near Trondheim (Norway) on August 7, 1960 (After MUNDA, 1964; modified)

Localities	°C	‰S	Ca + Mg (meq./l)
High water			
1	18.0	21.1	0.81
1-2	19.0	20.9	0.81
2	20.0	21.1	0.82
2-3	20.0	20.7	0.72
3	19.5	16.4	0.79
4	19.7	16.4	0.78
5	19.5	15.3	0.76
6	20.5	16.6	0.69
Low water			
1	19.0	22.2	0.84
2	19.6	10.3	0.43
3	19.5	7.0	0.31
4	19.0	6.8	0.41
5	19.0	5.0	0.22
6	18.8	3.1	0.20

MUNDA'S (1964) most important findings are listed in Tables 4-19, and 4-20; they can be summarized as follows: (i) *Fucus ceranoides* occurs in the Gaula estuary at salinities ranging from 19.3‰ to 2.0‰ (localities 1 to 6). (ii) The amounts of ash, dry matter and chlorine decrease with the degree of dilution of the surrounding water, while the amounts of Ca and Mg increase. A pronounced gradient of these compounds was thus observed towards the upper regions of the river. During water dilution at low tide, Ca and Mg are taken up by the tissue, while chlorine is washed out. The electrolyte content of the plants follows the variations in salinity. (iii) *Fucus ceranoides* plants, transplanted from brackish-water to sea-water habitats, are not able to survive under the new habitat conditions. (iv) In the outer part of the estuary, *Fucus ceranoides* occurs together with *Fucus vesiculosus*, the latter being represented mostly as forma *vadorum*. In addition to

Table 4-19  
 Chemical composition of *Fucus ceranoides* collected from different localities in the River Gaula estuary (Norway) on August 7, 1960 (After MUNDA, 1964; modified)

Localities	Dry matter (g/100g fresh weight)	Ash (g/100 g dry matter)	Ca + Mg (meq./g dry matter)	Cl (g/100 g dry matter)
High water				
1	21.9	28.31	1.40	5.41
1-2	22.6	22.34	1.12	5.41
2	20.2	22.18	1.18	5.50
2-3	19.4	23.80	1.27	4.96
3	18.4	22.91	1.24	4.67
4	18.5	21.30	1.37	3.58
6	17.3	27.31	1.88	4.33
Low water				
1	23.2	30.37	1.24	5.72
2	20.8	23.58	1.44	3.97
3	17.7	20.08	1.31	3.29
4	18.9	20.04	1.32	3.41
6	16.2	31.05	2.01	2.81

typical forms of *F. ceranoides*, intermediates were noticed which were provided with bladders and rounded receptacles. (v) The chemical components of the intermediates were compared with those of typical *Fucus ceranoides* and *F. vesiculosus* f. *vadorum* (Tables 4-19 and 4-20). This comparison indicated closer relationships to *F. ceranoides* than to *F. vesiculosus* (the amounts of the reducing compounds, protein and  $\beta$  carotene are different in the two species in question).

These findings confirmed previous results by HAUG and LARSEN (1958a, b) which indicate strongly that salinity exerts a pronounced influence on the chemical composition of *Ascophyllum nodosum*. Unfortunately, no salinity data are given in the last mentioned papers and so they cannot be discussed in more detail.

It is not possible to infer from these investigations whether the differences in chemical composition of the algae are directly caused by salinity. Therefore MUNDA (1967) conducted, in the same area, transplantation experiments and analyzed samples of the transplanted plants every month during a whole year. Dry weight and Cl content increase or decrease parallel to habitat salinity. In *Ascophyllum nodosum*, *Fucus ceranoides* and *F. serratus*, ash content, which is directly proportional to salt content (as are dry weight and Cl content), changes in correspondence with the salinity gradient. In *Fucus vesiculosus*, on the other hand, ash content increases with decreasing salinity. Extreme salinity reductions cause a decrease in ash content. A diminished ash content is also noticeable in algae transplanted into sea water. In the brackish-water population of *Fucus vesiculosus*, ash content is higher than in the sea-water population. Ca and Mg contents show a gain after transplantation from sea water to brackish water and vice versa; the Ca content is subject to greater fluctuations than that of Mg.

Table 4-20  
 Chemical composition of *Fucus* species collected from different Norwegian localities on August 7, 1960 (After MUNDA, 1964; modified)

Species	Dry matter (g/100g fresh weight)	Ash (g/100g dry matter)	Cl (g/100g dry matter)	Cl (g/100g fresh weight)	Ca-Mg (meq./g dry matter)	Mannitol (g/100g dry matter)	Protein (g/100g dry matter)	Fat (g/100g dry matter)	$\beta$ carotene (mg/kg)	Alginic acid (g/100g dry matter)	Iodine (g/100g dry matter)	Reducing power (meq./g matter)
<i>Fucus vesiculosus</i>	32.9	19.1	2.00	0.66	1.18	6.4	6.1	4.00	75	23.8	0.101	0.825
<i>F. vadorum</i>												
<i>Fucus ceranoides</i> (intermediate form)	18.2	22.4	3.52	0.65	1.32	6.6	9.8	4.81	116	21.3	0.052	0.566
<i>Fucus ceranoides</i>	19.5	23.1	2.81	0.55	1.27	5.3	9.6	5.13	128	20.5	0.019	0.413
<i>Fucus ceranoides</i> (innermost locality)	19.7	25.0	1.95	0.38	1.76	3.3	7.9	2.50	66	16.2	0.023	0.154

Following transplantation to brackish water, alginic-acid content decreases, whereas transplantation in the other direction causes no change. The mannitol content rises with increasing, and falls with decreasing salinity. Protein content increases with decreasing salinity; in *Fucus* species it varies more with salinity than in *Ascophyllum nodosum*. Ether-soluble compounds show no definite fluctuation trend under conditions of changing salinities. After a few months in sea water, the amount of reducing compounds increases; it decreases after transplantation into brackish water. The  $\beta$ -carotene content decreases after transplantation from brackish to sea water, while salinity decrease has no effect. Comparison of brackish and sea-water plants shows that the former undergo less changes in extremely diluted water. Under habitat conditions brackish-water plants survive during the period of low salinity (May to September) while sea-water plants die under similar conditions.

Another example of seasonal variation in the chemical composition of *Ulva lactuca* has been reported by PATIL and JOSHI (1967). In the area examined near Bombay (India), the chlorinity varies during the year between 10.8‰ and 20.9‰, due to heavy rainfall and extensive evaporation. It cannot be excluded that the chemical composition of *U. lactuca* is influenced also by environmental factors other than salinity. The monsoons certainly play an important and as yet unknown role; however, temperature does not appear to exert significant influences in this tropical area. The results obtained by PATIL and JOSHI are summarized in Table 4-21.

#### Rate of growth

In 1969, OHNO investigated the growth rates of early stages of *Ulva pertusa*, *Porphyra tenera*, *Scytosiphon lomentaria*, *Monostroma nitidum*, *Gelidium amansii* and *Eisenia bicyclis* in different salinities. Growth was measured by counting the number of cells after several days or by measuring the diameter or length of the sporelings. Some of OHNO's results are presented in Figs 4-30 and 4-31. The growth rates are influenced by salinity and temperature. Maximum growth rates occur in the vicinity of 1 sea water; growth rates decrease in diluted and concentrated sea water. The only exception is *M. nitidum* which attains, at 25°C, maximum growth already in 0.1 sea water. Obviously, growth-salinity relationships cannot be demonstrated, where temperature is the primary growth-limiting factor, e.g., in *Porphyra tenera* and *Scytosiphon lomentaria*.

The growth of the red alga *Dasya pedicellata* in relation to salinity has been investigated by NYGREN (1970). Material for cultures exposed to different salinities was collected in July. Germlings of carpospores, as well as tetraspores from isolated cystocarps and stichidia, were cultivated in media of 5‰, 10‰, 15‰, 20‰, 25‰ or 30‰S. Two months later, maximum growth rates were found in 15‰ to 25‰S. Experiments with germlings originating from a culture of isolated cells reveal maximum growth in 20‰S. In a 40-day-old culture, NYGREN found the following dry weight values (mg) in different salinities: 1.4 mg dry weight in 5‰S, 3.3 mg in 10‰S, 3.7 mg in 15‰S, 4.3 mg in 20‰S, and 3.7 mg in 30‰S.

MUNDA (1967) points out that maximum growth rates of algae occur in salinities similar to those in the normal habitat of the plants tested. Detailed experiments on salinity effects on growth rates of multicellular adult marine plants have thus

Table 4-21

Seasonal variations in inorganic and organic constituents of *Ulva lactuca* (expressed as g/100 g dry thallus) and of sea water (expressed as g/l). Moisture values are based on fresh weight (After PATEL and JOSHI, 1967; modified)

Inorganic constituents		August	September	October	November	December	January	February	March	April	May
Moisture (%)	<i>Ulva lactuca</i>	77.73	77.45	77.84	78.65	80.93	80.76	80.93	79.58	78.29	73.91
Ash (%)	Sea water	29.2	30.68	25.64	25.61	27.29	31.78	34.68	26.81	26.38	25.98
Sodium	<i>Ulva lactuca</i>	3.52	4.1	4.97	4.7	5.05	3.85	4.3	4.29	4.35	3.78
	Sea water	6.35	11.1	13.43	11.81	11.12	10.33	15.08	14.9	12.71	14.42
Potassium	<i>Ulva lactuca</i>	2.94	3.51	3.08	3.23	3.6	2.93	3.83	2.14	2.09	1.76
	Sea water	0.265	0.315	0.473	0.391	0.387	0.294	0.51	0.489	0.415	0.452
Na/K ratio		1.19	1.16	1.61	1.45	1.4	1.31	1.12	2.004	2.08	2.14
Magnesium	<i>Ulva lactuca</i>	2.96	3.74	3.09	3.41	3.67	3.55	4.42	3.82	3.49	2.02
	Sea water	0.797	1.35	1.51	1.48	1.44	1.23	1.57	1.51	1.38	1.42
Calcium	<i>Ulva lactuca</i>	0.31	0.348	0.345	0.449	0.419	0.38	0.427	0.389	0.423	0.443
	Sea water	0.212	0.364	0.405	0.371	0.356	0.299	0.413	0.406	0.343	0.378
Chlorides	<i>Ulva lactuca</i>	3.97	4.75	4.9	5.36	5.83	5.08	7.15	5.88	5.83	4.56
	Sea water	10.82	18.01	20.46	19.7	19.6	16.86	22.37	20.96	20.26	20.79
Organic constituents		August	September	October	November	December	January	February	March	April	May
Reducing sugars		0.148	0.145	0.216	0.279	0.747	0.287	0.221	0.414	0.167	0.148
Starch		3.69	4.23	11.09	5.96	4.24	4.61	7.37	9.90	8.39	8.15
Nitrogen		5.67	7.49	7.74	8.59	7.77	8.73	8.81	9.84	8.29	9.35
TAN*		10.6	16.89	21.29	16.68	16.28	14.58	8.56	7.934	18.71	36.58

\* TAN (titrable acid number): ml of 0.1N NaOH required to neutralize acid contents in the extract from 100 g of fresh material; values expressed on fresh weight basis.

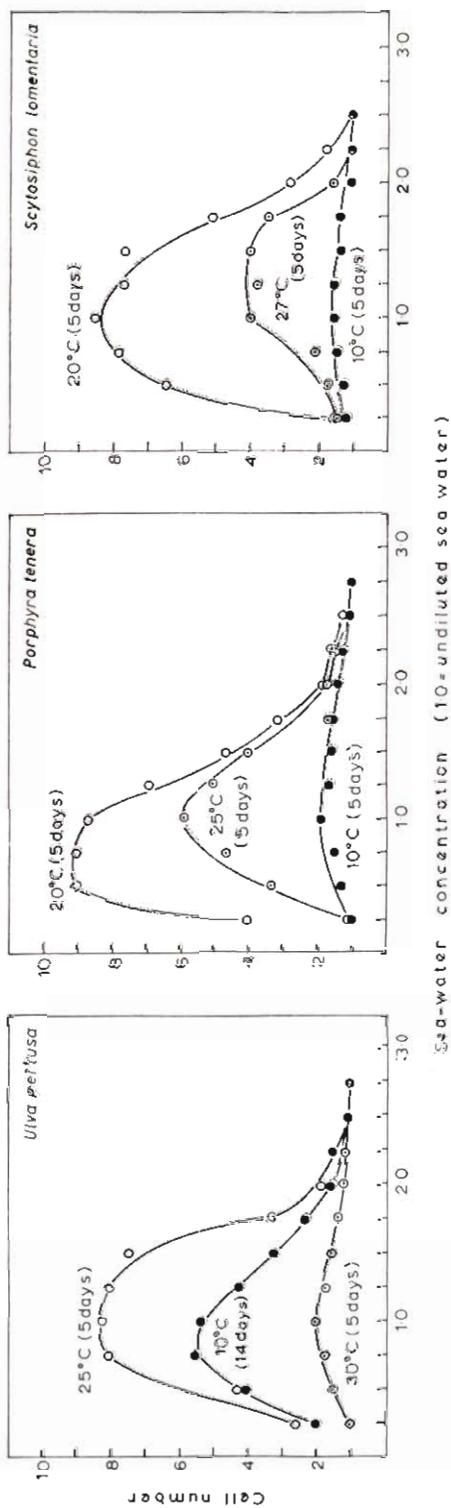


Fig. 4-30: Growth rates of early unicellular stages of *Ulva pertusa*, *Porphyra tenera* and *Scytosiphon lomentaria* exposed to different concentrations of natural sea water and to different constant temperatures. (After OHNO, 1969; modified.)

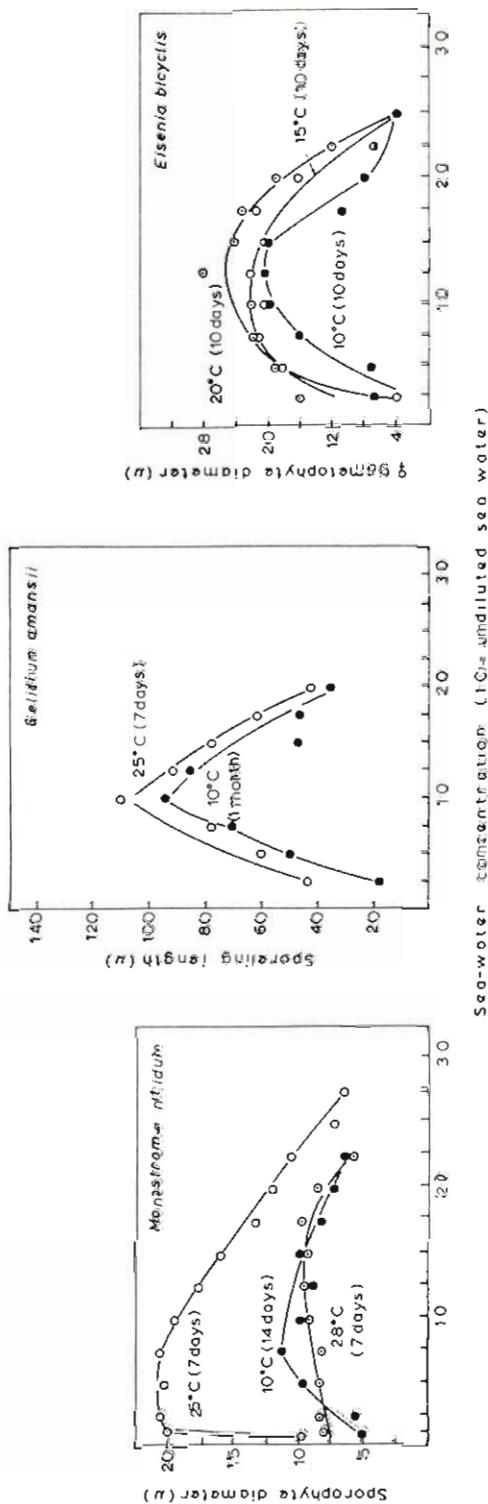


Fig. 4-31: Growth rates of sporophyte, sporeling and gametophyte of *Monostroma nitidum*, *Gelidium amansii* and *Eisenia bicyclis*, respectively, exposed to different concentrations of natural sea water and to different constant temperatures. (After OHNO, 1969; modified.)

far been carried out only in species of *Porphyra*, the most thoroughly investigated marine alga genus. OGATA and MATSUI (1967) cultivated *Porphyra* species on expanded nets, a method commonly used in Japan. The taut nets are submersed for different periods of time in localities with different salinities, and at different water depth levels. Fastest growth (based on plant surface area) occurs where the salinity is high and tidal salinity variations limited; however, in all experiments, the degree of exposure to water movement and temperature changes tends to modify the salinity effects on growth (Fig. 4-32).

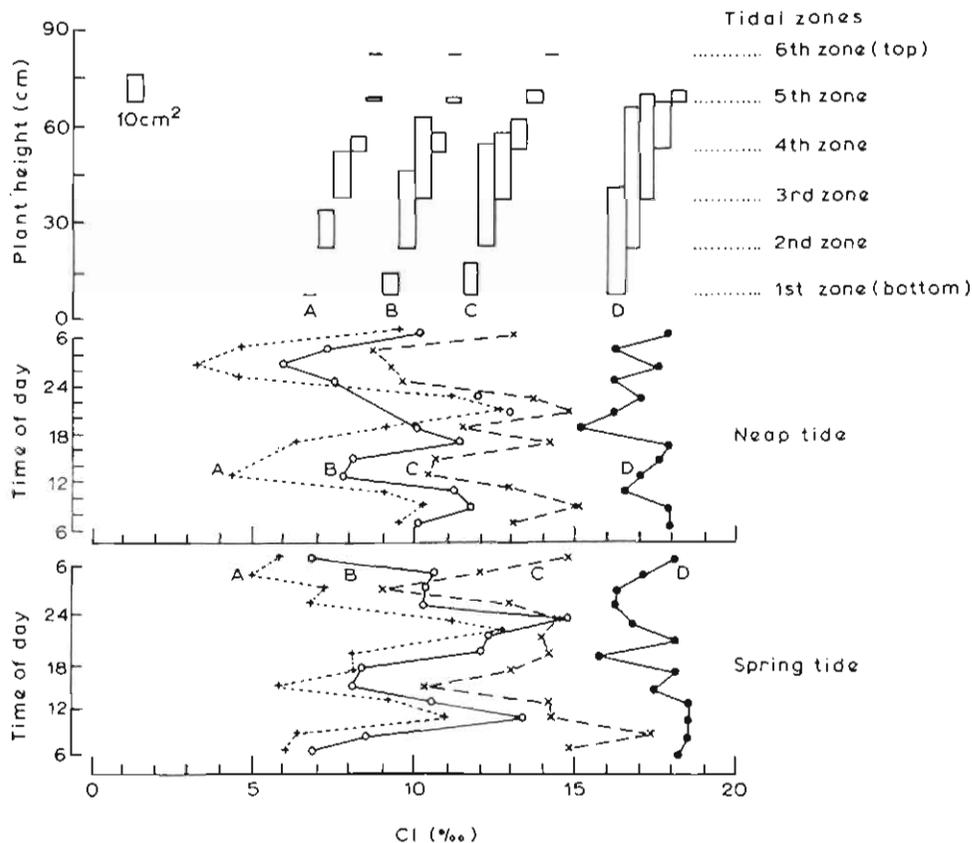


Fig. 4-32: *Porphyra yezoensis*. Growth in four localities (A, B, C, D) with different salinity regimes during 36 days. Growth rate was determined on the basis of increase in plant body surface in 6 different tidal zones. (After OGATA and MATSUI, 1967; modified.)

The results of OGATA and MATSUI (1967) are in contrast to newest information produced by OGATA and SCHRAMM (1971) on *Porphyra umbilicalis* from the North Sea: during a 3-week cultivation experiment in artificial sea water of different salinities, the surface area growth in a hyperosmotic medium (double the concentration of normal sea water) was slowest, while it was fastest in hypo-osmotic medium (half the concentration of normal sea water); likewise, the gain in dry weight was smallest in the higher concentrations, but attained approximately identical values in normal sea water and in 50% diluted sea water.

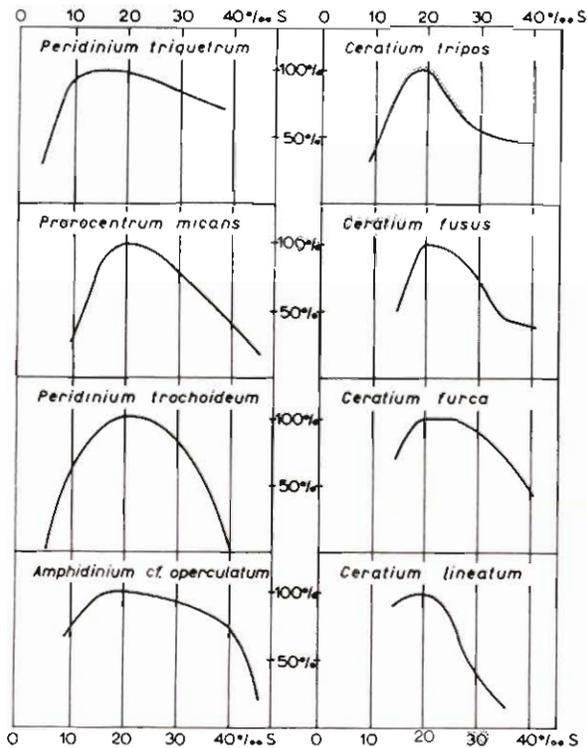


Fig. 4-33: Population growth of marine dinoflagellates at different salinities. Growth rates are expressed as percentages of maximum growth rates. (After various authors; from BRAARUD, 1961.)

More information is available on the influence of salinity on growth rates in unicellular algae. However, in unicellular algae growth rates are identical with rates of cell division and multiplication (BRAARUD, 1951, 1961), referring to growth parameters of populations but not individuals. Some information on salinity effects on population growth in dinoflagellates is presented in Fig. 4-33. There is considerable variation in the response pattern, both at the inter- and intraspecific level. Furthermore, the shape of population-growth curves depends on light, temperature and other concomitantly effective environmental factors. Several flagellates, growing in saline waters or in rock pools containing concentrated sea water, are adapted (restricted) to high salinities; they exhibit optimal cell division rates only in high salinities. The best examples may be found amongst species of the genus *Dunaliella* (Fig. 4-34), which are often responsible for the red colour in saline ponds.

Relationships between salinity, osmotic values and specific ion activities during cell division of *Cyclotella nana* were investigated by GUILLARD and MYKLESTAD (1970). Their growth experiments with synthetic media indicate that *C. nana* can survive at a magnesium concentration of 0.85 mM, a calcium concentration of 1 mM and a potassium concentration of 1 mM. A salinity equal to 1/10

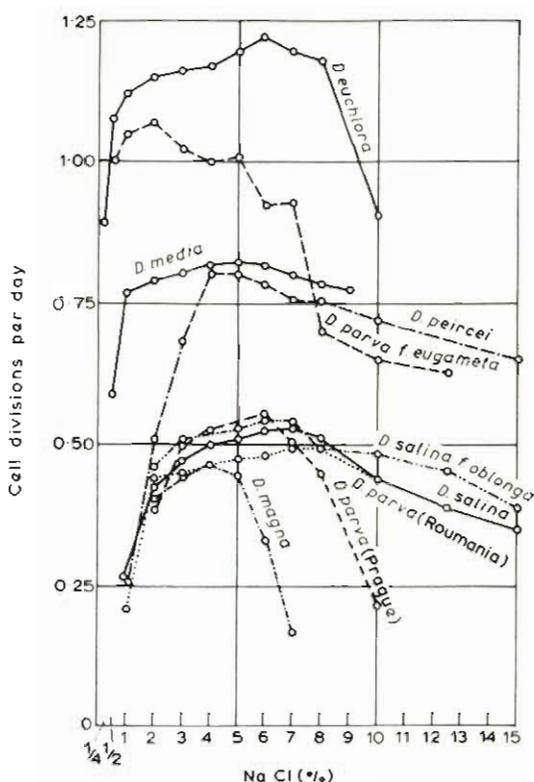


Fig. 4-34: Rate of cell division (number of divisions per day) as a function of salinity in different species of the flagellate genus *Dunaliella*. (After LERCHE, 1936, 1937; modified.)

sea water is equivalent to concentrations of potassium and calcium salts of about 1 mM. GUILLARD and MYKLESTAD suggest that the poor growth in 1/10 sea water is caused by too low concentrations of both potassium and calcium—or, at least, one of them. Relatively high calcium requirements have also been reported for other algae. These experiments demonstrate again that any salinity change results in a multitude of specific effects on the living systems considered. In many cases, it is not easy to pinpoint the factor actually responsible for the physiological responses observed under sub- or supranormal salinity conditions.

#### Metabolic water and salt regulation

Metabolic regulations of marine plants can be discussed under the subheadings: ion regulation, osmoregulation and turgor regulation. Depending on the perspective of the reviewer, the two latter may also be considered synonymous. Metabolic regulations require energy and hence may affect respiratory quotients. However, our present knowledge is insufficient for detailed assessments.

Most of our present information on the regulatory capacities of marine algae has been obtained on multicellular, macroscopic forms, especially on attached benthic species. Little, if anything, is known about metabolic regulations in unicellular planktonic forms.

Significant differences in osmoconcentrations of plant cells and surrounding sea water appear to occur only in euryhaline, coastal species. These are called osmoregulators, in contrast to oceanic osmoconformers which are often isosmotic to the surrounding medium and readily conform to salinity variations.

While in marine animals osmotic regulations occur both at the body fluid and cellular levels (Chapter 4.3), marine plants are largely, if not exclusively, restricted to intracellular regulations.

*Ion regulation.* All marine plants hitherto examined exhibit some degree of ion regulation. They tend to keep their cellular concentrations of Na and  $\text{SO}_4$  lower, and their K concentrations higher than in the surrounding sea water. Some species can accumulate ions or salts used as structural components of body parts.

In the marine flagellate *Noctiluca miliaris*, cellular osmoconcentrations, determined by employing the freezing-point depression technique, are comparable to values calculated for cellular inorganic cations and anions (Table 4-22).

Table 4-22

*Noctiluca miliaris*. Chemical composition and freezing point depression of cell fluid (After KESSELER, 1966; modified)

Components	Cell fluid		External medium		Relative accumulation
	Equivalent/l	g-Ion/l	Equivalent/l	g-Ion/l	
Na	0.414	0.414	0.418	0.418	0.991
K	0.034	0.034	0.0088	0.0088	3.865
$\text{NH}_4$	0.0585	0.0585	—	—	—
Ca	0.0095	0.0048	0.0185	0.0095	0.513
Mg	0.015	0.0075	0.095	0.0475	0.158
$\Sigma$ Cations	0.531	0.5188	0.5403	0.4838	1.072
$\Sigma$ Anions	0.5095	0.5095	0.5455	0.5222	0.975
Cl	0.4965	0.4965	0.4989	0.4989	0.995
$\text{H}_2\text{PO}_4$	0.013	0.013	—	—	—
$\text{SO}_4$	0.0	0.0	0.0466	0.0233	0.0
$\Sigma$ Anions + Cations		1.0283		1.0060	1.022
$\pi$ calculated (atm)		20.626		20.179	
pT calculated		0.447			
$\pi$ measured (atm)		20.95		20.35	
pT measured		0.60			
$\Delta_i$ calculated		-1.705		-1.67	
$\Delta_i$ measured		-1.730		-1.685	
pH = 4.35					

$\pi$  calculated = osmotic potential.

pT measured = cell turgor = difference of the osmotic potential of cell sap and ambient medium.

Variations in relative amounts of inorganic ions are responsible for the total resulting osmoconcentration of cell fluids not only in planktonic forms, such as *Noctiluca miliaris* or *Coscinodiscus wailesii* (KESSELER, 1967), but also in benthic marine algae (KESSELER, 1964; Table 4-23). As may be seen in Table 4-23, the ratio  $\text{Na}_i:\text{Na}_e$  is less than 1 (except for *Codium fragile*) while the ratio  $\text{K}_i:\text{K}_e$  is (except for *Codium fragile*) considerably greater than 1, reaching the highest

Table 4-23

Ion concentrations in cell fluids of 6 benthic marine algae from Helgoland (southern North Sea; ca 30‰S) (After KESSELER, 1964; modified)

Ions	<i>Chaetomorpha linum</i>	<i>Codium fragile</i>	<i>Bryopsis hypnoides</i>	<i>Desmarestia viridis</i>	<i>Ceramium rubrum</i>	<i>Poly-siphonia urceolata</i>	
H	—	—	—	0.383	—	—	
Na	0.044	0.483	0.345	0.111	0.031	0.096	
K	0.743	0.015	0.280	0.279	0.515	0.644	
Mg	0.033	0.081	0.004	0.099	0.150	0.095	
Ca	0.008	0.068	0.002	0.057	0.015	0.058	
$\Sigma$ Cations (Equivalents/l)	0.828	0.647	0.631	0.929	0.711	0.893	
$\Sigma$ Anions (Equivalents/l)	0.815	0.653	0.738	0.968	0.667	0.784	
Cl	0.762	0.551	0.705	0.089	0.575	0.583	
SO <sub>4</sub>	0.045	0.100	0.028	0.872	0.088	0.198	
PO <sub>4</sub>	0.008	0.002	0.005	0.007	0.004	0.003	
$\Sigma$ Cations	1.016	0.991	0.855	0.960	1.065	1.139	
$\Sigma$ Anions							
Ion relations	Na <sub>i</sub> :Na <sub>e</sub>	0.107	1.180	0.842	0.270	0.076	0.234
	K <sub>i</sub> :K <sub>e</sub>	84.7	1.71	31.9	31.75	58.6	73.3
	Cl <sub>i</sub> :Cl <sub>e</sub>	1.575	1.14	1.46	0.184	1.19	1.21
	SO <sub>4i</sub> :SO <sub>4e</sub>	0.985	2.18	0.61	19.2	1.925	4.32

*i* = internal (cell fluid), *e* = external (ambient sea water) medium.

value in *Chaetomorpha linum*. Excellent examples of potent ion regulators among green algae are species of the genus *Valonia*, particularly the tropical *V. ventricosa*. As early as 1891, MEYER reported extremely high K concentrations in the cell sap of *Valonia* species. Since then, numerous papers have been devoted to the phenomenon of the 'potassium-sodium-pump'. Unfortunately, in many cases potassium-sodium ratios have not been determined in the protoplasm, the major site for selective ion regulations. Some data are listed in Table 4-24. The regulation

Table 4-24

K:Na ratios in meq./kg (milli-equivalent/kg) in *Valonia ventricosa* (Calculated from values presented by BLEI, 1966)

Ion ratios	Sea water (artificial)	Protoplasm	Vacuole
K:Na (meq./kg)	0.02	4	21
K:Na (relative to sea water = 1)	1	200	1200

	SEA WATER	PROTOPLASM	VACUOLE	
				CONCENTRATIONS
Na	508	40	44	mM
K	12	434	625	
Cl	596	138	643	
				FLUXES
Na		3.6	3.3	$\mu\text{M}/\text{cm}^2\text{sec}$
K		89	86	
Cl		18	11	
				POTENTIALS
		$E_o = -71$	$E_v = -88$	mv

Fig. 4-35: Ionic relations in *Valonia ventricosa*. Provisional scheme showing concentrations, fluxes and potentials. Large arrows indicate active transport. (After GUTKNECHT, 1966.)

processes involved in ion pumps are summarized in Fig. 4-35. In the marine red alga *Gracilaria foliifera*, light stimulates the cation and anion fluxes; both processes are depressed by anaerobiosis (GUTKNECHT, 1965).

*Osmoregulation and turgor regulation.* Higher terrestrial plants maintain their cellular osmotic pressures, not only by accumulating inorganic ions, but also by employing sugars and organic acids (Table 4-25). In terrestrial halophytes, mineral salts (mainly NaCl) are responsible for 40 to 90% of the total osmotic pressure (*Atriplex hastata*: 62%, *Salicornia europaea*: 90%) (ARNOLD, 1955). In aquatic vascular plants, the osmotic values are formed to 80% by mineral compounds (GESSNER, 1956b). Using sugars for osmotic regulations amounts, of course, to 'wasting of energy'. It appears plausible, therefore, that marine algae use

Table 4-25

Composition of cell fluids in higher terrestrial plants, expressed as osmotic pressures in atmospheres (After GESSNER, 1950; modified)

Species	Sugars	Organic acids	Salts
<i>Syringa vulgaris</i>	3.9	1.8	8.4
<i>Zea mais</i>	3.1	1.3	3.5
<i>Picea excelsa</i>	9.9	2.6	2.4

primarily 'cheap' mineral salts of their medium to establish osmotic gradients required for the diffusion pressures and for plasmatic stability.

Employing the concept of the osmometer, DREVS (1896) conducted the first studies concerned with salinity effects on osmoregulation in algae. He came to the conclusion that organic substances incapable of passing the plasmatic layer are primarily responsible for establishing the cellular osmoconcentration, and that osmoregulation takes place by uptake or excretion (loss) of ions. As will be documented later, the osmometer concept is not, according to newer information, suitable for explaining the establishment and control of osmotic gradients between plants and environment.

Sixty years after DREVS, BIEBL (1956b) studied the osmoregulative capacities of the green alga *Enteromorpha clathrata*, a euryhaline form which can survive in fresh water as well as in salinities several times exceeding that of the ocean (brine waters, see Chapter 4.31). BIEBL cultivated *E. clathrata* and obtained the values listed in Table 4-26. The great differences recorded after exposure to distilled water

Table 4-26

Changes in cellular osmoconcentration in the euryhaline green alga *Enteromorpha clathrata* after transfer into distilled water and different salinities (expressed as proportions of normal sea water 1); pl: plasmolyzed, depl: deplasmolyzed, + : dead (After BIEBL, 1956b; modified)

Exposure time (days)	Distilled water	Salinity (proportion of normal sea water)				
		0.5	1.0	2.0	3.0	4.0
0	2.9	2.9	2.9	2.9	2.9	2.9
1	0.8	2.1-2.2	2.1-2.2	2.9	depl	pl
2	0.6	2.1-2.2	2.1-2.2	2.8	3.6	pl
3	0.6	2.0-2.1	2.1-2.2	2.8	3.6	pl
5	0.6	1.9-2.0	2.1-2.2	2.8	3.6	pl
7	+	1.9	2.1-2.2	2.8	—	—

and 0.5 sea water made it desirable to examine also the responses to intermediate salinities. Distilled water causes a breakdown of osmoregulative processes. Even in salinities as low as 0.1 sea water, cellular osmoconcentrations above 1.0 are maintained.

Freshwater-living plants which immigrate to brackish-water areas are, like marine plants, confronted with problems of osmoregulation. The cell sap of submersed freshwater plants is always hyperosmotic to the ambient medium. Consequently, the question arises: what kind of regulations occur if the osmotic gradient between plant and surrounding water is reduced as the plant immigrates to brackish-water habitats? LEHTORANTA (1956) tried to find an answer to this question. He found that, in *Ceratophyllum demersum* growing along the coast of Finland in between 0‰ and 6‰S, ion content of the cell sap increases with increasing habitat salinity, thus maintaining the gradient (Table 4-27). However, as in

Table 4-27  
*Ceratophyllum demersum*. Ion accumulation in the cell sap with increasing salinity (After LEHTORANTA, 1956; modified)

Ambient water				Cell sap				Cell sap/water				Cell sap		
Na	K	Ca	Cl	Na	K	Ca	Cl	Na + K Ca + Mg	Na	K	Ca	Cl	Na + K Ca + Mg	K/Na
0.03	0.025	0.33	0.00	54	99	1.1	55	169	1800	3667	3.3	611	327	1.83
0.09	0.035	0.20	0.08	42	143	1.3	—	206	467	4086	6.5	—	386	3.40
0.93	0.18	0.89	0.97	49	89	1.7	92	155	53	494	1.9	95	—	1.82
1.5	0.052	0.52	1.7	56	132	1.1	76	206	37	2358	2.1	45	65	2.36
4.6	0.12	0.55	5.7	43	119	1.1	84	218	9.4	992	2.0	15	32	2.77
26	0.56	1.2	31	31	182	0.18	72	231	1.2	325	0.15	2.3	6.8	5.87
54	1.5	4.3	77	94	123	0.96	82	231	1.7	82	0.64	1.1	3.1	1.31
66	1.7	4.8	85	119	148	0.88	87	286	1.8	87	0.18	1.0	3.3	1.24
80	1.8	5.0	88	148	203	0.94	98	379	1.9	113	0.19	1.1	3.7	1.37

*Chaetomorpha linum*, the *Ceratophyllum demersum* cell acts in accordance with the buffer principle and reduces the fluctuation range. This response may be regarded as an example of the universal biological 'law of equifinality'. If plotted, the external ion concentration multiplied by ion accumulation in the cell sap yields a hyperbolic curve with surprisingly high accuracy. The equations are,

$$\text{for Na } y = \frac{60}{x}, \text{ for K } y = \frac{110}{x}, \text{ and for Cl } y = \frac{90}{x}.$$

The most important experiments on osmo- and turgor regulation were carried out by KESSELER (1959) on *Chaetomorpha linum*, a euryhaline green alga with relatively large cells. The thalli were cultivated for 5 days in salinities ranging between 5‰ and 35‰. After this acclimation period the osmoconcentration of the cell fluid was measured microcryoscopically (Table 4-28). Other experiments

Table 4-28

Cellular osmoconcentrations in fully stabilized individuals of the euryhaline green alga *Chaetomorpha linum* (After KESSELER, 1959; modified)

Salinity (‰)	Salinity (atm)	Cellular osmoconcentration (atm)	Difference cell sap/salinity (atm)
5	3.2	21.2	18.0
10	6.5	22.2	15.7
15	9.7	27.3	17.6
20	13.0	27.6	14.6
25	16.3	31.7	15.3
30	19.6	34.5	14.9
35	23.1	37.9	14.8

had shown that it is not necessary to extend exposure periods beyond 5 days since the new osmotic steady state is normally attained within 8 hrs. The cellular osmoconcentrations remain hyperosmotic to the ambient medium in all test salinities. While the osmotic pressures in the test salinities vary between 3.2 and 23.1 atm, cell sap pressures range only between 21.2 and 37.9. The osmotic gradients between internal and external medium vary within rather narrow limits, i.e. between 18.0 and 14.6 atm. *C. linum* exhibits a considerable capacity for osmoregulation. Fully stabilized individuals are capable of maintaining similar osmotic gradients in salinities ranging from 5‰ to 35‰. Truly marine algae have lesser capacities for osmoregulation and turgor regulation. Most stenohaline marine algae tend to remain hyperosmotic and to establish fairly constant osmotic gradients over the salinity range tolerated; while the majority of marine animals are poikilosmotic, most marine plants are stenohyperosmotic.

Osmoregulative processes require energy provided by respiration. KESSELER (1962) transferred *Chaetomorpha linum* from 5‰ to 35‰S and recorded a brief increase in respiratory rate of 75% (Fig. 4-36, curve a). *C. linum*, previously adapted to 50‰S, exhibited upon transfer to 20‰S an increase in respiratory rate of only 30% (Fig. 4-36, curve b). These and related investigations by other authors

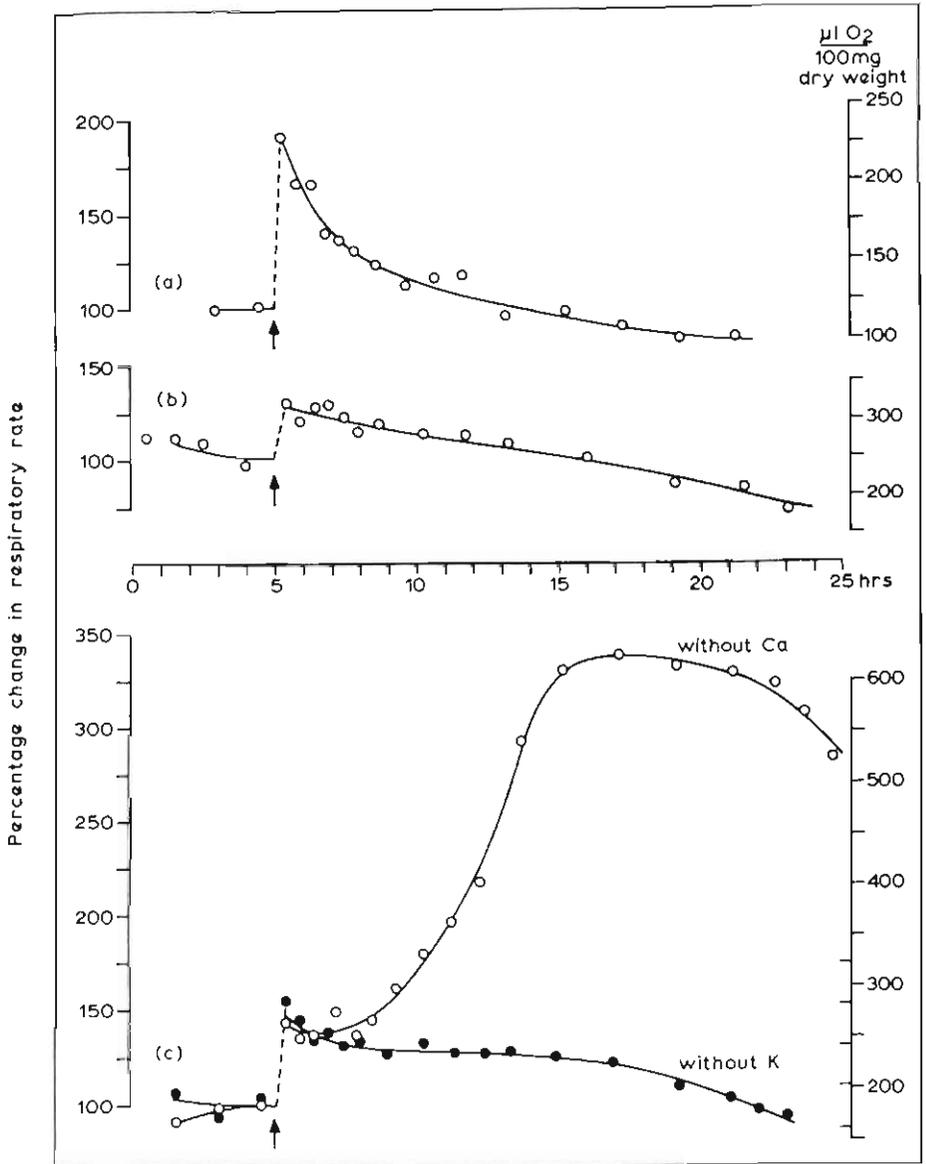


Fig. 4-36: *Chactomorpha linum*. Changes in respiratory rates due to variations in salinity. Arrows indicate times of salinity change. (a) Salinity increase from 5‰ to 35‰; (b) salinity decrease from 50‰ to 20‰; (c) salinity increase from 5‰ to 35‰ (addition of artificial sea water without Ca or without K). (After KESSELER, 1962; modified.)

demonstrate that salinity changes due to subsequent regulatory adjustments of salt and water balances, require additional energy. It is no wonder, therefore, that the capacity for turgor regulation can be significantly affected by KCN (KESSELER, 1959). In the absence of inorganic ions, turgor regulation is impossible. If *C. linum* is exposed to different sucrose concentrations no change of the osmotic values takes place (KESSELER, 1959).

From the information available, it may be concluded that cellular osmoconcentrations of marine algae are mainly due to inorganic ions. When aquatic plant thalli are exposed to distilled water, the conductivity of the external medium increases measurably after only a few minutes; this observation proves that exosmosis causes excretion or loss of ions. GESSNER and HAMMER (1968) demonstrated that marine benthic algae—due to high ion permeabilities—lose considerable amounts of ions if exposed to distilled water. Ion loss in distilled water can be demonstrated by chloride titrations or conductivity measurements performed on samples taken from the culture medium. The rapidity and complete reversibility of exosmosis show that ion movements out of and into the 'free space' are involved (Fig. 4-37). When *Laminaria saccharina* thalli, exposed to a series of increasing NaCl concentrations, are subsequently transferred into distilled water, the external concentration increases proportionally to the rate of ion loss. In small containers, the alga establishes via its 'free space' an ionic equilibrium with the

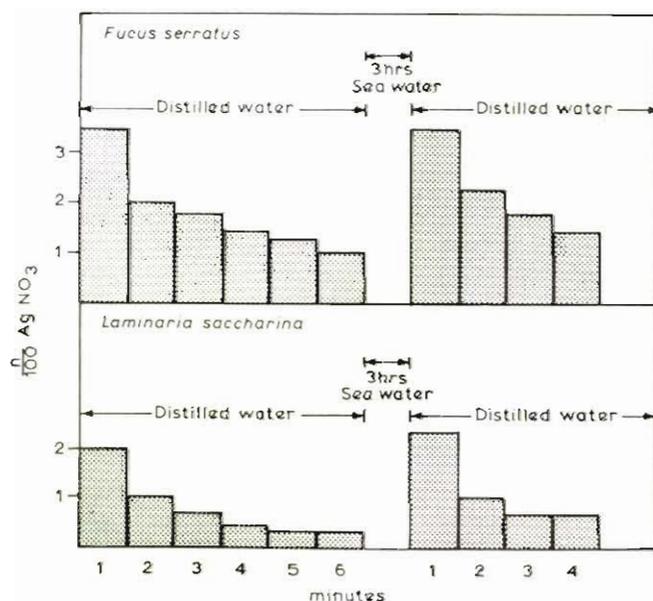


Fig. 4-37: Loss of Cl ions (ml n/100 AgNO<sub>3</sub>) in brown algae exposed alternately to sea water and distilled water. The subsequent series of determinations were conducted on one individual thallus in each case; they reveal reversibility of Cl loss and gain in *Fucus serratus* and *Laminaria saccharina*. Thalli re-transferred to distilled water after a 3-hr exposure to sea water exhibit Cl loss rates identical to those during the first distilled water treatment. (After GESSNER and HAMMER, 1968; modified.)

external medium. If the algal thallus is killed (20 secs of exposure to water steam) previous to the transfer experiment, the extent of chloride loss is much higher. Because of thermal destruction of the 'osmotic space', chloride can escape from the entire thallus. Since sublittoral algae die upon drying, chloride loss from dried thalli is much higher than that from wet thalli (Fig. 4-38). This difference is smaller in littoral algae, which tolerate short periods of dryness. A close relationship exists between the extent of chloride loss and the degree of resistance to drying. Table 4-29 summarizes rates of Cl loss of several marine algae briefly rinsed 3 times with distilled water, and then exposed to distilled water for 1 min.

A special case of exosmosis has been reported for the giant cells of *Valonia ventricosa* (GESSNER, 1967, 1969a). In distilled water, the osmoconcentration of the cell sap of this alga decreases within 2 hrs from 27 to 2 atm due to total loss of semipermeability. Distilled water acts in these giant cells like formalin and kills the cells within a short period of time (Fig. 4-39). It may be assumed that the sudden water uptake at 27 atm (instead of 2 to 3 atm in sea water) is followed by rapid cell expansion which destroys the plasmatic structure. In ion-free glucose solutions, isosmotic to the sea water, the cells survive for several days.

Table 4-29

Chloride loss (ml n 100 AgNO<sub>3</sub>) of marine algae exposed to distilled water. The values (individual determinations) were obtained within a 1-min period following transfer and expressed per g dry weight (After GESSNER and HAMMER, unpublished)

Chlorophyta	
<i>Ulva lactuca</i>	18.7, 16.0
<i>Anadyomene stellata</i>	47, 45
<i>Halimeda tuna</i>	572, 560
<i>Udotea desfontainii</i>	93.8, 95.7
<i>Codium tomentosum</i>	24, 21
<i>Codium bursa</i>	40, 38
Phaeophyta	
<i>Fucus virsoides</i>	9.4, 8.5, 7.8
<i>Padina pavonia</i>	22.2, 39.0, 33.6
<i>Sargassum linifolium</i>	17.5
<i>Cystoseira abrotanifolium</i>	37.4, 18.7
<i>Cystoseira crinita</i>	6.5, 6.6, 7.7, 10.8
<i>Dictyopteria membranacea</i>	21, 45.9
<i>Zanardinia collaris</i>	9.2, 10.2
<i>Cladostephus spongiosus</i>	35.0
Rhodophyta	
<i>Laurencia obtusa</i>	50.0, 59.2
<i>Peyssonnelia squamaria</i>	18
<i>Peyssonnelia rubra</i>	15.6
<i>Vidalia volubilis</i>	18, 25
<i>Halymenia floresia</i>	342, 288
<i>Rhodymenia corallicola</i>	21, 20

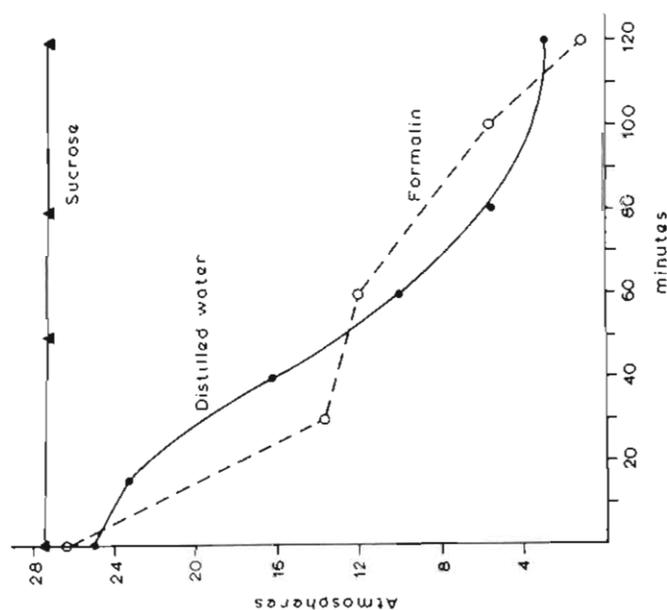


Fig. 4-39: *Valonia ventricosa*. Decreasing osmotic values (atm) of cell sap after exposure to distilled water and formalin. (After GESSNER, 1969a; modified.)

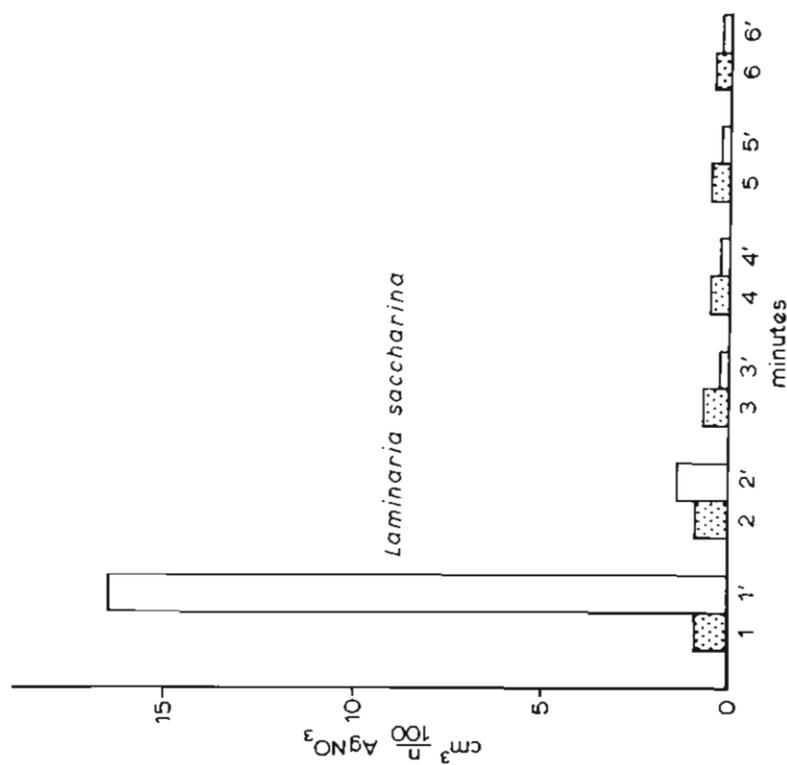


Fig. 4-38: Cl loss in the subtidal alga *Laminaria saccharina* exposed to distilled water. 1-6: wet thalli; 1'-6': dry thalli. (After GESSNER and HAMMER, 1968; redrawn.)

*Changes in volume or dimension*

As mentioned above, in many cases plasmolysis cannot be used as criterion for osmotic exchanges of water and salt since cell walls swell or deswell under the influence of different solutes. So increase or decrease in thallus length is not caused by loss or uptake of water by osmotic forces. Since volume or dimension changes occur also in dead thalli, neither physiological processes in the plasmalemma nor in the tonoplast can be responsible. These phenomena have been known for a long time, but exact experiments were conducted for the first time by OGATA and TAKADA (1955) on *Porphyra tenera* and *Ulva pertusa*.

Measurements on increase or decrease in dimensions of plant parts exposed to osmotic stress were carried out by employing a procedure which modifies the simplified method of URSPRUNG (1926) used for determining suction forces. The thallus was cut into narrow rectangular strips (17-19 mm in length and 4-6 mm in width) with sharp margins. The strips were then exposed to a series of solutions (ranging from hypo-osmotic over isosmotic to hyperosmotic concentrations) and the changes in strip length measured after defined periods of time (2.5-20 mins). The results obtained are illustrated in Figs 4-40 and 4-41.

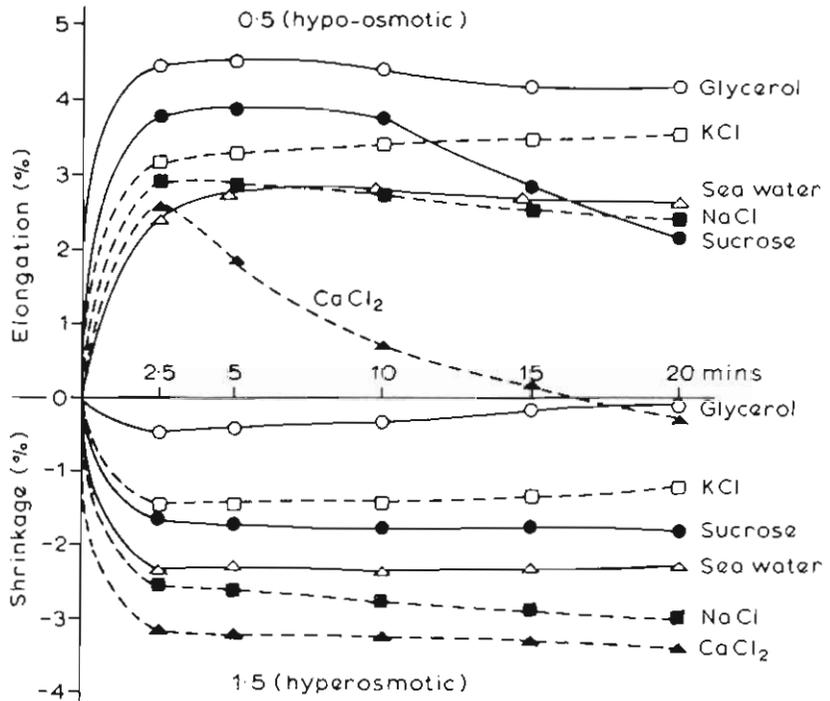


Fig. 4-40: Percentage elongation or shrinkage of *Porphyra tenera* thallus strips in hypo-osmotic (0.5; 8.3-9.0 atm) and hyperosmotic (1.5; 21.8-22.6 atm) solutions. Thallus strips were transferred into these test solutions from standard sea water (17.1 atm). (After OGATA and TAKADA, 1955; modified.)

Water adsorption by hydrophilic colloids results in swelling and consequently in increased length and width of the thallus strips. In regard to cellulose and similar colloid cell wall materials of marine algae, the role of chemically bound water is difficult to assess. In the thick-walled cells of marine algae, the presence of ions and molecules passing across or along cell walls, and the hydrostatic status of tissue water deserve special attention. After 5 mins exposure to hypo-osmotic test solutions, percentage strip elongation increases in the order  $\text{CaCl}_2$ , sea water,  $\text{NaCl}$ ,  $\text{KCl}$ , sucrose, glycerol in *Porphyra tenera* (Fig. 4-40), and in the order sucrose  $\text{CaCl}_2$ , sea water, glycerol,  $\text{NaCl}$ ,  $\text{KCl}$  in *Ulva pertusa* (Fig. 4-41). In hyperosmotic

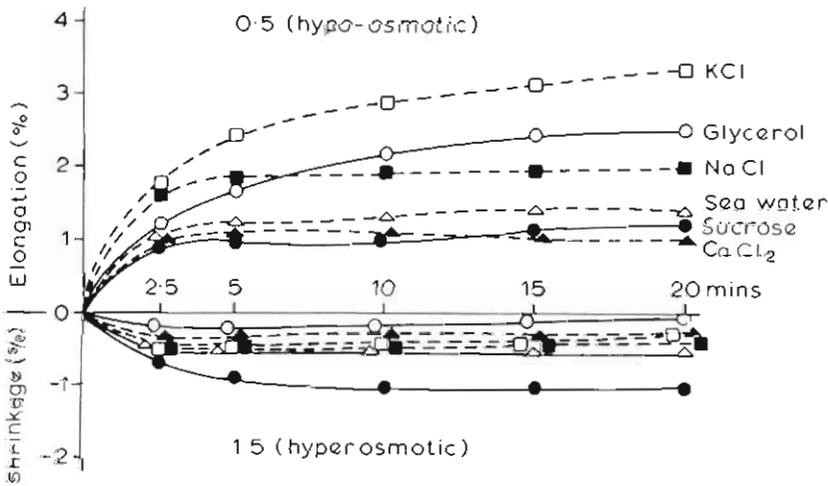


Fig. 4-41: Percentage elongation or shrinkage of *Ulva pertusa* thallus strips in hypo-osmotic (0.5; 8.3-9.0 atm) and hyperosmotic (1.5; 21.8-22.6 atm) solutions. Thallus strips were transferred into test solutions from standard sea water (17.1 atm). (After OGATA and TAKADA, 1955; modified.)

test solutions, the extent of shrinkage increases in the order glycerol,  $\text{KCl}$ , sucrose, sea water,  $\text{NaCl}$ ,  $\text{CaCl}_2$  in *Porphyra tenera*; shrinkage in hyperosmotic solutions is far less pronounced in *Ulva pertusa*. Sucrose causes a marked swelling of the cell wall in *Porphyra tenera*, even in hyperosmotic solutions, and cannot penetrate readily into the protoplast. In this respect, the cell wall of *Ulva pertusa* seems more rigid. A comparable relation is found in regard to glycerol, although it seems to penetrate into *U. pertusa* somewhat faster.  $\text{KCl}$  also promotes swelling of cell walls; the protoplasmic membranes of both alga species tested are permeable to K ions.

$\text{NaCl}$  solution and sea water differ in their effects from those of the other three test solutions (sucrose, glycerol and  $\text{KCl}$ ); they do not affect swelling of the cell wall. It is possible to distinguish the response of cell wall or protoplast to  $\text{NaCl}$  alone from that to sea water.

$\text{CaCl}_2$  hardly penetrates the protoplasts of both algae; in cell walls it leads to deswelling.  $\text{CaCl}_2$  reverses the physiological effects of  $\text{KCl}$ ; such antagonistic relations between  $\text{KCl}$  and  $\text{CaCl}_2$  may occur especially in the thallus of *Porphyra tenera*.

Changes in volume or dimensions of the alga body, or parts thereof, due to hypo- or hyperosmotic ambient media are largely caused by water uptake (swelling) or water loss (shrinkage) of cell walls. Such changes may also affect spore liberation. Swelling and shrinkage do not occur in the cell wall only. In 1923, WALTER documented on the supralittoral red alga *Bangia fuscopurpurea* that also the protoplasm takes part in swelling processes (see also WALTER and KREBB, 1970).

### Desiccation

Desiccation stress may affect significantly metabolism and activity of marine plants. The major aspects of desiccation effects on metabolic performance of plants will be considered here under the subheadings gas exchange, intermediary metabolism, plasmatic viscosity and permeability, and growth.

*Gas exchange.* The first detailed investigations on gas exchange of marine algae during desiccation stress were conducted by STOCKER and HOLDHEIDE (1937). In general, marine algae exhibit the same responses as other plant groups hitherto investigated: as water loss proceeds, the intensity of gas exchange becomes reduced.

In many surface algae, e.g. species of the Fucaceae, gas exchange appears to become stimulated during the initial phase of water loss. Maximum rates of photosynthesis are not attained at full water saturation, i.e. immediately after air exposure, but—similar to the situation in lichens (RIED, 1960)—after small losses of water (Fig. 4-42). STOCKER and HOLDHEIDE (1937) attribute this response, in the *Fucus* species investigated by them, to an initially purely physical inhibition of diffusion in the mucilaginous surface layers—a situation which may

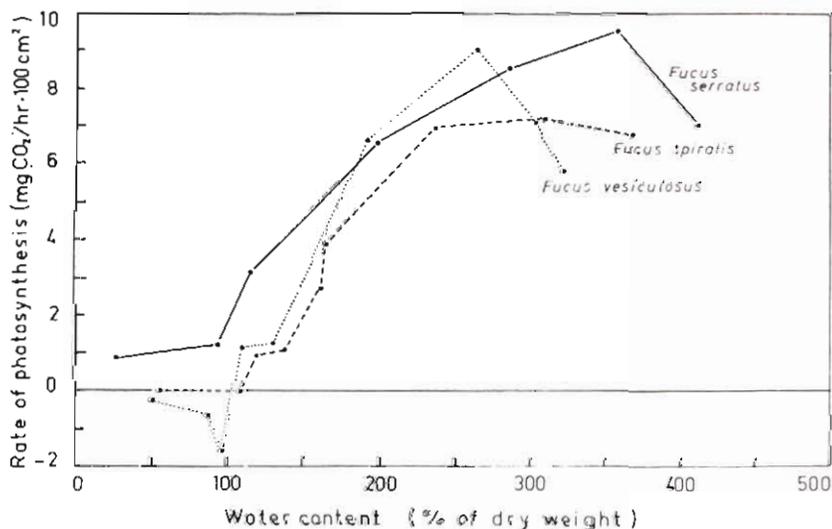


Fig. 4-42: Rate of photosynthesis as a function of desiccation stress in *Fucus* species from the southern North Sea (Helgoland). Photosynthesis measured under conditions of air exposure (80 to 87% relative humidity; 18° to 19°C; natural daylight; overcast sky). July; individual data. (After STOCKER and HOLDHEIDE, 1937; modified.)

possibly apply also to the submersed condition as already pointed out by KNIPEP (1907) and HARDER (1915).

'Die beginnende Austrocknung verbessert dann durch die Dickenabnahme der Quellschicht, vielleicht auch durch die Entstehung von Rissen, die Diffusionsgeschwindigkeit für  $\text{CO}_2$  und bedingt damit das Assimilations-optimum. . .' (STOCKER and HOLDHEIDE, 1937, p. 20).

In membranous forms, such as *Enteromorpha linza* or *Porphyra atropurpurea*, STOCKER and HOLDHEIDE could not establish such a photosynthesis maximum

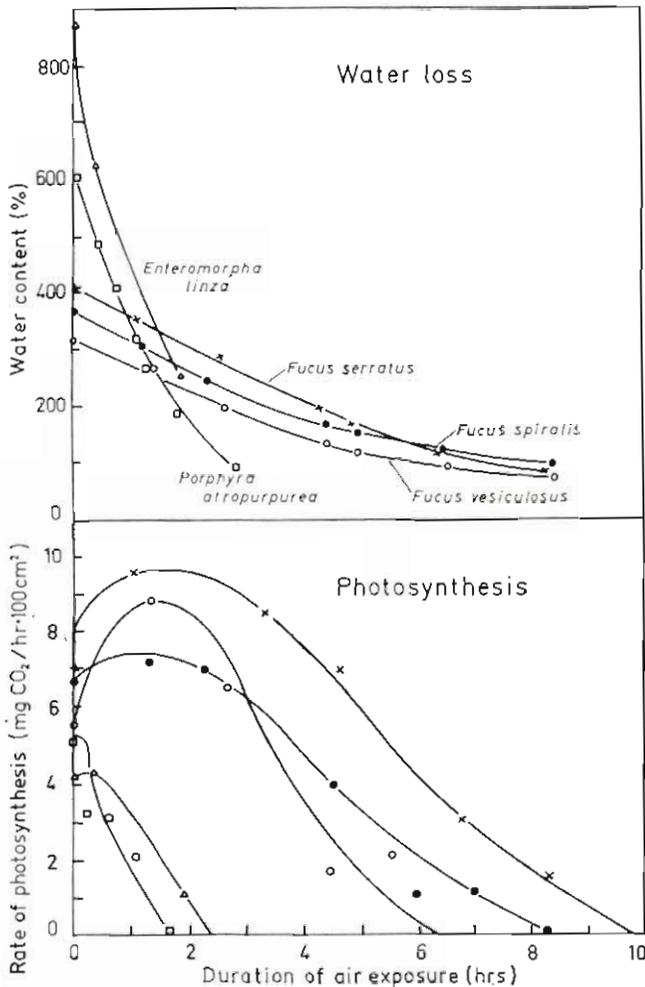


Fig. 4-43: Rate of water loss (in percent of dry weight) and rate of photosynthesis (carbon dioxide uptake in  $\text{mg CO}_2/\text{hr}\cdot 100 \text{ cm}^2$ ) as a function of desiccation stress in various benthonic algae from the southern North Sea (Helgoland). Photosynthesis measured in air (80 to 87% relative humidity) at  $18^\circ$  to  $19^\circ \text{C}$ ; natural daylight; overcast sky. July; individual data. (After STOCKER and HOLDHEIDE, 1937; modified.)

with the technical means at their disposal. Interspecific differences in peripheral structures also affect the time course of water loss-photosynthesis curves. The 'humidity-compensation point', i.e. the degree of water loss which causes the assimilation surplus to drop to zero, is attained much sooner in *Enteromorpha linza* or in *Porphyra atropurpurea* than in the more rigid Fucaeeae (Fig. 4-43).

Unfortunately, comparative measurements on absolute maximum performance of gas exchange in and outside water have not yet been conducted under identical, controlled conditions. Data available from literature and own unpublished measurements suggest, however, that surface algae differ essentially in this respect from algae growing in greater water depths. Sublittoral forms tend to exhibit pronounced reductions in photosynthesis when outside water; in addition, the photosynthesis maximum observed in many surface algae subsequent to weak dehydration, appears to be absent. This situation has already been reported by STOCKER and HOLDHEIDE (1937) in the brown algae *Laminaria saccharina* and *Laminaria digitata*. An example is illustrated in Fig. 4-44. It shows the photosynthetic behaviour of the New Zealand brown alga *Carpophyllum maschalocarpum* (Fucales), a characteristic species of the sublittoral fringe, occurring 0.45 m above to 2.15 m below extreme low water spring tide line (CHAPMAN, 1966). Upon emergence, respiratory rate drops, as does the rate of photosynthesis (in this example, to 35% of the value obtained in the submerged algae).

According to BIDWELL and CRAIGIE (1963), in the littoral surface alga *Fucus vesiculosus*, the rates of both photosynthesis and respiration fell rapidly to lower levels when the alga was removed from sea water. Photosynthesis rate was measured at 16°C and about 1000 or 1200 foot candles employing the <sup>14</sup>C method of

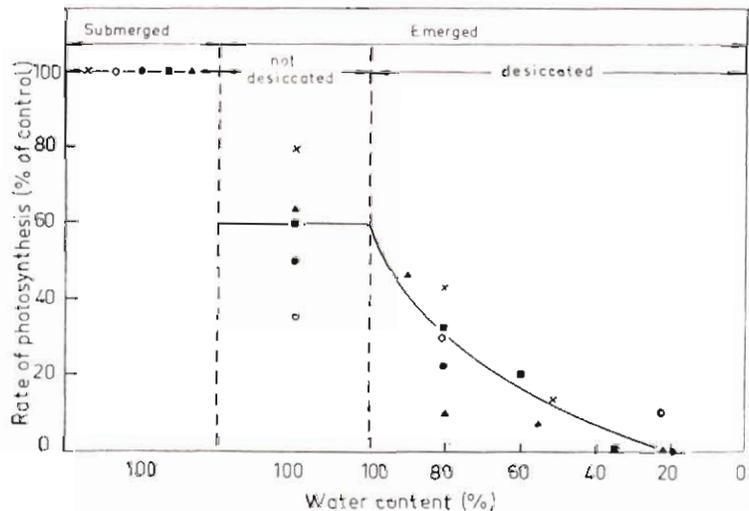


Fig. 4-44: *Carpophyllum maschalocarpum* (New Zealand). Rate of photosynthesis of various parts while submerged in sea water or exposed to air. Photosynthesis measured at 15° (20°) C, 1000 foot candles; submerged in buffered artificial sea water. ○ secondary pinnac, photosynthesis measured at 15° C, × at 20° C; ● secondary axes at 15° C, ■ at 20° C; ▲ primary pinnac at 20° C. (After CHAPMAN, 1966; modified.)

O<sub>2</sub> utilization; respiration was determined at 15° and 22° C by alkali titration. All measurements were made under conditions of water saturation. Their results are in contrast to own recent observations, which are in full agreement with results obtained by STOCKER and HOLDHEIDE (1937): *Fucus vesiculosus*, as well as other surface forms of the littoral investigated, are able to photosynthesize out of water at the same rates as their counterparts under submersed conditions; in some cases, emersed surface algae photosynthesize at even higher rates.

Respiration of marine algae reveals a similar dependence on the degree of dehydration as does photosynthesis (Fig. 4-45). Maximum values are not, in some

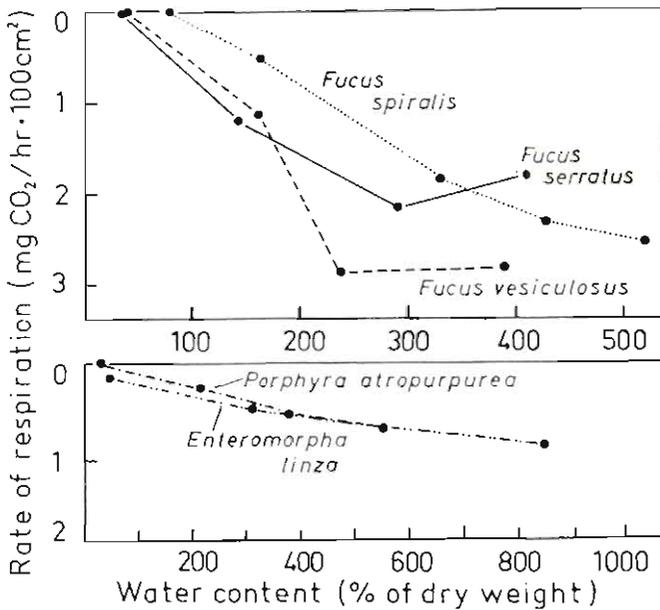


Fig. 4-45: Rate of respiration of various algae from the southern North Sea (Helgoland) under desiccation stress. Respiration measured in CO<sub>2</sub>-free air at 21° to 22° C in darkness. Between subsequent respiration measurements plants were exposed to sunlight. July; individual data. (After STOCKER and HOLDHEIDE, 1937; modified.)

cases, reached during full water saturation but after beginning dehydration. This observation is supported by results obtained by OGATA (1963, 1968). OGATA examined ten different species of marine plants, applying manometric techniques, at different degrees of water loss and after re-immersion in sea water. Respiration under exposed conditions was measured in plants placed in reaction flasks without aqueous phase. In the rehydration state, respiration was determined immediately after pouring sea water into the reaction flasks. All measurements were made at 25° C. The general trend in all plants examined was that algae, as well as marine phanogams, show recognizable O<sub>2</sub> uptake when emerged. A more or less pronounced enhancement of O<sub>2</sub> uptake due to slight desiccation was observed, for example, in *Ulva pertusa*, *Enteromorpha linza*, *Gloiopeltis tenax* and *Zostera marina* (Fig. 4-46). With increasing dehydration, O<sub>2</sub> uptake gradually declines. In his experiments, OGATA made an interesting observation: an unidentified gas, other

than  $\text{CO}_2$  was released when the plants were dehydrated to as little as about 10% of their initial water content.

Own, unpublished investigations—employing the infra-red gas analysis technique—demonstrate that the desiccation tolerant algae release  $\text{CO}_2$  even after prolonged exposure to air dry conditions. In *Porphyra umbilicalis* from the North Sea, for example,  $\text{CO}_2$  production after an 8-day exposure period at  $18^\circ$  to  $20^\circ$  C (water content 106% of dry weight) still amounted to approximately 1% of the  $\text{CO}_2$  production at water saturation.

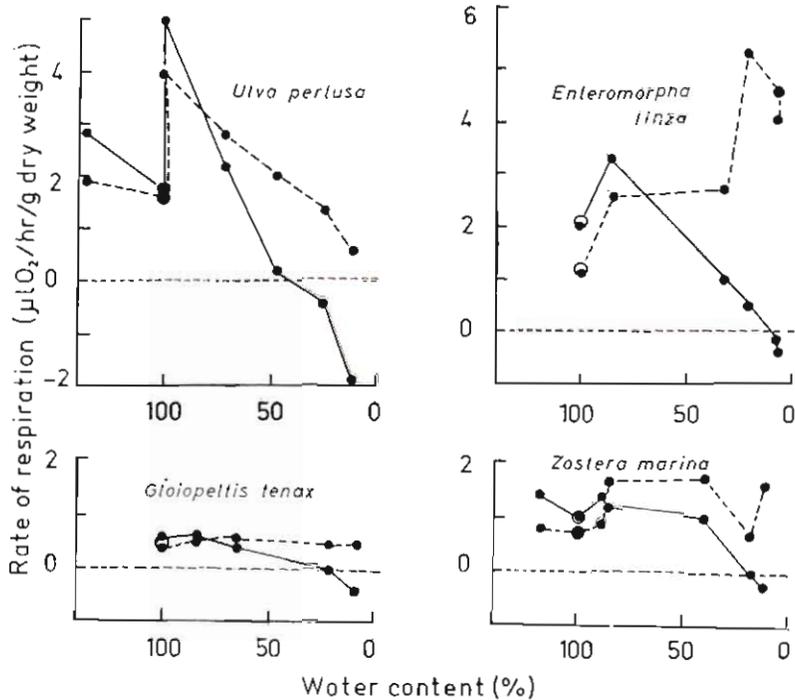


Fig. 4-46: Rate of respiration in dehydrated and rehydrated marine plants from the coast of Japan (Shimonoseki). Solid lines: dehydrated state; broken lines: rehydrated state (immediately after pouring sea water on the desiccated plant parts). Respiratory rates of controls (aqueous phase) are indicated by large circles;  $25^\circ$  C. Water content values of more than 100% are assumed to be due to the plant body absorbing ambient moisture (plant parts were kept over distilled water). June/July; individual data. (After OGATA, 1968; modified.)

Post-effects of dehydration on gas exchange are similar in marine plants and terrestrial thallophytes. Gas exchange, decreasing with dehydration and depending on the degree of tolerance of the plants tested, does not regain full intensity immediately after rehydration; photosynthesis and respiration become re-adjusted during a subsequent re-activation phase (activation, stimulation, equalization phase) as manifested in the form of the recovery curves obtained.

In marine algae, the post-effects of dehydration on gas exchange were first investigated in detail by MONTFORT (1937) and KALTWASSER (1938). In cases of weak dehydration, the subsequent depression of photosynthesis is compensated

for after periods of time ranging from a few minutes to several hours. If, however, the 'critical saturation deficit' (which varies in different species and with desiccation conditions) is surpassed, longer lasting post-effects result (see Fig. 4-3). In Baltic Sea *Fucus vesiculosus*, dehydrated in air at 18° to 22° C, the critical

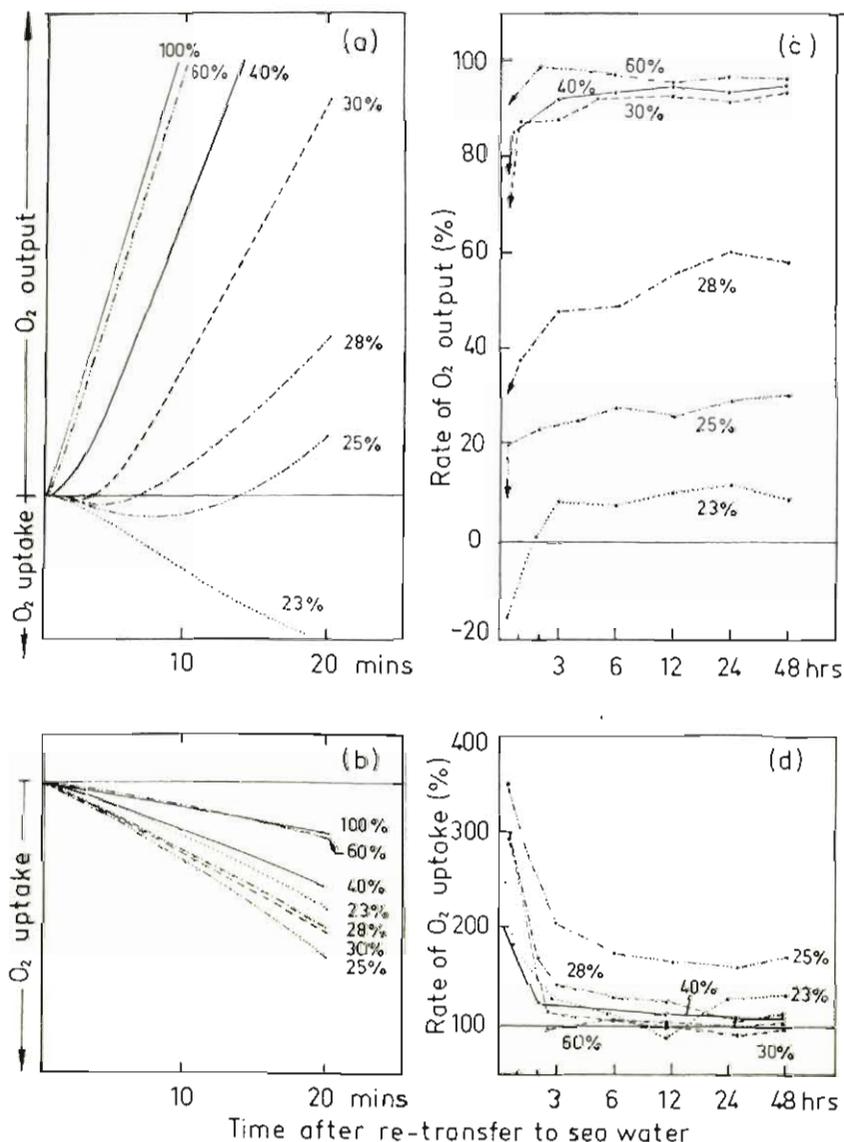


Fig. 4-47: *Fucus vesiculosus* (Baltic Sea). After-effects of desiccation on rates of photosynthesis and respiration following retransfer to Baltic Sea water. Percentages indicate degree of desiccation relative to saturation weight. (a) Time course of photosynthesis. (b) Time course of respiration during the first 20 mins after re-immersion. 100% indicates mean rates of photosynthesis or respiration of undesiccated material. (c) Rate of photosynthesis. (d) Rate of respiration. Percent initial values during a 48-hr period following re-immersion. Measurements in 15‰ S at 15° C; photosynthesis determined at 10 Klux. February; individual data. (After SCHRAMM, 1968; modified.)

saturation deficit lies at 10% of the total initial water content; in *Fucus serratus*, at 40 to 60%; in *Laminaria digitata*, at 50 to 70%; in *Furcellaria fastigiata*, at 60 to 70%; and in *Ulva lactuca*, at 60 to 80% (KALTWASSER, 1938). In extreme drought-resistant forms, such as *Pelvetia canaliculata*, a critical saturation deficit is hardly attained under natural conditions of desiccation; longer lasting post-effects on gas exchange occur only after maintenance in dried state (Fig. 4-4; see also p. 722).

Following more intensive dehydration, especially of the drought sensitive forms, re-activation of photosynthesis begins frequently with O<sub>2</sub> uptake. If employing sensitive recording devices, initial O<sub>2</sub> uptake can also be demonstrated after weaker dehydration or in drought-resistant forms such as *Fucus vesiculosus* (Fig. 4-47).

After-effects of dehydration on respiration vary almost opposite to photosynthesis (Fig. 4-48). They begin immediately with water uptake and attain values

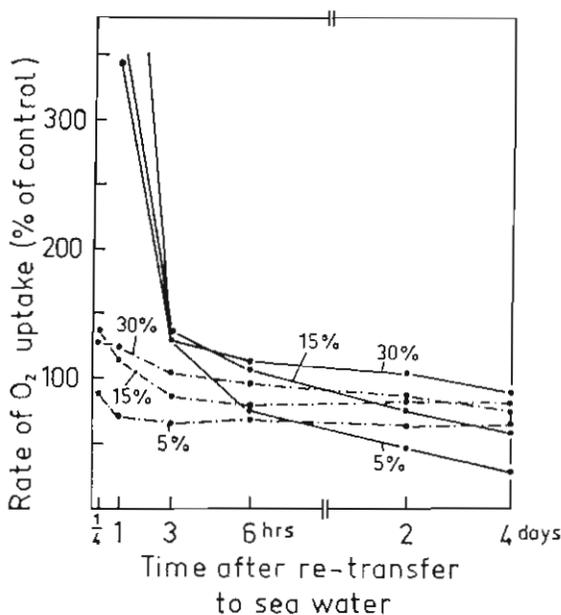


Fig. 4-48: Rate of respiration in brown algae following different degrees of desiccation. Solid lines: *Fucus serratus*; broken lines: *Laminaria digitata* (both from Baltic Sea, 8 to 10 m water depth). Percentages indicate the degree of desiccation relative to body water content. Desiccation in open air at room temperature (18° to 20° C). Respiration measured in Baltic Sea water of 17‰ S at 10° to 11° C. (After KALTWASSER, 1938; modified.)

more or less above the normal level of performance, depending on the degree of the preceding dehydration. Following pronounced desiccation, the respiratory rate may also fall below the normal value. Respiratory values, which, after the re-activation phase, do not regain the initial level, indicate that dehydration intensities extend the critical value; they may be accompanied by secondary after-effects which ultimately lead to death. Such a situation has been observed, for example, in *Fucus vesiculosus* from the Baltic Sea as water loss surpassed the critical saturation deficit (Fig. 4-49; SCHRAMM, 1968). O<sub>2</sub> uptake increases rapidly several days

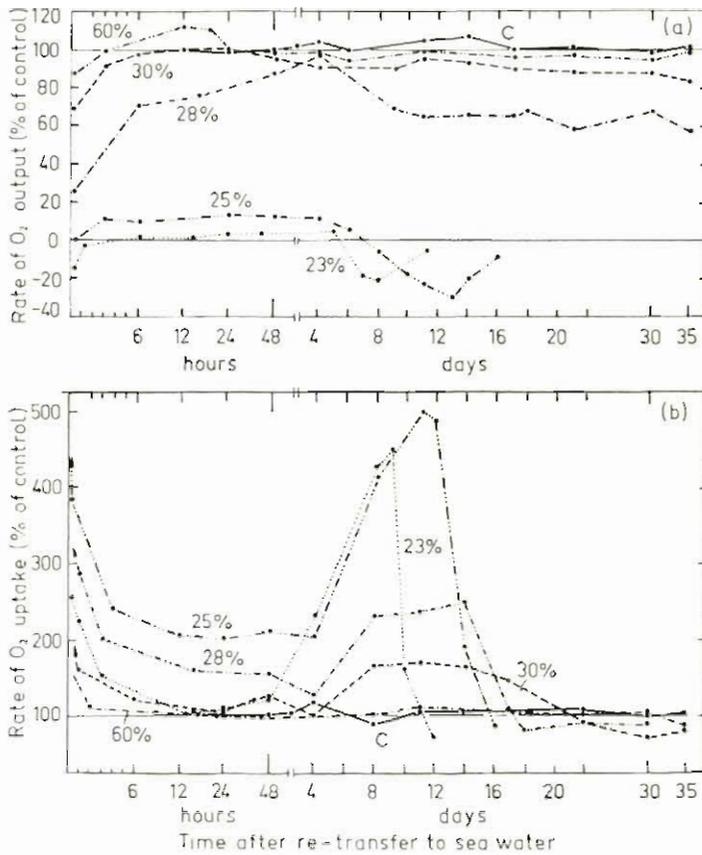


Fig. 4-49: *Fucus vesiculosus* (Baltic Sea). Time course of readjustment of photosynthesis and respiration, following different degrees of desiccation. Percentages indicate degree of desiccation relative to saturation weight. Rates of O<sub>2</sub> output (a) and O<sub>2</sub> uptake (b) are expressed as percentages of controls (C). Control values are expressed as percentages of the initial values of controls. Desiccation at 20° C. Measurements in sea water of 15‰ S at 15° C; photosynthesis determined at 10 Klux. March; individual data. (After SCHRAMM, 1968; modified.)

after dehydration ('respiratory fever'), while the rate of photosynthesis decreases and attains negative values. Extreme cases of dehydration result in complete breakdown of gas exchange. However, also water losses which cause, initially, only insignificant inhibitions of photosynthesis may lead to secondary damages over longer periods of time; such damages can manifest themselves, for example, in form of growth disturbances. Detrimental long-term effects of repeated dehydrations (to 30 to 40% saturation weight) during 2 months (15° C, 5000 lux for 14 hrs/day) have been recorded in *Fucus vesiculosus* from the Baltic Sea. The body parts grown during this time were luxurious, but irregularly branched; the branches themselves were reduced in width and very often constricted. Controls from the same material, which had not been desiccated, revealed normal growth (SCHRAMM, unpublished). Quite similar observations have been reported by RIED (1969) on fucoids following sublethal heat damages.

Nothing is known on after-effects of dehydration on gas exchange in other marine plant groups, except for a few measurements by OGATA and MATSUI (1965b) and OGATA (1968) on *Zostera marina* and *Zostera nana*. These two sea-grasses respond to desiccation in a way quite similar to the marine algae already mentioned (Figs 4-46, 4-50).

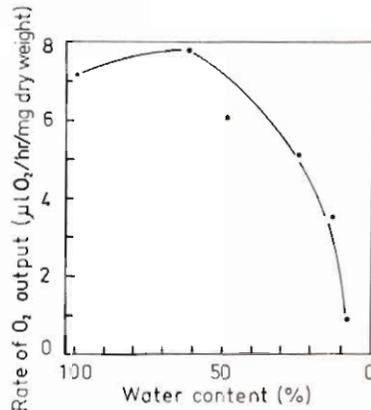


Fig. 4-50: *Zostera nana* from the coast of Japan (Shimonoseki). After-effects of desiccation on rate of photosynthesis after re-transfer to sea water. Desiccation in air. Photosynthesis measured in artificial, buffered sea water of 33‰S at 30°C and 10 Klux. (After OGATA and MATSUI, 1965b; modified.)

*Intermediary metabolism.* Most information available on desiccation effects on intermediary metabolism is restricted to higher terrestrial plants (MOTHESE, 1956). HAAS and HILL (1933) studied fat, sugar and nitrogen metabolism in a number of algae and report, especially for the brown algae tested, relations to the duration of emersion in the respective habitats (Table 4-30).

In the brown algae *Pelvetia canaliculata*, *Fucus vesiculosus* and *Laminaria digitata*, it was further possible to demonstrate certain relationships between the duration of emersion periods and the degree of saturation of the fats; the latter, as indicated by iodine values, increases with duration of emersion. HAAS and HILL (1933) correlate these results with the extreme environmental conditions experienced by plants in the higher intertidal region, especially with increased temperature and desiccation stresses. It was indeed possible to shift significantly the nitrogen balance in *Pelvetia canaliculata* via artificial prolongation of submersion periods under habitat conditions.

Recent investigations on the influence of desiccation on the intermediary metabolism have been performed by WATANABE and co-authors (1969). During a 2-month period (September to November) *Porphyra tenera* was cultivated on intertidal culture nets, under different emersion conditions (emersion periods during daytime 4.2 to 3.7 hrs, 3.2 to 2.7 hrs and 2.2 to 1.6 hrs, respectively). Growth rate was highest (4 cm average length increase in 2 months) at 2.2 to 1.6-hr emersion periods. Subsequent to the culture experiment, the influence of

Table 4-30

Ether extract and total nitrogen (expressed as percentage of dry weight) and the relative amount of biuret compound in various algae. (f) indicates material from a fresh-water habitat; all other material was obtained from sea-water habitats. ++ distinct, + weak, - no biuret reaction (After HAAS and HILL, 1933; modified)

Species	Ether extract	Total N	Biuret reaction
<i>Pelvetia canaliculata</i> f. <i>libera</i>	8.62	1.02	++
<i>Pelvetia canaliculata</i>	4.88	2.19	++
<i>Fucus vesiculosus</i> f. <i>volubilis</i>	3.76	2.82	
<i>Ascophyllum nodosum</i>	2.87	—	+
<i>Fucus vesiculosus</i>	2.60	2.56	+
<i>Halidrys siliquosa</i>	2.18	1.34	very weak
<i>Himantalia lorea</i>	1.21	1.39	—
<i>Desmarestia aculeata</i>	0.65	2.12	—
<i>Laminaria digitata</i>	0.46	1.49	—
<i>Bostrychia scorpioides</i>	0.31	2.84	—
<i>Chondrus crispus</i>	0.204	2.33	—
<i>Esteromorpha intestinalis</i>	0.217	3.14(f)	—
		4.34	—
<i>Ulva lactuca</i>	0.185	3.32	—

desiccation was tested (under habitat and laboratory conditions in light and darkness) on ATP-content, peroxidase activity, chlorophyll content, phyco-erythrin, soluble carbohydrates and proteins. In addition, after-effects of desiccation were determined on respiratory rates (manometric method; 18° C; measurements immediately after re-immersion into sea water). Fig. 4-51 illustrates the effects of desiccation in light and darkness on plants of different ages.

WATANABE and co-authors (1969) conclude from their findings that the ATP-balance plays a particularly important role in desiccation effects. They assume that the favourable growth obtained in *Porphyra tenera* exposed to its natural habitat is due to the restriction of competitors via desiccation stress, rather than to positive influences of desiccation on plant metabolism.

*Plasmatic viscosity and permeability.* STOCKER (1948, 1956) suggested that functional responses of plants to desiccation are ultimately based on changes in plasmatic structures (engagement or disengagement of intermolecular bindings). If we accept this view, we may expect that such changes will also manifest themselves in plasmatic properties such as viscosity or permeability. Whereas some information exists on such relationships in higher terrestrial plants (see the reviews by STÄLHJELT, 1949, 1956; STOCKER, 1956; BIEBL, 1962b), desiccation effects on plasmatic viscosity have not yet been investigated in marine plants.

Except for some indications, there is also nothing known in regard to desiccation effects on permeability of marine algae. One indication is related to the pheno-

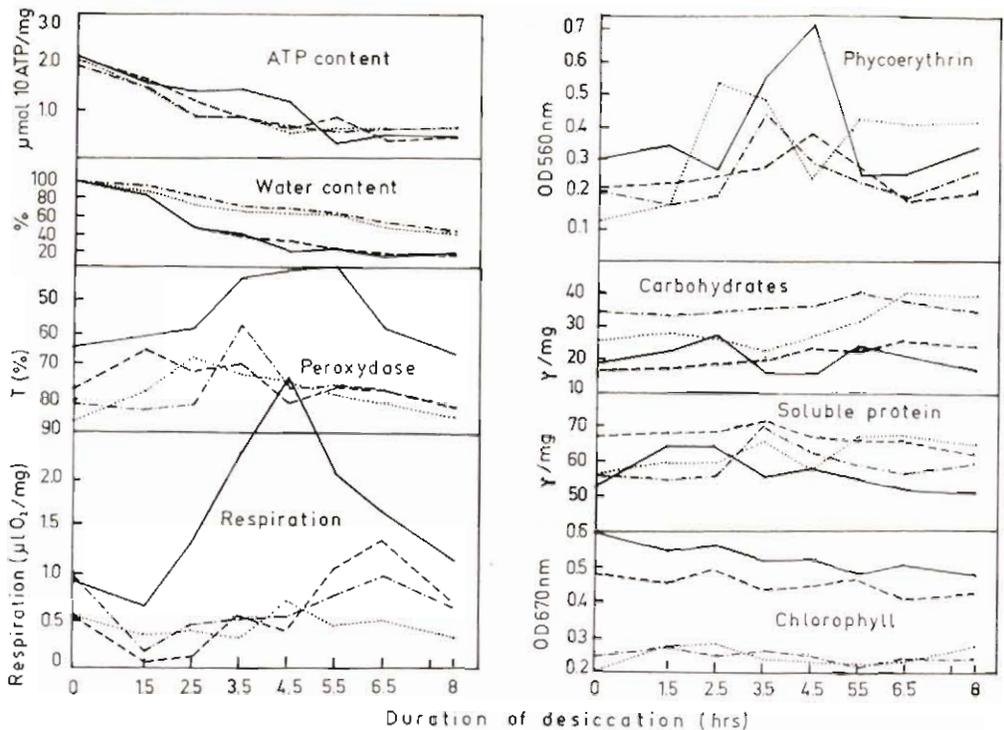


Fig. 4-51: Effects of desiccation on the intermediary metabolism of *Porphyra tenera* (coast of Japan, Matsushima Bay). After 40 days cultivation under field conditions, plants from upper and lower (i.e. shorter daily emersion periods) parts of culture nets were desiccated in light (on roof of laboratory) or in a darkroom. Plants from higher net levels had smaller average sizes than those from lower levels. Desiccation effects on ATP content (per mg dry weight), water content (%), peroxydase activity (relative transparency), respiration ( $\mu\text{l O}_2/\text{mg dry weight/hr}$ ;  $18^\circ\text{C}$ ), phycoerythrin (relative extinction at 560 nm), carbohydrates, soluble protein (per mg dry weight), and chlorophyll (relative extinction at 670 nm) were determined. No information on salinity. (After WATANABE and co-authors, 1969; modified.)

menon of 'exosmosis'—the release of cell constituents into the ambient water subsequent to desiccation. SIEBURTH (1969) investigated the influence of desiccation on exudation of organic matter in littoral algae. At hourly intervals, water loss and amount of exudate formed during a 10-min period of re-immersion in sea water were measured. After 3 hrs emersion of surface fronds of *Ascophyllum nodosum*, there is a water loss of 59.5% and an exudate of 17.4 mg C/100 g dry weight; after 5 hrs, a water loss of 77.0% and an exudate of 30.0 mg C/100 g dry weight. Under similar conditions (3 hrs and 5 hrs emersion), *Fucus vesiculosus* from the upper littoral loses 21.6 and 52.8 mg C/100 g dry weight, respectively; *Fucus vesiculosus* from the lower littoral as much as 159 and 382 mg C/100 g dry weight. Another hint has been presented by GESSNER and HAMMER (1968) in regard to the influence of desiccation on chloride release by marine algae (Fig. 4-52). If fresh and air-dried algae pieces are rinsed repeatedly at 1-min intervals in distilled water, the chloride content of the rinsing fluid differs markedly as a function of the habitat

(surface or deeper) water of the test algae. GESSNER and HAMMER interpret these results as follows: Undamaged algae release only chloride from the 'free space'; in previously dried drought-sensitive algae, however, the semipermeability of the plasma breaks down, with the result that chloride is released also from the 'osmotic space'. In drought-resistant forms, such as *Fucus vesiculosus*, the permeability properties of the plasma remain intact, even after more pronounced desiccation; consequently, also dried thalli release chloride only from the 'free space'.

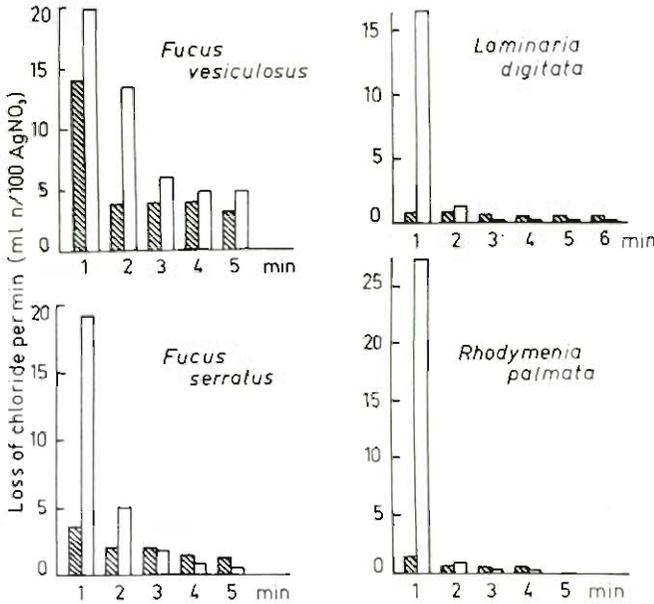


Fig. 4-52: *Fucus vesiculosus*, *Fucus serratus* and *Laminaria digitata* (Baltic Sea) and *Rhodymenia palmata* (Kattegat). Loss of chloride to ambient distilled water. Hatched columns: fresh material; white columns: air-dried material. (After GESSNER and HAMMER, 1968; modified.)

*Growth.* Desiccation affects plant growth via metabolism, e.g., through inactivation of gas exchange during prolonged dehydration, depression of photosynthesis and increased respiration as initial after-effects of water loss, or, in some surface algae, through increased gas exchange due to small amounts of water loss. In littoral algae, OLTMANN'S (1889, 1923) correlated growth rates to the degree of habitat desiccation, pointing out that, within one and the same species, significant variations occur in size and shape, depending on emersion conditions. This may be exemplified by referring to dwarf forms of *Fucus vesiculosus* var. *muscoides* COTTON which occupy salt marshes, only occasionally submersed during spring tides; or by reference to *Fucus vesiculosus* of the western Baltic Sea which develops luxurious growth in permanently submersed habitats but dwarf forms in the uppermost intertidal. Unfortunately, the existence of such relationships is based on not much more than assumptions. OLTMANN'S himself pointed out that variations in size and shape of intertidal algae may be caused not only by dehydration but also by other simultaneously effective environmental factors, such as tem-

perature, osmotic climate and light (see also OVERBECK, 1956; RIED, 1969). Desiccation effects on plant growth have hardly been documented as yet on the basis of detailed experimental evidence.

First attempts toward experimental analyses have been undertaken by BAKER (1909). She collected a considerable number of very small individuals of *Fucus ceranoides*, *Fucus vesiculosus*, *Fucus serratus* and *Ascophyllum nodosum*, each species being taken from the very centre of its distributional area. The young plants were divided up into three groups and cultivated in sea water, which was renewed once every 12 hrs. During the 12 hrs one group was left dry for 1 hr and under water for 11 hrs, the second group was left dry for 6 hrs, under water for 6 hrs, and the third group was immersed only for 1 hr. In this way a rough simulation of the periodic tidal exposure was obtained. Unfortunately, BAKER gives no information about cultivation conditions such as temperature, light or degree of water loss during emersion. Corresponding to their natural habitats, the test plants show marked differences in rates of growth and survival during the 24-day experiment (Table 4-31). From these results, BAKER concludes that seaweeds

Table 4-31

Relative growth and survival of young seaweeds as a function of desiccation. 24-day experiment with different air-exposure periods (1, 6, 11 hrs per 12-hr period). + slow, ++ medium, +++ rapid growth; - some test individuals survived, -- all dead (After BAKER, 1909; modified)

Species	Hours of exposure per 12-hr period		
	1	6	11
<i>Fucus ceranoides</i>	+	++	+
<i>Ascophyllum nodosum</i>	++	++	+ -
<i>Fucus vesiculosus</i>	+++	++	+ -
<i>Fucus serratus</i>	+++ -	+ -	--

which can resist desiccation best grow most slowly, while those which grow most quickly have the lowest tolerance to desiccation. Species with high desiccation tolerance must have maximum protection from water loss, and hence absorb water most slowly;

'Since these plants get their nourishment from general absorption of water by the thallus, the best protected plants must grow most slowly' (BAKER, 1909, p. 202).

The differences in absolute growth rates are significant only in the 1-hr exposure series, i.e., under conditions of optimum water supply. Furthermore, the (assumed) differences in speed of water absorption can hardly be expected to exert a significant influence on the gain in body substances, since even after intensive desicca-

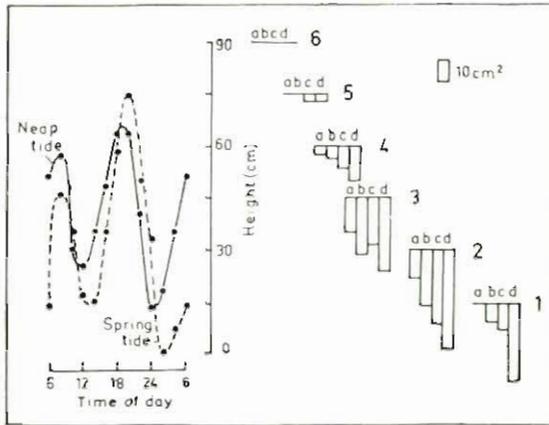


Fig. 4-53: Growth of *Porphyra* (*yezoensis*?) under different conditions of emersion during 36 days. Unit area: 10 cm<sup>2</sup>. Curves characterize diurnal tidal fluctuations. 1-6: growth zones (each 15 cm) over a total vertical distance of 90 cm above sea bottom. a-d: localities with different salinity regimes. (After OGATA and MATSUI, 1967; modified.)

tion, water saturation takes place in all algae within only a few minutes. The different growth rates recorded are based, therefore, on species-specific differences rather than on differential speeds of water uptake.

While *Fucus serratus*, *Fucus vesiculosus* and *Ascophyllum nodosum* grow best when exposed for 1 hr within the 12-hr test period, the 6-hr period greatly affects *Fucus serratus*, which inhabits the lowest intertidal level; in *Fucus vesiculosus* and *Ascophyllum nodosum*, recognizable damage occurs only after 11 hrs exposure. *Fucus ceranoides*, which inhabits the highest intertidal level, finds optimum conditions during even longer exposures (see also p. 717). The same applies to *Porphyra* (presumably *P. yezoensis*) according to information published by OGATA and MATSUI (1967).

Near Shimonoseki (Japan), culture nets with young *Porphyra* plants (1-2 and 2-3 cm long) were installed in intertidal localities characterized by different patterns of salinity fluctuations in such a way that during low tide the lower, and during high tide the upper parts of the nets are just submerged. Fig. 4-53 illustrates the results of a 36-day experiment conducted from end-December to end-January. Growth during this period was determined in six different vertical tidal levels (Table 4-32). During the day, air temperatures (determined at beginning and end of the experiment) ranged from 11.5 to 10.8°C, water temperatures (depending on the location of the culturing nets) from 4.2° to 14.2°C. In this and other experiments, growth rates were highest in the second and third intertidal level, i.e., under conditions of a mean daily emersion period of about 4 to 10 hrs. Unfortunately, no information has been provided on the degree of water loss of the test algae during emersion.

Table 4-32

Intertidal levels and exposure periods during growth experiments conducted on *Porphyra (yezoensis?)*, settled on culture nets near Shimonoseki (Japan) from end-December to end-January (After OGATA and MATSUI, 1967; modified)

Growth zone	Intertidal level	
	Height above sea level (cm)	Mean period of air exposure (hrs mins)
1	0	30
2	15	4 20
3	30	9 50
4	45	16 10
5	60	21 10
6	75	23 45

### (c) *Reproduction*

The amount of information available on salinity effects on reproduction in marine and brackish-water plants does not warrant a review at this time. However, there can be no doubt that salinity, particularly in coastal waters, greatly affects processes of sexual and asexual reproduction in aquatic plants. There is urgent need for a critical analysis.

MATSUI (1969) documented for the red algae *Gloiopeltis tenax* and *G. furcata* that liberation of tetraspores is not significantly influenced by salinities between 17‰ and 52‰. Above 60‰ and below 12‰S, liberation is delayed and the number of spores released decreases. But if the fronds, especially those of *G. tenax*, are transferred from either above 60‰S or below 12‰S to 35‰S, there is a tendency for spore liberation to be accelerated. The optimal salinity range for adhesion of spores is 26‰ to 43‰ in both species.

A few papers deal with desiccation effects on reproductive processes of benthonic littoral plants. FRIEDMANN (1963, 1969) investigated the occurrence of meiotic divisions in *Prasiola stipitata* and found that, within the *Prasiola stipitata* belt in the intertidal zone, there is a vertical zonation of meiotic and non-meiotic plants, the former being prevalent in the lower and the latter in the higher levels of the belt. FRIEDMANN suggests that humidity, i.e. desiccation (both its absolute quantity and its periodicity) might be the most potent environmental factor controlling this zonation. Considering vegetative growth, reproduction and germination, it becomes quite clear that desiccation is of special importance for all processes immediately related to reproduction. All aquatic plants require a liquid medium for successful sexual reproduction. Many inhabitants of the intertidal zone adjusted not only their vegetative development to the specific conditions brought about by air exposure and dehydration, but also reproductive processes and germination.

On the basis of his investigations on the physiology and biology of germination in the genus *Fucus*, KNIPE (1907) suggested the existence of relationships between

the morphology of reproductive organs and environmental conditions encountered in the natural habitat. He points out that, in *Fucus spiralis*, which produces hermaphroditic conceptacles, fertilization occurs probably during emersion also. Monoecious species, such as *Fucus serratus*, however, require submersion for successful fertilization. On the other hand, monoecious forms have adjusted to periodic emersion to such an extent that emersion appears to have become a necessary prerequisite, since gamete release depends largely on a preceding phase of dehydration.

OLTMANN (1889), FARMER and WILLIAMS (1898) and others showed that, during emersion, gametes of the Fucaceae are extruded by means of the mucilage in the conceptacles.

This effect of desiccation on the expulsion of gametes was investigated experimentally by BAKER (1910). Specimens of *Fucus spiralis*, *Fucus vesiculosus*, *Ascophyllum nodosum* and *Fucus serratus* were exposed to air by placing them on flat stones on the shore for defined periods of time. Of the drying conceptacles, 200 were covered with a measured quantity of sea water. After 12 hrs, the conceptacles were removed and the number of gamete bundles counted which were found in the water. Unfortunately, no information is available on desiccation and temperature conditions during emersion and during the 12-hr immersion period. BAKER's experiments suggest that exposure periods of a certain length (degree of desiccation) are required for the gamete expulsion to function efficiently and that these periods vary with the species examined. The lengths of the exposure periods required increase progressively as the seaweeds tested occupy increasingly higher shore levels (Fig. 4-54).

At this point, the question arises, to what extent may adjustments to intertidal life of reproductive processes become a limiting factor in regard to occupying greater water depths (SCHREIBER, 1930; ISAAC, 1933, 1935). ISAAC (1935, p. 116) writes:

'*Fucus serratus* may be restrained at the upper limits of the *Laminaria*-zone at Port Eynon because below that level the minimum of contraction necessary to bring about the liberation of gametes may not be possible.'

In contrast to this assumption, the major *Fucus serratus* vegetation of the western Baltic Sea lives permanently submerged.

In gametes sensitive to emersion, desiccation may exert negative effects (SAITO, 1960; this chapter, p. 726). As a result of such gamete sensitivity, the location of the reproductive organs on the thallus becomes an important factor which affects vertical zonation. The unilocular sporangia, e.g. of *Laminaria digitata*, are grouped together to form sori on the thallus surface; thus the vitality of the reproductive cells might be impaired by considerable desiccation. In the Fucaceae, however, oogonia and antheridia are embedded in the thallus and, therefore, sheltered. Only after release may the gametes become subject to critical water loss. In *Pelvetia canaliculata*, danger due to critical water loss is further reduced, since the eggs of this alga remain in the thick-walled oogonium. The oogonium wall persists and must be penetrated by the male gametes prior to fertilization.

Next to gamete release, zygote maturation and germination may be affected by

desiccation in intertidal algae. BAKER (1910) cultivated zygotes of *Fucus spiralis*, *Fucus vesiculosus*, *Fucus serratus* and *Ascophyllum nodosum* under different conditions of emersion over a 4-week period (July-August; Isle of Wight, England). She exposed developing plants for 1, 6 or 11 hrs per 12-hr period (data on degree of water loss and details on cultivation conditions are not available). Her experiments

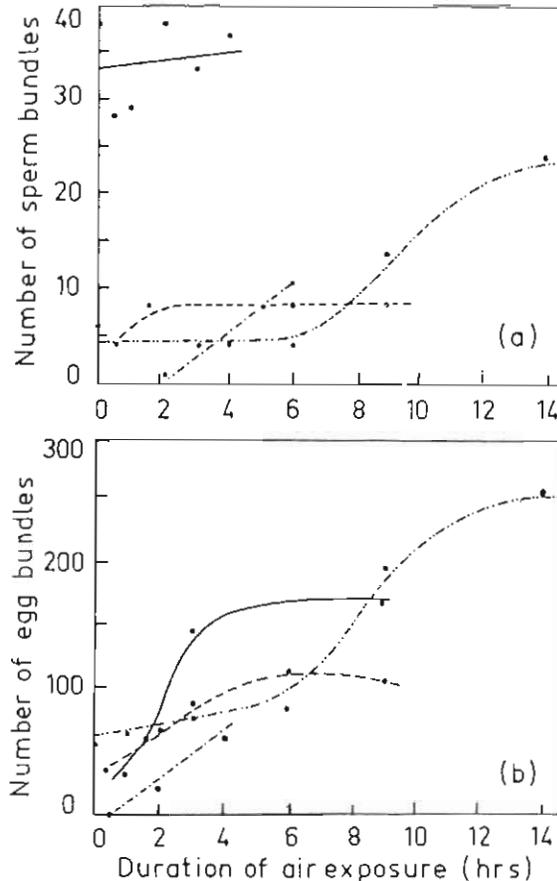


Fig. 4-54: Effect of desiccation on gamete expulsion of littoral algae (Isle of Wight, Great Britain).—*Fucus serratus*, — — — *Fucus vesiculosus*, - · - · - *Ascophyllum nodosum*, · · · · *Fucus spiralis*. Ordinates: Number of bundles of (a) spermatozoa from one conceptacle, (b) eggs from 200 conceptacles left in sea water for 12 hrs after different periods of air exposure. July/August. (After BAKER, 1910; modified.)

reveal that species occupying the highest shore levels can germinate, and their germlings attach themselves, even if submersion lasts only a very short time. However, species confined to lower shore level habitats cannot germinate under the tidal conditions prevailing in the highest zones. It is noteworthy that *Fucus vesiculosus*, in this respect, behaves as if occupying a higher shore level than *Ascophyllum nodosum*, whereas, in fact, it inhabits lower zones in the locality considered.

Not only germination, but also differentiation is influenced by the osmotic

climate. TORREY and GALUN (1970) demonstrated in *Fucus vesiculosus* that, under normal sea-water culture conditions, each embryo forms a single rhizoid. When grown in sea water supplemented with sugar concentrations above 0.4 mole, *F. vesiculosus* embryos develop as multicellular spherical bodies lacking rhizoids. In 0.6 mole sucrose sea water, 97% of the embryos are apolar at 2 days. Nuclear counts showed that sucrose sea water markedly inhibits the rate of cell division.

#### (d) Distribution

Since salinity influences all metabolic processes in plants, it may be assumed to affect also the geographical distributions of marine plants. Unequivocal evidence for relations between salinity and plant distribution has come from areas in which the salinity differs significantly from that of the open seas.

Two factors are mainly responsible for deviations in salinity: precipitation and dilution by river waters causing reduced salinities, and evaporation causing increased salinities (Chapter 4.0). Intracontinental seas such as the Baltic Sea, the Black Sea and Lake Maracaibo contain brackish waters with salt contents below the average oceanic salinity of 35‰. Semi-enclosed sea areas which remain in contact with the open seas and contain waters saltier than ocean water are of local importance and restricted in surface area. Intracontinental water bodies with no connection to the oceans—like the Dead Sea, Lake Urmia, Lake Tuz (Anatolia) and the Great Salt Lake (USA)—contain significantly concentrated sea water. Such water bodies are not considered marine environments here and hence will not be treated. (For further information see GESSNER, 1959.)

#### Major factors affecting plant distributions

Four ecological master factors determine primarily the distribution of marine plants: light (Chapter 2), temperature (Chapter 3), salinity (Chapter 4) and water movement (Chapter 5). It is obvious that numerous interrelations exist between the biological effects of these environmental factors and between their physical and chemical aspects. In order to exemplify such factor interactions, which will be discussed in detail in Chapter 12, the geographical distribution of three *Laminaria* forms, studied by DRUEHL (1967) in 15 localities in the vicinity of Vancouver Island (Canada), will be considered.

*Laminaria groenlandica* long stipe form occurs in areas exposed to heavy surf, while *L. groenlandica* short stipe form prefers more sheltered localities, as does *L. saccharina*. The salinity and temperature in the habitats occupied by the three forms are shown in Fig. 4-55. *L. saccharina* grows in wide ranges of salinity and temperature, whereas *L. groenlandica* long stipe form is cold stenotherm and stenohaline. The importance of salinity and temperature for the distribution of these forms is supported by measurements on rates of photosynthesis and respiration (Table 4-33). In *L. saccharina*, net photosynthesis increases with temperature but is hardly affected by salinity. In *L. groenlandica*, photosynthesis rapidly decreases at higher temperatures and in lower salinities, while the resulting respiratory rates vary irregularly; the ratio photosynthesis:respiration decreases considerably at higher temperatures, indicating that this alga prefers high salinities and low temperatures.

Table 4-33

*Laminaria saccharina* and *L. groenlandica*. Net photosynthesis, dark respiration, and ratio net photosynthesis: dark respiration of long stipe forms in different salinity-temperature combinations. Units:  $\mu\text{l O}_2/\text{cm}^2/\text{hr}$  (After DRUEHL, 1967; modified)

<i>Laminaria saccharina</i>		Net photosynthesis					Average		<i>Laminaria groenlandica</i>					Average		
$^{\circ}\text{C}$		20	24	26	28	30	32‰S		$^{\circ}\text{C}$	20	24	26	28	30	32‰S	
7	6.1	8.3	6.8	6.8	7.0	7.0	7.3	7.1	7	5.7	5.7	6.0	5.6	5.7	7.0	6.0
10	8.1	8.0	8.1	7.9	8.0	8.3	8.3	8.1	10	2.4	3.7	2.5	4.2	5.9	5.0	4.0
13	7.8	8.5	8.6	8.2	8.9	8.6	8.6	8.4	13	0	0	0	0	2.7	2.7	0.9
15	10.0	11.0	10.5	9.2	10.6	9.3	10.1	10.1	15	0	0	0	2.9	1.4	0	0.7
18	10.8	11.9	10.4	8.3	12.3	12.1	11.1	11.1	18	0	0	0	0	0	0	0
Average:	8.6	9.5	8.9	8.1	9.5	9.2				1.6	1.9	1.7	2.5	3.1	2.9	
		Dark respiration					Average		Dark respiration					Average		
7	0.5	0.5	0.6	0.7	0.5	0.7	0.7	0.6	7	1.6	1.2	1.2	1.1	1.0	0.7	1.1
10	1.0	0.5	0.6	0.4	0.8	0.5	0.5	0.6	10	1.8	1.8	0.8	1.9	1.1	1.2	1.4
13	0.7	0.7	0.6	0.7	0.6	0.7	0.7	0.7	13	2.2	2.3	2.2	1.6	2.4	1.8	2.1
15	0.7	1.0	0.7	0.8	0.9	0.7	0.8	0.8	15	2.2	2.2	2.5	2.6	2.8	2.4	2.5
18	0.6	0.8	0.7	0.7	0.8	0.9	0.9	0.8	18	1.2	0.5	1.5	1.6	1.8	2.1	1.5
Average:	0.7	0.7	0.6	0.7	0.7	0.7	0.7	0.7		1.8	1.6	1.6	1.7	1.8	1.6	
		Ratio net photosynthesis: dark respiration					Average		Ratio net photosynthesis: dark respiration					Average		
7	12.2	16.6	11.3	9.7	14.0	10.7	12.4	12.4	7	3.6	4.8	5.0	5.1	5.7	10.0	5.7
10	8.1	16.0	13.5	19.8	10.0	16.6	14.0	14.0	10	1.3	2.1	3.1	2.2	5.4	4.2	3.1
13	11.1	12.1	14.3	11.7	14.8	12.3	12.7	12.7	13	—	—	—	—	1.1	1.5	1.3
15	14.3	11.0	15.0	11.5	11.8	13.3	12.8	12.8	15	—	—	—	1.1	0.5	—	0.8
18	18.0	14.9	14.9	11.9	16.0	13.4	14.9	14.9	18	—	—	—	—	—	—	—
Average:	12.7	14.1	13.8	12.9	13.3	13.3	13.3	13.3		2.5	3.5	4.0	2.8	3.2	3.2	3.2

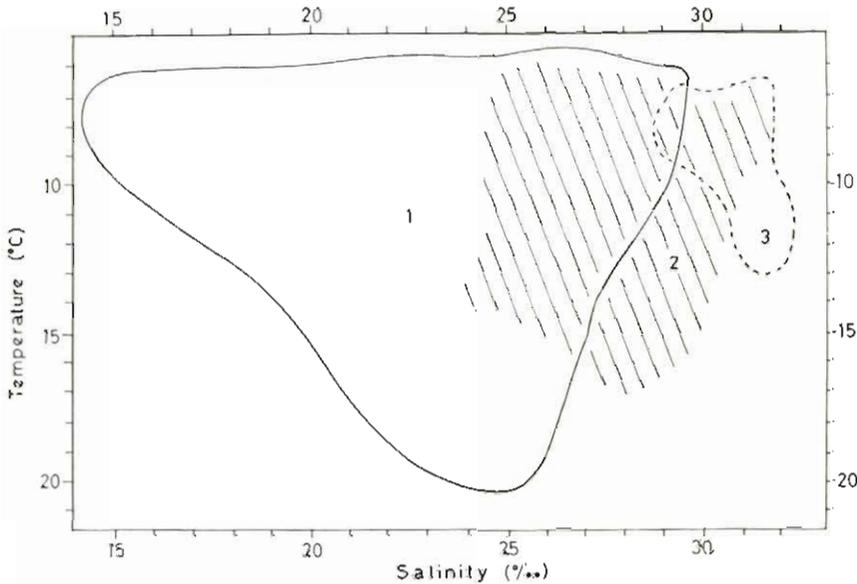


Fig. 4-55: Ranges of salinity and temperature variations in habitats occupied by *Laminaria saccharina* (1), *L. groenlandica* short-stipe form (2) and *L. groenlandica* long-stipe form (3). (After DREYER, 1967; modified.)

#### *Plant distributions in the Baltic Sea*

The Baltic Sea is one of the most thoroughly investigated brackish-water areas of the world. The conditions responsible for the brackish nature of the Baltic Sea have been summarized by GESSNER (1959). In the Kattegat, which connects the Atlantic Ocean and the Baltic Sea, the salinity decreases rapidly to values of about 20‰ to 13‰ at the surface, while in the depths salinities near 30‰ extend to the Danish islands. Towards the eastern parts of the Baltic Sea, the salinity decreases gradually to 2‰. Thus, for the marine ecologist, the Baltic Sea represents an almost ideal case of a natural salinity gradient ranging from marine to nearly limnic conditions; along some parts of the coast, lagoons ('Haffe') exist with only narrow connections to the open Baltic Sea; in these lagoons, the salinity is often as low as 1‰. Water of 1‰ S tastes like fresh water; however, it is normally still inhabited by a few brackish-water phytoplankters and benthonic algae which exist here together with true limnic species.

*Distribution of benthonic algae.* KYLIN (1907) recorded the number of red and brown algae occurring in various localities along the Swedish coast (Table 4-34). Since most parts of the coast are characterized by rocky substrates, the different localities studied appear to represent quite comparable habitats, except for the differences in salinity. Table 4-34 reveals that the number of red and brown algae species decreases with salinity toward the inner Baltic Sea.

In order to evaluate modern aspects of algal distribution, three localities are compared of which we possess an almost complete inventory of algal species. The localities are: the marine waters off the Atlantic coast near Roscoff (France),

Table 4-34

Number of marine algae species recorded in different coastal parts of the Baltic Sea (After KYLIN, 1907; modified)

Locality	S‰	Number of species	
		red algae	brown algae
Bohuslän	27-33	99	102
Middle and North Halland	19-32	72	67
South Halland and Schonen			
Småland	7-8	16	20

for which FELDMANN (1954) published a complete flora list; the brackish waters off the island of Hiddensee near Rügen (Baltic Sea) which has been studied algologically by KUNZENBACH (1955/56); and the highly diluted waters near Öregrund (1° north of Stockholm), the marine flora of which has been studied by WAERN (1952). The respective numbers of algal species are listed in Table 4-35. In regard to the Chlorophyceae, the species numbers listed for Roscoff and Öregrund are not very different; however, the majority of the species recorded from both localities are different; only 16 species occur in both localities:

<i>Enteromorpha intestinalis</i>	<i>Ectochaete leptochaete</i>
<i>Enteromorpha compressa</i>	<i>Entocladia viridis</i>
<i>Enteromorpha prolifera</i>	<i>Epicladia frustrae</i>
<i>Enteromorpha clathrata</i>	<i>Pringsheimiella scutata</i>
<i>Blidingia minima</i>	<i>Chaetomorpha melagonium</i>
<i>Percursaria percursa</i>	<i>Rhizoclonium riparium</i>
<i>Prasiola stipitata</i>	<i>Acosiphonia centralis</i>
<i>Pseudodendroclonium submarinum</i>	<i>Cladophora rupestris</i>

Table 4-35

Number of marine algae species recorded in different localities (After various authors; original)

Locality	S‰	Number of species		
		Chlorophyceae	Phaeophyceae	Rhodophyceae
Roscoff (France)	ca 36	79	136	299
Hiddensee (Baltic Sea)	8-6	36	27	18
Öregrund (Baltic Sea)	5	60	25	17

The number of Chlorophyceae is not very different in the open sea at ca 36‰S (79 species) and in the brackish waters of the Baltic Sea with salinities down to 5‰ (60 species). However, the number of Phaeophyceae and Rhodophyceae is considerably reduced near Hiddensee and Öregrund. Although salinities in these two Baltic Sea areas differ much less than those of the inner Baltic Sea and the Atlantic Ocean near Roscoff, the species composition is clearly different. Among the 41 Phaeophyceae of both regions, only 9 are identical; among the 27 Rhodophyceae only 11.

The species list published by WAERN (1952) comprises Chlorophyceae which penetrate into, or exist permanently, in the brackish waters of the Öregrund. This is a small number compared to the number of Chlorophyceae which are restricted to fresh water. The minimum number of species (near Hiddensee) exemplifies the long known 'law of poverty' (see also Chapter 4.31) regarding species diversity in brackish waters. With decreasing habitat salinity the reduction in the number of marine species is not compensated for by a comparable increase in the number of freshwater species. Recently, the problem of impoverishment in species numbers has been discussed quite frequently. In most cases reported, a single factor attaining extreme intensities or fluctuation ranges is responsible for the decrease in species diversity. Attempts have been made to ascribe the decrease in species diversity not to salinity itself but to critical fluctuations in salinity (i.e. to the rough osmotic climate characteristic of most brackish waters). However, such critical fluctuations do not exist in the major parts of the Baltic Sea, and the largest number of species is found in the area with the most pronounced salinity variations (Belt Sea). Furthermore, it was assumed that decreasing salinities cause a decrease in community diversity and, indirectly, in the number of species per community; however, this is not quite true either (REMANE, 1934). The same algal community (Furcellarietum) which accomodates more than 20 sessile animals in the Bay of Kiel (ca 15‰ to 17‰S), comprises only three sessile animal species in the 'Greifswalder Bodden' (ca 7‰S), although habitat conditions, except salinity, are quite the same in both localities.

Historical reasons rather than others may explain the reduced species diversity in brackish waters. In the course of millions of years, aquatic organisms have adapted to sea water on the one hand, and to fresh water on the other. In contrast to sea-water and freshwater habitats, brackish waters are ephemeral, appearing and disappearing so rapidly over geological time spans that there is insufficient time for adjusting to and populating of such new environments. Newly formed brackish waters challenge potential immigrants physiologically and force them to adapt to deviated salinity conditions. Hence the first immigrants of new brackish-water areas are euryhaline species. Immigration may take place rather rapidly; this was demonstrated in the Kiel Canal (connecting North Sea and Baltic Sea) which was built 74 years ago. Presumably the origin of new species in brackish water is so slow that it is not only beyond human observation but yields little or no progress during the 'lifetime' of a given brackish-water system.

The poverty of endemisms is a direct consequence of the geological youth of the Baltic Sea as a brackish-water area. Among the 457 algal species of the Baltic Sea, 44 were claimed to be endemic (LAKOWITZ, 1929). When HOFFMANN (1950) examined this claim in detail, he found that 29 of the 44 'endemic' species also

occur elsewhere; even the endemic character of the remaining 15 species is questionable. Truly endemic species are only *Monostroma baltica* and *Anabaena baltica*, perhaps also *Kjellmania sorifera*.

Since brown and red algae are scarcely, or not at all, represented in fresh waters, their minimum of species diversity is less pronounced than that of green algae. With decreasing salinity, the disappearance of brown and red algae is not compensated for by a reciprocal appearance of freshwater representatives. Only a few euryhaline species can penetrate into the inner Baltic Sea; especially in the Gulf of Bothnia, red and brown algae are extremely scarce. In this Gulf, VÄLIKANGAS (1933) found the distributional limits of *Sphacelaria racemosa*, *Pylaiella littoralis*, *Phyllophora brodiaei*, *Polysiphonia violacea*, *P. nigrescens* and *Furcellaria fastigiata* close to 4.5‰S; those of *Elachista fucicola*, *Fucus vesiculosus*, *Chorda filum*, *Dictyosiphon foeniculaceus*, *Gobia baltica*, *Stictyosiphon tortilis*, *Asterocystis racemosa* and *Ceramium diaphanum*, close to 3‰S.

The distribution of benthonic marine algae is not only limited directly by reduced salinities, but also by the fact that waters of lower salinities freeze more readily, thus introducing additional physiological barriers.

*Distribution of vascular plants.* Due to extensive investigations, mainly by Scandinavian scientists (SAMUELSSON, 1934; LUTHER, 1951), it is possible to provide a fairly detailed picture of the distribution of vascular plants in the peripheral regions of the Baltic Sea. General viewpoints can only be obtained if the major sources of errors are recognized and severe mistakes avoided. Even in restricted littoral areas, salinities may vary considerably. It is necessary, therefore, to state the salinity of the immediate place where the plant in question was found. General statements of salinity values obtained in off-shore waters are, in most cases, worthless for a critical assessment of the distributional relations between plant and salinity. The second point which deserves attention concerns the drifting of higher and lower marine plants via water currents. In the Baltic Sea, drifting parts of *Zostera marina* occur more frequently than intact sessile individuals; drifting parts are even carried far into the Finnish Gulf where settling is apparently impossible (LUTHER, 1950). Hence, in benthic marine plants we must distinguish between distributional areas of normally growing plants and those of drifting specimens or parts thereof.

If seasonal and annual salinity variations are small, one or a few determinations will allow us to characterize sufficiently the prevailing salinity conditions. Such situations exist in the inner Baltic Sea where distributional salinity boundaries of single species can be clearly defined. In the western mixing zone between Baltic Sea and North Sea waters, however, the resulting salinities may fluctuate enormously within short periods of time. Consequently, it would be wrong to base ecological considerations on average salinities. Not average but extreme salinities decide if a plant can establish itself permanently in a given geographical area.

Adaptation to new levels of environmental factor intensities appears to proceed more effectively under constant than under fluctuating conditions. An example, presented by LUTHER (1951), is the comparison of salt requirements of various phanerogams in two regions with completely different amplitudes of salinity fluctuations. While the salinity in the coastal region near Ekenäs (Finland)

fluctuates but little, the salinity of the Randers Fjord (Norway) is subject to periodical seasonal oscillations and often varies between 0‰ and 15‰S. On the basis of the mean values calculated, the phanerogams from the Randers Fjord (OSTENFELDT, 1918) tolerate salinities far lower than those prevailing in the Ekenäs region (Fig. 4-56). However, such conclusions would be misleading.

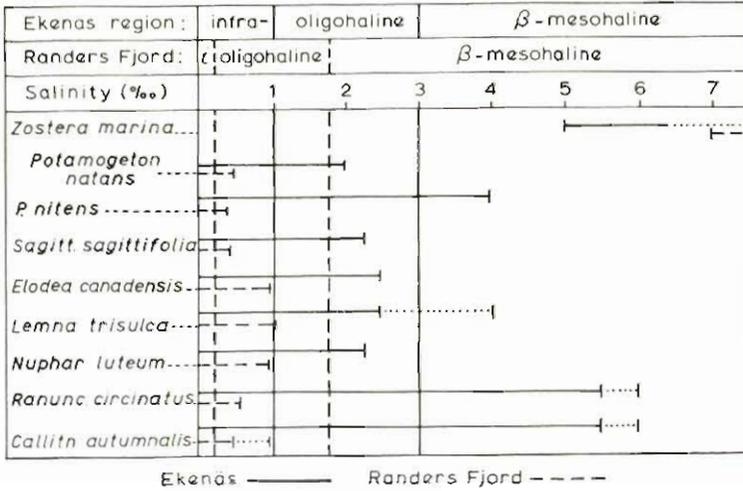


Fig. 4-56: Salinity limits of hydrophytes near Ekenäs (Finland) and Randers Fjord (Norway). *Sagitt.*: *Sagittaria*, *Ranunc.*: *Ranunculus*, *Callit.*: *Callitriche*. (After LUTHER, 1951; modified.)

Randers Fjord species could certainly exist in salinities between 1‰ and 3‰ (perhaps even in higher ones), if they were not excluded from such average salinity zones by much higher salinities which occur only during rather short periods of time and therefore hardly affect the calculated average values.

Following these general remarks, we shall now consider the higher vegetation of the Baltic Sea. According to SAMUELSSON (1934), there exist approximately 160 species, varieties and bastards of halophytes and submerged aquatic plants; this amounts to about 1/10 of the total species number of vascular plants found in northern Europe. Only 6 of these 160 taxonomic units are entirely restricted to sea water, and hence considered obligatory halophytes with high salt requirements: *Zostera marina*, *Z. nana*, *Ruppia maritima*, *R. spiralis*, *Zanichellia palustris* var. *major* and *Scirpus parvulus*.

The distribution of *Zostera marina* has already been discussed. Its close relative *Zostera nana* is quite unable to penetrate into the brackish waters of the Baltic Sea. Figs 4-57 and 4-58 illustrate the distribution of *Ruppia maritima* and *Scirpus parvulus*. We recognize a distributional limit similar to that of marine algae.

The following species, though also obligatory halophytes, have lower salt requirements: *Potamogeton vaginatus*, *P. pectinatus*, *Najas marina*, *Zanichellia palustris*, *Ranunculus baudotii*, *Scirpus maritimus* and *S. tabernaemontani*. They also populate regions of the Baltic Sea with very low salinities, and *Potamogeton vaginatus* (Fig. 4-59) is even restricted to such regions.

All other aquatic phanerogams of the Baltic coasts are considered facultative

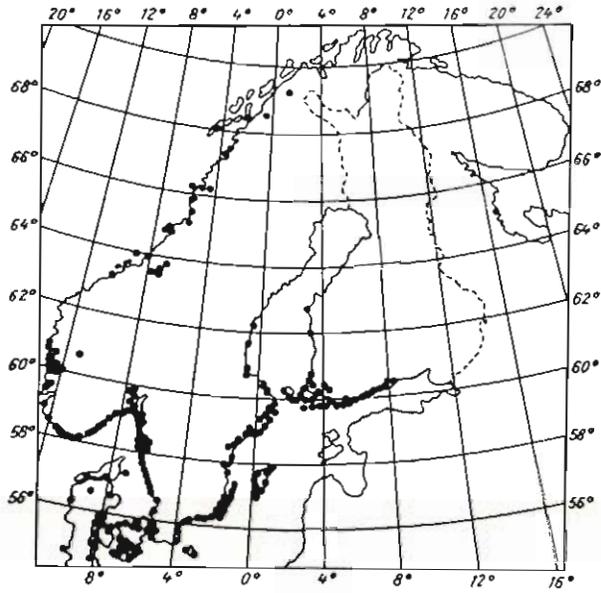


Fig. 4-57: Distribution of *Ruppia maritima* in Northern Europe. (After SAMUELSSON, 1934.)

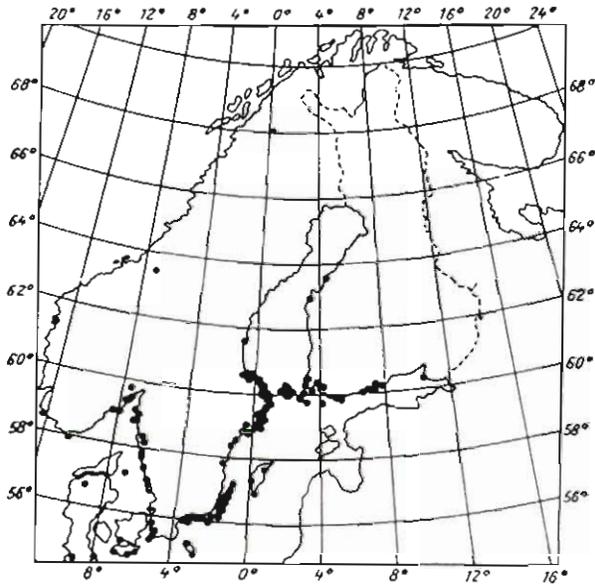


Fig. 4-58: Distribution of *Scirpus parvulus* in Northern Europe. (After SAMUELSSON, 1934.)

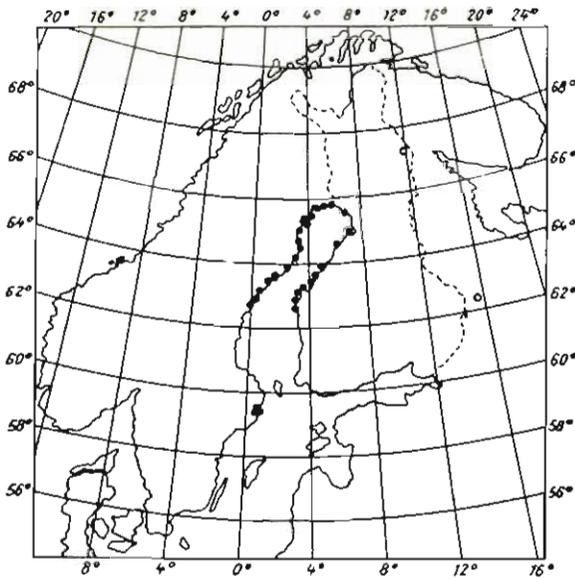


Fig. 4-59: Distribution of *Potamogeton vaginatus* in Northern Europe. (After SAMUELSSON, 1934.)

halophytes; from more or less limnic habitats they populate brackish waters because they can resist certain increases in salinity; their distributional limits are clearly related to the maximum salinities tolerated. Although facultative halophytes live primarily in fresh waters, they may be distributionally restricted to coastal areas of brackish waters. However, the primary factors determining their distribution may be others than salinity: (i) there is no competition with species incapable of existing in salty waters; (ii) the plants may have procured better assimilation conditions due to the increase of bicarbonate concentration in brackish waters; in soft fresh waters from igneous mountains bicarbonate concentrations are insufficient.

Interestingly, the decrease in number of species of marine plants from the west to the east of the Baltic Sea has no parallel in terrestrial halophytes. On the coasts of Gotland (7‰S) the same species occur as in the marshland of the North Sea (ENGLUND, 1942). This uniformity may be explained by the fact that, in terrestrial habitats close to the sea, salts frequently accumulate due to evaporation (GESSNER, 1930; POMPE, 1940). The salt accumulation periods may be often only short, but sufficient for providing the terrestrial halophytes with the required amounts of salt (Fig. 4-60). Terrestrial halophytes pose numerous fascinating problems to the ecologist; however, since they are members of the land vegetation, these problems cannot be treated here. For pertinent information consult CHAPMAN (1964).

Another remarkable fact is the absence of natural land reclamation in the Baltic Sea due to lack of marine helophytes. In 1927, the rice grass *Spartina townsendii*, a hybrid between *S. stricta* and *S. alternifolia*, was introduced to the German North Sea coast; but the hope that this plant would favour natural land reclamation was not fulfilled. Natural land reclamation ('Verlandung'), supported by *Scirpus maritimus* and *S. lacustris*, proceeds only in the middle parts of the Baltic

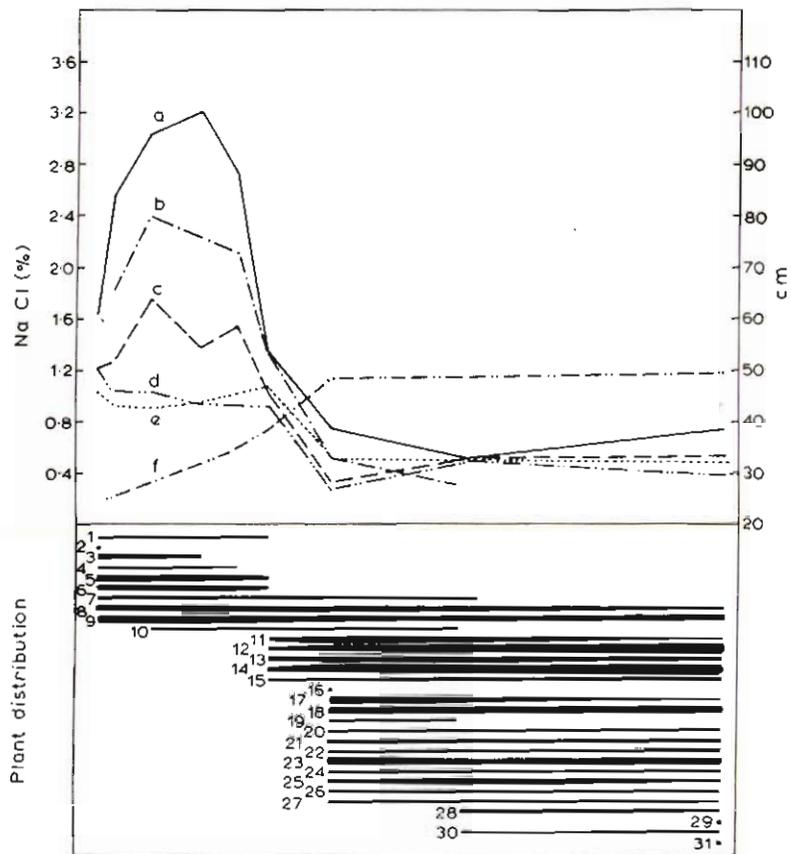


Fig. 4-60: Sections through a salt marsh on the Island of Hiddensee (Baltic Sea). Salinity: 8‰. Left: sea side, right: land side. a-e salinity in different depths of the soil; a: 1-2 cm, b: 6 cm, c: 15 cm, d: 30 cm, e: 45 cm; f: level above mean water (right cm scale). 1: algal distribution, 2-32 distribution of the following terrestrial halophytes: 2 *Festuca distans*, 3 *Spergularia salina*, 4 *Salicornia herbacea*, 5 *Glaux maritima*, 6 *Aster tripolium*, 7 *Triglochin maritima*, 8 *Juncus gerardi*, 9 *Plantago maritima*, 10 *Armeria vulgaris* var. *maritima*, 11 *Plantago coronopus*, 12 *Trifolium fragiferum*, 13 *Festuca arundinacea* var. *baltica*, 14 *Festuca rubra*, 15 *Agrostis alba*, 16 *Apium graveolens*, 17 *Leontodon autumnalis*, 18 *Potentilla anserina*, 19 *Potentilla reptans*, 20 *Lotus tenuifolius*, 21 *Erythraea pulchella*, 22 *Sagina nodosa*, 23 *Sieglingia decumbens*, 24 *Trifolium repens*, 25 *Bellis perennis*, 26 *Odontites litoralis*, 27 *Taraxacum officinale* var. *palustre*, 28 *Carex goodenoughii*, 29 *Carex distans*, 30 *Bupleurum tenuissimum*, 31 *Brunella vulgaris*. (After POMPE, 1940; modified.)

Sea in sheltered areas; in the innermost parts of the Baltic Sea, lenitic areas are always inhabited by *Phragmites communis*. It is well known that most of the European lakes, formed after the last Ice Age, have disappeared due to 'Verlandung'. It seems worthwhile to point out that this process has not been observed in marine habitats, not even under very sheltered conditions, and that 'Verlandung' plays

a very limited role also in brackish waters, except in regions with salinities below 5‰.

#### *Phytoplankton distributions in Baltic Sea and North Sea*

It is difficult to study salinity effects on the species composition of phytoplankton communities. Although the plankton communities in the Baltic Sea and North Sea have been investigated most extensively, it is hard to find two regions with identical species lists prepared with the same degree of completeness and taxonomical reliability. Furthermore, different authors differentiate between truly planktonic species of the open waters and those of coastal areas in different ways, so that the resulting species lists are not entirely comparable.

The problems due to drifting of marine plants via water currents, already mentioned in connection with benthonic plants, are of even greater significance in planktonic species (see also Chapter 5). If, for example, large amounts of fresh water enter the sea in estuaries, sea water diluted 1/10 by fresh water may contain 100 times more limnic than marine plankters per unit water volume. Since critical cell damages are frequently not detectable by means of microscopic inspection, the observer may be misled to assume that the (actually dying) limnic forms represent a permanent floristic element in his study area. The danger of such misinterpretations can only be reduced either by parallel experiments under controlled environmental conditions or by comprehensive observational evidence *in situ*, based on numerous single records.

When it comes to distinguishing between marine, limnic and brackish-water communities, however, every marine ecologist familiar with the respective plankton forms will be able to differentiate between these major groups upon a brief look into his microscope. The only major source of errors in such cases are diatom species with shells resisting biological or mechanical degradations; empty shells of marine diatoms may be carried with tidal currents far upstream into the fresh water of rivers (BROCKMANN, 1940; HALLIK, 1959). Thus GESSNER and SIMONSEN (1968) found marine diatom shells in the River Amazon 300 km upstream from the river mouth together with living desmids (see also GESSNER, 1959).

An example of the importance of salinity for the species composition of phytoplankton communities is provided if we compare the species lists reported by VÄLIKANGAS (1926) for the Port of Helsinki to that published by GESSNER (1959) for the southern North Sea (Table 4-36). While both localities maintain about the same total number of phytoplankton species, they have only 6 species in common: *Ebria tripartita*, *Peridinium pellucidum*, *Skeletonema costatum*, *Actinocyclus ehrenbergii*, *Achnanthes taeniata* and *Bacillaria paradoxa*. Also the distribution of higher taxonomic units, even that of algal classes, is different in both localities. While blue-green and green algae dominate in the brackish waters of the Port of Helsinki, they are almost absent or of little ecological importance in the marine waters of the North Sea. On the other hand, peridinean forms and diatoms are more strongly represented in the southern North Sea than in the Finnish Bay. Possibly, flagellates occur more frequently in brackish waters than in marine waters. However, evidence in support of such an assumption is largely based on collections taken at a time when the importance of nanoplankton forms (consisting to a large extent of flagellate species) was not appreciated. Especially the

Table 4-36

Species composition of phytoplankton communities from the Port of Helsinki and the German Bight, southern North Sea.  
(After GESSNER, 1959; modified)

Locality	‰S	Cyanophyceae	Flagellata	Number of species Dinoflagellata	Chlorophyceae	Diatomeae	Total
Finnish Bay (Port of Helsinki)	0-25-ca.6	14	13	13	12	44	96
German Bight (North Sea)	30-35	0	3	28	1	68	100

coccolithophorids are represented abundantly in the North Sea and may be considered a truly marine flagellate family (with few exceptions).

*Plant distributions in the Black Sea*

The Black Sea is connected with the Atlantic Ocean via the Mediterranean Sea through the Bosphorus, a channel only a few hundred metres wide. No unequivocally accepted picture exists yet in regard to water exchange patterns between Black Sea and Mediterranean Sea, in spite of extensive research on this matter. The major discrepancies between current views are related to the question as to how the outflowing brackish water is replaced by inflowing salt water. Table 4-37 gives salinity and temperature values as a function of water depth in the Bosphorus. The values shown characterize a momentary situation; water exchange between the Black Sea and the Marmara Sea varies with the prevailing wind direction. Regrettably, until now no papers have been published on the vertical zonation of algae in the Bosphorus. A study of the effects of factor combinations (especially of salinity and temperature) is likely to provide important information on the forces controlling plant distributions in this unique area.

Table 4-37

Salinity and temperature as a function of water depth in the Bosphorus (August 8, 1955) (Original)

Water depth (m)	‰S	°C
0	17.79	23.9
10	17.88	23.8
20	18.12	21.0
30	19.79	15.1
40	28.87	15.5
50	36.42	15.4
60	37.12	15.4
70	37.12	15.4

The surface salinity of the Black Sea is 17‰ to 18‰. Deep-water salinity rises to about 22.5‰. A substantial decrease in salinity occurs only near the coast, under the effect of outflowing river water. Thus, the main part of the Black Sea has a salinity approximately 3 times higher than that of the central basin of the Baltic Sea. It may be assumed that the number of marine algae species is higher in the Black Sea than in the middle or eastern Baltic Sea. A comparison of Tables 4-34 and 4-38 demonstrates that this assumption is correct.

Table 4-38 further reveals that, in the Mediterranean Sea, Black Sea and Sea of Azov—similar to the findings reported for the Baltic Sea—the number of marine algae species decreases significantly with decreasing salinity. Attention must be drawn to the fact that the numbers given for the Mediterranean Sea refer only to species recorded for the Gulf of Naples, while the number reported for the Black and Azov Seas include all species found there to date. Consequently, we can be

Table 4-38

Number of marine algae species recorded in the Mediterranean, Black and Azov Seas, respectively (After CASPERS, 1958; modified)

Locality	%S	Number of species		
		Chlorophyceae	Phaeophyceae	Rhodophyceae
Mediterranean Sea (Gulf of Naples)	ca 38	88	94	289
Black Sea	ca 18	54	64	103
Azov Sea	ca 11	19	4	10

quite sure that the total number of all Mediterranean species is considerably higher than the values presented in Table 4-38. Surprisingly, FELDMANN (1937) found a very similar number of taxa in the western Mediterranean Sea (Côte des Albères): 87 Chlorophyceae, 92 Phaeophyceae, and 279 Rhodophyceae; however, it is obvious that the Gulf of Naples and Côte des Albères are populated partly by different plant species.

The most abundant red algae genus in the Black Sea is probably *Phyllophora* with *P. nervosa* and *P. brodiaei*. These species make up the long known 'Sernovic *Phyllophora* meadows' growing, on a substratum which consists mostly of mollusc shells, in water depths between 0 and 47 m. Near Odessa, they are harvested for iodine exploitation and agar production.

The phytoplankton of the Black Sea reveals manifold similarities to the phytoplankton of the western Baltic Sea and of the North Sea. The three seas have in common 13 species of *Chaetoceros*, 9 of *Rhizosolenia* (among them *R. calcar avis* and *R. shrubsolei*), 6 species of *Melosira* (*M. nummuloides* and others), 13 *Coscinodiscus* species, as well as *Cerataulina bergoni*, *Leptocylindrus danicus*, *Thalassionema nitzschioides*, *Thalassiothrix longissima*, *Thalassiosira* sp., *Fragilaria* sp., *Asterionella* sp. and *Ditylum* sp. (VASILESCU-MARINESCU, 1956).

The most abundant coastal species of the northern Azov Sea is *Skeletonema costatum*. The dinoflagellates are represented by 23 species of *Peridinium*, 9 of *Dinophysis*, 7 of *Gonyaulax*, 4 of *Ceratium*, several species of *Glenodinium*, and by *Prorocentrum micans* and *Exuviaella cordata* (CASPERS, 1957). Surprisingly, no coccolithophorids have been found in the Black Sea; they occur frequently in the Mediterranean Sea and in great abundance in the western Baltic Sea.

#### *Plant distributions in the fjords of Norway and Sweden*

Effects of salinity on plant distributions are particularly obvious in the fjords of Norway and Sweden (SUNDENE, 1953; JORDE and KLAVESTAD, 1963). The great amounts of fresh water which enter the innermost fjord parts reduce the salinities gradually down to freshwater values. Since the amount of freshwater inflow varies considerably throughout the year, especially due to the large masses of ice which melt in early spring, fluctuation ranges of salinity (rather than average values) are of ecological importance.

An especially detailed account on algae distributions has been published by JORDE and KLAVESTAD (1963) who studied the Hardanger Fjord (Norway).

Fig. 4-61 illustrates how far the various algal species penetrate into the interior parts of the fjord. Table 4-39 exemplifies the reduction in number of algae towards the innermost fjord area and lists the 4 fjord areas which can be distinguished on the basis of their algal flora. The number of species clearly decreases with increasing

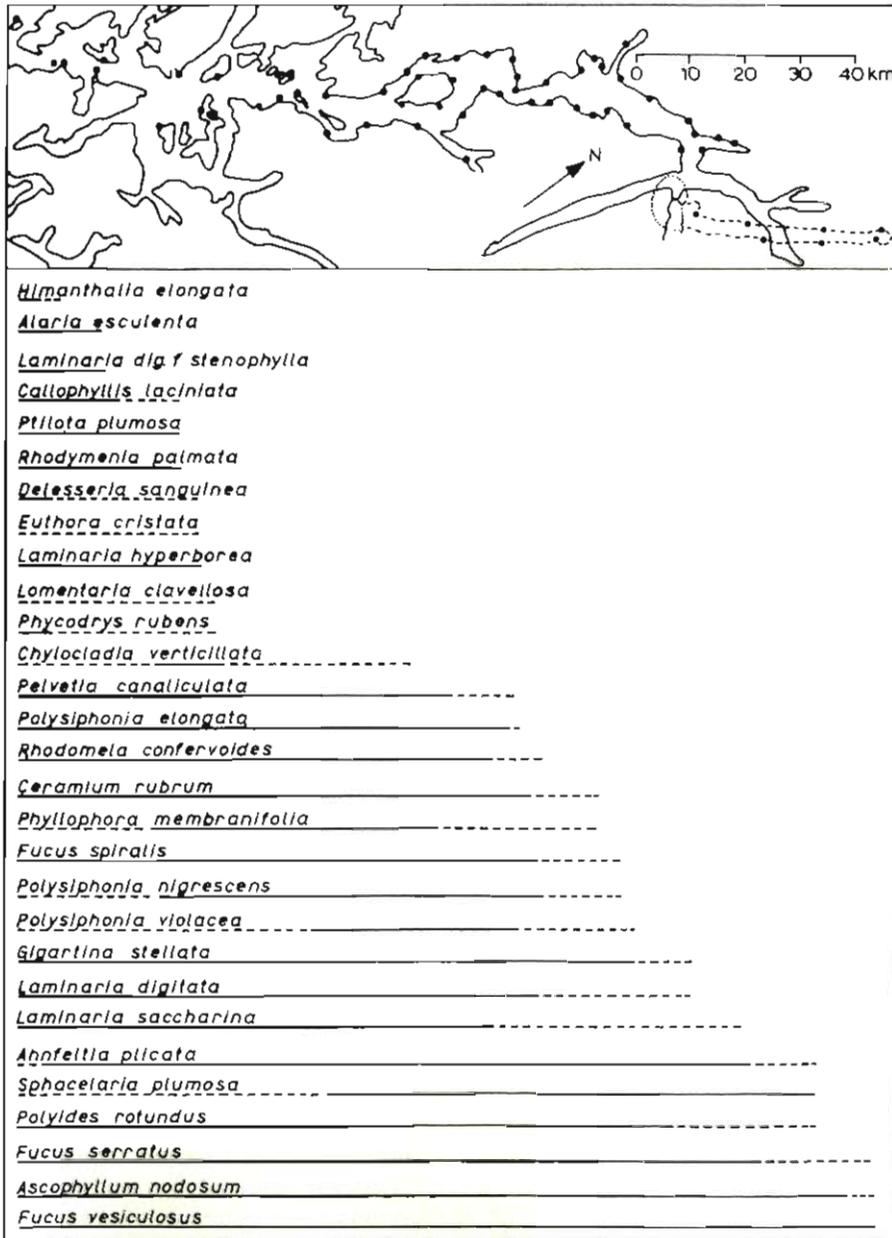


Fig. 4-61: Horizontal distribution of selected algal species in the Hardanger and Sør Fjords (the broken line shows the Sør Fjord turned to the right). In the lower part of the figure, solid lines indicate common, broken lines scattered occurrence. (After JORDE and KLAVESTAD, 1963; modified.)

Table 4-39

Total number of algae species recorded in the 4 parts of Hardanger Fjord (Norway) (After JORDE and KLAVESTAD, 1963; modified)

Area	Chlorophyceae	Phaeophyceae	Rhodophyceae	Total
Outer fjord	21	70	75	166
Intermediate fjord	27	49	53	129
Inner fjord	27	48	36	111
Sor Fjord and Eid Fjord	11	29	19	59

distance from the mouth of fjord; the decrease is most pronounced in the Rhodophyceae; in the innermost fjord parts the total number of species amounts to about one half to one third of the maximum species numbers recorded.

The reduction in species numbers applies, however, only to sessile, relatively long-living algae. Phytoplankton algae respond differently to the fluctuation patterns of salinity. In southeast Norway, a fjord exists with very narrow entrances; the name of its inner part is Hunnebunnen. The benthonic vegetation of this fjord has been investigated by KLAVESTAD (1957), the phytoplankton by BRAARUD and FØYN (1958). The salinity of the surface water fluctuates over the year from 2‰ to 28‰. The deeper waters (total depth 11 m) have a higher salinity throughout the year resulting in a stable vertical density gradient which prevents vertical water circulation. In the lower, stagnating water layers, H<sub>2</sub>S accumulates permitting only Euglenaceae to exist. Also the water of the upper 6 m shows a pronounced salinity stratification at all seasons (on March 25, 1954 the salinity was 0.1‰ at the surface and 31.4‰ in 6 m depth). The uppermost metres contain mainly brackish-water phytoplankton and limnic forms, while the deeper waters harbour marine forms, especially dinoflagellates which reach high cell numbers per unit water volume. The salinity gradient greatly affects the vertical distribution and, during certain seasons, leads to the establishment of different vertically separated phytoplankton communities. In Hunnebunnen, a total of 78 phytoplankton species was found—a very large number as compared to the benthonic species present. Phytoplankton forms, with their shorter life spans and generation times, can obviously adjust more easily to changing salinity regimes by parallel changes in population succession.

#### *Brackish-water submergence*

Since sea water has a higher density than brackish or fresh water, all habitats containing insufficiently mixed sea and freshwater components are characterized by more or less pronounced vertical salinity stratifications, with lower salinities at the surface and higher ones near the bottom. As all marine plants require certain minimum salinities they tend to follow the deep salt-water layers when entering coastal waters. This 'brackish-water submergence' was first described by REMANE (1955), who also pointed out that this phenomenon is more pronounced in

animals, since they do not directly depend on light, than in plants. Nevertheless, many examples have come to the reviewer's attention which illustrate brackish-water submergence also in algal species of coastal waters. A striking example is *Corallina officinalis* which grows in the upper littoral under marine conditions, but between 6 and 9 m depth in the innermost parts of the Hardanger Fjord (JORDE and KLAVESTAD, 1963). This alga penetrates also into the western parts of the Baltic Sea, becoming increasingly restricted to depths of 5 to 12 m.

Algae which follow saltier waters in greater depths are -due to decreasing amounts of light—in a conflict situation, and it may be expected that, in greater depths, only dwarf forms can be found. An example, not yet published, which supports this view has been reported to the author by Professor T. LEVRING. Under marine conditions near Bergen (Norway), the red alga *Callophyllis laciniata* grows near the water surface and reaches a normal thallus height; in the waters of the Gullmar Fjord near Kristineberg (salinity at surface: 25‰; at 25 m depth: 30‰), it is restricted to depths below 25 m and occurs only in the dwarf form (Fig. 4-62).



Fig. 4-62: *Callophyllis laciniata*. Normal habitus, Bergen (Norway) near water surface (36‰S); lower right: dwarf form, Kristineberg, 25 m water depth (salinity 0 m: 25‰, 30 m: 30‰). (Original.)

Since the quantity of light penetrating the water is drastically reduced in the innermost parts of the fjords ('fjord effect'), the brackish-water submergence is a phenomenon of limited ecological importance in the fjord ecosystem.

*Plant distributions in subtropical lagoons*

In 1964, CONOVER investigated the salinity requirements of 74 species of marine vascular plants and algae in some lagoons of Texas (USA). He found 47 stenohaline, 9 euryhaline, and 18 intermediate species. CONOVER classified the species studied according to their distributional salinity ranges (Table 4-40) and their lower and

Table 4-40

Distributional salinity ranges of marine plant species in Texas lagoons, USA (After CONOVER, 1964; modified)

Salinity range	Number of species	Salinity range	Number of species
smaller than 20‰	23	larger than 40‰	15
smaller than 10‰	13	larger than 50‰	4
smaller than 5‰	5	larger than 60‰	4

upper distributional salinity limits (Table 4-41). The numbers listed are higher in sub- than in supra-oceanic salinities, indicating that immigration of marine plants into waters with reduced salinities is easier than into waters with supra-oceanic salinities. At the same time, it is a well-known fact that water bodies with sub-oceanic salinities are more common than those with supra-oceanic salinities.

The main part of the Texas lagoon system under consideration is the hypersaline Laguna Madre.

'The plant life of the Laguna is highly seasonal, dying down during the high summer temperatures in August and September, and remaining dormant until spring. The macroscopic algae begin to appear in February and the grasses start to grow in March' (HEDEPETH, 1967).

In the northern part of the system (Baffin Bay) the salinity ranges from 50‰ to 75‰. No benthic algae or vascular plants have been recorded from that area, but 33 diatom species exist under these conditions.

*Plant distributions in hypersaline rock pools*

Rock pools with supra-oceanic salinities often occur in tropical and subtropical regions, but also in the Mediterranean Sea, due to high evaporation rates and low precipitation. The high, and frequently fluctuating, salinities as well as high temperatures (up to 40°C or more) create difficult conditions for unicellular algae. BOURRELLY (1958) studied the unicellular algae of 10 rock pools (Dinard, France) with salinities fluctuating between 25‰ and 65‰, and listed the number of species found according to their belonging to higher taxa (Table 4-42). The most abundant species recorded was *Brachiomonas submarina*.

Table 4-41

Benthic marine plants of Texas lagoons, USA. Lower and upper distributional salinity limits and habitat salinity allowing maximum growth rates (After CONOVER, 1964; modified)

Species	Lower salinity limit (‰)	Salinity allowing maximum growth (‰)	Upper salinity limit (‰)
<i>Cymodocea manatorum</i>	3	36	63
<i>Diplanthera wrightii</i>	28	—	36
<i>Halophila engelmannii</i>	27	—	36
<i>Ruppia maritima</i>	12	32	41
<i>Thalassia testudinum</i>	3	23	51
<i>Ulva lactuca</i> var. <i>latissima</i>	18	23	28
<i>Ulva lactuca</i> var. <i>rigida</i>	30	—	38
<i>Ulva fasciata</i>	29	34	39
<i>Enteromorpha intestinalis</i>	18	30	—
<i>Enteromorpha plumosa</i>	27	—	33
<i>Enteromorpha prolifera</i>	7	23	29
<i>Enteromorpha flexuosa</i>	28	36	40
<i>Enteromorpha clathrata</i>	20	32	—
<i>Chaetomorpha brachygonia</i>	29	—	33
<i>Cladophora fascicularis</i>	28	33	40
<i>Cladophora refracta</i>	33	38	43
<i>Cladophoropsis macromeres</i>	22	33	42
<i>Cladophora luteola</i>	22	—	33
<i>Cladophoropsis membranacea</i>	31	34	40
<i>Rhizoclonium riparium</i>	26	31	33
<i>Acetabularia crenulata</i>	19	40	80
<i>Batophora oerstedii</i>	20	41	80
<i>Bryopsis hypnoides</i>	30	35	40
<i>Penicillus capitatus</i>	20	38	48
<i>Caulerpa crassifolia</i>	28	32	37
<i>Ectocarpus confervoides</i>	30	—	34
<i>Ectocarpus duchassaingianus</i>	27	32	36
<i>Ectocarpus siliculosus</i>	32	—	36
<i>Giffordia mitchellae</i>	28	—	33
<i>Sphacelaria furcigera</i>	28	32	38
<i>Pylaiella antillarum</i>	30	—	36
<i>Phycocoelis floridana</i> (?)	27	—	33
<i>Eudesme zosterae</i> (?)	27	—	35
<i>Dictyota dichotoma</i>	30	—	36
<i>Dictyota indica</i>	31	—	35
<i>Padina rickersiae</i>	32	—	37
<i>Sargassum natans</i>	32	—	37
<i>Sargassum filipendula</i>	32	—	36
<i>Petalonia fascia</i>	29	33	37
<i>Stictyosiphon</i> spp.	3	30	35
<i>Erythrotrichia carnea</i>	29	—	38
<i>Bangia fuscopurpurea</i>	8	36	49
<i>Porphyra leucosticta</i>	27	38	47
<i>Amphiroa fragilissima</i>	26	31	36
<i>Corallina officinalis</i>	33	—	38

Table 4-41—Continued

Species	Lower salinity limit (‰)	Salinity allowing maximum growth (‰)	Upper salinity limit (‰)
<i>Fosliella le jolisii</i>	18	33	—
<i>Gelidium corneum</i>	13	—	37
<i>Gelidium crinale</i>	30	33	37
<i>Gracilaria verrucosa</i>	23	—	31
<i>Gracilaria cornea</i>	13	27	32
<i>Gracilaria crassissima</i>	27	—	33
<i>Gracilaria blodgettii</i>	24	—	33
<i>Gracilaria foliifera</i>	24	32	—
<i>Gracilaria foliifera</i> var. <i>angustissima</i>	7	—	43
<i>Grateloupia filicina</i>	31	—	37
<i>Grateloupia gibbesii</i>	21	31	38
<i>Agardhiella tenera</i>	32	—	36
<i>Hypnea cornuta</i>	28	—	34
<i>Hypnea musciformis</i>	28	—	33
<i>Acanthophora spicifera</i>	27	—	33
<i>Rhodymenia pseudopalmata</i>	29	—	36
<i>Chondria sedifolia</i>	24	—	32
<i>Chondria atropurpurea</i>	23	30	43
<i>Chondria tenuissima</i>	22	30	34
<i>Digenea simplex</i>	18	27	32
<i>Laurencia poitei</i>	12	33	47
<i>Polysiphonia</i> spp. ( <i>P. ferulacea</i> )	13	26	31
<i>Polysiphonia havanensis</i>	28	33	37
<i>Polysiphonia fracta</i> ( <i>P. echinata</i> )	12	—	32
<i>Polysiphonia macrocarpa</i>	28	—	34
<i>Centroceras clavulatum</i>	27	33	37
<i>Spyridia aculeata</i>	27	32	36
<i>Bryocladia cuspidata</i>	28	34	36
<i>Lyngbya confervoides</i>	2	52	200

Table 4-42

Number of unicellular algae found in 10 rock pools (Dinard, English Channel) (After BOURRELLY, 1958; modified)

Taxonomic group	Number of species found	Taxonomic group	Number of species found
Cyanophyta	1	Xanthophyta	1
Flagellata	2	Euglenophyta	1
Craspedomonada	1	Dinoflagellata	1
Cryptophyta	2	Chlorococcales	1
Chrysophyta	2		

A completely different type of algal vegetation has been described by SCHILLER (1956) as existing in a rock pool of the Los Aves Islands (Caribbean Sea) with salinities from 40‰ to 50‰. These pools were coloured deep red due to an enormous production of *Haematodinium gessneri*; in addition to this dinoflagellate, only blue-green algae were found in enormous quantities (13 species, 4 genera and 1 family). This prevalence of Cyanophyta is certainly related to the extremely high temperature.

#### *Plant distributions in Lago Maracaibo*

This large land-locked water body in the northwest of Venezuela was first investigated by GESSNER (1956a). A narrow channel connects the shallow 'lake' (maximum depth 34 m) with the Gulf of Venezuela, a part of the Caribbean Sea. The surface salinity distribution is shown in Fig. 4-63; it reveals that Lago

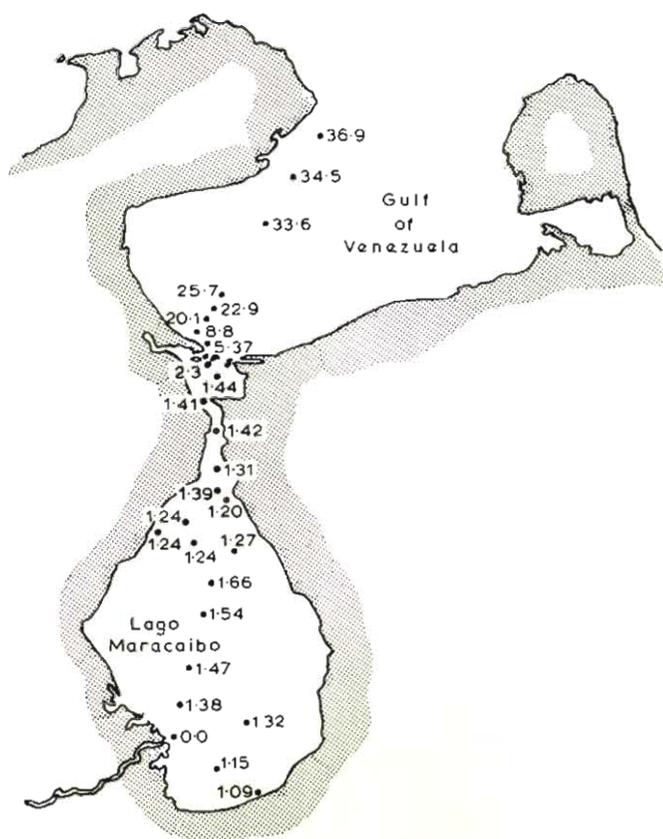


Fig. 4-63: Lago Maracaibo and Gulf of Venezuela; surface salinity distribution. (After GESSNER, 1956a; modified.)

Maracaibo contains extremely oligohalinic brackish water. The salinity regime greatly influences plant life in the 'lake'. Due to the absence of rocky shores, the only multicellular benthonic algae genera found in the inner part of Lago Maracaibo are *Enteromorpha* and *Bostrychia*.

The phytoplankton seems to represent a real freshwater community, in which blue-green algae play the most important role. The planktonic green algae present underline the limnic character of the ecosystem (Table 4-43). Even representatives of three species of desmids (*Staurastrum manfeldtii*, *Cosmarium phaseolus* var. *minutus* and *C. abbreviatum* var. *minor*) have been found.

Table 4-43

Planktonic green algae of Lago Maracaibo, Venezuela  
(After GESSNER, 1956a)

<i>Eudorina elegans</i>	<i>Dictyosphaerium pulchellum</i>
<i>Scenedesmus quadricauda</i>	<i>Coelastrum reticulatum</i>
<i>S. dimorphus</i>	<i>C. microsporum</i>
<i>S. ecornis</i>	<i>Pediastrum clathratum</i>
<i>Tetraedron caudatum</i>	<i>P. duplex</i> var. <i>reticulatum</i>
<i>T. muticum</i> var. <i>punctulatum</i>	<i>P. duplex</i> var. <i>rotundatum</i>
<i>T. limneticum</i>	<i>P. simplex</i>
<i>Ankistrodesmus falcatus</i>	<i>P. tetras</i>

Nevertheless, the distribution of diatom populations shows that the salinity influence should not be underestimated. HUSTEDT (1956) published a detailed description of 129 diatom species found in samples collected by GESSNER (1956a); among these, 27 species were new to science, 60 halophytes, and 42 oligohalobionts or indifferent. A list of the most abundant halophilic diatom species is presented in Table 4-44.

Table 4-44

The most abundant halophilic diatom species of Lago  
Maracaibo, Venezuela (After HUSTEDT, 1956)

<i>Achnanthes curvirostrum</i>	<i>Terpsinoe americana</i>
<i>Amphora gigantea</i>	<i>Thalassiothrix frauenfeldii</i>
<i>A. turgida</i>	<i>Chaetoceros similoides</i>
<i>Amphiprora alata</i>	<i>Actinocyclus oceanicus</i>
<i>Cocconeis pensacolae</i>	<i>Biddulphia regia</i>
<i>Mastogloia pumila</i>	<i>Rhizosolenia hebetata</i>
<i>Navicula arenicola</i>	<i>Thalassiosira gessneri</i>
<i>N. maculata</i>	<i>Coccinodiscus excentricus</i>
<i>Nitzschia filiformis</i>	<i>C. perforatus</i>
<i>Synedra tabulata</i>	<i>C. oculus iridis</i>

Most of the blue-green and green algae found in the phytoplankton of Lago Maracaibo apparently cannot distinguish between fresh water and brackish water of very low salinity. Such discrimination can only be made by diatoms which are, among the plants, the best salinity indicators. Of the diatom species of Lago Maracaibo, 77 are distributed world wide; only 18 species are distributionally restricted to tropic and subtropic areas (it is obvious that nothing can be said yet about the geographic distribution of the newly described species).

*The halobic system of diatoms ('Halobiensystem')*

Due to the world-wide distribution of most of the known diatom species, a general system can be presented which illustrates distributional tendencies of diatoms in regard to different habitat salinities. In 1927, KOLBE began his investigations on diatom distributions in a salty inland water system near Berlin (Germany). He attempted to distinguish different areas on the basis of diatom occurrence and salinity regime. KOLBE's system was revised by BUDE (1931, 1933) and later adapted by HUSTEDT (1953, 1957) to cover also marine conditions (Table 4-45).

Table 4-45

Halobic system of diatoms, based on species distributions in waters of different salinity (After HUSTEDT, 1953, 1957; modified)

## (1) Polyhalobic diatoms

30‰S or higher (euryhaline representatives may also tolerate salinities somewhat below 30‰)

## (2) Mesohalobic diatoms

(a) euryhaline mesohalobics—about 0.2‰ to 30‰S

(b)  $\alpha$  mesohalobics—species inhabiting brackish waters of higher salinities

(c)  $\beta$  mesohalobics—species inhabiting brackish waters of lower salinities

## (3) Oligohalobic diatoms

(a) halophilic diatoms

(b) indifferent diatoms

## (4) Halophobic (haloxene) diatoms

Polyhalobics and mesohalobics comprise the halobionts proper, the true salt-water living diatoms; oligohalobics and haloxenes comprise all species which are conventionally called freshwater diatoms. The halophile oligohalobics interconnect the two groups. Not all the euryhaline mesohalobics occur over the whole Cl spectrum.

There are three major differences between the new classification after HUSTEDT (1953, 1957) and that proposed earlier by BUDE (1931, 1933). Firstly, the polyhalobionts no longer comprise forms which have salinity requirements exceeding oceanic salinities; in fact, as far as is known, such forms do not exist. The species listed by BUDE also grow in lower Cl concentrations. Secondly, HUSTEDT leaves the question of the limit between  $\alpha$ - and  $\beta$ -mesohalobics open. The mesohalobium was first subdivided by REDEKE (1933) into an  $\alpha$  and  $\beta$  region, and the borderline set at about 10‰S. A similar borderline (about 8‰S) was drawn by VÄLIKANGAS (1933) who studied the Baltic Sea. VÄLIKANGAS also introduces an  $\alpha$ -meio- or  $\beta$ -mesohaline zone (2‰ to 8‰S) and a pleio- or  $\alpha$ -mesohaline zone (8‰ to 16.5‰S). Consequently, salinities between 8‰ and 10‰ seem to represent a salinity barrier which many organisms have in common (see also Chapter 4-3). However, the ecological importance of such distributional barriers should not be overestimated, as long as we ignore their physiological basis. Thirdly, according to HUSTEDT, halophilic species are those which occur in fresh water but grow in somewhat higher Cl levels, while the indifferent species are independent of variations in Cl content (within the characteristic salinity range). To the group of oligohalobic diatoms belong: *Cyclotella meneghiniana*, *Caloneis amphisbaena*, *Gomphonema*

*parvulum*, *Navicula gregaria*, *Thalassiosira fluviatilis*; to the  $\beta$ -mesohalobic diatoms: *Amphora commutata*, *Amphiprora paludosa*, *Achnanthes brevipes*, *Caloneis formosa*, *Nitzschia apiculata*; to the  $\alpha$ -mesohalobic diatoms: *Amphipleura rutilans*, *Melosira nummuloides*, *Navicula pygmaea*, *Nitzschia closterium*. As examples of a euhalobic form, BUDDE (1933) names *Nitzschia frustulum*, of a polyhaline form *Gomphonema exiguum*, *Navicula longirostris* and *Nitzschia closterium*.

#### Importance of desiccation for the distribution of intertidal plants

The pronounced vertical distribution patterns of the littoral vegetation have attracted the attention of marine ecologists since the very beginning of biological research. From LAMOUROUX (1824) until recent times, the fluctuations in tidal water levels have been held responsible as the primary factor influencing the vertical distribution of intertidal plants (e.g. BERTHOLD, 1882; GRAN, 1893; BÖRGESEN, 1908; BAKER, 1909, 1910; JOHNSON and YORK, 1915; MUENSCHER, 1917; JOHNSON and SKUTCH, 1928; COLMAN, 1933; ISAAC, 1933, 1935; GRUBB, 1936; DOTY, 1946; EVANS, 1947; BARKMANN, 1950; ZANEVELD, 1969). In fact, there can be hardly any doubt about the dominant role of water level fluctuations since they modify, during emersion, the intensity patterns of important environmental factors, such as temperature, light and osmotic climate to a significant, if not extreme, degree. The vertical zonation of littoral plants depends on their ability to survive such environmental fluctuations.

In general, the most important vertical distribution levels can be characterized by different lengths of emersion periods. Figs 4-64 and 4-65 document this fact

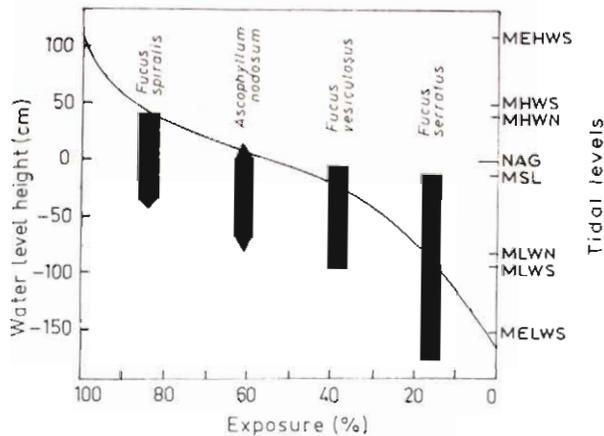


Fig. 4-64: Vertical distribution of some Fucaceae near Den Helder (The Netherlands) in relation to tidal levels (height in cm above or below New Amsterdam Water Gauge, NAG). MEHWS mean extreme high water—spring tide, MHWS mean high water—spring tide, MHWN mean high water—neap tide, MSL mean sea level, MLWN mean low water—neap tide, MLWS mean low water—spring tide, MELWS mean extreme low water—spring tide. The curve shows the percentage exposure at different water level heights. (After ZANEVELD, 1937; modified.)

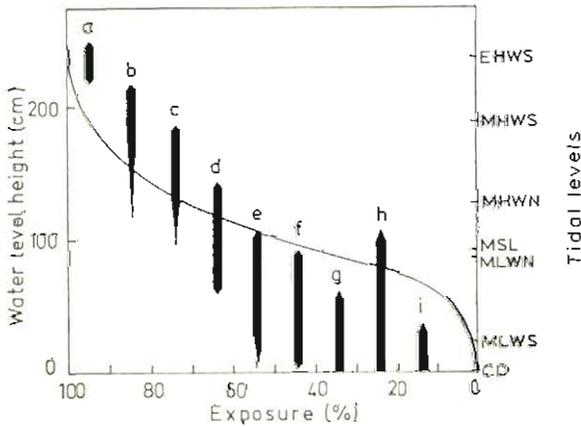


Fig. 4-65: Vertical distribution of some littoral algal associations at Peyeril Point (Dorset, England) in relation to tidal levels. (a) Blue-green association, (b) *Porphyra* association, (c) *Fucus spiralis* association, (d) bare zone, (e) *Ulva* association, (f) *Laurencia-Corallina* association, (g) *Himantalia* association, (h) *Fucus serratus* association, (i) *Laminaria* association. Height in m above chart datum (CD). For abbreviations of sea levels consult Fig. 4-64. The curve shows the average percentage exposure (based on four fortnights' tidal fluctuations) at different heights above CD. (After GRUBB, 1936; modified.)

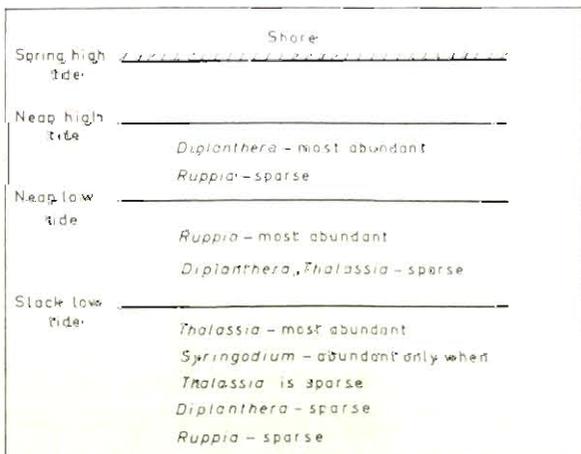


Fig. 4-66: Schematic presentation of sea-grass zonation in the shallow water of Tampa Bay (Florida, USA) related to tidal levels. (After PHILLIPS, 1960; modified.)

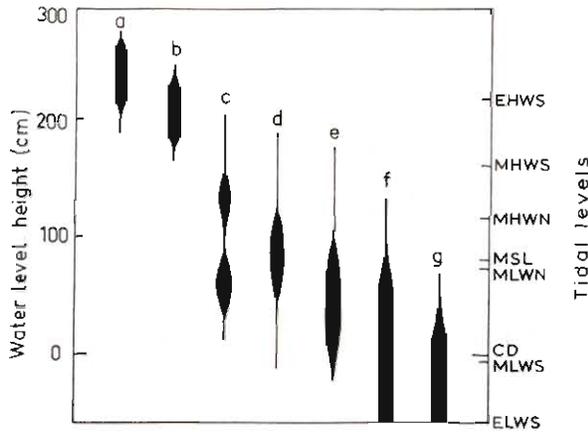


Fig. 4-67: Vertical distribution of some diatom communities at wave-exposed Peveril Point (Dorset, England) in relation to tidal levels. (a) *Achnanthes*—blue-green algae, (b) *Amphiptera rutilans*, (c) *Fragilaria*—*Melosira*, (d) *Schizonema ramosissima*, (e) *Schizonema grevillei*, (f) *Grammatophora*—*Cladophora*, (g) *Rhabdonema*—*Licmophora*. Height in m above and below chart datum (CD). For abbreviations of sea levels consult Fig. 4-64. (After ALLEEM, 1950; modified.)

for marine benthonic algae. These two examples of vertical distributions of marine benthonic algae related to emersion are paralleled by observations on phanerogams (Fig. 4-66), diatoms (Fig. 4-67) and blue-green algae (e.g. ERCEGOVIĆ, 1932).

First attempts to analyze such relationships on the basis of experimental evidence have been undertaken by MUENSCHER (1917). Near Friday Harbour (Washington, USA), he removed algae from different water depths and spread them on the beach for periods of 1 to 96 hrs. The experiments were carried out in June and July on sunny days. At the end of the emersion period the specimens were returned to the sea and their ability to survive tested over a period of up to 7 days. The death of the algae was determined by their changes in colours. In Table 4-46 the species tested are arranged in the order of their ability to withstand emersion. This order corresponds well to the sequential vertical distribution on the habitat shoreline. MUENSCHER points out that the varying, uncontrolled environmental conditions during emersion limit the value of the information produced by his experiments. Nevertheless, he assumes that it is primarily the degree of dehydration experienced during emersion which determines the vertical distribution in the intertidal habitat.

Among the environmental factors which undergo considerable changes during emersion, it is particularly the desiccation factor which has been held responsible for controlling intertidal plant distributions. This is hardly surprising in view of the morphological organization of marine plants; in contrast to their predominantly homeohydric terrestrial counterparts, marine plants are, as typical representatives of a poikilohydric organization, not able to control reductions in water loss without modifications in gas exchange. In order to survive emersion periods, two main

Table 4-46

Ability to withstand emersion in marine algae from different water depths. Friday Harbor, Washington, USA (After MUENSCHER, 1917; modified)

Species	Average emersion periods (hrs)
<i>Fucus evanescens</i>	48
<i>Gloiopeltis furcata</i>	48
<i>Gigartina mamillosa</i>	24-48
<i>Porphyra perforata</i>	24
<i>Halosaccion glandiforme</i>	2-6
<i>Colpomenia sinuosa</i>	2-6
<i>Rhodomela larix</i>	2-6
<i>Iridaea laminarioides</i>	4
<i>Ulva lactuca</i>	2-3
<i>Nereocystis luetkeana</i>	1-2
<i>Sarcophyllis californica</i>	-1
<i>Desmarestia aculeata</i>	-1
<i>Alaria valida</i>	-1
<i>(Colpomenia sinuosa</i> on <i>Rhodomela larix</i> in tide pools; <i>Desmarestia aculeata</i> on <i>Nereocystis luetkeana</i> )	

avenues have been followed: (i) Binding of a maximum initial water reserve and retardation of water loss via thickening of cell walls, slime production, etc. with the result that photosynthesis may continue at least for some time. Since these measures are insufficient, lack of water may fast become a limiting factor for proper continuation of life processes during emersion. (ii) Increased capacity of protoplasm to maintain life processes under limited saturation or to persist periods in a dehydrated, and at the same time inactivated, physiological state. Close relationships between these two avenues (i.e. drought avoidance and drought resistance) and vertical distributions of different intertidal plants do indeed exist. They have been referred to in various sections of the present review and suggest a direct effect of desiccation on distributions of coastal plants.

Unfortunately, experimental-ecological evidence for such relationships is still scarce. For detailed ecological evaluations of the importance of desiccation for plant distributions it is insufficient to correlate more or less theoretical emersion periods with organismic responses obtained in model experiments. We must know more about the whole desiccation complex *in situ* (e.g. microclimate conditions and the resulting water losses) and the long-term effects of such conditions, including concomitant effects of simultaneously fluctuating cofactors, on all life-cycle stages of the plant under consideration.

An impressive example of the importance of desiccation conditions for plant distributions has been provided by BØRGESEN (1908). On the wave-exposed coasts of the Faroes, the large surf waves break and their water droplets continually moisten the littoral rocks several metres above the water level. This permanent water supply allows some of the local algae to occupy habitats (spray zone) far higher above the water line than in more wave-protected areas (Fig. 4-68). Just

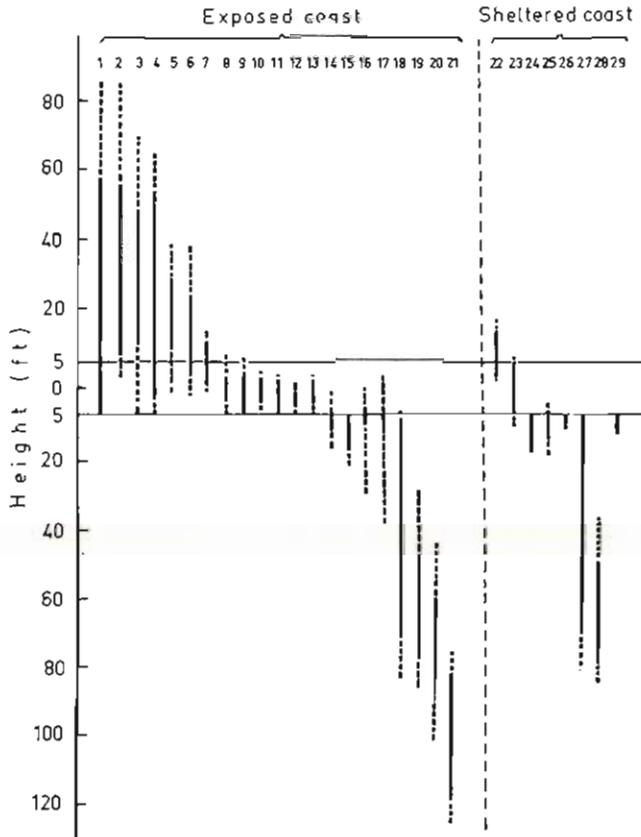


Fig. 4-68: Vertical distribution of algal formations and associations on the coast of the Faeroes.

Exposed coast: 1 *Hildenbrandia* formation with lichens, 2 Chlorophyceae formation (*Prasiola crassa*, *Rhizoclonium*, *Enteromorpha* and *Prasiola stipitata* association), 3 *Porphyra* association, 4 *Rhodochorton* association, 5 *Bangia-Urospora* association, 6 Fucaceae formation (*Fucus spiralis*, *Fucus inflatus* association), 7 *Callithamnion* association, 8 *Rhodomyenia* association, 9 Littoral *Corallina* formation, 10 *Monostroma grevillei* association, 11 *Acrosiphonia-Polysiphonia* association, 12 *Gigartina* association, 13 *Himantalia* association, 14 *Phymatolithon* association, 15 Sublittoral *Corallina* formation, 16 *Laminaria digitata* association, 17 *Alaria* association, 18 *Laminaria hyperborea* association, 19 *Desmarestia* association, 20 *Lithoderma* association, 21 Sublittoral Florideae formation;

Sheltered coast: 22 Chlorophyceae formation (*Enteromorpha* association), 23 Fucaceae formation (*Pelvetia* association, *Fucus vesiculosus-Aecophyllum* association, *Fucus inflatus* association), 24 *Stictyosiphon* association, 25 *Monostroma-Enteromorpha* association, 26 *Halidryx* association, 27 *Laminaria* formation (*Laminaria faeroensis* association, *Laminaria hyperborea* association), 28 *Desmarestia* association, 29 (*Zostera* association).

Dotted parts of vertical lines indicate level of reduced abundance. Height in ft above and below mean sea level. The zone between +5 and -5 ft marks has been enlarged in order to make it more distinct. (After BÖRGESEN, 1908; modified.)

as the degree of wave exposure modifies the desiccation conditions, and consequently the vertical distribution of algae, in this case, climatic aspects may additionally modify the total resulting ecological situation. OLTMANN (1923) has suggested that these algae are able to maintain their high levels on wave-exposed coasts not least because of the high relative humidity and the overcast skies characteristic of such areas.

The importance of microclimate for desiccation conditions has been stressed by various authors (e.g. JOHNSON and YORK, 1915; CASTENHOLZ, 1963). Reduced sun radiation in north-exposed habitats or wind protection in narrow rock crevices lessen evaporation rates and, consequently, allow the plants to inhabit higher coastal levels. Unfortunately, such microclimatic differences have not yet been correlated with water loss measurements *in situ* and the distribution of algae. The few pertinent values available in literature represent mostly occasional recordings, (e.g. ISAAC, 1933, 1935; STOCKER and HOLDHEIDE, 1937; PRIOU, 1963; CHAPMAN, 1966; JENIK and LAWSON, 1967; SCHRAMM, 1968). However, the recordings indicate that water losses during average emersion periods rarely attain the critical limits and hardly ever the lethal limits of desiccation tolerances of adult plants, as determined in laboratory experiments. Especially in the inhabitants of the upper vertical distribution levels, desiccation tolerance is, relative to environmental habitat conditions, surprisingly high; it 'out-dimensions' the stress to be anticipated (RIED, 1969). Thus *Pelvetia canaliculata* from the North Sea suffers a 50% irreversible inhibition of photosynthesis (Fig. 4-5) only after a desiccation period of 4 weeks (40% relative humidity, 14°C); for *Pelvetia canaliculata* on the French coast near St. Malo, PRIOU (1963) has recorded an average daily emersion period of only 9 hrs (during spring tides several days; compare the calculations by SCHRAMM, 1968, on emersion conditions for *Fucus vesiculosus* from the Baltic Sea). The data discussed above suggest that desiccation influences the vertical distribution of these plants only during occasional periods of extreme emersion stress, and primarily via sublethal damages leading to impaired energy balances.

Another, most important aspect is related to the possibility that the degree of desiccation tolerance may vary in different life-cycle stages of one and the same plant (see also section *Tolerance*). CHAPMAN (1966) assumes that, in many littoral algae, the sensitivity to drought during germination and of the youth stages determines the distributional limits of the species (see also BAKER, 1910). In practice, however, it is just the young settling stage which—due to favourable microclimatic conditions (e.g. in the undergrowth protected by the higher adult vegetation or in crevices, folds, etc.)—survives even extreme drought periods. According to RIED (1969), distribution-limiting desiccation stress may also affect later stages and adult individuals; this is witnessed by the fact that zonation borders rarely reveal dead thalli, but underdeveloped and sterile individuals.

Little is known about the importance of desiccation for horizontal distributions and seasonal successions. Therefore, we must restrict ourselves here to discussing a few general aspects. The hypothesis, based on observations by KNIEP (1914) and HARDER (1915), according to which the rich algae flora of colder climates is a consequence of the adjustments of marine algae to live under conditions of weak light and low temperatures, has already been questioned by MONTFORT (1929, 1930, 1935) and STOCKER and HOLDHEIDE (1937). Even if, as suggested by STOCKER and

HOLDHEIDE, the degree of mass development in colder seas has been overestimated, the more abundant algal life in cold-temperature climates as compared to tropical ones is obvious, at least in regard to littoral plants. The attempt to offer an explanation for this phenomenon brings up the ecologically interesting question, to what extent may desiccation be considered as secondary aspect of the large-scale geographical temperature gradient (GESSNER, 1955).

JONNSON (1912) as well as OLTMANN (1923) have mentioned air humidity and cloud covering as factors which may affect dehydration of emersed littoral algae. STOCKER and HOLDHEIDE (1937) conclude from their results that colder climatic regions with predominantly cloudy skies, in which light intensities still allow high rates of photosynthesis and which retard dehydration are especially favourable for maximum gain of body own substances. CONWAY (1954) attributes her observation that, on the English coasts, the intertidal algae tend to occupy higher habitats towards the North, to wave action as well as to the increasingly frequent fog and cloudiness (see also BURROWS and co-authors, 1954). However, detailed evaluations require more information about microclimate and water loss under *in situ* conditions. The same is true for proper assessment of the importance of desiccation for the distributional periodicities of littoral plants (e.g. ALEEM, 1950).

Seasonal successions due to desiccation could have various causes: (i) changes in emersion conditions, e.g., annual variations in water level height as in the Baltic Sea; (ii) changes in desiccation conditions brought about by climatic influences, e.g., increased desiccation stress during summer; (iii) changes in desiccation tolerance caused by environmental (exogenous) fluctuations or by development-dependent (endogenous) variations. To the reviewer's knowledge such relationships have not yet been documented experimentally.

### (3) Structural Responses

In the preceding sections of this chapter, many examples have been presented which illustrate that salinity variations influence nearly all functional responses of marine plants. It is obvious that many of the functional responses must have structural consequences. The fact is that salinity changes may bring about a multitude of structural responses. A few examples must suffice to document this statement.

#### (a) Size

Reduction in body size is a rather general phenomenon in marine plants inhabiting waters with progressively decreasing salinities. Such a tendency towards dwarf forms parallels structural responses reported for marine animals (Chapter 4.3). One of the most instructive examples is the brown alga *Fucus vesiculosus* forma *subcostata* from the coasts of Finland (5‰-6‰S). Its reductions in size (Fig. 4-69) may be due to individual non-genetic adjustments, or to selection, or both.

In regard to desiccation, SCHILLER (1928) believes that the larger body size of *Fucus virsoides* from the northern Adriatic Sea, compared to that of the middle Adriatic Sea (about half the size), can be attributed to the regular rhythm of

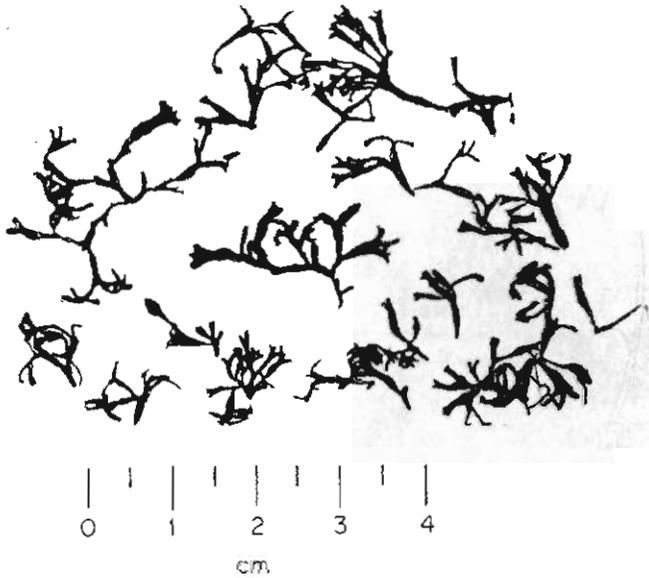


Fig. 4-69: *Fucus vesiculosus* forma *subecostata* from the coast of Finland. (Original.)

emersion (dehydration) and immersion (rehydration) in the north. However, in the Baltic Sea, permanently submersed *Fucus vesiculosus* ('deep-water form') are mostly larger and better developed than frequently emersed specimens growing in the littoral ('littoral form'). Similarly, CHAPMAN (1961, 1966) found in the emerging mangrove form of *Hormosira banksii* (maximum daily emersion periods 6 to 6.5 hrs) larger leaves than in the submersed deep form.

Of course, in all these reports, which are based exclusively on observations in the natural habitat, it cannot be excluded that, in addition to salinity and desiccation, other environmental factors may affect the size of the plants concerned. The same is true in regard to external and internal structures.

#### (b) External Structures

Many dwarf forms exhibit not only reductions in body size but also variations in body shape, indicating that salinity exerts differential effects on growth rates of different body parts. The red alga *Delesseria sanguinea* exhibits quite different structural features in individuals obtained from the North Sea (ca 33‰-35‰S) and the Baltic Sea (ca 16‰-22‰S; Fig. 4-70). It may be assumed that these differences are caused primarily by the different habitat salinities. No transplantation experiments have been carried out yet to put this assumption to a critical test.

In the diatom *Caloneis amphisbaena*, supranormal salinities cause increased longitudinal growth upward to the apical axis and smoothing of the tips which have a pointed shape in subnormal salinities (Fig. 4-71; HUSTEDT, 1925; KOLBE, 1927). It must be pointed out, however, that such cases of structural responses are rare among diatoms, otherwise these could hardly be used as salinity indicators (p. 809).

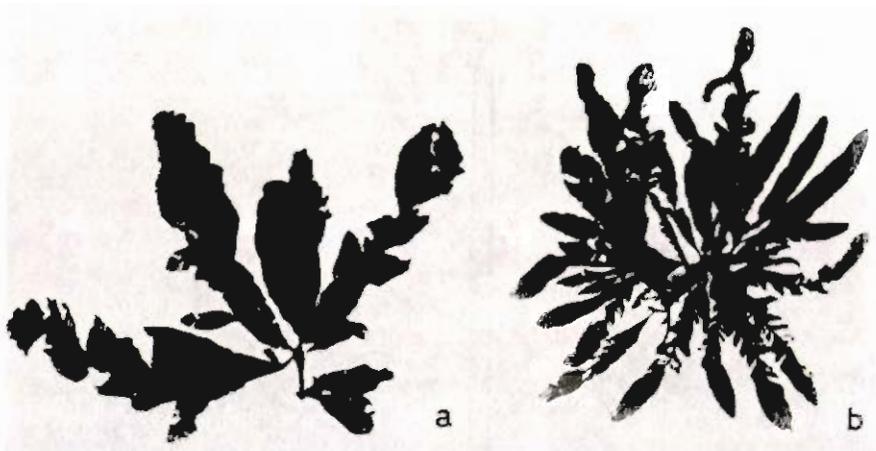


Fig. 4-70: *Delesseria sanguinea*. (a) North Sea form; (b) Western Baltic Sea form. (After NELLEN, 1966; modified.)

OLTMANN'S (1889) called attention to variations in external structures of *Pelvetia canaliculata* which may be related to desiccation. In specimens which live permanently submerged in tide pools, the thallus was not rolled up in the characteristic way; the branches were somewhat wider, and conceptacles were never observed. In freshwater plants which grow partly above the water surface, external structures frequently differ significantly in submerged and emerged body parts.

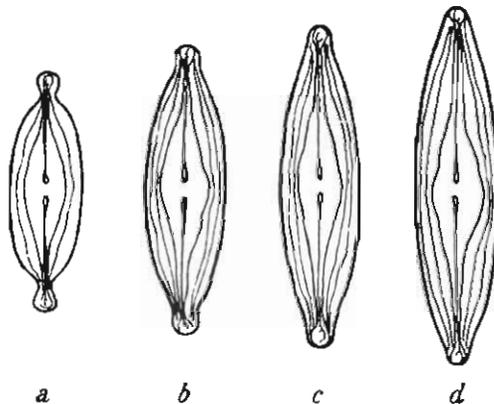


Fig. 4-71: *Caloneis amphibiaena*. Changes of diatom shell shape and size with increasing habitat salinity; (a) forma *typica* from fresh water; (b), (c) transition forms from habitats with 1300–1900 mgCl/l; (d) var. *aequata* from ca 9000 mg Cl/l. (After KOLBE, 1932.)

(c) *Internal Structures*

The green alga *Enteromorpha intestinalis* and *E. marginata* grow in the sea as well as in fresh water. However, the internal structures of individuals exposed for months to fresh water (tap water) differ entirely from those grown in sea water (Fig. 4-72). FELDMANN and FELDMANN (1941), who reported these interesting differences, stressed the need for studying these structural responses in more detail.

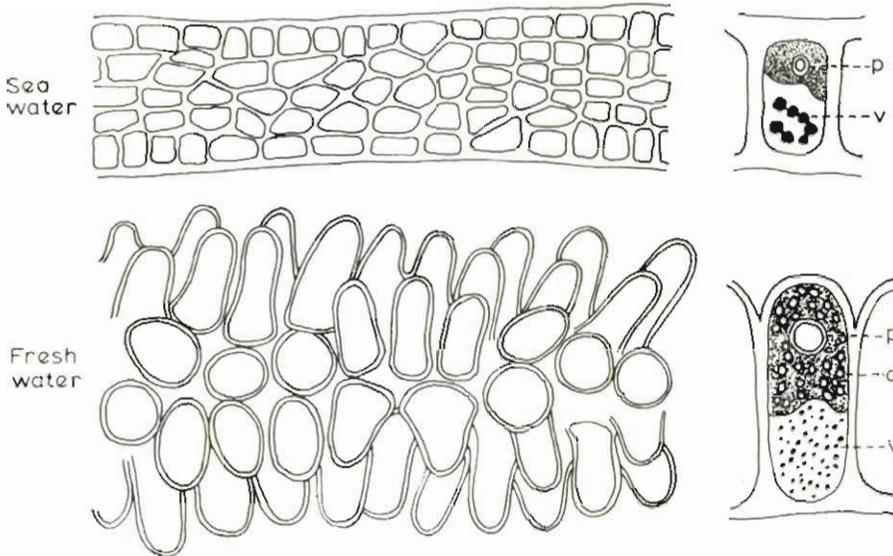


Fig. 4-72: *Enteromorpha marginata*. Variations in internal structures due to salinity. Left side: filaments in sea water and fresh water respectively ( $\times 960$ ). Right side: cells in sea water and fresh water respectively ( $\times 1920$ ); p: chloroplast, v: vacuoles, a: amyloids coloured with cresyl blue. (After FELDMANN and FELDMANN, 1941; modified.)

In his investigations concerned with the vertical zonation of *Fucaceae* and *Ascophyllum nodosum* along the Dutch coasts, ZANEVELD (1937) observed that the thickness of the cell walls increases with the habitat height of the alga species examined (Table 4-47). ZANEVELD found, furthermore, that the saturation water content reaches maximum values in the algae occupying the highest habitats. The ecological importance of these differences is interpreted by ZANEVELD as being related to (i) retardation of water loss and (ii) the larger amounts of body water available to the higher growing forms at the beginning of the emersion period. He could demonstrate, in fact, that the percentage water loss is smallest in algae inhabiting the highest shore levels. Similar results have been obtained by PÉRIOU (1963) on *Fucaceae* of the French Atlantic coast: even under different conditions of desiccation (temperature, relative humidity, air movement), the highest growing algae dehydrated slowest. In contrast, PRINGSHEIM (1923) found no clear relations between dehydration rate and habitat height of *Fucus spiralis*, *Fucus vesiculosus* and *Fucus serratus*. These problems have recently been re-investigated by KRISTENSEN (1968) on large amounts of test material. In the three *Fucus*

Table 4-47

Variations in cell wall thickness as a function of habitat height in intertidal algae. The four species listed occupy increasingly higher shore habitats

(After ZANEVELD, 1937; modified)

Species	Thickness of cell wall ( $\mu$ )
<i>Fucus serratus</i>	0.42 $\pm$ 0.03
<i>Fucus vesiculosus</i>	0.69 $\pm$ 0.09
<i>Ascophyllum nodosum</i>	1.02 $\pm$ 0.03
<i>Fucus spiralis</i>	1.47 $\pm$ 0.15

species mentioned, *Pelvetia canaliculata* and *Ascophyllum nodosum*, KRISTENSEN could neither establish unequivocal relationships between habitat height and body water content, nor a significant influence on the speed of water loss by differences in cell wall thickness. Furthermore, cell wall thickness of the various species could not always be correlated with habitat height. However, the degree of exposure to wave action appears to have a significant influence on cell wall thickness.

Other authors also have pointed to the considerable thickness of the cell walls of intertidal algae (BIEBL, 1938; POST, 1963). It would be of interest, therefore, to test to what extent cell wall thickness—in addition to water balance—may affect, via mechanical properties and water imbibition capacity, the resistance to desiccation. Small, thick-walled cells with a small vacuole appear to be particularly protected against detrimental protoplasmic deformations during desiccation (ILJIN, 1933, 1953; BIEBL, 1938). If the very drought-resistant representatives of *Porphyra* species are exposed to dehydration, the thick, extremely elastic membranes contract around the increasingly reduced cell content, with the result that the whole cell becomes smaller but otherwise appears completely normal. The secretion of slime in many marine algae may possibly affect the process of desiccation (increased capacity to hold water; retardation of water loss).

The relationships between osmotic stress and submicroscopical structure have only been studied in *Dunaliella salina* (TREZZI and co-authors, 1965). Uptake or loss of water do not affect the submicroscopical structure of the protoplasm; all cell contents undergo equal changes in water balance and reveal no significant morphological changes. However, water uptake leads to the formation of 'sacks' between the double lamellae of the nucleus membranes; upon water loss, the double lamellae move closely together again.

Further research is required before we are able to analyze the various environmentally induced structural responses of marine plants to salinity (including desiccation) in sufficient detail.

## 4. SALINITY

### 4.3 ANIMALS

#### 4.31 INVERTEBRATES

O. KINNE

##### (1) Introduction

The salinity of the open oceans is fairly constant and so is the ionic composition of ocean water. Hence the study of organismic responses to salinity is largely concerned with forms inhabiting coastal or inland waters characterized by salinities significantly below or above 35‰, or by considerable salinity fluctuations.

This subchapter concentrates on responses to salinity of whole intact invertebrates. Physiological mechanisms of regulation and adaptation, as well as biochemical aspects, will be dealt with in Volume II of this treatise.

Salinity may affect functional and structural responses of invertebrates through changes in (i) total osmoconcentration, (ii) relative proportions of solutes, (iii) coefficients of absorption and saturation of dissolved gases, (iv) density and viscosity; possibly, also through changes in surface tension, absorption of radiation, transmission of sound, and related parameters.

The concept of salinity has been coined by physical oceanographers. It is of limited use to the marine ecologist unless its biologically significant components are realized and separately assessed.

Salinity may exert indirect effects by modifying the species composition of an ecosystem and thus change the biotic background for the remaining forms. The many aspects of salinity as an ecological and physiological entity frequently make it difficult to assess the specific causes of the organismic responses observed.

As has been pointed out in Chapter 4.0, the average oceanic salinity of 35‰ may decrease to about 32‰ or increase to about 38‰ in certain surface areas of the oceans. In secondary seas, estuaries, bays, etc., exposed to intensive freshwater influxes, or much rain, salinities may fall to a few ‰ and even approach freshwater conditions. In the Red Sea, salinity of main water masses attains values up to 41‰; in the Laguna Madre of Texas (USA) and the Crimean Sivash (USSR), salinities of 50‰ to 80‰ are common and maximum values near 100‰S have been recorded; in the tropical Bahamas of the West Indies, shore ponds may have salinities of up to 155‰ (PEARSE and GUNTER, 1957). In the deep, hot brine areas of the Red Sea, salinities of from 250‰ to well above 300‰ (at maximum temperatures near 56° C) have been measured (BREWER and co-authors, 1969; DIETRICH and KRAUSE, 1969; EMERY and co-authors, 1969). The total range of salinities on earth extends from 0‰ to full saturation (about 360‰S, subject to ionic composition and temperature).

More than 95% of the water on earth is sea water. Most of the rest is fresh water, a small fraction brackish water (mixture of sea and fresh water), and a still smaller

one hypersaline or brine water. The major differences between these waters and their respective faunas and floras are evident; yet a detailed evaluation of such divergencies is difficult. Numerous attempts have been made to classify waters with different salinity conditions and their respective faunas on the basis of differences in (average) salinity (e.g. MÖBIUS and HEINCKE, 1883; JOHANSEN, 1918; REDEKE, 1922, 1933; SCHLIENZ, 1924; VÄLIKANGAS, 1926, 1933; GURNEY, 1928-1929; REMANE, 1934, 1940, 1959; EKMAN, 1935, 1953; HILTERMANN, 1949; CASPERS, 1959a, b). The proposed classifications have been reviewed, discussed or modified (DAY, 1951, 1964; HEDGPETH, 1951, 1957; ROTTGARDT, 1952; DAHL, 1956; SMITH, 1957, 1959; REMANE and SCHLIEFER, 1958; D'ANCONA, 1959; PETIT and SCHACHTER, 1959; SEGERSTRÅLE, 1959; SYMPOSIUM ON THE CLASSIFICATION OF BRACKISH WATERS, 1959; ZENKEVITCH, 1959; DEN HARTOG, 1960, 1961, 1964; CARRIKER, 1967; HUSMANN, 1967; ACKEFORS, 1969a; KHLEBOVICH, 1969; SCHACHTER, 1969; see also p. 959). Most classifications reflect local rather than general aspects and several have led to 'cumbersome and conflicting terminologies' (SMITH, 1959, p. 59). This is not surprising. Habitat or fauna classifications based on a single environmental factor can hold only in situations in which that factor represents the dominating ecological master factor for all, or at least the majority of, species present. Such situations appear to be indicative of extreme rather than normal conditions; usually species composition and dynamics of an ecosystem depend on several ecological master factors. Furthermore, the biological effects of a given master factor may depend more on occasionally attained extreme values and fluctuation patterns than on average values. Finally, one and the same salinity may cause different responses, depending on ionic composition and other simultaneously effective abiotic environmental factors (especially temperature, water movement, dissolved gases and substratum), as well as on biotic factors. Supranormal temperatures tend to accentuate salinity-dependent variations in organismic functions and structures, while subnormal temperatures tend to diminish them; optimum intensities of other concomitant environmental entities are often prerequisites for maximum salinity tolerances or maximum adjustments to salinity stress.

Unless otherwise specified, in this subchapter, water with salinities from 30‰ to 40‰ is referred to as sea water and water of less than 0.5‰S as fresh water. Natural water with reduced concentrations of dissolved constituents equivalent to salinities between 0.5‰ and 30‰ is called brackish water, natural water containing dissolved constituents in concentrations equivalent to salinities of 40‰ to 80‰ hypersaline water, and all higher concentrations, brine water (KINNE, 1964a). Sea-water and freshwater habitats have endemic classes but practically no species in common (KHLEBOVICH, 1969). Comparative studies of functional and structural responses to salinity variations of marine and freshwater organisms promise new insights into aspects of salinity tolerance, adaptation and regulation, and into the evolutionary origin of the freshwater fauna. Brackish waters are inhabited by species evolved from closely related marine or freshwater forms. The brackish-water fauna consists largely of secondary or derivative elements. There are no high-ranking endemic (primary) brackish-water taxa (ZENKEVITCH, 1963). A similar situation exists in hypersaline and brine waters. Hypersaline waters are colonized by extremely euryhaline marine and freshwater species. Brine waters

support only unusually salt-resistant forms such as the protozoan *Monas dunalii*, the rotatorian *Diaschiza* sp., the crustaceans *Cletocamptus* sp., *Tigriopus fulvus*, *Artemia salina*, and larvae of the aquatic insects *Ephydra macellaria*, *Chironomus halophilus* and *C. salinaricus*. These forms are, at least in part, derivatives of fresh-water species. The relative numbers of marine, brackish-water and freshwater animal species are illustrated diagrammatically in Fig. 4-73.

Organisms capable of existing under a wide variety of salinity conditions are euryhaline or euryhaline, those restricted to narrow salinity ranges stenohaline or stenohaline. These terms are relative in connotation; they refer to groups of organisms which obviously differ in their potential to tolerate different levels, or fluctuation intensities, of salinity. In general, invertebrates considered euryhaline tolerate salinity ranges of 10‰ to 30‰ or more, while those considered stenohaline tolerate salinity ranges of 10‰ or less. Important prerequisites for euryhalinity are high cellular osmotic tolerances and/or high capacities for osmoregulation; cellular osmotic tolerance is more widespread among euryhaline invertebrates and obviously the more important prerequisite since, under salinity stress, even the most potent osmoregulators cannot avoid variations in osmoconcentration of their body fluids. On the other hand, several invertebrates without capacities for osmoregulation can tolerate very low or high salinities and hence are euryhaline (e.g. the lamellibranch *Mytilus edulis*). Most stenohaline species live in the open oceans. Stenohaline forms confined to oceanic salinities are called orthostenohaline; those restricted to fresh water oligostenohaline (Table 4-74), and those restricted to supra-oceanic salinities polystenohaline. Truly polystenohaline species are rare and occupy hypersaline or brine waters. A few invertebrates can exist in fresh, brackish and sea water; examples of such holeuryhaline species are the turbellarians *Gyratrix hermaphroditus*, *Breslauilla relicta*, *Macrostomum appendiculatum*, the rotifers *Encentram marinum*, *Colurella colurus*, *C. adriatica*, *Notholca bipalium*, *N. striata*, *Proales reinhardti*, the oligochacte *Pachydrius (Lumbricillus) lineatus* and the crustaceans *Mysis oculata* (REMANE and SCHLIEPER, 1958) and *Eriocheir sinensis*. Some aquatic invertebrates are truly holeuryhaline only during certain periods of their lives; others migrate from the sea into fresh water, or vice versa, in connection with their reproductive activities, e.g. the crab *Eriocheir sinensis*. Such facultative holeuryhaline forms change their responses to salinity during their freshwater, brackish-water or sea-water phases. Holeuryhaline invertebrates are much fewer in number than euryhaline invertebrates, and these, in turn, are less numerous than stenohaline ones.

While establishment in habitats with pronounced salinity fluctuations, e.g. in estuaries, may be paralleled by evolutionary augmentation of osmotic tolerance and regulative capacities, it does not seem to promote evolutionary processes in general. In fact, extreme salinity fluctuations in the sense of environmental instability (not diversity) appear to act as brake rather than as motor of speciation and evolution. High genetic salinity tolerance and evolutionary conservatism often go hand in hand. The diversity of aquatic invertebrates and the number of species per genus or family often attain maximum values in the oceans; they decrease in the order fresh waters, brackish waters, hypersaline and brine waters.

In contrast to the uniform composition of oceanic water, ionic constituents of coastal waters, and of inland salt lakes or rivers, may vary significantly according

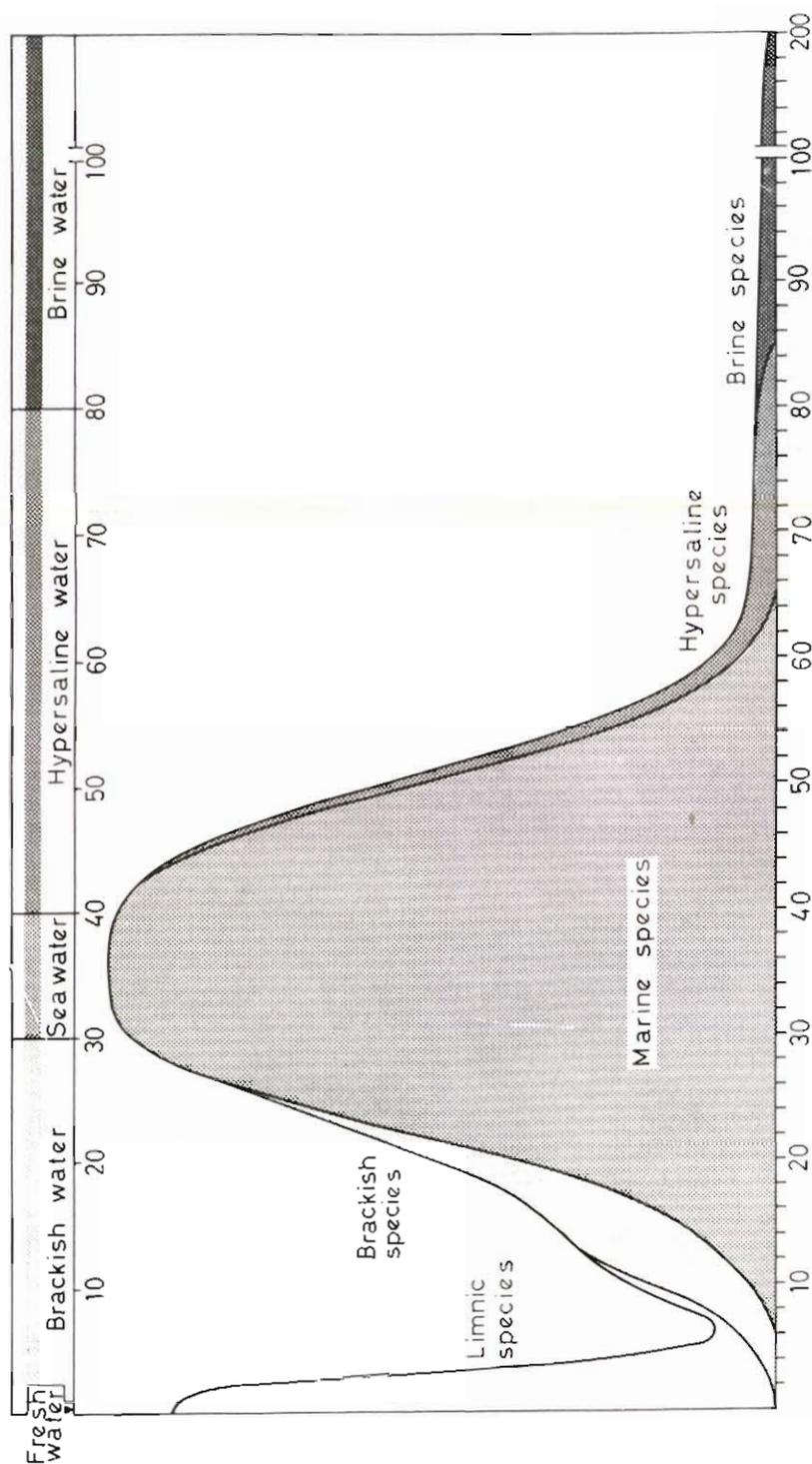


Fig. 4.73: Quantitative relations between aquatic invertebrate species occupying fresh, brackish, sea, hypersaline or brine waters. For each salinity (0‰-200‰), the relative number of species is indicated by the vertical extension of the respective areas. Rough estimations, based on REMANE (1934), HEDGPETH (1959) and own data. (Original.)

to the chemical properties of the sea bottom, lake or river bed and the introduction of substances by natural processes or man. Among the most important ions, sodium and chloride are more abundant in ocean water, while calcium and carbonate occur in relatively higher concentrations in freshwater lakes or rivers; for details consult CLARKE (1924), BALDWIN (1937), WITTIG (1940), SVERDRUP and co-authors (1942), LOBZA (1945), RANKAMA and SAHAMA (1950), RUBEY (1951), BARNES (1954, 1959), CARPELAN (1954), ALMAZOV and DENISOVA (1955), PEARSE and GUNTER (1957), ALMAZOV and co-authors (1959), VINETSKAYA (1959), ALMAZOV (1962), TSURIKOVA (1962), ZENKEVITCH (1963), TSURIKOVA and SHULGINA (1964), TSURIKOVA and TSURIKOV (1966), DEGENS and ROSS (1969). For information concerning the ionic composition and other properties of ocean water in the past, see WALTHER (1911), SCHUCHERT and DUNBAR (1937), RAYMOND (1939), CONWAY (1943, 1945), RUBEY (1951), PEARSE and GUNTER (1957), CRAIG (1969).

In the last two decades, reviews concerned with responses of marine and brackish-water invertebrates to salinity have been published by SCHLIEPER (1955, 1964, 1966), PEARSE and GUNTER (1957), ROBERTSON (1957a, 1960), KINNE (1958b, 1963a, b, 1964a, b, 1966, 1967a), MOORE (1958), REMANE and SCHLIEPER (1958), NICOL (1960), SHAW (1960b), PROSSER and BROWN (1961), LOCKWOOD (1962), POTTS and PARRY (1964) and THEEDE (1965b).

## (2) Functional Responses

### (a) Tolerance

In marine invertebrates, the degree of tolerance to salinity variations often varies during ontogeny. While developing eggs and newly hatched larvae of some invertebrates (and teleosts, Chapter 4.32) may tolerate extremely wide ranges of salinity, early ontogenetic stages of many invertebrates exhibit lesser tolerances to salinity than the respective later stages or adults. Thus gastrula, trochophora and young larva of the polychaete *Nereis diversicolor* die in salinities below 5‰ while older stages can tolerate such salinity reductions for long periods of time (BOGUCKI, 1953, 1954). Eggs of the shore crab *Carcinus maenas* develop normally only in salinities between 28‰ and 40‰, while adults tolerate salinities down to 4‰ for long periods (BROEKHUYSEN, 1936). Eggs of the amphipod *Gammarus duebeni* (from near Kiel, Germany) do not develop in salinities below 1‰, yet the adults tolerate pure fresh water (KINNE, 1953a). Eggs of the gastropod *Littorina littorea* need a minimum salinity of 20‰ while adults can live in much lower salinities (HAYES, 1927). Eggs of the gastropod *Purpura lapillus* are killed by low salinities tolerated by adult specimens (FISCHER-PIETTE, 1931). Gametes and larvae of the clam *Mytilus californianus* die in diluted sea water in which adults can survive 'indefinitely' (FOX, 1941). Zygotes of the ascidian *Ciona intestinalis* have narrower tolerance ranges of salinity than larvae or adults (DYBERN, 1967). Similar findings have been reported for *Ostrea madrasensis* (RANSON, 1948; RAO, 1951), several species of *Balanus* (BARNES, 1953) and the intertidal gastropods *Limapontia depressa*, *L. capitata*, *Ovatella myosotis* (SEELEMANN, 1968); see also GRESENS (1928).

Resting (dormant) life-cycle stages, such as spores, cysts or menonts of proto-

zoans, sponges, hydrozoans and other invertebrate groups are characterized by considerably higher salinity tolerances than active stages. Ecologically, such maximum tolerances within the total life span of a given organism are of great importance for assessing the chances of a population to survive temporary detrimental salinity conditions. Little, if any, detailed research has been conducted on salinity tolerances of dormant life-cycle stages.

Minimum (or reduced) salinity tolerances are frequently related to maximum (or elevated) metabolic rates and vice versa. This relationship can be found both interspecifically (active compared to sluggish species) and intraspecifically (life cycle stages with high metabolic activities compared to those with lower activities or resting stages). Less differentiated tissues tend to be more resistant than highly differentiated ones; thus, in the colonial hydroid *Cordylophora caspia*, salinity tolerance of tissues decreases in the order stolons, hydranth body, tentacles, gonophores (KINNE, 1956b, 1958a). In more complex marine invertebrates, such as molluscs and crustaceans, nerve cells often appear to be less tolerant to changes in osmoconcentration of body fluids than reproductive cells, and these, in turn, less tolerant than somatic cells.

Usually, salinity tolerances tend to decrease as test temperatures, concentrations of dissolved gases and other environmental factors become sub- or supra-optimal. Salinity tolerances may be subject to significant intraspecific (inter-populational) differences, especially in euryplastic invertebrate populations occupying habitats with different salinity conditions (average salinities, extent and speed of salinity fluctuations). Hence salinity tolerances determined in individuals of a given population cannot, without further qualification, be taken to comprise species-specific responses. Species-specific response patterns can only be assessed on the basis of comparative tolerance tests performed on populations from different habitats, representative of the whole distributional area occupied by the species in question. Interpopulational differences in salinity tolerance may have both a genetic (selection) and a non-genetic (individual adjustments) basis (pp. 841, 842).

#### *Critical salinities in the sea*

In general, death from sub- or supranormal salinities does not occur in the open oceans, except at the uppermost surface layers, which may be subject to salinity variations due to extensive rainfall or evaporation. However, coastal waters, such as estuaries, lagoons, bays, beach and rock pools, are frequently characterized by considerable salinity fluctuations (dilution by rain, excessive evaporation during prolonged periods of drought), and significant variations in ionic composition which may surpass the tolerance limits.

In the state of latent life (spores, cysts), a few invertebrates inhabiting brackish water, hypersaline water or brine water have survived considerable periods of time in salt concentrations ranging from distilled water to wet crystallized salt; in the state of active life, brief periods of time in distilled water to full salt saturation near 360‰S. The salinity ranges tolerated by invertebrates inhabiting sea or fresh water are usually considerably smaller.

Very few invertebrates can exist permanently in salinities above 200‰, e.g. the brine shrimp *Artemia salina* and larvae of the dipteran genus *Ephydra*. In the Red

Bulack lake near the Caspian Sea, the following forms have been reported to occur at a salinity of 285‰ (for details consult REMANE and SCHLIEPER, 1958): the flagellate *Dunaliella* (*Monas dunalii*), the cyanophycean *Lyngbya* sp., larvae of 2 unknown dipteran species, 1 unknown oligochaete, the copepod *Cletocamptus* sp. and the rotatorian *Diaschiza* sp. At a comparable salinity, CASPERS (1952) reported larvae of the dipteran *Halliella casperi* and *Ephydra macellaria*, as well as some *Artemia salina*, from brine pools of the Anchialo salt-works near the Black Sea. FRASER (1936) found living copepods *Tigriopus fulvus* in brine pools; they died only after evaporation proceeded to a point where salt crystals began to form.

Habitats with salinities between those of oceans and fresh waters are critical to the majority of aquatic invertebrates. In fact, salinities between 5‰ and 8‰ constitute a significant ecophysiological boundary line, characterized by minimum numbers of species (Fig. 4-73; REMANE, 1934, 1940, 1969; REMANE and SCHLIEPER, 1958; KHLEBOVICH, 1965, 1966, 1968, 1969). In the present review, the boundary range 5‰ to 8‰S is referred to as 'horohalanicum' (from the Greek horos: limit, boundary line; see also pp. 959, 961).

KHLEBOVICH (1968) has attempted to analyze the hydrochemical aspects of the horohalanicum. He recalls that WITTIG (1940) has determined the relative calcium content in water samples of different salinities taken in the Norwegian Sea and at various stations in the Baltic Sea, demonstrating a distinct relative increase of calcium in salinities below 5‰ (Fig. 4-74). LOBZA (1945) presented information on ion ratios, indicating pronounced changes in salinities below 4‰, and data by KIRSCH

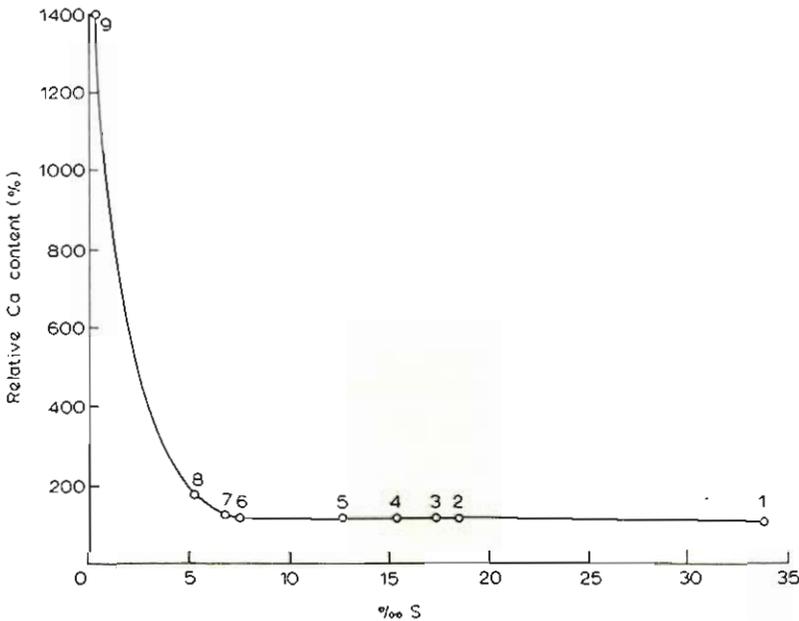


Fig. 4-74: Relative calcium content as a function of salinity at various localities: 1: near Oslo (Norway), 2: Kiel Bay, 3: Bornholm Deep, 4 and 7: east coast of Baltic Sea, 5: Kiel Inlet, 6: Arkona Deep, 8 and 9: estuary of Schwentine River (2 to 9 Baltic Sea). (After KHLEBOVICH, 1968; based on data by WITTIG, 1940; redrawn.)

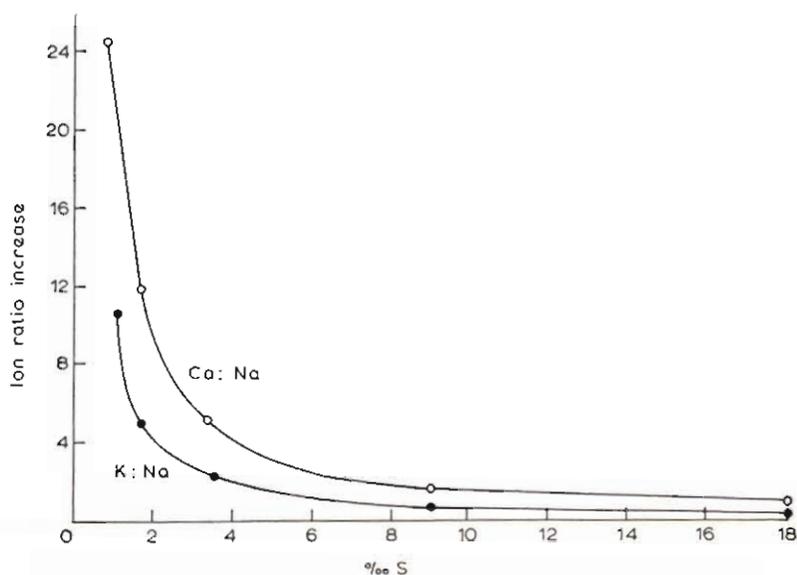


Fig. 4-75: Relative increase in the ion ratios K:Na and Ca:Na in waters of different salinities of the Bute and Knight Inlets, British Columbia (Canada). Ordinate: Ion ratio increase above 100% (normal sea water). (After KHLEBOVICH, 1968; based on data by KIRSCH, 1956; redrawn.)

(1956) reveal sudden changes in important hydrochemical characteristics in water samples obtained near the Bute and Knight Inlets (British Columbia) between 4‰ and 7‰S (Fig. 4-75). ALMAZOV and DENISOVA (1955), ALMAZOV and co-authors (1959) and ALMAZOV (1962) noted sudden changes of the ion ratio at salinities near 3‰, and marked divergencies from the normal chlorine coefficient at 5‰S in estuarine waters of the Black Sea. TSURIKOVA (1962) reported a lability of the carbonate-calcium system in Taganrog Inlet (USSR) water at a chlorine content of less than 4‰ (equivalent to a salinity of about 7‰). As KHLEBOVICH (1968) points out further, TSURIKOVA and SHULGINA (1964) found that the correlation between salinity and chlorinity in water of the Azov Sea shows a marked discontinuity at 2‰S (Fig. 4-76); the standard correlation between electroconductivity and salinity is no longer applicable at salinities below 5.5‰. According to TSURIKOVA and TSURIKOV (1966), different formulae for carbonate-calcium calculations should be applied at salinities below about 4‰. VINETSKAYA (1959) called attention to relations between the flow magnitude of the River Ural, salinities in the eastern part of the north Caspian Sea and changes in ion ratio; below 7‰S ion ratios change, possibly by removal of certain ions from the solution. KHLEBOVICH and NIKULICHEVA (1966) studied the calcium-chlorine ratio in the estuary of the River Keret (White Sea); during high tide, the salinity changed from fresh water to 14.4‰ over a distance of not more than 100 m; in this steep gradient, the relative calcium contents did not differ essentially from those reported by WITTIG (Fig. 4-74) over distances of hundreds of kilometres. Experimental mixings of waters of different origins have led KHLEBOVICH (1968) to conclude that the causes of ion-ratio changes in natural waters are associated primarily with the mixing of

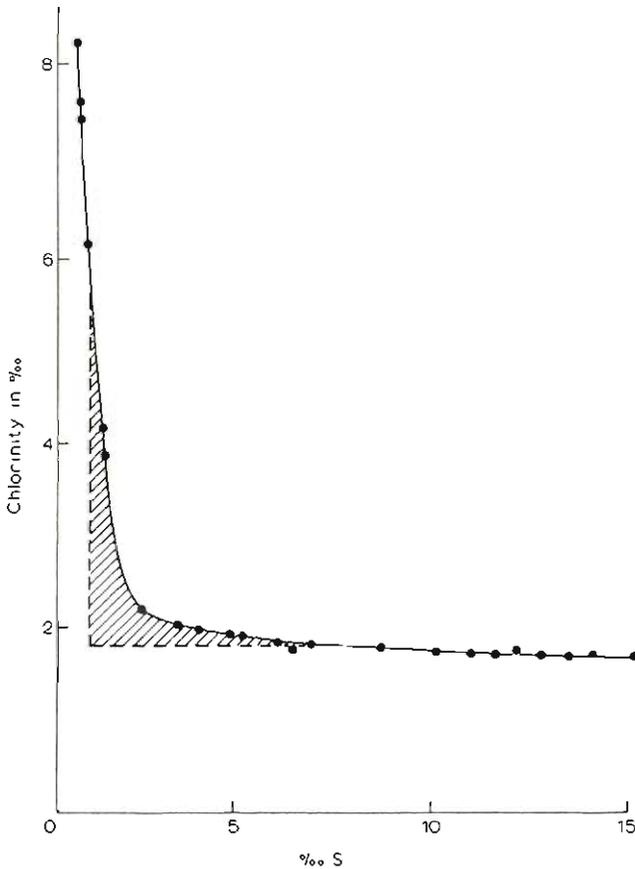


Fig. 4-76: Correlation between salinity and chlorinity in water from the Azov Sea. Hatching: mixed water zone. (After TSURIKOVA and SHULGINA, 1964; redrawn.)

waters of different hydrochemical properties, but cannot be explained merely by changes in ionic strength. The information at hand reveals that—as the salinities of the different waters studied decrease to values between 7‰ and 4‰S—several hydrochemical properties vary considerably. Since these variations may be of ecological importance (BEKLEMISCHEW and BASKINA, 1933), hydrochemical properties, rather than total salinities, may represent the principal causes for the ecophysiological barrier characterizing the horohalinicum (see also p. 959).

With regard to the horohalinicum (5‰ to 8‰S), KHLEBOVICH (1969) suggests at least six types of *in situ* tolerance relationships between larvae (embryos) and adults of hydrobiont invertebrates:

(i) Adults tolerate salinity reductions down to 5‰ to 8‰; ontogenetic development is possible only in higher salinities. Examples: *Carcinus maenas*, *Corbulomya maotica*.

(ii) Larvae tolerate salinity reductions down to 5‰ to 8‰; adults require higher salinities. Examples: marine euryhaline forms such as *Crassostrea virginica*.

(iii) Adults tolerate fresh, or almost fresh, water; larval development is possible only in salinities not less than 5‰. Examples: marine euryhaline forms such as *Nereis diversicolor*, *Eriocheir sinensis*.

(iv) None of the life-cycle stages tolerates salinities above 5‰ to 8‰; in general, salinity tolerance of adults is somewhat higher than that of developmental stages. Examples: limnic forms such as *Pelmatohydra oligactis*, *Herpobdella atomaria*.

(v) Larvae cannot, but adults can, tolerate salinities above 5‰ to 8‰. Examples: limnic forms such as *Acanthocyclops viridis*, *Asellus aquaticus*.

(vi) Free-living adults perish in salinities above 5‰ to 8‰; endoparasitic larvae require salinities (represented by body fluids of host) not lower than 5‰. Examples: limnic forms, probably restricted to the mollusc family Unionidae.

Several experimental studies indicate that many estuarine invertebrates are more tolerant to deviations in ionic composition than to the variations in total salinity encountered (e.g. KINNE, 1964a, 1966, 1967a). Deviations in ionic composition of coastal waters may, however, override the effects of variations in total external osmoconcentration if the ionic composition is severely altered. Critical changes can be caused by local geological peculiarities or introduction of large amounts of water pollutants.

In estuaries and other habitats with extensive short-term salinity fluctuations, certain clams and barnacles may establish populations in critically low or high average salinities as long as the lengths of the active periods, allowed by temporarily normalized salinity conditions, are sufficient for feeding, defecation and reproduction.

In sediment-dwelling invertebrates, physicochemical properties of the substrate, the degree of water exchange and the fact that salinity variations may be less extreme in the substrate than in the free water above, play an important role. Dampening of salinity fluctuations in the substrate has been reported for coastal waters with extensive short-term salinity variations (REID, 1930, 1932; ALEXANDER and co-authors, 1932, 1935; CAPSTICK, 1957), especially for regions of estuaries in which the proportions of sea water and freshwater inflow vary considerably, due to tidal rhythms (Fig. 4-77). For the Pocasset River (USA), SANDERS and co-authors (1965) report that (at their station 3) the salinity in the sediment below 5 cm is uniform and steady at about 20.5‰, while the salinity of the water

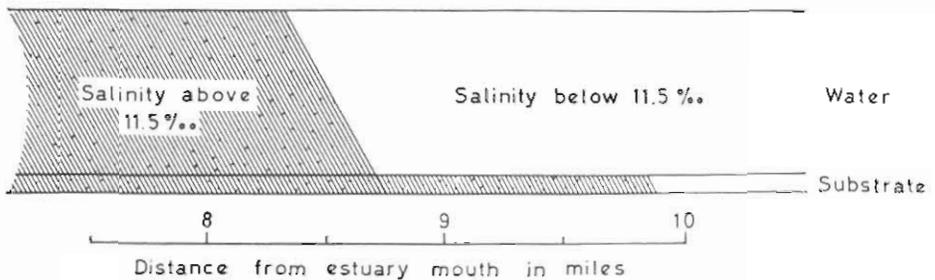


Fig. 4-77: Diagrammatic illustration of salinity conditions in an estuary during low tide. With increasing distance from the mouth of the estuary, salinity decreases faster (and fluctuates more intensively) in the free water than in the substrate. (After KINNE, 1966; adapted from ALEXANDER and co-authors, 1935; redrawn.)

above the sediment ranges from 2.3‰ to 29.3‰ during the tidal cycle, with a nett time-averaged salinity of 18.7‰. Thus the steady sediment salinity is higher than the time-averaged salinity of the free bottom water by 1.8‰. The difference becomes even more pronounced if one considers the intermediate steps of tidal salinity variations. The integrated salinity deficit of the free bottom water at low tide, compared to that of the substrate (mud), is 1.6 times as great as the integrated salinity excess at high tide. This means that the high salinity water is much more effective in determining the sediment salinity than the low salinity water. According to McLUSKY (1968a), the interstitial salinity of the mud or muddy sand of the River Ythan estuary (Aberdeenshire, Scotland) is controlled by the salinity of the high-tide water overlying the substrate, but interchange is slow; only persistent changes in salinity conditions are reflected in variations of the interstitial salinity. Thus the population of the amphipod *Corophium volutator* which inhabits the muddy substrate is exposed to lesser salinity fluctuations than organisms occupying the free water of the immediate vicinity. *C. volutator* can tolerate reductions of average salinity down to 2‰ (the same lower tolerance limit was found in laboratory experiments; McLUSKY, 1967). However, even fed individuals cannot survive in 2‰S for more than 500 hrs. Unfed individuals require salinities above 5‰ for moulting, growth and survival (McLUSKY, 1968a, b). NELSON (1962) reported that the chlorinity of interstitial water tends to exceed slightly that of the overlying water layers. Replacement of interstitial fresh water by salt water is rapid, but replacement of salty interstitial water by overlying fresh water rather slow (LAEVASTU and FLEMING, 1959). Interstitial salinities and their effects on substrate-living invertebrates have also been studied by REID (1932), SMITH (1955c, 1956), EMERY and STEVENSON (1957a, b), JANSSON (1962, 1966, 1967) and JOHNSTON (1964). Among the various techniques employed to measure interstitial salinities, electrical conductivity determinations appear to be most appropriate since they refer to total solutes (COX, 1963).

In commercial oyster (*Crassostrea virginica*) plants in five parishes of southeast Louisiana (USA), summer salinity and temperature conditions appear to affect the yield in the following season. When the air temperature was 27.8°C or higher and the rainfall 7.0 cm or lower for prolonged periods during the preceding summer, there was a significant decrease in the production of oysters in the following year. Conversely, the yield increased if preceded by a cool, wet summer. Mortality rather than failure to grow seems to be responsible for the decreased productivity of the oyster plants (OWEN, 1953).

Detailed assessments of salinity tolerances, on the basis of field studies alone, are difficult because salinity effects proper may be modified (increased, reduced, masked) by other simultaneously effective environmental factors such as light (Chapter 2), temperature (Chapter 3), water movement (Chapter 5), dissolved gases (Chapter 9), nutrition, and interactions between co-existing organisms. In many cases, relatively low temperatures tend to reduce the detrimental effects of subnormal salinities, while high temperatures are sometimes beneficial in supra-normal salinities. Similarly, intensive water movement (surf-beaten shores, strong currents or circulation) and high rates of water oxygenation frequently reduce the stress endured at subnormal salinities.

*Critical salinities in the laboratory*

More detailed information on tolerances to salinity variations is available from laboratory experiments conducted under controlled environmental conditions. In these experiments, stabilized individuals (acclimated for days or weeks to defined environmental and nutritive conditions) with comparable genetic backgrounds are exposed to slowly declining or increasing salinities, or abruptly transferred into critically low or high salinity levels. Their lethal salinities are then determined in a way similar to that described in Chapter 3.3 (p. 414) in regard to temperature.

*Lethal salinity effects due to changes in total osmoconcentration* have been studied in several invertebrates, e.g. free-living ciliates from brackish and fresh waters (Ax and Ax, 1960), the parasitic ciliate *Ichthyophthirius multifiliis* (TESCH, 1968), the mysid *Gastrosaccus sanctus* (PORA and BACESCU, 1939), the amphipods *Pontogammarus maeoticus* (PORA and CARAUSU, 1939) and *Gammarus duebeni* (KINNE, 1953a, 1959), the polychaete *Nereis diversicolor* (PORA and ROSCA, 1944), the gastropod *Theodoxus fluviatilis* (NEUMANN, 1960) and larvae of the mosquitoes *Chironomus thummi*, *C. halophilus* and *C. salinarius* (NEUMANN, 1961a).

Abrupt changes in total osmoconcentration may be tolerated better by young life-cycle stages than by fully grown adults. Young stages of *Artemia salina*, for example, tolerate a sudden transfer into supra- or subnormal salinities better than adults (MARTIN and WILBUR, 1921; BOONE and BAAS BECKING, 1931). According to D'AGOSTINO and PROVASOLI (1968), newly hatched *A. salina* can be transferred without difficulties to salinities ranging from 5‰ to 205‰; nauplii not older than 6 hrs reveal survival rates of 80% when transferred to salinities between 5‰ and 90‰.

JANSSON (1962, 1967) conducted tolerance and preference experiments on mesopsammic invertebrates. He tested the responses to several important environmental factors including salinity. In his 1967 study, JANSSON used the euryhaline brackish-water copepod *Parastenocaris vicesima* as test organism. Tolerance experiments conducted by transferring adult *P. vicesima* abruptly into 8 different salinity levels (15°C) revealed maximum survival rates in salinities between 0.1‰ and 10‰. The lethal dose to kill 50% of the test population (LD<sub>50</sub>) was not attained between 0.2‰ (habitat salinity) and 10‰S within 3 weeks. Surprisingly, tolerance was greater in distilled water than in 15‰S; in distilled water, 50% of the test population died after about 13 days, in 15‰S after 1 or 2 days. This result requires confirmation. Preference experiments revealed a preferred salinity zone between 0.1‰ and 2.5‰S.

REISH and HETHERINGTON (1969) studied the chlorinity tolerance of three species of the marine wood-boring isopod genus *Limnoria*. The lower LD<sub>50</sub>-28 day levels for *L. lignorum*, *L. tripunctata* and *L. quadripunctata* were 6.5‰, 9.5‰ and 14.5‰ chlorinity, respectively; the upper levels, 27.5‰, 32.0‰ and 21.0‰ chlorinity (Fig. 4-78). *L. lignorum* can tolerate lower chlorinities than the other two species; it occurs along the northeastern Pacific coast characterized by intensive rain falls and hence frequently reduced chlorinities. The authors attribute the narrow tolerance range of *L. quadripunctata* to the relatively high test temperature of 25°C.

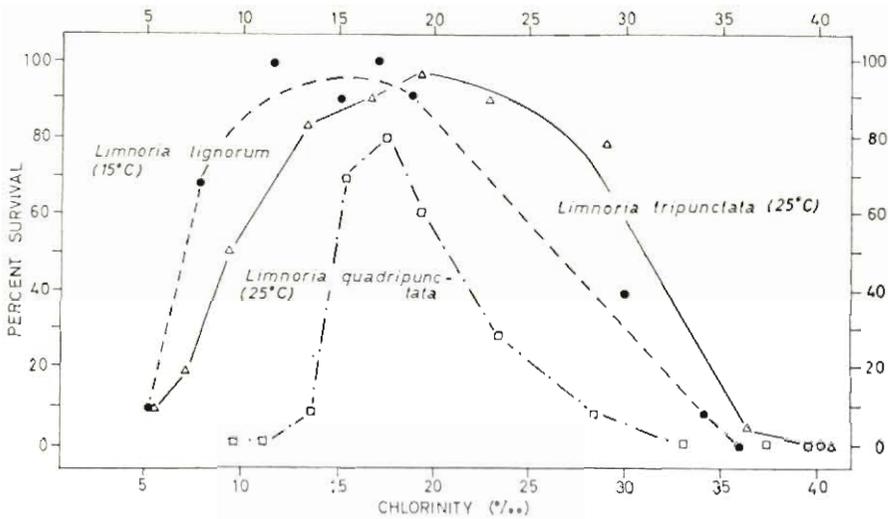


Fig. 4-78: Tolerance of three species of the marine wood-boring isopod genus *Limnoria* to different constant chlorinities. Exposure time: 28 days. Test temperatures indicated in brackets. (After REISH and HETHERINGTON, 1969; modified.)

The euryhaline copepod *Tigriopus fulvus* dies 84 hrs after transfer into distilled water; it survives in salinities between 4.2‰ and 90.0‰, but above 90‰ falls into a state of locomotory inactivity (ISSEL, 1914). Soon after transfer into salinities above 90‰, swimming activities cease and the copepods sink to the bottom. Recovery experiments (RANADE, 1957) revealed that maximum immersion periods after which no recovery occurs are 60 hrs in 98‰S, 30 hrs in 135‰ to 180‰S, and 3 hrs in 225‰S. In its natural habitat—small coastal water bodies such as rock pools—*T. fulvus* is frequently confronted with rapid reductions (rain) or increases (evaporation) in salinity. Near the Marine Biological Station, Port Erin (Great Britain), pools which had almost dried up and, apparently, contained no *T. fulvus*, revealed actively swimming specimens after rain, even though the sea had not meanwhile covered the pools.

BATTAGLIA and BRYAN (1964) compared the ability of homozygous adult females of the *trifasciata* and *violacea* forms of the polymorphic copepod *Tisbe reticulata* from Chioggia (Lagoon of Venice, Italy) to tolerate subnormal salinities. Both forms appear to be equally capable of tolerating concentrations between 100‰ and 33‰ sea water. Comparisons between the *trifasciata* form from Plymouth (Great Britain) and three different geographical populations of *Tisbe furcata* revealed that the latter are less tolerant to low salinities.

CARGO and SCHULTZ (1966, 1967) tested the tolerance to changes in salinity in polyps of the cnidarian *Chrysaora quinquecirrha* under winter conditions (Chesapeake Bay, Maryland, USA). Polyps kept in 5‰S encysted, whereas those kept in 30‰ and 35‰S appeared to be ready to, but did not actually, encyst. The 5‰S polyps seem to have been adversely affected compared to the polyps exposed to higher salinities.

Salinity tolerances of intertidal gastropods often parallel their vertical distributions. Tolerance to sub- or supranormal salinities tends to increase with the shore levels occupied (e.g. BROEKHUYSEN, 1941; SEELEMANN, 1968).

*Lethal salinity effects due to changes in relative proportions of solutes* hardly ever occur in purely marine habitats. But variations in solute contents of the water may reach critical values in fresh, brackish, hypersaline or brine waters. Laboratory studies on critical values of ionic ratios have been conducted on the colonial hydroid *Cordylophora caspia* (ROCH, 1924), gammarids (SCHUMANN, 1928), *Chironomus* larvae (HAAS and STRENZKE, 1957; STRENZKE and NEUMANN, 1960; NEUMANN, 1961a, 1962) and developing eggs of various echinoderms.

Particular attention has been paid to changes in relative amounts of calcium. In low total salt concentrations, high proportions of calcium may exert a stabilizing effect on protein structures and metabolic processes, resulting in an over-all increase in tolerance, especially to high temperatures. This has been shown, for example, in the turbellarian *Gunda ulvae* (PANTIN, 1931a), the polychaete *Nereis diversicolor* (ELLIS, 1937) and the mollusc *Mytilus edulis* (SCHLIEPER and KOWALSKI, 1956). The estuarine *Gunda ulvae* can tolerate temporary exposure to fresh water only if sufficient ambient calcium is available; in fresh water, and in brackish water of low salt content, it suffers from extensive water uptake and salt loss, unless both media have a supranormal calcium content (PANTIN, 1931a, b; WEIL and PANTIN, 1931). In *Mytilus edulis*, additional amounts of calcium and magnesium increase the thermal stability of tissues, while addition of potassium decreases it.

The freshwater-living amphipod *Dikero gammarus haemobaphus* survived (more than 50% of the test individuals) after transfer into water from Lake Aral of 12‰S but died (100%) in water of Lake Balkhash (USSR) of 9.5‰S within 6 days—probably because of the higher potassium content of the Balkhash water (BIRSHTEIN and BELIAEV, 1946). Negative biological consequences of supranormal potassium contents are also suggested by experiments conducted on the mysid *Mesomysis kowalevskyi*; this crustacean tolerates a salinity range of 0‰ to 1.5‰ in Balkhash water but of 0‰ to 10‰ in Aral water (KARPEVICH, 1958).

Copper concentrations of 1 mg/l kill the gastropod *Australorbis glabratus* in fresh water within a few hours. 15 $\gamma$ Cu/l sea water leads to developmental retardation in larvae of the echinoderm *Paracentrotus lividus*; 25 $\gamma$ Cu/l causes damage (BOUGIS, 1959). These copper concentrations lie within the ranges of variation of natural sea water. BOUGIS was therefore able to interpret the findings of WILSON and ARMSTRONG (1958), who reported developmental disturbances in *Echinus esculentus* in bottom waters of sea areas which were later found to contain copper concentrations of up to 25 $\gamma$ /l.

Table 4-48 presents some critical lower concentrations of sodium and chloride, below which sufficient absorption of chloride from the external medium is no longer possible; the invertebrates concerned continue to lose chloride and finally die, unless they succeed in replenishing their chloride ions via food intake.

Changes in ionic composition of the ambient medium have been shown to modify tolerance to cold and heat (Chapter 3.3). A recent example has been provided by KÄHLER (1970; see also p. 866), who studied the effects of the chlorides of Na, K,

Table 4-48

Lower critical concentrations (mMol/l) of sodium and chloride established for some aquatic molluscs and crustaceans (Based on data from various authors)

Invertebrate group	Species	Na	Cl	Author
Mollusca	<i>Limnaea stagnalis</i>		0.1	KROGH (1939)
	<i>Paludina viviparus</i>		0.1	"
	<i>Dreissena polymorpha</i>		0.1	"
	<i>Unio pictorum</i>		0.1	"
	<i>Gammarus duebeni</i>	0.2		SHAW and SUTCLIFFE (1961)
Crustacea	<i>G. pulex</i>	0.06		" "
	<i>Asellus aquaticus</i>	0.09		LOCKWOOD (1960)
	<i>Potamon johnstoni</i> (?)	0.01-		
		0.02		SHAW (1959b)
	<i>P. niloticus</i>	0.05		"
	<i>Astacus fluviatilis</i>	0.05		KROGH (1939)
	<i>A. pallipes</i>	0.04	0.03	SHAW (1960a)

Ca and Mg on cold and heat resistance of the euryhaline supralittoral oligochaete *Enchytraeus albidus*. By adding these ions to the acclimation salinity of 10‰, KÄHLER increased the total resulting salinity to 12‰, 15‰, 20‰ or 30‰ and recorded the thermal tolerances of test groups previously acclimated to 5° or 23° C. The effect of the added ions depends on total osmotic concentration and acclimation temperature. Na, K, Ca and Mg reduce cold tolerance (exposure to -13.2° C) in 5° C-acclimated worms, i.e. in individuals which have already acquired considerable resistance to cold. 23° C-acclimated worms become more cold tolerant when K and Ca are added. Heat tolerance (exposure to 35.8° C) of 23° C-acclimated individuals decreases when Ca and Mg are added. Addition of ions beyond the levels mentioned causes tolerance reductions in all cases. Interestingly, addition of the anti-freeze substance dimethyl sulphoxide leads to considerable increase in cold tolerance, both in cold and warm acclimated worms, eliminating the respective thermal adaptations.

Further laboratory experiments on tolerances of marine and brackish-water living invertebrates to salinity variations have been conducted on littoral turbellarians (GOMPEL and LEGENDRE, 1928), polychaetes (ELLIS, 1933; SAYLES, 1935; PORA and ROSCA, 1952; SMITH, 1957; KRISHNAMOORTHY, 1962; HOHENDORF, 1963; KRISHNAMOORTHY and KRISHNASWAMY, 1966a), gastropods (BROEKHUYSEN, 1941), lamellibranchs (DAVIS, 1958; STICKNEY, 1964; REISH and AYERS, 1968), crustaceans (MCLEESE, 1956) and tunicates (DYBERN, 1967).

Studies on tolerances of freshwater invertebrates to elevated salinities are fewer in number (e.g. GRESENS, 1928; LAGERSPETZ, 1955; MEIJERING, 1966).

Salinity ranges occupied in the sea are not necessarily the same as those tolerated for prolonged periods in the laboratory. A distinction between the 'ecological

potential' exhibited in the field and the 'physiological potential' revealed in the laboratory is therefore necessary (KINNE, 1953a, 1956d). The marine sipunculid *Themiste dyscritum*, for example, appears to be stenohaline in the sea but tolerates a wide range of salinities in the laboratory (OGLESBY, 1968a). There exists a multitude of further examples illustrating discrepancies between salinity tolerances (death, growth, reproduction, etc.) in the sea and in the laboratory. Combined studies in the sea and in the laboratory (KINNE, 1956d) are, therefore, the safest way of assessing ecologically meaningful tolerance limits.

#### *Salinity tolerance at the subindividual level*

Studies on salinity tolerance at the subindividual level will be considered here only as far as they can be expected to be of immediate relevance to marine ecological considerations.

For a number of bivalve species, close correlations between cellular salinity tolerance and ecological parameters (field tolerances, geographic distributions) have been claimed (e.g. PILGRIM, 1953; SCHLIEPER and KOWALSKI, 1956; SCHLIEPER and co-authors, 1960, 1967; RESHÖFT, 1961; ZHIRMUNSKY, 1962; VERNBERG and co-authors, 1963; THEEDE, 1965a, 1969b; SCHLIEPER, 1966; THEEDE and LASSIG, 1967).

Excised gill pieces of poikilosmotic marine bivalves can survive for several days; their exact survival periods can be determined microscopically using the rate of ciliary activity as criterion. SCHLIEPER and co-authors (1967) transferred isolated small gill pieces into a series of petri dishes containing water of different salinities and determined, after certain time intervals, the intensity of ciliary beating (consult Chapter 3.31, p. 420 for further methodological details). Among the lamellibranch species listed in Fig. 4-79, excised gill tissue of *Spisula solida* (which inhabits 10 to 50 m water depths in the North Sea) reveals the lowest degree of salinity tolerance. After 24 hrs, ciliary activity of 4 to 8 mm<sup>2</sup> gill pieces can be observed in salinities ranging from 15‰ to 50‰. Comparable gill pieces of *Cardium edule* from shallower parts of the North Sea survive from 10‰ to 60‰S. Excised gill pieces of *Mytilus edulis* from the North Sea littoral survive 24 hrs in salinities ranging from 5‰ to 65‰. In contrast, *M. edulis* individuals from the western Baltic Sea (brackish water) reveal a significantly lower tolerance to salinities of 35‰ and higher, but increased tolerance to reduced salinities (total range: 5‰ to 45‰S). These differences in salinity tolerance at the subindividual level parallel those found in intact whole individuals.

Employing the same method, gill tissues of several other bivalve species have been tested by SCHLIEPER and co-authors (1960), RESHÖFT (1961) and VERNBERG and co-authors (1963). Ciliary activities in the littoral tropical bivalves *Chama cornucopia* and *Modiolus auriculatus* reveal higher tolerances to high salinities but lower tolerances to low salinities than in the littoral temperate bivalves *Ostrea edulis* and *Mytilus edulis*. The differences are also related to the respective salinity tolerances of intact individuals, and may be used as indicators of the population- or species-specific ecological potential for tolerating different salinity regimes.

THEEDE and LASSIG (1967) studied the 24-hr survival of excised gill pieces from the euryhaline lamellibranchs *Mytilus edulis*, *Macoma baltica*, *Cardium edule* and *Mya arenaria* collected in habitats with different average salinities (about 30‰S:

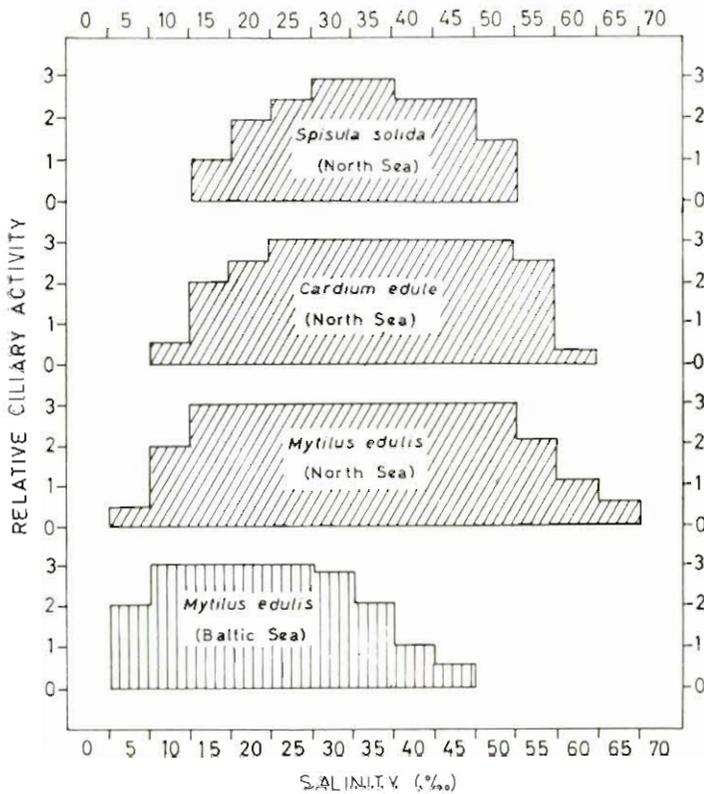


Fig. 4-79: Salinity tolerance of excised gill pieces obtained from adult representatives of three different lamellibranch species. Averages of 10 individual measurements; relative activity: 3 denotes normal ciliary activity, 2 somewhat reduced activity, and 1 strongly reduced activity (50 to 90% of the cilia have ceased to beat). Size of gill pieces: about 4 to 8 mm<sup>2</sup>; test period: 24 hrs; test temperature: 10° C. (After THEEDE, 1965a; modified.)

Büsum, S.E. North Sea; about 15‰: 'Kieler Förde', western Baltic Sea near Kiel; about 6‰S: near Tvärminne, Gulf of Finland, Baltic Sea). The results of this study are illustrated in Fig. 4-80. Interestingly, the major differences in tissue tolerance occur in test salinities above 35‰, i.e. in salt concentrations higher than those encountered in the respective habitats. At the lower end of the test salinity scale tolerances of individuals from about 6‰ or 15‰ habitat salinities lie rather close together. Thus, in *Mytilus edulis* from Büsum (North Sea) and from the Gulf of Finland (Baltic Sea), the difference between the respective upper salinity tolerances amounts to about 30‰S, while the corresponding difference in lower salinity tolerances is only about 5‰S. Under habitat conditions, the small differences in tolerance to low salinities may, however, be of greater ecological importance than the more pronounced differences in high salinities. Both at the upper and lower critical salinities, the sequence in tissue tolerance parallels the differences in habitat salinities: in the representatives of all four species, upper tolerances decrease in

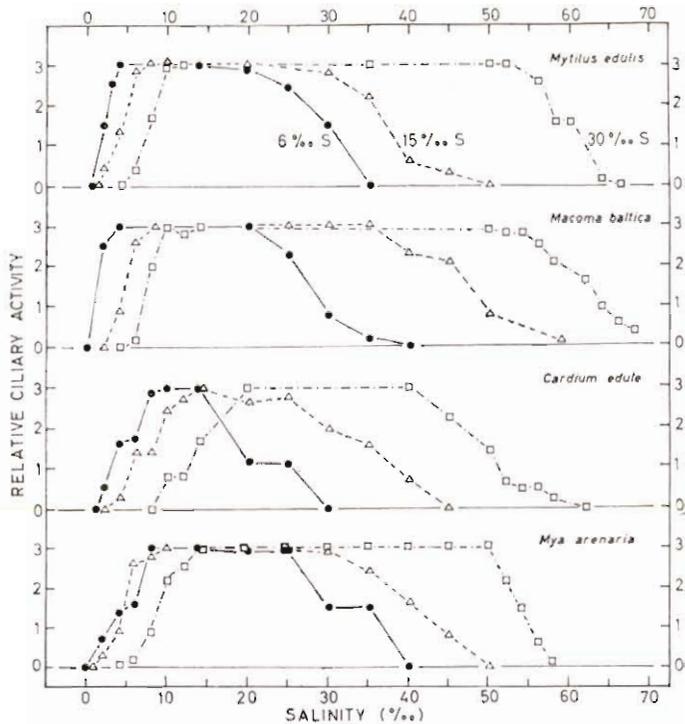


Fig. 4-80: Influence of habitat salinity conditions on salinity tolerances of excised gill pieces from adults of four different lamellibranch species. Averages of 8 to 10 individual measurements. Relative ciliary activity and size of gill pieces as in legend to Fig. 4-79. Ciliary activity was determined 24 hrs after transfer of gill pieces into test salinities. Average habitat salinities were 6‰ S; near Tvärminne, Gulf of Finland, Baltic Sea; 15‰ S; western Baltic Sea near Kiel; 30‰ S; North Sea near Büsum, Federal Republic of Germany. (After THEEDE and LASSIG, 1967; modified.)

the order 30‰, 15‰, 6‰ habitat salinity, while lower tolerances decrease in the order 6‰, 15‰, 30‰ S. The total range of salinities tolerated during the 24-hr experiments is widest in tissues of North Sea individuals of all four species; it decreases with decreasing habitat salinity.

The causes of the pronounced intraspecific differences in excised tissue tolerance appear to be related largely to long-term non-genetic salinity adaptation. THEEDE (1965a) cross-acclimated adult *Mytilus edulis* from the Baltic Sea and the North Sea (at 10° C) and found that the differences in salinity tolerance of excised gill pieces are practically reversible after 30 days (see also p. 865 and Fig. 4-98).

While in some molluscs salinity tolerances of excised gill tissues are congruent to salinity stresses endured in the field, in others they far exceed habitat demands. Tolerance potentials which exceed immediate environmental demands may be indicative of historical changes in habitat salinity or of phylogenetic relations to more euryhaline ancestors. They can also be considered as pre-adaptations for

extending or shifting the present salinity range of the populations or species concerned.

In regard to differences in tissue tolerance to salinity variations among the four bivalves studied by THEEDE and LASSIG (1967), *Mytilus edulis* and *Macoma baltica* exhibit the greatest tolerance capacities (total range of North Sea *M. edulis*: about 5‰ to 67‰S). Tolerance to high salinities decreases in the order *Macoma baltica*, *Mytilus edulis*, *Cardium edule*, *Mya arenaria*; in regard to the tissue tolerance to low salinities, no significant differences have been observed between *Mytilus edulis*, *Macoma baltica* and *Mya arenaria* from the North Sea, while *Cardium edule* from the North Sea shows a lower degree of tolerance.

Salinity tolerances of excised tissues are also a function of the ionic composition of the test medium. SCHLIEPER and KOWALSKI (1956) tested the salinity tolerance of gill pieces from *Mytilus edulis* in western Baltic Sea water (15‰S; 236 m Mol/l), which was diluted to 30 m Mol/l by adding either pure distilled water or distilled water containing 200 mg Ca/l (Fig. 4-81). The salinity tolerance of excised gill

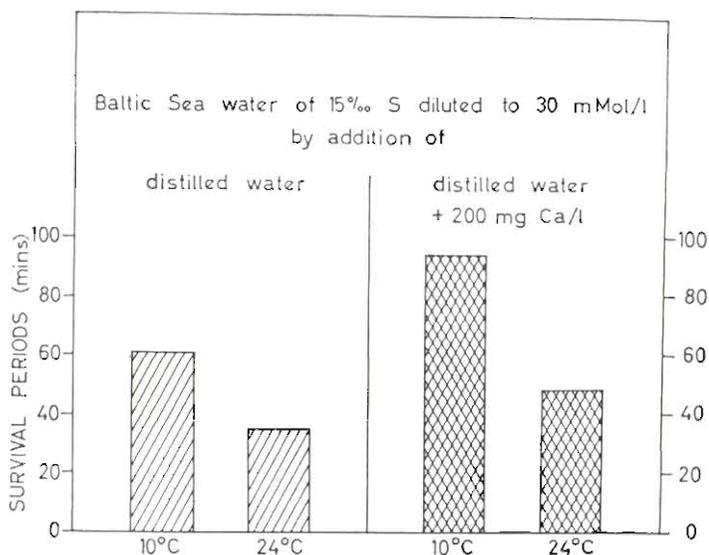


Fig. 4-81: Effect of ionic composition of the test medium on the salinity tolerance of excised gill tissues of the lamellibranch *Mytilus edulis* from the western Baltic Sea (15‰S; 236 m Mol/l). Salinity tolerance is significantly higher if  $\text{CaCl}_2$  is added to the distilled water used as dilutant; survival is enhanced by lower temperatures in both media; test temperatures are indicated at the bottom of the respective columns. (After SCHLIEPER and KOWALSKI, 1956; modified.)

tissues proved to be considerably higher if calcium had been added to the dilutant. Calcium addition to the external medium is also known to increase the degree of salinity tolerance in intact whole individuals (p. 834). The decisive factor in both cases is, according to SCHLIEPER and KOWALSKI, the cellular calcium level. Supranormal amounts of calcium have been reported to counteract detrimental tissue effects of low salinities in other organisms also (e.g. PANTIN, 1931a, b; BREDER,

1933; ELLIS, 1937; HEUTS, 1944). Calcium ions appear to increase the structural stability of protoplasmic protein molecules and thus augment the general tolerance to environmental stress.

Further information on the physiological effects of calcium, magnesium and potassium at the subindividual level has been obtained by increasing the respective concentrations of these ions, using natural brackish water of 15‰S as basic medium. Exposed to the resulting test media, isolated gill pieces of *Mytilus edulis* exhibit different degrees of thermal tolerance (Fig. 4-82). Addition of 100% of the

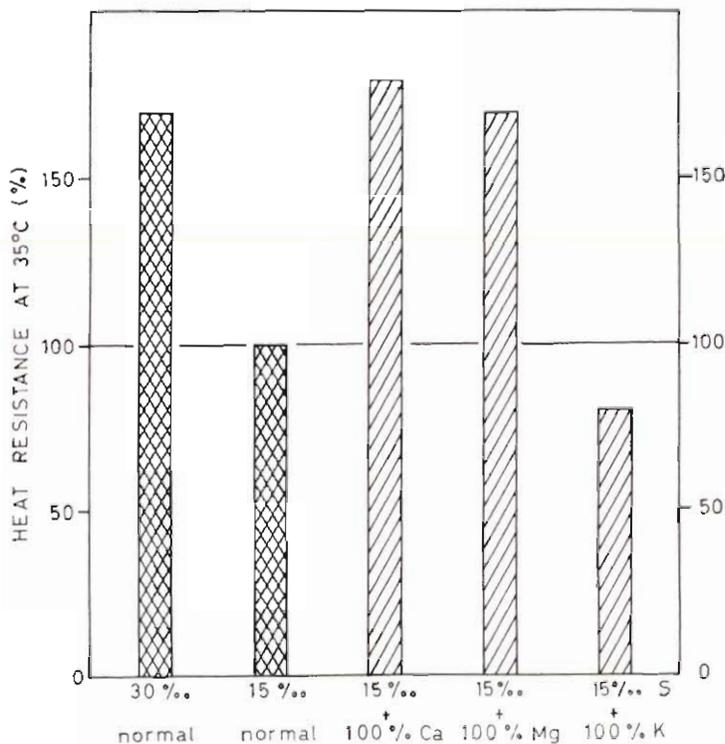


Fig. 4-82: Effect of ionic composition of the test medium on heat resistance (35°C) of excised gill tissues of the lamellibranch *Mytilus edulis*. (After SCHLIEPER and KOWALSKI, 1956; modified.)

amount of calcium or magnesium normally present in brackish water of 15‰S increases heat resistance significantly, while the addition of potassium lowers heat tolerance far below the resistance levels observed in normal sea water of 30‰S or in normal brackish water of 15‰S. Parallel to these changes in tolerance, the beating activity of the gill cilia decreases in test media with added amounts of calcium and magnesium, but increases in the medium with additional amounts of potassium (SCHLIEPER and KOWALSKI, 1956). Such an inverse correlation between the degrees of tolerance and activity appears to be a fairly general phenomenon. For further information the reader is referred to recent reviews by KINNE (1964a, 1967b), POTTS and PARRY (1964), ROBERTSON (1964), FOGG (1965) and SCHOF-FENIELS (1967).

*Salinity tolerance at the supra-individual level*

Salinity tolerances may be subject to significant variation at the population level. Interpopulational tolerance differences are of considerable ecological importance. They represent means for supra-individual adjustments to different environments. Knowledge of interpopulational gradients of functional and structural properties is a prerequisite for a complete assessment of the ecological potential of a given species. Apparently, different (conflicting) strategies are required for maximum ecological success at the individual and population levels. It seems that, in individuals, a perfect match of maximum tolerance or performance and environmental stress can be achieved only by adjusting, at the expense of versatility, to a specific condition. In contrast, populations must preserve versatility (a broad spectrum of genotypes) at the expense of individual lives and maximum individual performance, in order to meet the danger of population death due to sudden, extreme environmental changes.

BATTAGLIA (1964, 1967) compared the tolerances to diluted sea water of three geographically separated populations of the copepod *Tisbe furcata*. Adult representatives from England (Plymouth: high average salinities) and Italy (Chioggia, Lagoon of Venice: low and considerably fluctuating salinities; Gargano, Lake of Varano, Apulia: still lower and also considerably fluctuating salinities) were transferred from his standard laboratory sea water (34‰S) into brackish water (18‰S). Previous to tolerance tests, all populations were kept in the laboratory under standard salinity and temperature conditions for more than 2 years (more than 60 generations). Upon transfer into 18‰S, the test individuals suffered a shock, from which they recovered after certain periods of time. These recovery periods were recorded (Fig. 4-83). The differences in recovery time of the three populations are statistically significant. Proof of the genetic nature of the differences has been obtained by testing the salinity tolerance to diluted sea water of the  $F_1$  and  $F_2$  generations of the cross Gargano  $\times$  Plymouth. The greater tolerance of the  $F_1$  hybrids, compared to the parental populations, indicates that they are strongly heterotic. In the  $F_2$  an increase of variance occurs, which is due to segregation. The highest degree of tolerance to low salinities is exhibited by the population from Gargano, medium tolerance by that from Chioggia, and the lowest tolerance by the Plymouth population. These differences in tolerance are related to the different salinity conditions in the three original habitats. BATTAGLIA assumes that the different, genetically fixed salinity tolerances may be caused, not only by the effect of specific genes (not necessarily many) but also by the degree of heterozygosity.

Colour forms of the isopod *Isocladus armatus*, an inhabitant of rocky shores of New Zealand, reveal temporal and spatial variation in frequency correlated with differences in habitat temperature. In the laboratory, colour forms exhibit differences in tolerances to salinity and temperature. While other factors, such as concealment from predators, non-random mating, differential fecundity, cannot be excluded from contributing to populational frequency gradients of colour forms, field and laboratory data are consistent with the hypothesis

'that the geographic variations and seasonal changes in local populations are, at least in part, produced by the selective effects of temperature and salinity' (JANSEN, 1968, p. 120).

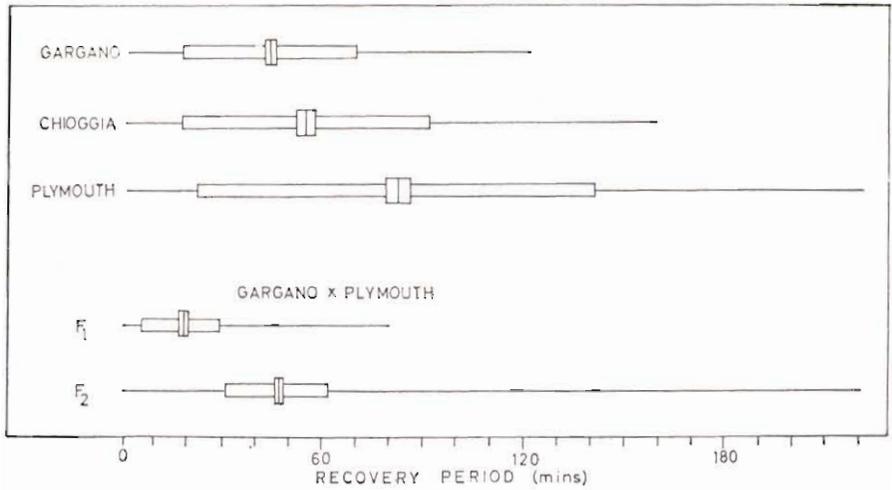


Fig. 4-83: Genetic resistance adaption to salinity variations in three populations of the copepod *Tisbe furcata* (from Gargano, Chioggia and Plymouth) and in hybrids of the cross Gargano  $\times$  Plymouth. Criterion: recovery period of adult individuals after shock suffered from abrupt transfer from 34‰S to 18‰S. Horizontal lines: range of variation; horizontal bars: standard deviation from mean (vertical lines); vertical bars enclosing the means: standard error  $\times$  2. (After BATTAGLIA, 1967; modified.)

According to BELIAEV (1949), populations of the barnacle *Balanus balanoides* are adjusted to lower salinities in the White Sea than in the Barents Sea, with its higher salinities (see also SAVVATEEV, 1952 and FOSTER, 1969a).

Another example of interpopulational differences in salinity tolerance has been reported by DYBERN (1967). Adult ascidians *Ciona intestinalis*, collected from populations living under different salinity conditions, show different salinity tolerances; parallel differences occur in their eggs and larvae.

The biological significance of supra-individual gradients in environmental resistance lies in the increased capacity to enlarge the distributional area of the species. The gradients are established by differential extension of the ecological potential of populations, paralleled by modifications (shifting, reduction) in the environmental ranges of individuals.

Salinity may also affect communities or ecosystems. These terms refer to multi-species assemblages, characterized by specific functional (flow of energy and matter) and structural (presence and abundance of species) properties and usually associated with a particular set of physical conditions (habitat). In the Possjet Bay (Sea of Japan), GOLIKOV and SCARLATO (1967) studied salinity effects at the ecosystem level and claim to have found differences in tolerance. Employing skin-diving techniques, GOLIKOV and SCARLATO report that, in estuaries and lagoons, salinity greatly affects the species composition (presence and abundance) of the ecosystem (bottom biocoenosis) and that the effect of salinity variations increases from phytal and epifauna to infauna—a fact which may be related to the relatively higher and more stable salinities in interstitial spaces. In half-closed bays, the patchiness of bottom biocoenoses tends to increase and the respective territories occupied decrease in total area. According to GOLIKOV and SCARLATO, these

changes may be related to (a) more intensive fluctuations in physicochemical conditions and their increased variety, and (b) accelerated successions. Ecosystems of shallow waters and half-closed coastal sea areas are reported to be 'less resistant' than those existing off the open coasts and in greater water depths. GOLIKOV and SCARLATO define resistance or stability of ecosystems in terms of their remaining in an invariable state (relative constancy; period of time during which they remain in a state close to climax). Reduced constancy and the corresponding acceleration of successions in shallow waters and half-closed bays are assumed to be connected with a greater influence of environmental changes upon the components of the ecosystem. Quality and quantity of the bottom organisms studied depend not only on abiotic environmental factors but also on the 'biocoenotic background', i.e. conditions produced by aggregations of certain species which create additional, new niches (see also GOLIKOV, 1966).

Major changes in salinity conditions of large areas, due to changes in geomorphology, climate or man-made constructions, may lead to death at the population, species or ecosystem level. Important studies on the effect of progressive reductions in the salinities of bays regained from the sea are being conducted by Dutch scientists. From these studies, new insights may be expected into the effects of salinity variation on species composition and dynamic interrelations of ecosystems exposed to gradual salinity changes.

#### *Salinity tolerance under multivariate conditions*

As has already been pointed out, the degree of salinity tolerance is subject to modification by other environmental factors, especially temperature (Chapter 3, p. 427), water movement (Chapter 5), substratum (Chapter 7), dissolved gases (Chapter 9), as well as food, competition, biochemical interaction, etc. Responses to such factor combinations are treated *in extenso* in Chapter 12. It may suffice here, therefore, to refer to two typical examples.

COSTLOW (1967) maintained megalops of the blue crab *Callinectes sapidus*, reared from hatching through all zoeal stages at 25° C and 30‰ S, in 23 salinity/temperature combinations until metamorphosis and determined their survival rates (Fig. 4-82). The analysis of mortality was performed by fitting a response surface (BOX and YOUNG, 1955; COSTLOW and co-authors, 1960, 1962, 1966) where the response equals

$$Y = \text{arc sine} \sqrt{\text{percentage mortality}}$$

The functional form fitted is fully quadratic in salinity and temperature. In the plotting of the contours of mortality, the choice is in part dictated by the computer programme employed. The programme requires that a constant increment be used once an initial value has been set. Thus the mortality contours represent even intervals in the variable *Y* which accounts for the uneven contours 6.7‰ and 93.3‰ S in Fig. 4-84. Individual regression coefficients of linear and quadratic effects of salinity (*S*, *S*<sup>2</sup>), linear and quadratic effects of temperature (*T*, *T*<sup>2</sup>), and interactions between the linear components of salinity and temperature (*S* × *T*) are determined in regard to mortality of the megalops stage. The individual regression coefficients are then compared with their respective standard errors as a test of significance; Table 4-49 represents a summary of these tests.

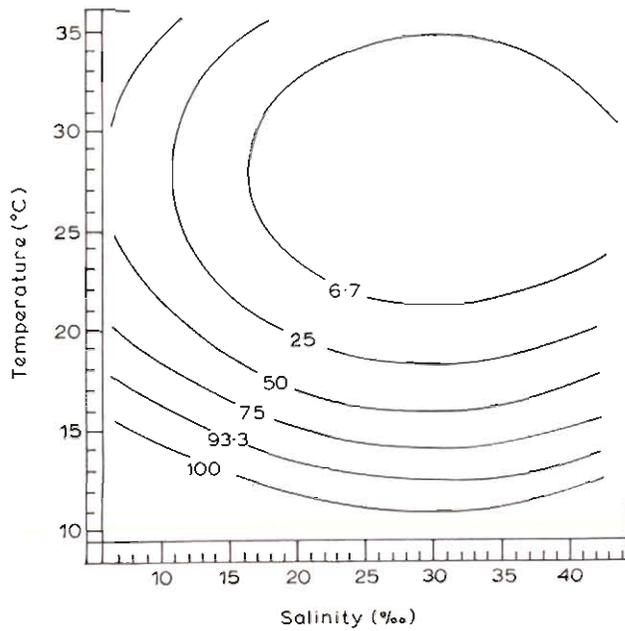


Fig. 4-84: Estimation of percentage mortality of megalops of blue crabs *Callinectes sapidus* based on fitting a response surface to mortalities observed under 23 different combinations of salinity and temperature. (After COSTLOW, 1967; redrawn.)

According to Fig. 4-84, within wide ranges of salinities and temperatures (11‰S to more than 44‰S, 18° C to more than 35° C), 25% mortality or less is predicted. A steady increase in mortality can be expected, however, if a decrease in salinity is accompanied by a decrease in temperature. COSTLOW (1967) further points out that any effect due to direct interaction of salinity and temperature ( $S \times T$ ) is absent; the mortality contours approximate perfect circles and are not skewed as would be expected if interaction were a significant factor in regard to the salinity tolerance of the megalops larvae. COSTLOW presents the hypothesis that survival

Table 4-49

Statistical analysis of salinity/temperature tolerance experiments on megalops stages of the crab *Callinectes sapidus* (After COSTLOW, 1967)

Mortality	Significance	Duration	Significance
$S$	1% level	$S$	not significant
$S^2$	1% level	$S^2$	5% level
$T$	1% level	$T$	1% level
$T^2$	1% level	$T^2$	1% level
$S \times T$	not significant	$S \times T$	not significant

and duration of the megalops of *Callinectes sapidus* in the field are directly associated with the time of hatching, the time at which the megalops is reached in relation to seasonal changes in water temperature, and the salinity in which the final zoeal moult occurs. Comparable papers have been published on the salinity tolerances of larval stages of other decapod crabs, e.g. *Sesarma cinereum* (COSTLOW and co-authors, 1960), *Panopeus herbstii* (COSTLOW and co-authors, 1962), *Rhithropanopeus harrisii* (COSTLOW and co-authors, 1966); see also COSTLOW and BOOKHOUT (1965).

CRISP and COSTLOW (1963) studied the combined effects of salinity and temperature on tolerances of developing embryos of the cirripedes *Balanus eburneus*, *B. amphitrite amphitrite* and *Chelonobia patula*. In salinities between 25‰ and 40‰, embryos develop (*in vitro*) at the normal speed; in salinities between 15‰ and 25‰ or between 40‰ and 60‰, developmental rates become retarded and only some of the eggs hatch. Salinity tolerance is not influenced appreciably by temperature within the thermal range normally encountered in the habitat. Salinity tolerance of the first and second stage nauplii is similar to that of the embryos; however, the actual limits are to some extent dependent on the salinity to which the eggs have been exposed during development. In *Balanus eburneus*, interaction between salinity and temperature is scarcely significant (Fig. 4-85); there is a tendency,

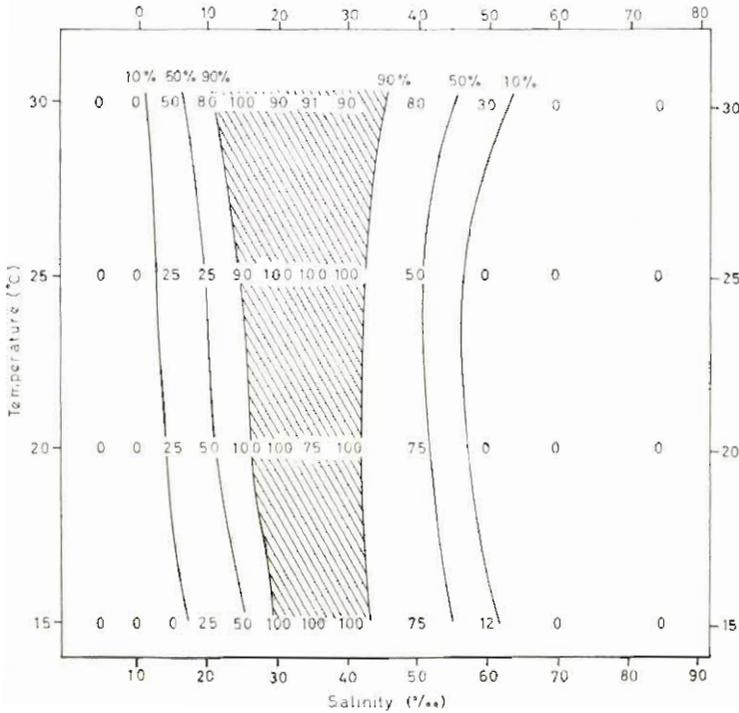


Fig. 4-85: Salinity tolerance of embryos (stages 5 to 9) of the cirripede *Balanus eburneus* as a function of temperature (15°, 20°, 25°, 30° C). The hand-fitted lines represent the probable position of contours of equal survival percentages. Hatched area: highest survival and hatching rates. (After CRISP and COSTLOW, 1963; modified.)

however, for the survival area to enlarge at higher test temperatures. The experimental conditions covered only the temperature range normally encountered in the habitat during the breeding season; more extreme temperatures might have yielded more pronounced interaction. Similar observations on *Chelonobia patula* at 25° and 30° C, and on *Balanus amphitrite amphitrite* at 15°, 25° and 30° C, indicated little influence of temperature on salinity tolerance in these cirripedes.

JANSEN (1968) investigated the tolerances to salinity and temperature in intertidal species (New Zealand) of the isopod family Sphaeromidae. At the lowest test temperature (10° C), salinity tolerances differ widely, increasing from 18‰ to 35‰S in *Amphoroidea media* to 0‰ to 70‰S in *Pseudosphaeroma campbellensis*. The narrowest tolerance ranges occur in the rocky shore species *Scutuloidea maculata* and *Amphoroidea media* which inhabit algal fronds in exposed areas. Tolerances are wider in algal-cryptic species, being broadest in *Dynamenella cordiforaminalis* (distributed highest and most widely in this group), and narrowest in *D. hirsuta* (restricted to wave-exposed shores). Also in the other species examined, salinity tolerances at 10° C are directly related to the degree of salinity variations encountered by each species in its habitat. At 20° or 30° C, salinity tolerances become reduced in all isopod species studied.

Exposure to subnormal salinities may result in reduced tolerances to other simultaneously effective environmental factors such as temperature, dissolved gases or hydrostatic pressure (e.g. KINNE, 1954a, 1956a, 1964a, 1967a, b). On the other hand, supranormal salinities may lead to increased tolerances to high temperatures (Chapter 3). Of course, such phenomena can only be observed in sub-critical salt concentrations, since very extreme salinities will, *per se*, lead to severe injuries, overriding all other potential responses.

In low salinity habitats (about 6‰S) of the Gulf of Finland (Baltic Sea), the lamellibranchs *Mytilus edulis*, *Cardium edule*, *Macoma baltica* and *Mya arenaria* lose almost completely their ability to survive freezing (freezing tolerance is well developed in populations occupying waters of 30‰ or 35‰S), while the ability to tolerate long periods of exposure to water temperatures just above freezing point (chilling tolerance) does not seem to be affected (THEEDE, 1965a). In northwest Spain, the oyster *Ostrea edulis* suffers increased mortality if salinities decrease during winter (FIGUERAS, 1970).

#### *Tolerance to desiccation*

The term 'desiccation' refers here to the stress endured by intertidal organisms during temporary air exposure. Desiccation is characterized by body water loss which, in turn, is a function of the morphology of the organism involved, as well as of air movement, humidity and temperature, and of the sun radiation received. Body water loss affects directly organismic water and salt balances. Consequently, tolerance to desiccation is related to salinity tolerance. The number of investigations concerned with tolerance to desiccation of invertebrates is rather limited. Intertidal plants have received appreciable attention (Chapter 4.2).

In the intertidal limpet *Acmaea limatula*, desiccation causes responses quite similar to those recorded in high salinities. At normal temperatures, *A. limatula* can easily tolerate normal desiccation periods due to tidal exposure; however, body fluid osmoconcentration may rise appreciably. Extreme osmotic and thermal

conditions appear to be buffered somewhat by the extravisceral water (SEGAL and DEHNEL, 1962). Surprisingly, the low shore level limpet *Siphonaria aspersa* exhibits a higher tolerance to desiccation than *S. capensis* and *S. deflexa* which occupy higher shore levels, but *S. aspersa* loses water at a faster rate, possibly because of greater air exposure of soft body parts, due to lack of a home scar (ALLANSON, 1958). The limpets *Patella aspersa* and *P. vulgata* migrate to favourable microhabitats and vary their preferred intertidal level with age and size (DAVIES, 1969). Proper adjustment of such motile forms to rock area or crevice occupied may increase the total resulting tolerance to air exposure and water loss (e.g. KENSLER, 1967). For *Patella aspersa* and *P. vulgata*, DAVIES (1969) reports some inter- and intraspecific differences in rates of, and tolerances to, water loss; both are correlated with the intertidal distribution of these two species.

BROEKHUYSEN (1941) investigated the tolerances to desiccation of six African intertidal gastropods, *Littorina knysnaënsis*, *Oxystele variegata*, *Thais dubia*, *O. tigrina*, *Cominella cincta* and *O. sinensis*. According to BOKENHAM and co-authors (1938), adults of these species exhibit sequential vertical distributions (Fig. 4-86). The observations by BROEKHUYSEN confirm the findings of BOKENHAM and co-authors, but *T. dubia* extends somewhat higher up than *O. variegata*. With the exception of *C. cincta*, the sequence of zonal distribution and of tolerance to desiccation is parallel. There is, however, little correlation between rate of desiccation (water loss) and zonation sequence. In contrast, BROWN (1960) reports some correlation between rate of water loss and distribution in six species of intertidal gastropods. Direct parallelism of desiccation tolerance and intertidal distribution can only be expected in cases in which the stress imposed by desiccation represents the primary limiting environmental entity (ecological master factor) over longer periods of time.

Semiterrestrial and terrestrial crabs often have to tolerate extended periods of desiccation. It appears that their ability of hypo-osmotic regulation assists in tolerating water evaporation from the branchial chamber (JONES, 1941). However, the amount of salt contained in the small volume of branchial fluid, e.g. in the crab *Pachygrapsus crassipes*, is, according to GROSS (1955), insufficient to cause a harmful rise in osmoconcentration of body fluids, even if it were completely absorbed. Nevertheless, when out of water, gills must be kept moist in order to facilitate respiration; consequently, gills exposed to air tend to lose water. Continued extensive water loss from evaporation may lead to significant increases in blood and tissue osmoconcentration (JONES, 1941; PARRY, 1953). When the terrestrial *Gecarcinus lateralis* is desiccated, its blood sodium concentration is not elevated as much as in desiccating *Pachygrapsus crassipes*; nor does its intracellular potassium shift into the blood space as in *P. crassipes* (GROSS, 1963b). The inability of *P. crassipes* to regulate its blood potassium under desiccation stress has been suggested by GROSS (1958) as a factor limiting its capacity to occupy truly terrestrial habitats.

Intertidal isopods from New Zealand vary greatly in their ability to tolerate desiccation (JANSEN, 1968). At 10° C and 100% relative humidity, 100% of the representatives (10 individuals per temperature-humidity combination) of each species tested survived for 24 hrs, except *Scutuloidea maculata* (50% survival) and *Amphoroidea media* (80%). These two less tolerant species live on exposed shores

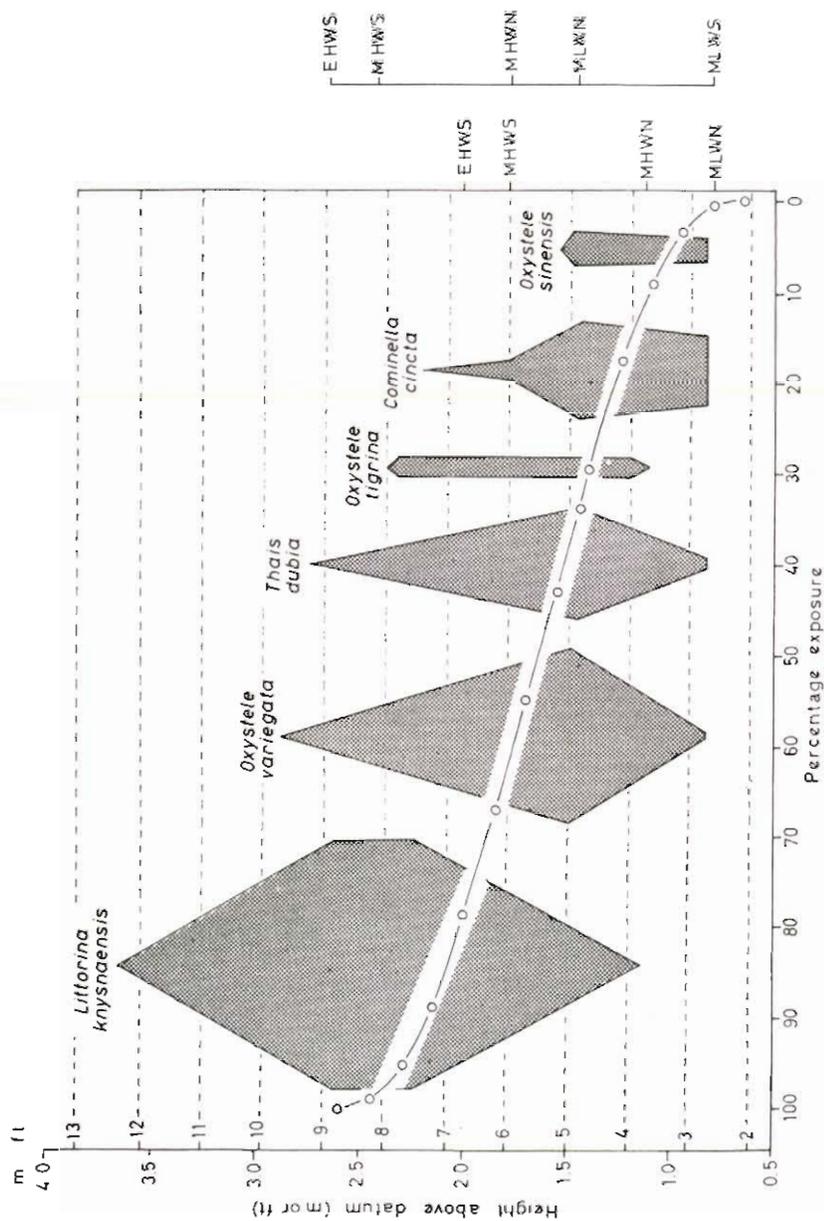


Fig. 4.86: Tolerances to desiccation, expressed as differences in vertical distribution, in six African intertidal gastropods. Two series of tide levels are indicated (right scale); the lower ones represent levels calculated from tide-gauge records, the upper ones are raised 67 cm (2.2 feet) above the lower ones to allow for wash-zone influences. EHWS: extreme high water—spring tides; MHWS: mean high water—spring tides; MEHW: mean high water—neap tides; MLWN: mean low water—neap tides; MLWS: mean low water—spring tides. Superimposed upon the figure is a curve, calculated from tide-gauge records, showing percentage exposure at the various levels; this curve is related to the upper series of tide levels at St. James and Simonstown, False Bay (South Africa). (After BOKENHAM and co-authors, 1938; modified.)

on algal fronds, rarely exposed to air. At 10° C and 70% relative humidity, survival is reduced in all species, except *Isocladus armatus* and *Dynamenopsis varicolor*; none of the *Scutuloidea maculata* and *Amphoroidea media* tested was able to survive (Table 4-50). At 20° and 30° C, all isopods died, except *Exosphaeroma planum*.

Table 4-50

Tolerance to desiccation in intertidal Sphaeromidae from New Zealand waters. Percentage survival (of 10 individuals in each case) after 24 hrs at 100 or 70% relative humidity (r.h.) and at 10°, 20° or 30° C. Specimens of middle size range (After JANSEN, 1968, 1971; modified)

	10° C		20° C		30° C	
	100% r.h.	70% r.h.	100% r.h.	70% r.h.	100% r.h.	70% r.h.
<b>Marine species living among stones</b>						
<i>Isocladus armatus</i>	100	100	0	0	0	0
<i>Exosphaeroma obtusum</i>	100	85	0	0	0	0
<i>Isocladus calcareus</i>	100	65	0	0	0	0
<i>Cymodoceella egregia</i>	100	25	0	0	0	0
<b>Marine algal-cryptic species</b>						
<i>Dynamenella cordiforaminalis</i>	100	70	0	0	0	0
<i>Dynamenopsis varicolor</i>	100	100	0	0	0	0
<i>Dynamenella huttoni</i>	100	90	0	0	0	0
<i>Dynamenella hirsuta</i>	100	60	0	0	0	0
<b>Marine algal-frond species</b>						
<i>Scutuloidea maculata</i>	50	0	0	0	0	0
<i>Amphoroidea media</i>	80	0	0	0	0	0
<b>Brackish-water species</b>						
<i>Pseudosphaeroma campbellensis</i>	100	60	0	0	0	0
<i>Exosphaeroma planum</i>	100	90	90	75	35	0

GLYNN (1968) examined the ability of intertidal echinoderms to withstand desiccation under unprotected and protected habitat conditions in Puerto Rico. He studied representatives of five species: *Brissus unicolor*, *Lytechinus variegatus*, *Tripneustes ventricosus*, *Diadema antillarum* and *Echinometra lucunter*. Twenty-one individuals of each species were exposed on coral rubble in the open sunlight (unprotected) over a period of 6 hrs. First after half an hour, and then at hourly intervals, the wet weights of 3 individuals were recorded and thereafter the test individuals returned to sea water, where they were allowed to recover for 15 to 20 hrs. Parallel experiments were conducted under conditions of some degree of sun protection (*T. ventricosus*, *E. lucunter* and *D. antillarum* were shaded under rocks; *B. unicolor* remained buried just below the surface of wet sediment; *L. variegatus* was allowed to cover itself with algae, coral shingle, etc. (Figs. 4-87, 4-88)). Water loss (weight loss) as a function of time is essentially linear in unprotected and protected individuals. However, in unprotected individuals, water loss is considerably faster. Weight loss due to defecation amounted to less than 1% of wet body weight and therefore was omitted from calculations. The ranges in wet weight of

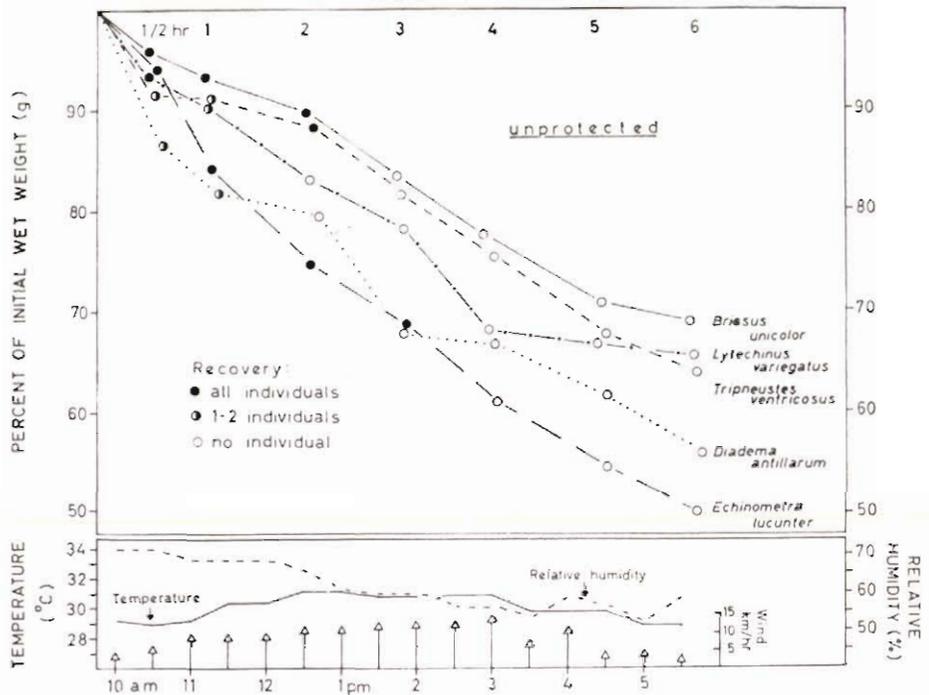


Fig. 4-87: Desiccation tolerance of five littoral echinoids exposed directly to atmospheric conditions (unprotected). Each symbol denotes the mean percentage wet weight of three individuals and their ability to recover (symbol explanation lower left). A summary of habitat weather conditions (atmospheric temperature, relative humidity, wind velocity) is presented in the lower part of the figure. The sky was clear until 3.30 p.m. (After GLYNN, 1968; modified.)

unprotected individuals were: *Lytechinus variegatus* 18.4 to 59.1 g, *Tripneustes ventricosus* 25.6 to 101.6 g, *Echinometra lucunter* 8.2 to 12.4 g, *Diadema antillarum* 80.3 to 212.1 g, *Brissus unicolor* 30.0 to 48.7 g; the corresponding values of protected individuals were: 9.9 to 47.4 g, 15.2 to 82.6 g, 5.2 to 24.5 g, 106.2 to 254.7 g and 29.2 to 70.6 g. Unprotected urchins of all species died (open circles in Fig. 4-87) after 3 hrs, all *Lytechinus variegatus* and *Diadema antillarum* within 2 hrs; water loss was lowest in *Brissus unicolor* (about 30% of initial wet weight after 6 hrs) and highest in *Echinometra lucunter* (50% after 6 hrs). Among the protected urchins, *Tripneustes ventricosus* exhibited the highest tolerance to desiccation, while *Lytechinus variegatus*—despite the habit of heaping debris on its aboral body surface during daylight hours—showed the lowest tolerance (Fig. 4-88); survival rates of *L. variegatus* remained essentially the same, indicating that heaping of large amounts of moist algae thalli does not significantly prolong its ability to withstand desiccation. In *B. unicolor*, desiccation tolerance was less than in unprotected individuals; GLYNN (1968) assumes that the explanation for this apparent discrepancy lies in the intense heating of the moist sediment: by 2.17 p.m., sediment temperature had climbed to 37.7° C (in thermal tolerance experiments all *B. unicolor* died at 38° C within 2 hrs).

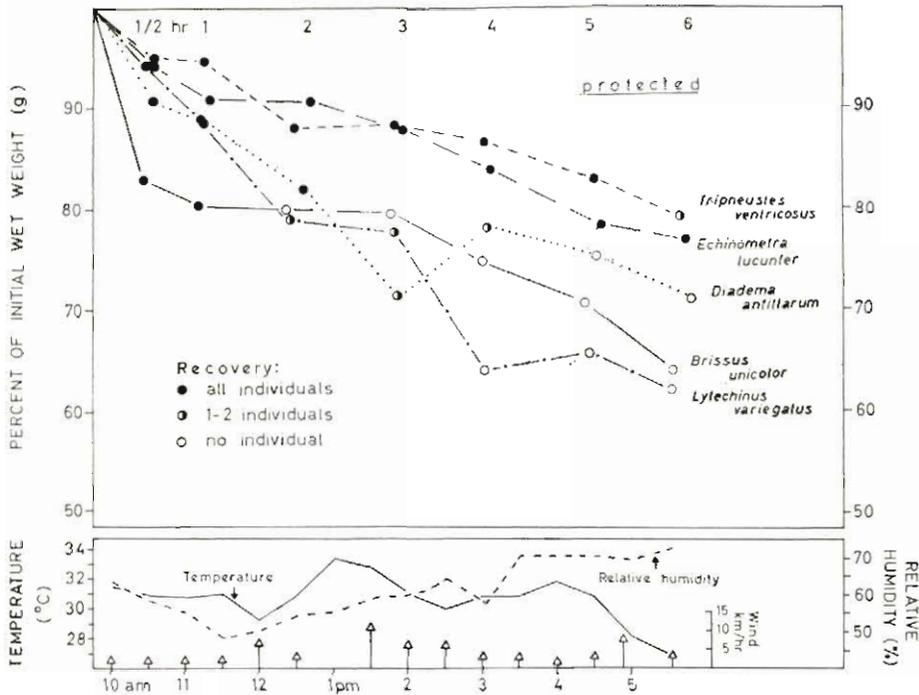


Fig. 4-88: Desiccation tolerance of five littoral echinoids exposed to atmospheric conditions with some degree of protection. See also legend to Fig. 4-87. The sky was clear until 5.00 p.m. (After GLYNN, 1968; modified.)

Tolerance to desiccation is of utmost ecological importance in young intertidal invertebrates which, once attached, cannot leave their chosen site. Newly settled barnacles, for example, depend greatly on desiccation conditions, even though adult specimens may survive long periods of air exposure. Adult *Chthamalus depressus* survived at least 119 days at normal temperatures on a laboratory bench (MONTEROSSO, 1930). In 1932, MONTEROSSO (consult for further references) reported that *C. depressus* tolerates immersion in oil for 14 days. Specimens survive over periods of many months if immersed in sea water for a few hours at infrequent intervals. Controlled use of opercular valves allows intertidal barnacles to use their mantle cavity as a 'lung' while air exposed, with a minimum loss of water (BARNES and BARNES, 1957, 1964; CRISP and SOUTHWARD, 1961; BARNES and co-authors, 1963; GRAINGER and NEWELL, 1965; AUGENFELD, 1967).

BARNES and BARNES (1964) have looked into the functional prerequisites which enable intertidal cirripedes to withstand desiccation. Intertidal barnacles first allow access of oxygen through the opercular micropyle and minimize water loss; with increased desiccation stress, the mantle cavity may remain completely closed and an anaerobic milieu set up. Under these conditions, metabolic rates, aerobic or anaerobic, are grossly reduced. This reduction is related, apparently, to a fall in ATP, concomitant with a similar reduction in ATP-ase; there may also be recourse to an alternative metabolic pathway. In *Chthamalus depressus*, the fall in ATP content, associated with reduced oxygen uptake, occurs within 3 days after air exposure. Accumulation of glucose-6-phosphate within 6 days indicates that

subsequent reactions become limiting. On resorting to anaerobic metabolism, ATP production per unit substrate will be lowered further. Body water loss (whether due to evaporation or high salinity) reduces respiratory rates even more; it is probably this extremely lowered metabolic level which allows intertidal barnacles to survive long periods of air exposure.

'The following sequence of events may be envisaged: on transference to air, access to the latter is at first maintained via the micropyle, and aerobic respiration, at the reduced rate under conditions characteristic of inanition, continues; there will be water loss at this stage. Eventually dehydration stress causes complete occlusion of the mantle cavity and a resort to anaerobiosis; this point is nicely adjusted so that the amount of dehydration is adequate to make a reduced metabolic rate acceptable without affecting the viability. Reserves are only slowly used up and the animal can remain alive for long periods. Once a certain proportion of the carbohydrate has been used up both protein and fat are mobilized . . . and in the case of fat the metabolic water may help to maintain optimal hydration. Ultimately the accumulation of toxic products such as lactic acid or the depletion of reserves and cellular destruction kill the animal' (BARNES and BARNES, 1964, p. 26).

Detailed experiments on desiccation tolerance in intertidal barnacles have been conducted by FOSTER (1969a), employing the desiccation apparatus designed by KENSLER (1967). FOSTER examined the tolerance to desiccation of *Balanus*

Table 4-51

Tolerance to desiccation in embryos of *Balanus balanoides*. Numbers are given of adults that, after 24-hr recovery, yielded ovigerous lamellae; these were removed and placed in sea water. Good hatch: most of the nauplii swimming vigorously within 1 hr; poor hatch: only a few nauplii swimming; no hatch: no swimming nauplii observed. Mean rostro-carinal diameter of adults: 10.7 mm. 0% relative humidity; 10° C (After FOSTER, 1969a)

Desiccation period (hrs)	Adults recovered			Adults died			Adult mortality (%) from probit regression on mortality data
	good hatch	poor hatch	no hatch	good hatch	poor hatch	no hatch	
86	11	0	0	0	0	0	0
97	5	1	0	0	0	0	0
109	4	1	0	0	0	0	0
132	5	0	0	0	1	0	6
146	5	0	0	0	4	1	14
164	5	0	0	0	0	5	27
182	5	1	0	3	0	4	43
192	12	1	0	1	1	8	54
204	3	1	0	0	0	9	65
214	11	1	0	0	0	11	71
228	0	0	0	0	1	11	80
258	0	1	0	0	0	11	92
Totals	66	7	0	4	7	60	

*balanoides* at different life-cycle stages: in embryos within the mantle cavity of adults, in freshly settled cyprids, in settled cyprids and spat, and in adult specimens.

The embryos of *Balanus balanoides* are retained within the mantle cavity of the parent and therefore experience environmental stresses comparable to those endured by the parent individual. The tolerance to desiccation of embryos ready to hatch, in relation to the tolerance of the parent barnacles, is exemplified in Table 4-51. Following the desiccation periods listed, the adults were allowed to recover for 24 hrs in running sea water. The ovigerous lamellae from recovered and dead barnacles were then removed and teased apart in finger bowls containing sea water. Hatching of nauplii occurred within 1 hr, if at all. There exists a strong correlation between hatching of nauplii and recovery of adults on the one hand, and failure of nauplii to hatch and death of adults on the other. It is unlikely that the embryos receive prolonged protection from water retained in the adult's mantle cavity as the latter appears dry well before any noticeable shrinkage occurs of prosoma or mantle tissue. Some lamellae crumble readily, yet still yield vigorously swimming nauplii. Hence the nauplii must have been protected sufficiently by the thin common lamella membrane, their individual egg membranes and their external integument to allow them to survive as long as the parents. Of course, both embryos and parents are protected by adult shell and operculum.

Cyprids of *Balanus balanoides*, after an exploratory phase of settlement activity, cement their antennules to the substratum and undergo metamorphic re-organiza-

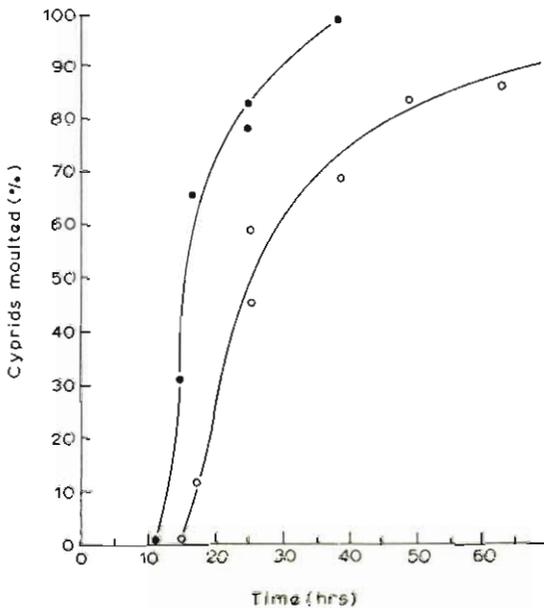


Fig. 4-89: *Balanus balanoides*. Time to moulting in recently settled cyprids. Filled circles: immersion in still sea water; open circles: exposure to air of 100% relative humidity; 15°C. No moulting occurred at or below 75% relative humidity. (After FOSTER, 1969a; redrawn.)

tion, culminating in the moult to the young adult-form barnacle or spat (FOSTER, 1969a). In FOSTER's experiments, small Tufnol panels, on which many cyprids had previously been settled and removed ('conditioned' panels), received many more exploring cyprids than did previously unused panels. On conditioned panels, settlement began as early as 19 mins after exploratory attachment. It is assumed that, under field conditions aiding settlement, a cyprid can cement itself permanently within 30 mins. After settlement, cyprids kept in well oxygenated, running sea water moult to the spat in about 20 hrs at normal temperatures. On a shore with semidiurnal tides, freshly settled cyprids are thus likely to be air exposed for one or two tides before the moult. In water-saturated air, the Tufnol panels retain a film of sea water and most of the cyprids complete metamorphosis and moult to the spat (Fig. 4-89), although they take longer to shed the carapace than individuals fully immersed. Cyprids exposed continuously to dry air do not moult. In order to assess the effect of desiccation on the process of metamorphosis,

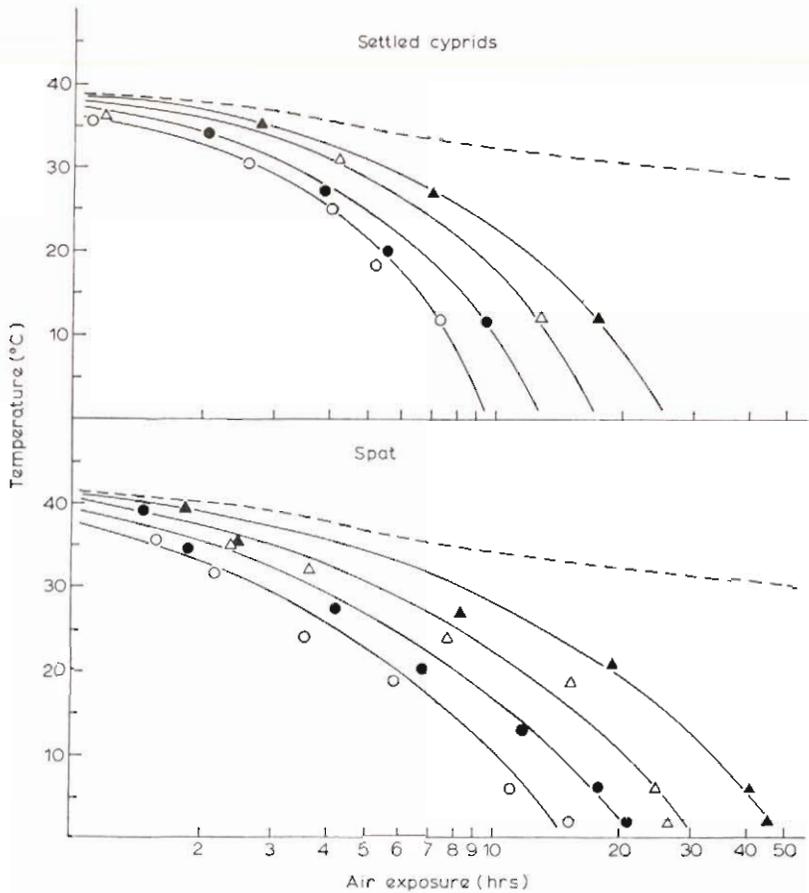


Fig. 4-90: *Balanus balanoides*: Median lethal times (hrs) of settled cyprids and spat. Filled triangles: 75% relative humidity (r.h.); open triangles: 50% r.h.; filled circles: 25% r.h.; open circles: 0% r.h. Broken curves: temperature survival curves of continuously submerged individuals. (After FOSTER, 1969a; redrawn.)

three batches of recently settled cyprids were exposed to 75% relative humidity in desiccators at 21°, 13° and 4° C. After the surface had dried, the time required to complete moulting increased roughly in proportion to the desiccation period. It is clear, however, that the delay in metamorphosis is normally less than the time spent out of water. FOSTER concludes that either some premoult changes take place during emersion, or such changes proceed faster than normal after re-immersion. Prolonged emersion at high temperatures (e.g. 9 hrs at 21° C) results in a delay at least equivalent to the desiccation period, indicating that such conditions further retard metamorphosis or prevent compensatory acceleration. After 12 hrs at 21° C, 42% of the cyprids fail to complete metamorphosis within 48 hrs of re-immersion, and after 24 hrs at 4° C, 20% fail to recover. Desiccation effects are externally apparent first as lateral indentations of the anterior carapace; later the cyprid literally shrivels and dics. In summary then, recently settled cyprids under desiccation stress can proceed with premoult metamorphic processes, but if the stress becomes too severe (prolonged periods of low humidity, high temperatures) metamorphosis is retarded and eventually stopped, at first temporarily, then permanently, with ensuing death.

For settled cyprids and spat of *Balanus balanoides*, median lethal times (determined from regression lines fitted to probit-logarithmic time transformations of mortality data) were plotted (Fig. 4-90). At lower temperatures, a quicker kill is obtained at lower humidities, while at higher temperatures the convergence of the

Table 4-52

*Balanus balanoides*. Median lethal times (to the nearest hr) of settled cyprids and spat. The data, extracted from Fig.4-90, reveal increased survival times of spat over cyprids under similar conditions of humidity and temperature (After FOSTER, 1969a)

Relative humidity (%)	Temperature (°C)	Median lethal times (hrs)		Increased survival time of spat over cyprids
		cyprids	spat	
0	20	5	5	0
	15	7	8	1
	10	8	10	2
	5	9	11	2
25	20	7	8	1
	15	8	11	3
	10	10	14	4
	5	11	18	7
50	20	9	12	3
	15	11	16	5
	10	13	21	8
	5	16	25	9
75	20	12	20	8
	15	15	26	11
	10	18	33	15
	5	22	42	20

curves for each humidity towards the time-temperature curve indicates the increasing importance of temperature in directly causing death (FOSTER, 1969a). A comparison of the curves for settled cyprids and spat (Table 4-52) reveals higher desiccation (and temperature) tolerance of spat. This difference increases with increasing humidity. For spat, the contours of median lethal times as a function of humidity and temperature are given in Fig. 4-91. The interpretation of this diagram is aided by describing the 'desiccation potential' (KENSLE, 1967) of various humidity-temperature combinations in terms of the saturation deficit which is the amount  $A$  by which the water vapour present falls short of the saturation value:

$$A = p_s - p_o = p_s(1 - r.h.)$$

$p_o$  is the actual,  $p_s$  the saturated water vapour pressure;  $r.h.$  represents relative humidity). Contours of equivalent desiccating conditions—all other factors being taken as equal—are shown as broken lines. The desiccation potential refers to the

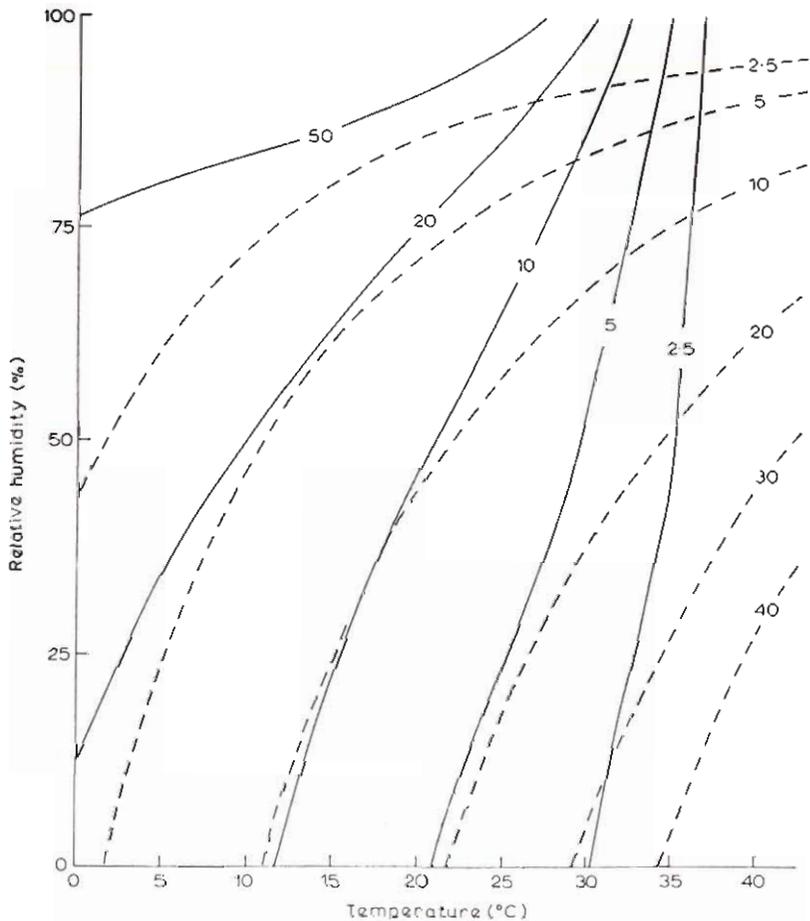


Fig. 4-91: *Balanus balanoides*. Contours of median lethal times (in hrs; solid curves) of spat as a function of relative humidity and temperature. Broken curves represent contours of desiccation potentials in mm Hg aqueous vapour pressure deficiency. (After FOSTER, 1969a; redrawn.)

main amount of air in the desiccator, not necessarily to the air at the surface of the test individuals, where evaporation occurs. The rate of evaporation from the integument depends on the humidity and temperature gradients between body surface and main amount of air; moving air, which is a major feature of the KENSLER apparatus, will tend, however, to reduce such gradients. At low relative humidities, the desiccation-potential curves parallel to some extent the survival-time contours (median lethal times are roughly proportional to the reciprocal of desiccation potential). At high relative humidities and at high temperatures, the survival curves depart from the desiccation-potential curves, and become nearly parallel to the humidity axis. This implies that temperature becomes the main determinant of survival time (FOSTER, 1969a, b). At low humidities and very low temperatures, evaporation causes the survival curves to become separated from the temperature-death curves; apparently dehydration becomes the main cause of death here.

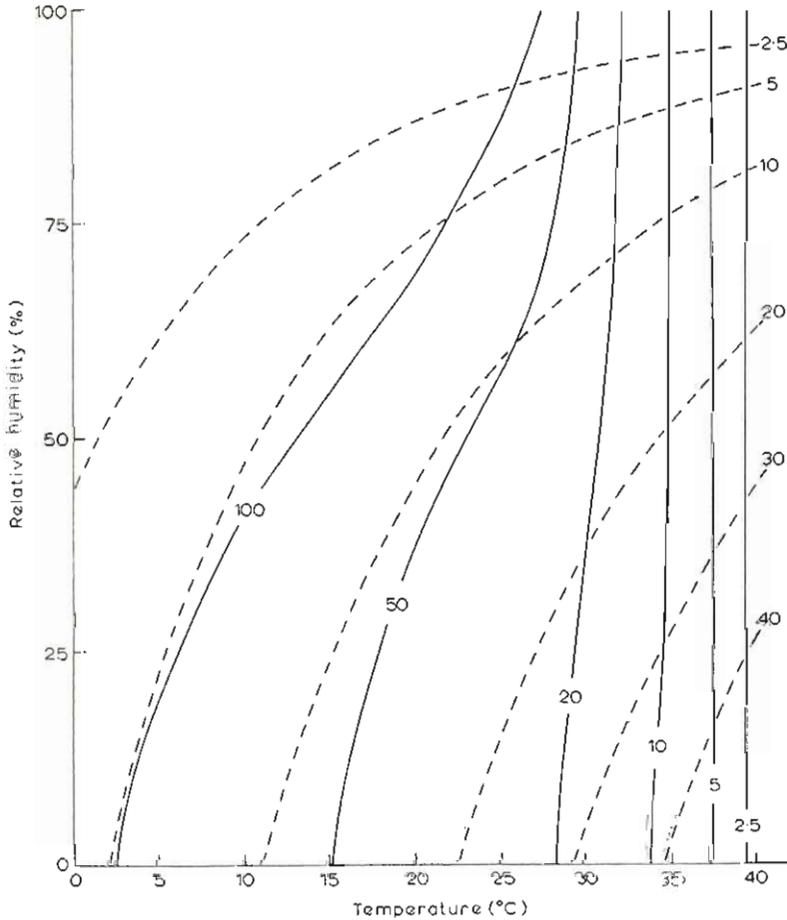


Fig. 4-92: *Balanus balanoides*. Contours of median lethal times (in hrs; solid curves) of barnacles of 5 mm basal diameter as a function of relative humidity and temperature. Broken curves represent contours of desiccation potentials in mm Hg aqueous vapour pressure deficit. (After FOSTER, 1969a; redrawn.)

The contours of the median lethal times for *Balanus balanoides* of 5 mm basal diameter are given in Fig. 4-92. Survival chances are similar but somewhat increased as compared to settled cyprids and spat. Stronger calcification of shell plates and valves results in close-fitting structures which further reduce water loss from the integument. The tolerance to desiccation increases linearly with body size. The larger the barnacle, the greater the ratio volume : surface area, and the longer the period of time in which a given proportion of the body water is lost.

FOSTER (1969a) arranged the contour diagrams along a third axis representing a characteristic linear dimension, the basal rostro-carinal diameter. The resulting three-dimensional diagram—relating median lethal time to humidity, temperature and size—is illustrated in Fig. 4-93 for *B. balanoides*; comparable diagrams for *B. crenatus* and *Elminius modestus* are shown in Figs 4-94 and 4-95 respectively. The form of the contours representing the interaction of humidity and temperature of the air in causing death of each size group lies on the *XOY* plane. The advantage of increased size in delaying death under otherwise identical desiccation conditions becomes obvious by following the curves along the *Z* axis. The most favourable

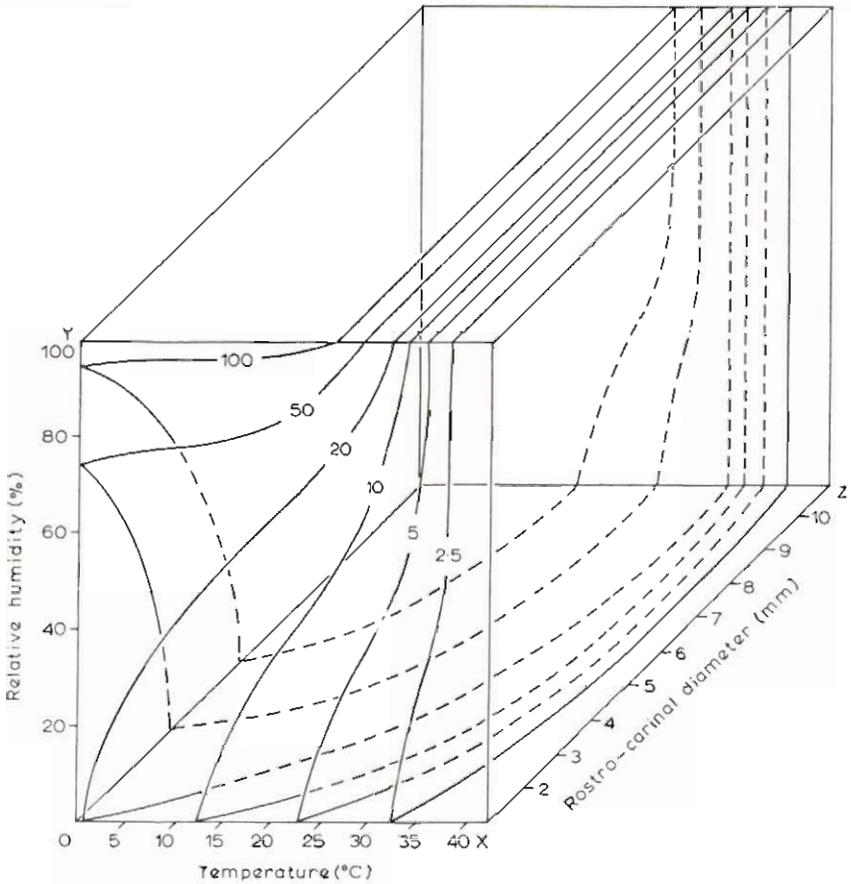


Fig. 4-93: *Balanus balanoides*. Contours of median lethal times (hrs) at different humidities (OY) and temperatures (OX) in relation to basal rostro-carinal diameter (XZ). (After FOSTER, 1969a; redrawn.)

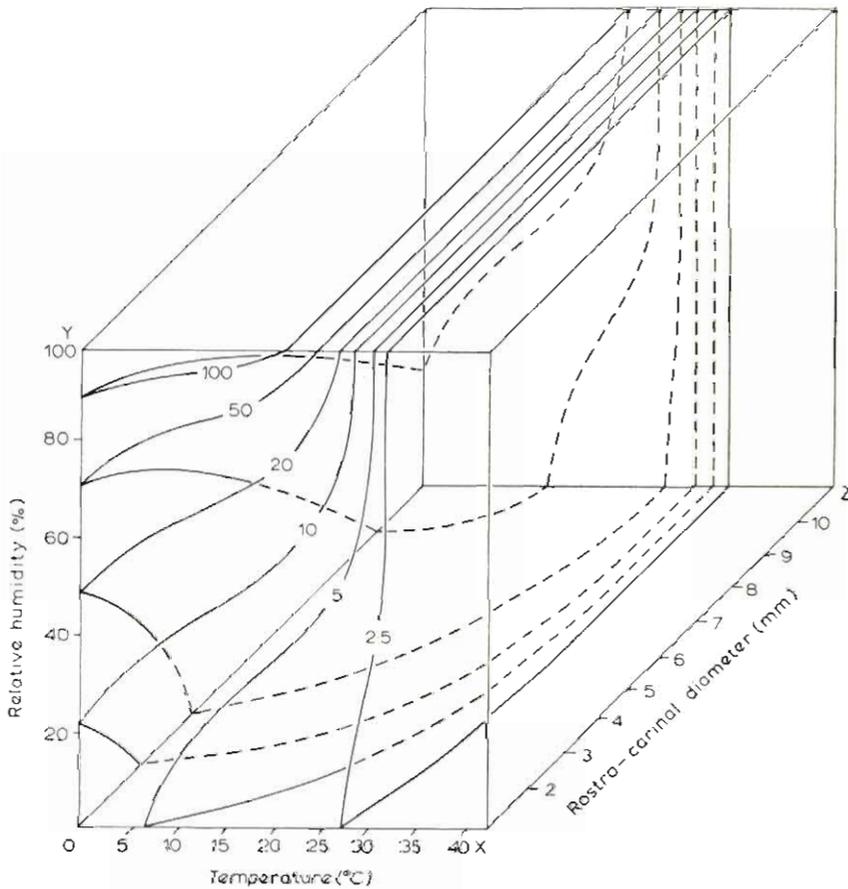


Fig. 4-94: *Balanus crenatus*. Contours of median lethal times (hrs) at different humidities (OY) and temperatures (OX) in relation to basal rostro-carinal diameter (XZ). (After FOSTER, 1969a; redrawn.)

region for survival in the space enclosed by the axes is that of highest relative humidity, lowest temperature and greatest diameter. Since lethal temperatures as such are not size dependent in adult barnacles, the larger individuals may be killed directly by high temperatures whereas smaller specimens exposed to identical conditions may die earlier, primarily due to desiccation.

Survival times under desiccation stress are plotted against rostro-carinal diameters of the three barnacle species in Fig. 4-96. This diagram provides empirical evidence that survival is linearly proportional to a characteristic linear dimension of the barnacle. *Balanus crenatus* is most susceptible to desiccation; if significant, the small differences between *Elminius modestus* and *Balanus balanoides* suggest slightly longer survival of the *B. balanoides* under critical desiccation stress; however, near the upper critical temperature, *E. modestus* survives slightly longer, due to its higher tolerance to heat. In an attempt to relate the survival times of barnacles of various sizes to desiccation conditions in the intertidal zone, FOSTER (1969a) compared the temperatures causing 50% mortality at zero

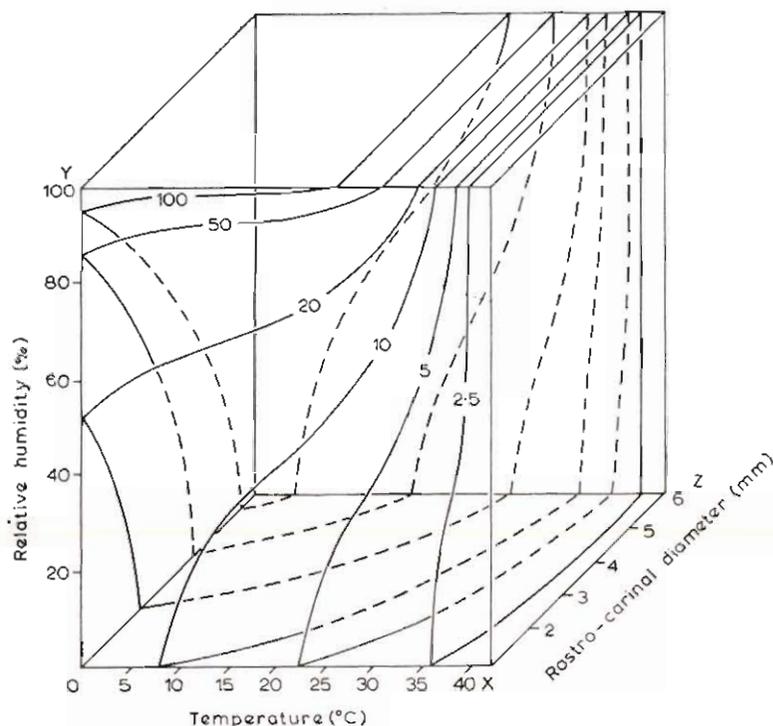


Fig. 4-95: *Elminius modestus*. Contours of median lethal times (hrs) at different humidities (OY) and temperatures (OX) in relation to basal rostro-carinal diameter (XZ). (After FOSTER, 1969a; redrawn.)

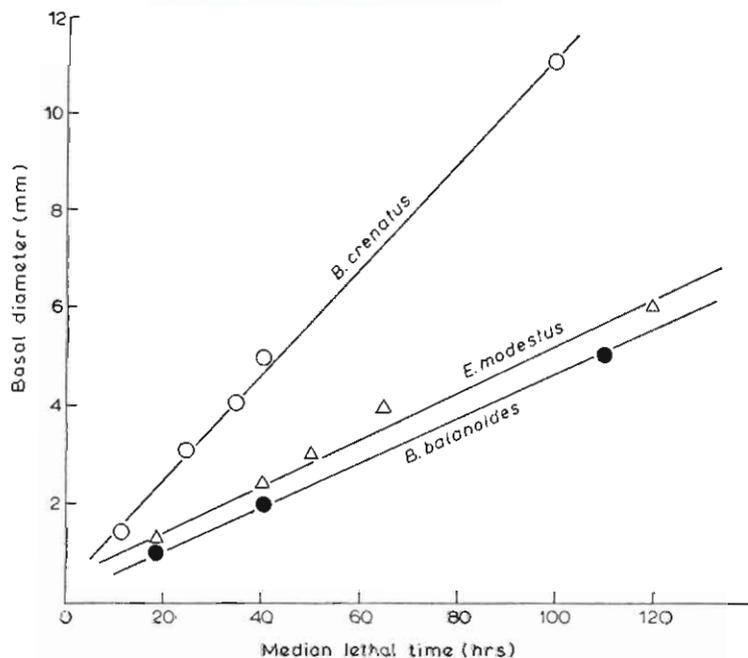


Fig. 4-96: Relationship between median lethal times and basal diameters of *Balanus crenatus*, *Elminius modestus* and *B. balanoides* under critical desiccation stress, i.e. at a desiccation potential of 5 mm Hg aqueous vapour pressure deficiency. (After FOSTER, 1969a; redrawn.)

humidity after 6 hrs exposure. He found that smaller individuals, which are more quickly susceptible to water loss, become lethally dehydrated at temperatures well below the upper thermal limit in less than 6 hrs. Young settled stages of the three species tested are in danger of desiccation at field temperatures commonly experienced. *Chthamalus stellatus* is very well adapted to withstand desiccation stress; the spat survive as long or longer than *Balanus crenatus* well over a thousand times greater in volume.

FOSTER (1969a) also determined the rate of water loss from *Balanus crenatus*, *Elminius modestus*, *Balanus balanoides* and *Chthamalus stellatus* by measuring the increase in blood osmoconcentration (freezing-point depression) of individuals exposed to known humidity-temperature combinations. Mortality and rates of water loss reveal comparable trends in cirripedes of the same base diameter exposed to identical desiccation stress (Fig. 4-97). The low-tidal *B. crenatus* is killed soonest and loses water at the fastest rate; equal-sized *E. modestus* and *B. balanoides* survive for similar lengths of time and lose water at similar rates (in Fig. 4-95, *E. modestus* of 6 mm base diameter is compared to *B. balanoides* of 11 mm diameter); the high-tidal *C. stellatus* exhibits much lower mortality than the

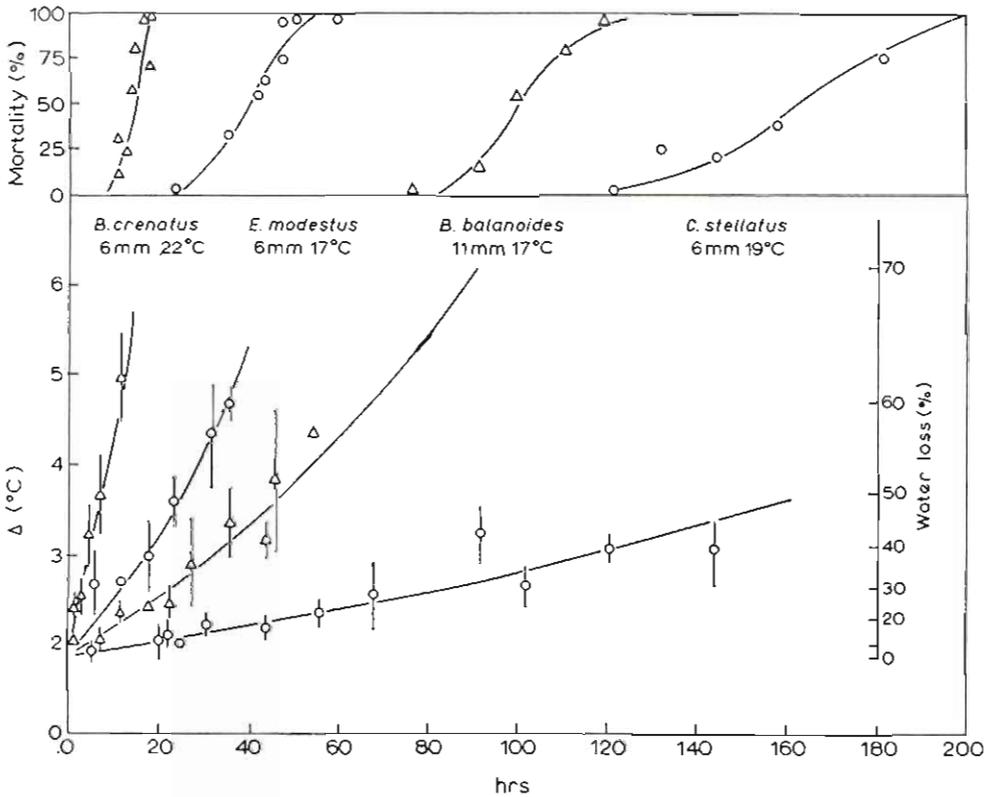


Fig. 4-97: Water loss (%) and blood osmoconcentration ( $\Delta^{\circ}\text{C}$ ), at zero humidity and at the temperatures indicated, in the barnacles *Balanus crenatus*, *Elminius modestus*, *Balanus balanoides* and *Chthamalus stellatus*. Mean values of 5 to 10 individuals; vertical lines: standard deviation. Top: mortality curves of barnacle samples from the same experimental series. (After FOSTER, 1969a; redrawn.)

other three species and loses water at a much slower rate. FOSTER conducted these experiments on laboratory-raised *B. crenatus*, *E. modestus* and *B. balanoides*, but on *C. stellatus* specimens which had settled under habitat conditions on the shore. The *C. stellatus* individuals tested may have been better acclimated, therefore, to retard water loss than those of the other two species which had been kept continually submerged.

There is no correlation between the estimated degree of water loss endured up to the point where death results from desiccation at normal temperatures and the respective intertidal levels occupied by each species (FOSTER, 1969a). *Chthamalus stellatus*, which is most tolerant to desiccation, dies at blood osmoconcentrations no higher than those leading to death in the most susceptible *Balanus crenatus*. Tolerance to desiccation, expressed as the length of survival periods under critical exposure conditions, seems to be related primarily to the ability to restrict the rate of water loss. Interspecific differences in rates of water loss appear to be related to (i) the size of the pneumostome (occasionally formed between the opercular flaps underlying the valves in order to facilitate gaseous exchange during air exposure), (ii) the frequency of its formation, (iii) differing shell porosities. With prolonged exposure to otherwise tolerable desiccation conditions, toxic metabolic waste products may increasingly become the primary cause of death, overriding the detrimental effects of water loss (BARNES and BARNES, 1964).

Some euryhaline marine worms reveal considerable tolerance to desiccation. The sipunculid *Themiste zosterocolum*, for example, can tolerate quite large water losses during air exposure (PEEBLES and FOX, 1933; GROSS, 1954). The worms recover fully upon return to normal sea water after having lost up to 43% of their total body water by evaporation; however, a total water loss of 45% is lethal. The worms do not recover fully if slowly desiccated to comparable degrees over periods of time exceeding those during normal low-tide exposure. Possibly, osmotically active particles are removed from body fluids during desiccation stress—either via particle fixation in tissues or by urinary excretion—resulting in a retardation of increase in internal osmoconcentration. The results obtained by GROSS (1954) suggest fixation of osmotically active particles in tissues, rather than excretion, because no urinary salt loss could be established during desiccation. For further details, the reader is referred to a pertinent discussion by OGLESBY (1969b).

VANDEL (1943, 1954) arranged the families of terrestrial isopods, on the basis of their fitness to tolerate dry air, in the following order: Ligiidae, Trichoniscidae, Oniscidae, Porcellionidae, Armadillidiidae. As a first approximation, this order is also indicative of the progressing degree of morphological specialization to increasingly drier habitats. The Oniscidae are fairly well adjusted to terrestrial life but depend on minimizing water loss through evaporation and on replacing the water lost (EDNEY, 1954). Moisture cannot be absorbed from the air, but can be imbibed through mouth and anus (SPENCER and EDNEY, 1954) or extracted from the food consumed (KEUNEN, 1959). The woodlouse *Tracheoniscus rathkei* can attain its normal life span only if exposed to saturation deficits near zero. In this species, survival time is inversely related to saturation deficit rather than simply to the relative humidity (WHITE and ZAR, 1968).

### Non-genetic resistance adaptation

Non-genetic resistance adaptations (acclimations, acclimatizations) have been defined and discussed in Chapter 3.31 (p. 435). Papers dealing with non-genetic resistance adaptation of invertebrates to salinity variations are fewer in number than those dealing with thermal acclimations. They refer largely to occasional,

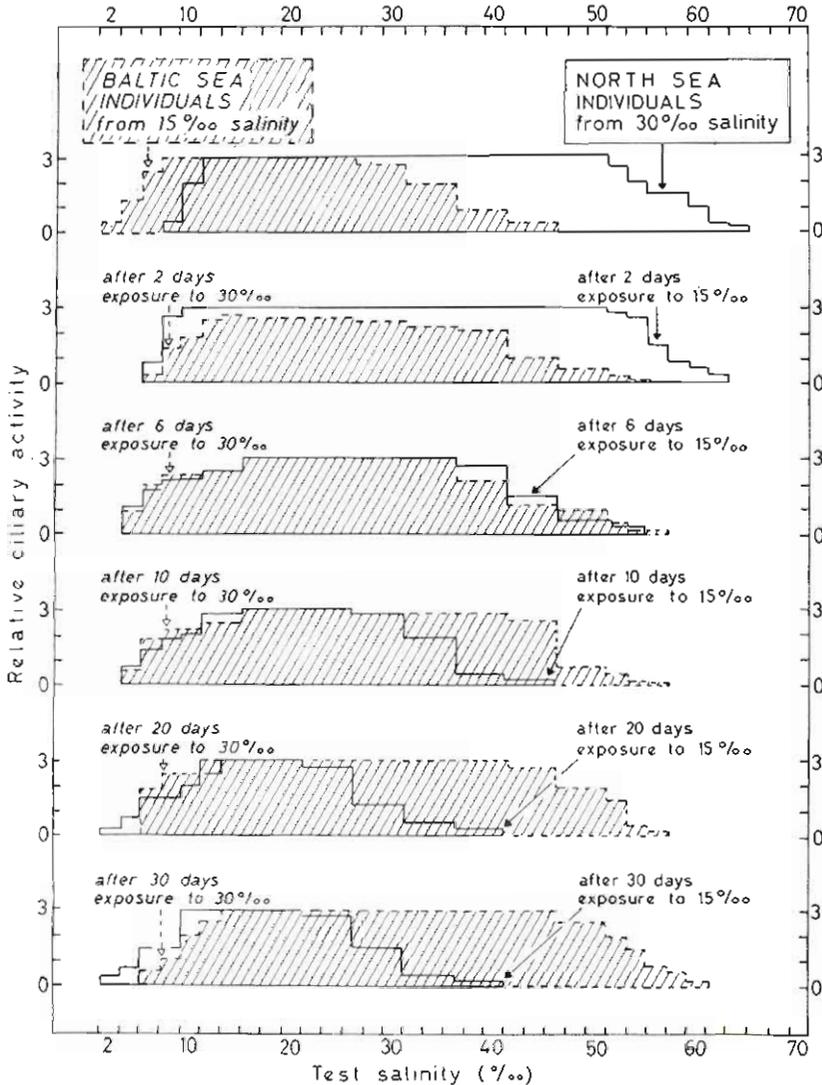


Fig. 4-98: Non-genetic resistance adaptation to salinity in the lamellibranch *Mytilus edulis*. Individuals from Baltic Sea and North Sea were cross-acclimated and gill pieces removed after intervals of 2, 6, 10, 20 and 30 days. The ciliary activity of the excised gill pieces (about 4 mm<sup>2</sup>) was then tested, 24 hrs after transfer into the test salinities. Average values of 10 observations in each case. For quantitative assessment of relative ciliary activity levels consult legend to Fig. 4-79. Test temperature: 10°C. (After THEEDE, 1965a; modified.)

not well-documented observations made under conditions of constant salinities; practically nothing is known about resistance acclimation to salinity fluctuations or to alternations in solute composition, although some investigations on ionic requirements have been carried out (e.g. ROCH, 1924; BERGER, 1929; LOOMIS, 1954; FULTON, 1960, 1962; LENHOFF and BOVAIRD, 1960).

Non-genetic resistance adaptations to different salinity conditions may lead to shiftings in lower and upper salinity tolerance limits, particularly in euryhaline invertebrates of estuaries and other coastal waters characterized by considerable salinity variations (e.g. KINNE, 1964c, d, 1967b).

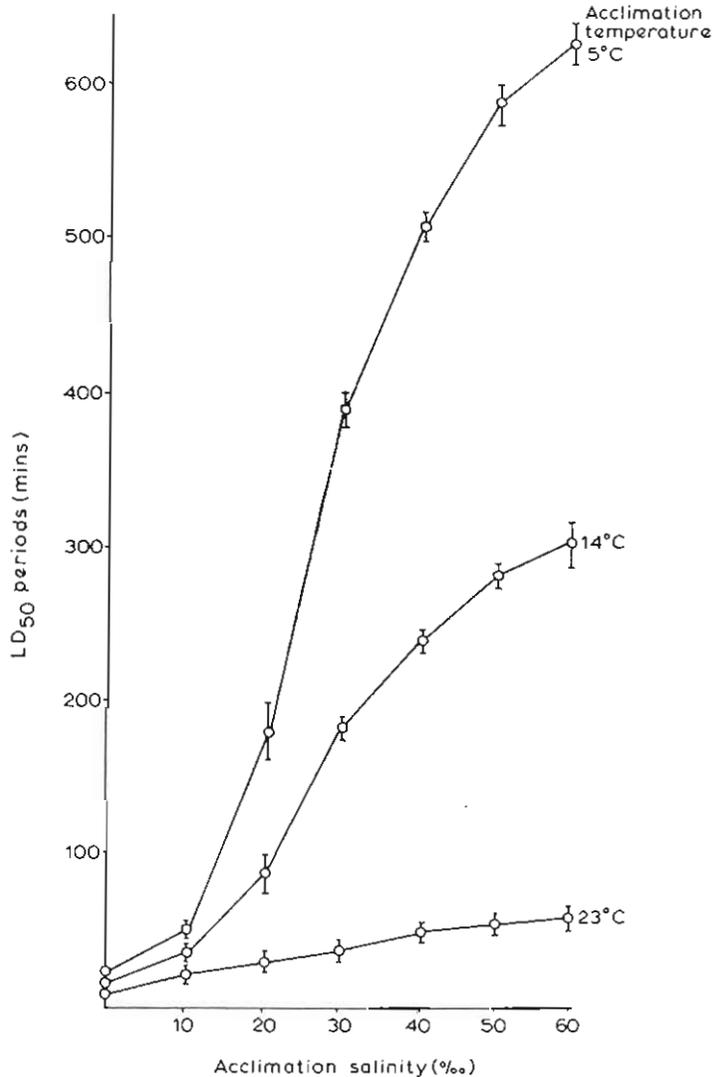


Fig. 4-99: *Enchytraeus albidus*. Effect of different combinations of acclimation salinities (0‰ to 60‰) and temperatures (5°, 14°, 23° C) on cold tolerance; test temperature: -13.2° C. Average values, based on 8 groups of 20 to 25 adult individuals in each case. Vertical lines: reliability intervals. (After KÄHLER, 1970; modified.)

A well worked-out example of non-genetic resistance adaptation to salinity has been published by THEEDE (1965a). THEEDE cross-acclimated *Mytilus edulis* individuals from the Baltic Sea (habitat salinity about 15‰) and the North Sea (habitat salinity about 30‰) and used the ciliary activity of isolated gill pieces (p. 836) as criterion for the states of acclimation. Previous to cross-acclimation, Baltic Sea specimens exhibited a somewhat higher tolerance to low salinities but considerably less resistance to higher salinities than their counterparts from the North Sea (Fig. 4-98, top). During cross-acclimation, these differences diminish and practically disappear after 6 days. Cross-acclimation is completed after about 30 days (Fig. 4-98, bottom). The original differences in salinity tolerance are now essentially reversed: tissues from North Sea specimens show a somewhat higher tolerance to low salinities but a significantly reduced tolerance to higher salinities than do the individuals from the Baltic Sea.

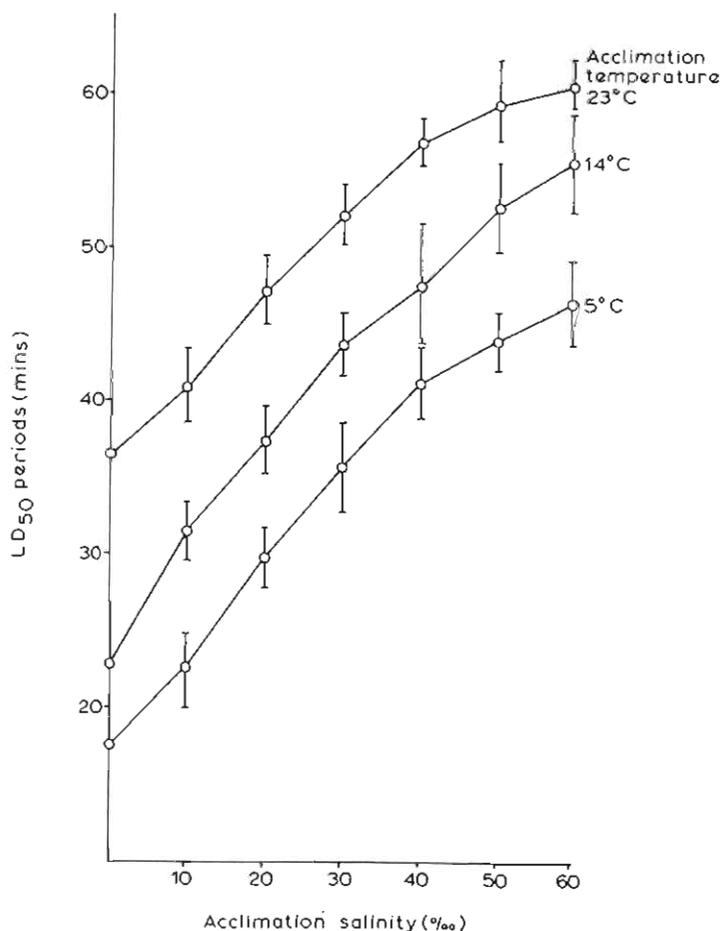


Fig. 4-100: *Enchytraeus albidus*. Effect of different combinations of acclimation salinities and temperatures on heat tolerance; test temperature: 35.8°C. Average values, based on 8 groups of 20 to 25 adult individuals in each case. Vertical lines: reliability intervals. (After KÄHLER, 1970; modified.)

KÄHLER (1970) investigated the influence of non-genetic salinity adaptation on cold and heat tolerance in the oligochaete worm *Enchytraeus albidus*. This euryhaline inhabitant of environmentally unstable habitats, such as the supralittoral, is, phylogenetically, in the state of re-migration into salty waters (TYNEN, 1969). It tolerates salinities between 0‰ and 60‰S and tends to be homeo-osmotic between 2‰ and 15‰S (FLEGLER, unpublished). KÄHLER acclimated his test worms (in sand moistened with water of the respective salinities) for 12 days to the following salinity-temperature combinations: 0‰, 10‰, 20‰, 30‰, 40‰, 50‰, 60‰S; 5°, 14°, 23° C (12-hr day). He then transferred them to 14° C water of the acclimation salinity for 20 to 30 mins and determined their cold tolerance at -13.2° C, and their heat tolerance at 35.8° C. From the percentage mortalities of the different test groups, LD<sub>50</sub> periods were computed. *E. albidus* exhibits a meaningful non-genetic resistance adaptation (Chapter 3.31, p. 438) to cold and heat. Increase of acclimation salinity causes augmented cold and heat resistances (Figs 4-99, 4-100). Cold resistance (Fig. 4-99) increases with decreasing acclimation temperature; the absolute gain in cold tolerance increases with increasing acclimation salinity (diverging curves). Heat resistance (Fig. 4-100) increases with increasing acclimation temperature; the absolute gain in heat tolerance is about the same in the various acclimation salinities (parallel curves). Salinities above 60‰ may be expected to reduce progressively the gain in heat tolerance; still higher salinities to cause severe damage (see also pp. 834-835).

Non-genetic adaptations to habitat salinities may be accompanied by genetic ones.

#### *Genetic resistance adaptation*

In contrast to directly environmentally induced non-genetic adaptations, genetic adaptations involve changes in genotype and are the result of genetic variations, selection, speciation and evolution (Chapter 3.31, p. 437; see also KINNE, 1963a, 1964a). While non-genetic resistance adaptations can be measured in short-term survival studies, genetic resistance adaptations must be assessed in terms of population or species survival, involving vast periods of time and, hence, lie outside the realm of the experimenter, except for genetical cross-breeding tests. Present evidence for genetic resistance adaptations to salinity comes largely from organisms existing in habitats with widely different salinity conditions. Assessments of genetic adaptations are, therefore, primarily descriptive and rather speculative (see, however, p. 841 and Fig. 4-83).

*General aspects.* There is evidence that the salinity of the oceans has not changed significantly since palaeozoic times (e.g. RUBEY, 1951; VINOGRADOV, 1959; ZENKEVITCH, 1966) and reason to assume that the relations between external medium and body fluids have remained similar from the remote past to the present situation (KHLEBOVICH, 1969). The horohaliniem, i.e., the limiting salinity range 5‰ to 8‰ (REMANE, 1934, 1940, 1969; ZENKEVITCH, 1959; MORDUCHAI-BOLTOVSKOI, 1960; KHLEBOVICH, 1968, 1969) must also have existed for geological time spans and divided aquatic animals into osmoconformers (p. 905) devoid of effective osmoregulative mechanisms and restricted to salinities above 5‰ to 8‰, and osmoregulators (p. 906), capable of maintaining their internal osmoconcen-

trations at levels equivalent to 5‰ to 8‰ or higher, even in fresh water. Genetic adaptation of marine forms to life in fresh water is, according to KHLEBOVICH (1969), first of all, a problem of passing the horohalimum (p. 827, pp. 959–961). Evolutionary transition of this boundary line requires such pronounced re-organization that it is largely irreversible, and even if certain forms return to the sea, they retain features acquired during their presence in freshwater habitats.

Some glacial relicts of Eurasia and North America have become genetically adapted to freshwater conditions but retained their original capacity to tolerate brackish water. Glacial relicts, especially from Northern Europe, have repeatedly been subjected, during glacial and interglacial periods, to shiftings from brackish to fresh water and vice versa and, apparently, achieved genetic adaptations to their alternating environments in the course of several thousand to more than a hundred thousand years (SEGERSTRÅLE, 1966).

In addition to acquiring hyperosmotic regulation (pp. 868, 906) in subadults and adults, marine invertebrates penetrating into fresh waters must also evolve adjustments for protecting early developmental stages. Examples of such genetic adaptations are: internal fertilization; eggs equipped with salt depots and membranes with low permeability; and hatching at advanced stages of ontogenetic development.

Marine invertebrates conquered freshwater habitats via different routes. They employed a great diversity of genetic adaptations to life in media with drastically reduced salt contents and deviating ionic ratios, elaborating pre-existing, basic cellular properties such as active transport, ion regulation and permeability control. Depending on genetic background, functional and structural peculiarities of the immigrant, and the particular ecological situation met, these elaborations resulted in a variety of co-operative and often highly effective regulatory systems.

*Examples of genetic resistance adaptation in crustaceans.* A variety of evolutionary adjustments—which may be considered genetic resistance adaptations involving shifts in salinity tolerance—made it possible for numerous macrocrustaceans to leave their oceanic home and to establish themselves in habitats with fluctuating, reduced or increased salinities, and even on land. The adjustments include changes in (i) absorption and excretion of salt and/or water, (ii) surface permeability to salt and/or water, (iii) chemical composition of body fluids, (iv) tissue tolerance to variations in total osmoconcentration and ionic composition, (v) salt and/or water storage in tissues or organs, (vi) biochemical aspects of metabolism and (vii) behaviour (e.g. KINNE, 1963a, b, 1964a, b, d, 1967a).

In an attempt to classify different degrees of genetic resistance adaptation to salinity variations, five groups of crustaceans may be distinguished: (i) Orthostenohaline inhabitants of the ocean; (ii) euryhaline inhabitants of coastal, estuarine or brine habitats characterized by extremely low, high or significantly fluctuating salinities; (iii) holcuryhaline inhabitants of sea-water, brackish-water and freshwater habitats; (iv) oligostenohaline inhabitants of freshwater; and (v) inhabitants of semiterrestrial and terrestrial habitats.

(i) Orthostenohaline crustaceans are osmoconformers with ion regulation (p. 885), but small, or no, capacities for volume regulation (p. 898) and osmoregulation (p. 904); examples are: *Macropipus puber*, *Maia verrucosa*, *Hyas araneus*, *Cancer*

*antennarius*, *Emerita talpoida*, *Speocarcinus californiensis*, *Lophopanopeus heathii*, *Pagurus longicarpus*, *Palinurus elephas*, as well as species of *Callinassa* (DUVAL, 1925; SCHLIEFER, 1929; SCHWABE, 1933; ROBERTSON, 1949, 1960; GROSS, 1957a; POTTS and PARRY, 1964). Presumably, most other truly oceanic crustaceans belong to this group.

(ii) Euryhaline crustaceans are characterized by reduced surface permeability to water and salt and improved mechanisms for differential absorption and excretion of ions; examples are: *Carcinus maenas* (DUVAL, 1925; SCHLIEFER, 1929; NAGEL, 1934; SHAW, 1961a; FLÜGEL, 1963; POTTS and PARRY, 1964; THEEDE, 1969a), *Rhithropanopeus harrisi* (JONES, 1941; KINNE and ROTTHAUWE, 1952; COSTLOW and SASTRY, 1966; SMITH, 1967), various species of *Gammarus* (WIDMANN, 1935; BEADLE and CRAGG, 1940a; KINNE, 1952b; WERNTZ, 1963), *Palaemonetes varians*, *Palaemon serratus*, *Palaemon squilla*, *Penaeus indicus*, *Penaeus carinatus*, *Metapenaeus dobsoni* (PANIKKAR, 1939, 1940a, b, 1941a, 1950), *Metapenaeus monoceros* (PANIKKAR and VISWANATHAN, 1948), *Crangon crangon* (BROEKEMA, 1941; FLÜGEL, 1963), *Upogebia pugettensis*, *U. affinis* (THOMPSON and PRITCHARD, 1969), *Artemia salina* (CROGHAN, 1958b), *Uca crenulata*, *Pachygrapsus crassipes* (JONES, 1941; GROSS, 1955, 1957a, b, 1959; PROSSER and co-authors, 1955; GROSS and CAPEN, 1966), *Uca minax*, *U. pugilator*, *U. pugnax* (GREEN and co-authors, 1959), *Ocyropode (albicans) quadrata* (FLEMISTER and FLEMISTER, 1951), *Hemigrapsus oregonensis* (GROSS, 1957a, 1961; DEHNEL and STONE, 1964), *Heloccius cordiformis*, *Leptograpsus variegatus* (DAKIN and EDMONDS, 1931; EDMONDS, 1935), *Gecarcinus lateralis* (GROSS, 1963b) and *Birgus latro* (GROSS, 1955, 1957a, 1964b). On the basis of genetic differences in osmoregulative performance, euryhaline crustaceans can be subdivided into two groups: (a) hyperosmotic regulators (see also p. 906) which tend to maintain significantly hyperosmotic body fluids in diluted sea water, but become poikilosmotic in higher salinities (e.g. *Carcinus maenas*, *Rhithropanopeus harrisi*, *Upogebia pugettensis*, various species of the genus *Gammarus*); and (b) hyper- hypo-osmotic regulators (see also p. 906) which tend to remain significantly hyperosmotic in diluted sea water and hypo-osmotic in higher salinities (most shore shrimps, brine shrimps, semiterrestrial and terrestrial crabs). Hyper-hyporegulation is found also in sea-water inhabiting insects and represents the most elaborate genetic adaptation to osmotic stress in aquatic invertebrates.

Hyperosmotic regulation is based on active salt uptake from the surrounding medium and from food, in counteraction to salt loss from external surfaces and excretory glands. In the euryhaline amphipods *Gammarus duebeni*, *G. locusta* and *G. obtusatus*, changes in blood osmoconcentration are caused by salt rather than water exchange (BEADLE and CRAGG, 1940a). In lowered salinities, *Gammarus duebeni* can reduce the degree of salt loss (SHAW and SUTCLIFFE, 1961); below 17‰S, such reduction is accomplished by producing urine which is hypo-osmotic to the blood (LOCKWOOD, 1961) and possibly also by changes in surface permeability (LOCKWOOD, 1961; SHAW and SUTCLIFFE, 1961). As the salinity decreases further, *G. duebeni* increases the rate of urine flow (until, in fresh water, it reaches the equivalent of 70% total body water/day) and progressively decreases its urine concentration. Blood hypo-osmotic urine is presumably produced also by *G. zaddachi* and *G. salinus* when exposed to dilute media (LOCKWOOD, 1961). In the

crab *Carcinus maenas*, genetic adaptation to subnormal salinities includes reduced surface permeability to water and salt, high tissue tolerance to lowered osmo-concentration of body fluids, and active salt absorption from the external medium. The most important osmoregulatory organ seems to be the gill. In sea water and brackish water, antennal glands produce approximately blood-isosmotic urine; they play no significant part in osmoregulation. Urine output increases with decreasing salinity; it is assumed that the gills replace the resulting salt loss by a reciprocal increase in salt absorption (e.g. NAGEL, 1934; see also pp. 915-918).

Hypo-osmotic regulation is still insufficiently investigated. The brine shrimp *Artemia salina* (CROGHAN, 1958a-e) 'drinks' continuously from its surrounding medium and re-absorbs water from its gut lumen. The osmotic pressure of its gut fluid is higher than that of the blood but, in supranormal salinities, remains below that of the surrounding medium. Regulation occurs in gills (salt balance) and gut (water balance). Ionic ratios of the haemolymph are fairly constant and quite different from those of the external medium. Changes in haemolymph osmo-concentration, which may occur as salinity varies, are due more to net movements of salt than to water exchange. *A. salina* shows an appreciable degree of permeability, especially in its gut epithelium. It can actively excrete (first 10 pairs of gills) and absorb (probably first 10 pairs of gills plus gut) sodium chloride. The gut exhibits considerable capacities for active water uptake and water-balance control in hyperosmotic media (CROGHAN, 1958b, c, d). The low osmoconcentration of body fluids, the type of ionic regulation and the low internal magnesium concentration resemble conditions found in freshwater invertebrates and have been interpreted as evidence of the freshwater ancestry of brine-living animals (e.g. ROBERTSON, 1960). The shrimps *Palaemonetes varians* and *Palaemon longirostris* produce rather large amounts of blood isosmotic urine over a wide range of salinities (PANIKKAR, 1939; PARRY, 1955, 1957); hence there must be an intensive absorption of salt, particularly in subnormal salinities. The semi-terrestrial crab *Pachygrapsus crassipes* produces slightly blood hypo-osmotic urine when in a diluted medium, and blood isosmotic urine when in sea water (PROSSER and co-authors, 1955). By immersing *P. crassipes* in different salinities containing varying concentrations of magnesium, it was shown that urine magnesium concentrations are not a direct function of magnesium influx, but rather of water influx. Furthermore, it could be demonstrated that the muscle tissue of *P. crassipes* swells if the crab is immersed in dilute sea water, and shrinks if it is exposed to concentrated sea water. Volume change of muscles take place at the expense of the blood space; the crab does not change weight (GROSS and MARSHALL, 1960). In the semiterrestrial crabs *Uca pugnax* and *Uca pugilator* kept in 100% and 175% sea water, urine osmotic and electrolyte concentrations are blood hyperosmotic. Chief sites of entrance of water and salt are stomach and gills; chief sites of regulation are gills and antennal glands, with some regulation by the stomach and possibly the midgut gland (GREEN and co-authors, 1959). The semiterrestrial crab *Ocyropode quadrata* re-absorbs water in its antennal glands when in air or in blood hyperosmotic salinities; it excretes water by antennal glands, and may also excrete chloride, when in hypo-osmotic salinities. Its gill membrane is assumed to function in the reverse way (FLEMISTER and FLEMISTER, 1951). Water re-absorption in antennal glands has also been demonstrated in the terrestrial crab

*Gecarcinus lateralis* (FLEMISTER, 1958). On the other hand, the terrestrial *Cardisoma carnifex*, the amphibious *Sesarma meinerti*, and the euryhaline aquatic *Varuna litterata*—brachyuran crabs with powerful hyper hyporegulation—have antennary glands which are ineffective for osmoregulation, but capable of regulating magnesium and calcium.

It seems that, in most euryhaline crustaceans, antennal glands play little or no part in osmoregulation, but assist in ionic regulation, and that only in some semi-terrestrial and rather terrestrial crabs may antennal glands become progressively capable of re-absorbing water and of excreting ions against the gradient—adaptations which aid hypo-osmotic regulation.

(iii) **Holeuryhaline** crustaceans are rare. They are able to inhabit all three aquatoria—sea, brackish and fresh water; they either migrate as individuals from one aquatorium to the other during their life cycle, or establish populations in all three media simultaneously. The best investigated example is the migrating holeuryhaline crab *Eriocheir sinensis* (BERGER, 1931; SCHOLLES, 1933; SCHWABE, 1933; SCHLIEPER, 1935; CRONKLIN and KROGH, 1938; KROGH, 1939; KOCH and co-authors, 1953, 1954; KOCH and EVANS, 1956a, b, c; SHAW, 1961b; POTTS and PARRY, 1964; DE LEERSNYDER, 1967); another example is its Indian relative *Varuna litterata* (PANIKKAR, 1950). Genetic adaptation to life in the whole salinity range from fresh water to sea water includes considerable capacities for non-genetic adaptation, low surface permeability to water and salt, absorption and excretion of salt against steep gradients, and high tissue tolerance to fluctuations in blood osmoconcentration. The high degree of osmotic independence (homeo-osmoticity) represents a remarkable achievement shared with only a few other invertebrates. Holeuryhalinity is as rare as it seems, once established, evolutionary conservative. In *Eriocheir sinensis* exposed to fresh water, blood osmoconcentration is high ( $\Delta = 1.1^\circ$  to  $1.2^\circ$  C) and urine output low (3 to 5 ml/day in a 60 g individual). The urine is isosmotic or slightly hyperosmotic to the blood, both in fresh water and in sea water (SCHOLLES, 1933; SCHLIEPER, 1935; DE LEERSNYDER, 1967), and chloride and ammonia losses are the same, whether the excretory pores are open or closed. Sodium chloride and other salts are actively absorbed from very dilute media by the gills (SCHWABE, 1933; KOCH, 1954; KOCH and EVANS, 1956a, b, c). The existence of a potassium pump, separate from the sodium absorbing mechanism, has been indicated, suggesting the presence of a mechanism similar to that reported for larvae of insects, i.e. in the genera *Chironomus* and *Aedes*. *Eriocheir sinensis* resembles the river crab *Potamon edulis* in (i) maintaining a high blood osmoconcentration in fresh water; (ii) actively absorbing sodium and potassium; and (iii) excreting small amounts of more or less blood isosmotic urine.

(iv) **Oligostenohaline** crustaceans inhabit fresh water and are characterized by a well-developed hyperosmotic regulation meeting osmotic requirements in very dilute media. Their osmoregulation collapses in salinities above 5‰ to 8‰; examples are *Potamon edulis* (SCHLIEPER and HERRMANN, 1930), *Potamon niloticus* (SHAW, 1959b), *Astacus fluviatilis* (BRYAN, 1960a, b, c), *Palaemonetes antennarius* (PARRY, 1957, 1961a), *Asellus aquaticus* (LOCKWOOD, 1959, 1960), *Gammarus pulex*, *Gammarus lacustris* (LOCKWOOD, 1961; SHAW and SUTCLIFFE, 1961) and presumably most other freshwater-living crustaceans. The main osmotic problems facing a marine crustacean immigrating to fresh water are: increased water inflow,

paucity of ions and increased variations in chemical and physical properties of the ambient medium. Genetic resistance adaptation of crustaceans to life in fresh water includes: very low differential surface permeability to water and salt; active salt absorption by gills and gut; salt re-absorption; reduction of normal osmoconcentration of body fluids; water expulsion; accumulation of nutrients and salt in the egg, making the organism more independent of the surrounding water during early ontogeny. Gaining the capacity for intensive hyperregulation usually goes hand in hand with losing the ability to tolerate increased salinities. On the basis of their genetically different osmoregulative potentials, oligohaline crustaceans can be subdivided into two groups: (a) producers of (more or less) blood isosmotic urine (e.g. *Potamon edulis*, *Potamon niloticus*, *Palaemonetes antennarius*) and (b) producers of blood hypo-osmotic urine (e.g. family Astacidae, *Gammarus pulex*, *G. lacustris*, and numerous other freshwater-living crustaceans).

Among the producers of (more or less) blood isosmotic urine, the river crab *Potamon edulis* appears to be osmotically ill-adapted to life in fresh water; it has a high blood osmoconcentration ( $\Delta = 1.1^\circ$  to  $1.2^\circ$  C), is more permeable to water and salt than many other freshwater invertebrates, and produces urine which is practically blood isosmotic. However, *Potamon edulis* releases only small amounts of urine and actively absorbs sodium and potassium from the external medium (SCHLIEFER and HERRMANN, 1930; SHAW, 1959b). The shrimp *Palaemonetes antennarius* has a lower blood osmoconcentration ( $\Delta = 0.75^\circ$  C) than *Potamon edulis*, but loses large amounts of salt via an almost blood isosmotic urine ( $\Delta = 0.67^\circ$  C) produced at the rate of about 2% body weight/hr (PARRY, 1957). Regarding its osmoregulative potential, *Palaemonetes antennarius* does not seem to have completed its genetic adaptation to life in fresh water. It must still expend considerable energy in order to compensate for large salt losses via diffusion and excretion; in addition, it appears to be limited by a critical lower ambient sodium concentration (between 0.125 and 0.183  $\mu$ M Na/l) beyond which the uptake mechanism begins to fail. Similar critical thresholds seem to exist for other monovalent ions and may contribute to the prawn's discontinuous geographic distribution. Possibly, divalent ions are equally important; they can seriously affect the permeability of the prawn's body surface. Thus a low concentration of calcium in the external medium tends to increase cuticle permeability which, in turn, increases salt loss and urine flow, forcing the prawn to increase the rate of active salt uptake (PARRY, 1961a).

Among the producers of blood hypo-osmotic urine, the blood osmoconcentration of members of the family Astacidae has been found to vary between  $\Delta = 0.6^\circ$  and  $0.8^\circ$  C (ROBERTSON, 1960). In an external medium of  $\Delta = 0.018^\circ$  C, the crayfish *Astacus astacus* maintains a blood osmoconcentration of  $\Delta = 0.81^\circ$  C and excretes urine of  $\Delta = 0.09^\circ$  C. In fresh water, urine output amounts to 4% of its body weight per 24 hrs (HERRMANN, 1931) or to 0.175% body weight/hr (SCHOLLES, 1933); urine output decreases with increasing salinity, approaching zero in a blood isosmotic medium. *Procambarus clarkii* compensates for osmotic water inflow in fresh water by excreting blood hypo-osmotic urine at the rate of 5.2% of its body weight per 24 hrs (LIENEMANN, 1938).

Smaller freshwater crustaceans such as *Gammarus pulex* and *Asellus* sp. have low blood  $\Delta$ 's of  $0.4^\circ$  to  $0.6^\circ$  C (BEADLE and CRAGG, 1940a; PARRY, 1953; POTTS and PARRY, 1964); *Daphnia magna* of  $0.2^\circ$  to  $0.3^\circ$  C (FRITZSCHE, 1917). *Gammarus*

*pulex* lacks the capacity (present in *G. duebeni*) to vary its urine concentration; in solutions more concentrated than 20 to 30 mM/l, its urine becomes hypo-osmotic not only to the blood but also to the medium (LOCKWOOD, 1961). Its main genetic adaptations to life in fresh water seem to be active ion uptake and differential surface permeability. *Asellus aquaticus* is fairly permeable to salt and water; maintenance of its internal osmoconcentration against a gradient of approximately 100 : 1 must result from fast replacement of ions from the medium. Constancy of blood osmoconcentration during 8 days of starvation indicates that salt loss can, if necessary, be replaced solely by active uptake from the external medium, i.e. independent of the food supply (LOCKWOOD, 1959). The freshwater-living branchiopod *Triops cancriformis* maintains its blood osmoconcentration by very low surface permeability and salt uptake from food. Its osmoregulation breaks down in slightly blood hyperosmotic media (PARRY, 1961b). Salt uptake from food has also been demonstrated or suggested in other freshwater crustaceans, e.g. *Branchipus* (presumably *B. schaefferi*; KROGH, 1939) and *Chirocephalus diaphanus* (PANIKKAR, 1941b).

BEADLE and CRAGG (1940a, b) have suggested that genetic adaptation to life in fresh water proceeds in two stages: (i) Maintenance of high blood osmoconcentration (as in *Potamon edulis* and *P. niloticus*) associated with a large blood/tissue chloride gradient; at this early stage, sudden salinity increase can still be tolerated. (ii) Evolution of renal salt re-absorption and lowering of both blood osmoconcentration and blood/tissue chloride gradient to levels more easily maintained (as in *Gammarus pulex* and most other truly freshwater species); at this advanced stage, higher salinities are lethal. PEARSE and GUNTER (1957) consider the most essential requirement for permanent population establishment in fresh water to be the accumulation of food and salt in the egg, making the most critical ontogenetic stage more independent of the external medium.

(v) Inhabitants of semiterrestrial and terrestrial habitats have acquired high tolerances to desiccation and to changes in internal osmoconcentration. The different conditions of air-exposure encountered may affect greatly water and salt balances and produce physiological phenomena in body fluids and cells, which are comparable to those faced under salinity stress. Genetic adaptations of crustaceans to life on land are well documented (e.g. EDNEY, 1960; KINNE, 1963a; TERRESTRIAL ADAPTATIONS IN CRUSTACEA, 1968). The major route of land immigration has been, and still is, from the sea via the littoral zone. Thus terrestrial crustaceans are usually more closely related to marine species than to estuarine or freshwater ones (VANDEL, 1943). In spite of a variety of genetic adaptations to terrestrial habitats, crustaceans have 'never quite made it'. Compared to insects, land-living crustaceans are rather poorly equipped for life in dry air; even their most successful representatives, the isopods, cannot fully exploit the ecological opportunities offered by the terrestrial habitat and must avoid truly terrestrial conditions. In order to occupy their present niches on land, crustaceans did not have to change very much; they were pre-adapted. Their most important pre-adaptations to land life are: (i) hard exoskeleton, (ii) jointed, strong extremities, (iii) internal or quasi-internal fertilization, (iv) carapace-covered gill chambers of crabs, and (v) egg-protecting brood pouches of amphipods and isopods. In his reviews, EDNEY (1960, 1968) comes to the conclusion that remarkably few profound changes have

resulted from assuming the terrestrial way of life, and that even in land isopods, all devices required for land life were present in their aquatic ancestors, or if not, are to some degree makeshift. Thus there is no effective protection against surface evaporation (no wax layer in epicuticle); respiration is still accomplished by (slightly modified) gills and the pseudotracheae are but short bunches of tubes; the eggs are by no means cleidoic and must be carried by the parent; excretion is still predominantly ammonotelic; osmotic changes are tolerated rather than controlled; and high ambient temperatures are suffered only at the expense of increased evaporation.

BLISS and MANTEL (1968) pointed out that, among the three groups of crustaceans occupying terrestrial habitats, amphipods have succeeded primarily by behavioural means, while isopods and decapods have developed a diversity of morphological, physiological and biochemical adaptations as well. In all three groups, behavioural adaptations to land life ensure that water loss is minimal and that a suitable compromise between detrimental dehydration and evaporative cooling is maintained. In most crustaceans, excretion of nitrogenous wastes requires copious amounts of water for washing away soluble metabolic end-products. Terrestrial isopods, such as *Oniscus asellus* (HARTENSTEIN, 1968), are able to excrete ammonia as a gas. In terrestrial decapods, either ammonia (especially when sufficient water is available), or insoluble uric acid (when water is scarce) is excreted. In adult land crabs, water balance is controlled through the concerted action of gills, pericardial sacs and gut; their larvae still develop in the sea.

Decapod crabs, which occupy rather terrestrial habitats, tend to accumulate more magnesium in their urine than their more aquatic relatives (GROSS, 1964a). An exception to this apparent rule is the terrestrial *Gecarcinus lateralis*, the only brachyuran crab known to be incapable of concentrating urine magnesium at the expense of sodium. High urine magnesium, however, does not necessarily reflect strong magnesium regulation in the blood (GROSS and CAPEN, 1966). While the semiterrestrial crab *Coenobita perlatus* can still use sea water as its exclusive water source, its terrestrial relative *Gecarcinus lateralis* requires additional low-salinity water sources. *G. lateralis* appears to regulate its blood sodium and magnesium in a way fundamentally different from that employed by other land-living crabs, which suggests a different evolutionary pathway towards land life (GROSS, 1963b). There is also evidence that the antennal glands of *Coenobita perlatus*, *C. brevipaninus* and *Birgus latro* are especially adapted to life on land (GROSS, 1964b).

We may summarize the most obvious genetic adaptations of crustaceans to life on land as follows: (i) reduction of evaporation rates; (ii) collection of water from small sources and water absorption against gradients; (iii) active salt secretion; (iv) reduction of the amount of nitrogen excreted per unit weight; (v) reduction of normal osmoconcentration of body fluids; (vi) increased tolerance to osmotic and ionic deviations in fluids of body cavities and cells; (vii) elaboration or development *de novo* of devices for: selection of suitable microhabitats, body temperature compensation, sensory perception, orientation, feeding, walking and mating under semiterrestrial or terrestrial conditions; and (viii) increased over-all tolerance to environmental stress.

*Causes of death due to sub- or supranormal salinities*

The causes of death in critically low or high salinities are not yet well understood. They are related primarily to critical disturbances in the water and mineral balance: (i) functional or structural damage at the protein, cell and tissue levels via osmotic phenomena; (ii) functional or structural damage via deviations in relative proportions of solutes; and (iii) damage caused by critical variations in metabolic rate or performance, or by disharmonizing effects on mechanisms of organismic integration.

Salinity-induced disturbances in metabolic rate, activity or integration may lead to insufficient rates of energy liberation, locomotion, ciliary activities, water pumping and filtration (e.g. in protozoans, planarians, sponges, molluscs, polychaetes, cirripedes), and to insufficient performance in regard to escaping predators, holding on to the substratum, burrowing, or selecting more convenient habitat locations. Severe reductions of metabolic performance may, furthermore, increase the susceptibility to parasitic infestation and microbial infection.

*(b) Metabolism and Activity*

Within tolerable ranges of salinity, functional responses can be subdivided into two general aspects: metabolism and activity. Rates of metabolism and activity are functionally correlated: changes in metabolic rate tend to alter the scope for activity, and changes in the level of activity (e.g. locomotion) tend to modify the speed of metabolic processes (see also Chapter 3.3).

*Metabolism*

*Rate of oxygen consumption in whole individuals.* Variations in salinity may modify the rate of metabolism of aquatic invertebrates. This fact has been established primarily on the basis of respiration experiments. A detailed analysis of such modifications must differentiate between short-term responses (overshoot reactions, shocks) and long-term responses of stabilized individuals. Even in regard to long-term responses, salinity effects can only be assessed sufficiently if the environmental past (previously effective environmental factors; status of non-genetic adaptation) and present (concomitantly effective environmental factors; ontogenetic stage, sex, degree of locomotory activity, nutrition, behavioural aspects) are considered. Few of the papers available contain enough information for critical assessments. Nevertheless, certain general trends have become apparent (KINNE, 1964a, c). Within tolerable ranges of salinity, rate of oxygen consumption of marine and brackish-water invertebrates may (temporarily)

- (i) increase in subnormal salinities and/or decrease in supranormal salinities;
- (ii) increase in sub- and supranormal salinities;
- (iii) decrease in sub- and supranormal salinities;
- (iv) remain essentially unaffected.

Types (i) and (ii) are represented largely by euryhaline invertebrates, type (iii) by stenohaline forms—which suffer from osmotic damage whenever the salinity deviates significantly from the normal level—type (iv) by holeuryhaline or extremely euryhaline forms.

Numerous examples are available for type (i): the polychaete *Nereis diversicolor* (SCHLIEPER, 1929), the crustaceans *Carcinus maenas*, *Eriphia spinifrons* (SCHLIEPER, 1929; SCHWABE, 1933), *Gammarus locusta* (SCHLIEPER, 1929), *Potamon edulis* (RAFFY, 1934), *Gammarus duebeni* (KINNE, 1952b), *Uca* spp. (GROSS, 1957a), *Hemigrapsus oregonensis* (DEHNEL, 1960), *Balanus balanoides* (BARNES and co-authors, 1963; FOSTER, 1969a), and the mollusc *Alderia modesta* (FRIEDRICH, 1937). Examples of type (ii) are the crustaceans *Ocypode (albicans) quadrata* (FLEMISTER and FLEMISTER, 1951), *Palaemonetes varians* (LOFTS, 1956) and *Metapenaeus monoceros* (RAO 1958). Examples of type (iii) are the sea anemone *Metridium marginatum* (SHOUP, 1932), the clam *Mytilus edulis* (BOUXIN, 1931; BELIAEV and TSCHUGUNOVA, 1952; THEEDE, 1964), and various species of the sea-star *Asterias* (SCHLIEPER, 1929; MEYER, 1935; MALOEUF, 1938; BOCK and SCHLIEPER, 1953). Decrease in metabolic rate in sub- and supranormal salinities may be preceded by a brief period of increased metabolism and locomotory activity immediately upon transfer. Examples of type (iv) are the wool-handed crab *Eriocheir sinensis* (SCHWABE, 1933; KROGH, 1939), the brine shrimp *Artemia salina* (GILCHRIST, 1956, 1958), the snail *Theodoxus fluviatilis* (LUMBYE, 1958), the isopod *Cyathura polita* (FRANKENBERG and BURBANCK, 1960) and the amphipod *Corophium volutator* (McLUSKY, 1968c); see also ELTRINGHAM (1965), McFARLAND and PICKENS (1965), THEEDE (1965b) and PALMER (1968).

In freshwater-living crayfish of the genus *Astacus*, respiratory rate is higher in fresh water than after a few days' exposure to a diversity of salinity levels ranging up to 100‰ sea water. The freshwater mussel *Lamellidens marginalis* exhibits maximum respiration in 10‰ sea water (RAMAMURTHI, 1965). In euryhaline invertebrates, rates of oxygen consumption and of related metabolic processes have been reported to be subject to changes, particularly in the salinity range 5‰ to 8‰ (e.g. KHLEBOVICH, 1969; p. 827).

Salinity-induced changes in respiratory rates have been shown to depend on temperature, body size and dissolved gases. Supranormal temperatures tend to increase salinity-dependent variations in metabolic rate, while subnormal temperatures frequently reduce them. DEHNEL (1960) acclimated *Hemigrapsus oregonensis* and *H. nudus* to temperatures of 5°, 10°, 15° and 20° C and salinities of 8‰ and 24‰, respectively. He then tested their oxygen consumption at 10° C. Individuals acclimated to 5° C show higher respiratory rates in 8‰ and (to a lesser extent) in 24‰S than those acclimated to 20° C. Amongst the individuals acclimated to 5° C, respiratory rate in 8‰S increases, largely independent of body size; amongst the 20° C acclimated ones, however, respiratory rate of small (0.8 g) individuals is higher in 24‰ than in 8‰S. This difference decreases with increasing body size; it disappears in individuals heavier than 5 g. Also in some other crustaceans, smaller specimens show more pronounced differences in rates of oxygen consumption if exposed to different salinities than larger ones, e.g. in *Artemia salina* (ELIASSEN, 1953) and *Metapenaeus monoceros* (RAO, 1958).

*Corophium volutator*, acclimated to 1‰, 10‰, 20‰ and 30‰S at 10° C and forced to swim actively during the experiments, exhibit practically the same rates of oxygen consumption in all salinities if similar sized individuals are compared. Oxygen consumption is logarithmically related to the dry weight of the amphipods (McLUSKY, 1968c). Changes in the amounts of ambient dissolved gases may con-

siderably modify rates of oxygen consumption and locomotory activity. Water solubility of oxygen and carbon dioxide—and hence the amounts of these gases which can be held in solution—decrease with increasing salinity (Chapter 9).

Rates of oxygen consumption become dependent upon ambient partial pressures of oxygen and carbon dioxide at some critical value. In crustaceans, lower critical partial pressures of oxygen occur approximately at 10% air saturation in *Eriocheir sinensis* (CHEN, 1932), 20 to 40% in *Orconectes immunis* (HELFF, 1928), 25% in *O. virilis* (HIESTAND, 1931) and *Astacus astacus* (KALMUS, 1930), 45% in *Gammarus locusta*, 49% in *G. pulex* (WÄLSHE-MAETZ, 1956), 50% in *Calanus finmarchicus* (MARSHALL and ORR, 1955), *Palaemonetes* sp. (AMBERSON and co-authors, 1924), and *Pugettia producta* (WEYMOUTH and co-authors, 1944), 57% in *Pherusa fucicola* (WÄLSHE-MAETZ, 1956), and 70% in *Orchestia mediterranea* (WÄLSHE-MAETZ, 1956). All values are subject to modification due to changes in temperature, carbon dioxide, size or age. Active metabolism is more dependent than resting metabolism. Low partial pressures of oxygen, which decrease the rate of active metabolism, reduce the scope for activity and hence place the individual concerned at an ecological disadvantage. At certain low partial pressures, the active metabolic rate becomes reduced to bare maintenance requirements, and the individual is no longer capable of performing external work. Still lower levels quickly lead to death. For further information consult FRY (1957), WOLVEKAMP and WATERMAN (1960), Chapter 3.31 (p. 445) and Chapter 9.3.

It is difficult to interpret experimental results obtained on non-stabilized individuals. In many cases, investigators have measured respiratory rates soon after the salinity change and without sufficient knowledge about the time course of stabilization processes. For ecological considerations new steady-state performances are most revealing. One should further keep in mind that determinations of respiratory rates (frequently obtained under inadequate conditions in 'respiratory chambers') are of greater value to the ecologist if combined with measurements on (locomotory) activity as well as on rates and efficiencies of growth and reproduction. There is great need for such comprehensive studies, and they can be expected to provide a more objective basis for a critical evaluation of salinity effects on metabolic processes than is currently available.

Our present information allows only two generalizations: (i) Many aquatic invertebrates respire at most economic rates in salinities to which they are genetically adjusted, or to which they have been acclimated over prolonged periods of time; (ii) respiratory demands due to salinity stress can be reduced by beneficial intensities of other concomitantly effective environmental factors (possibly also by reductions in muscular activity).

*Rate of oxygen consumption in isolated tissues.* VAN WINKLE (1968) measured oxygen consumption of excised gill tissues of the lamellibranchs *Crassostrea virginica*, *Mercenaria mercenaria*, *Modiolus demissus* and *Mytilus edulis* in 5‰, 10‰, 15‰, 20‰ and 30‰S and at temperatures of 10°, 18° and 26° C respectively, during winter and summer. Oxygen consumption proved to be relatively constant from 5‰ to 30‰S in *C. virginica* and *M. edulis*, but to be greater at low salinities in *M. mercenaria* and *M. demissus* (Fig. 4-101). This effect of reduced salinities on respiratory rates of isolated gill tissue does not appear to be correlated with the

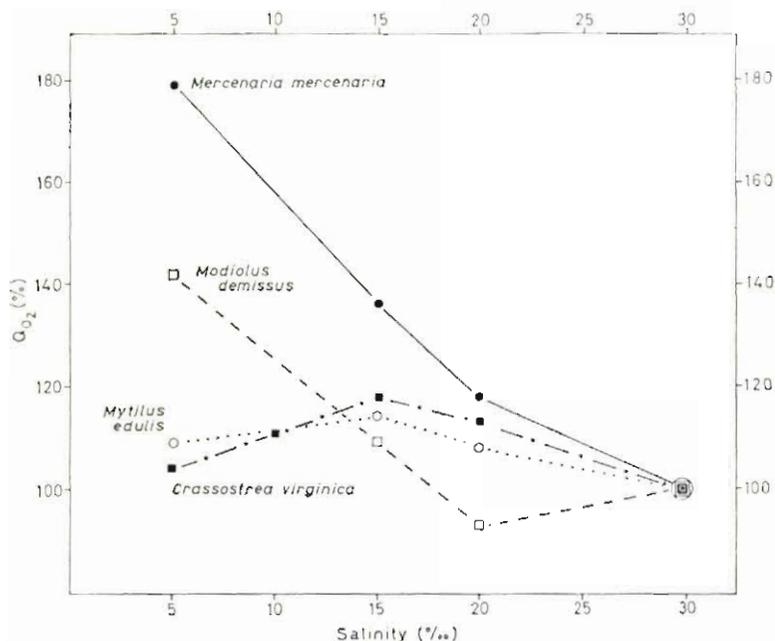


Fig. 4-101: Oxygen consumption of isolated gill pieces from representatives of four lamellibranch species as a function of salinity. Values obtained by averaging over seasons and experimental temperatures after conversion of  $Q_{O_2}$  values to percentage  $Q_{O_2}$  values.  $Q_{O_2}$ :  $\text{mm}^3$  oxygen consumed per g dry weight of gill tissue per min. (After VAN WINKLE, 1968; modified.)

lower salinity boundaries of intact whole specimens. While *Mytilus edulis* gill tissues (SCHLIEPER, 1955) and *Mercenaria mercenaria* gill, mantle and muscle tissues (HOPKINS, 1949) exposed to reduced salinities either increase or do not alter significantly rates of oxygen consumption, intact whole specimens of *Mytilus edulis* reveal reduced rates of oxygen consumption (SCHLIEPER, 1929; BOUXIN, 1931; BELIAEV and TSCHUGUNOVA, 1952).

A similar discrepancy between results obtained on excised tissue pieces and intact individuals has been reported by KING (1965) in decapod crabs, indicating that isolated tissues and whole animals do not necessarily show parallel respiratory responses to salinity variations.

The reason for the increased oxygen consumption of excised gill pieces of *Mercenaria mercenaria* and *Modiolus demissus* in diluted sea water is not clear (VAN WINKLE, 1968). The increase appears to be due to tissue damage and osmotic swelling of mitochondria (MUNDAY and THOMPSON, 1962; KING, 1966), rather than to additional energy expenditure for active salt or water transport.

Expressing oxygen consumption of excised gill pieces from *Mytilus edulis* as 'enzyme activity' per unit volume of tissue instead of per unit wet or dry weight, LANGE (1968) obtained quite similar values in *in vitro* and *in vivo* studies. He points out that, in poikilosmotic organisms exposed to different salinities, calculations of oxygen consumption per tissue weight must lead to comparison of respiratory rates of different numbers of cells (LANGE, 1964; LANGE and MOSTAD, 1967).

Calculations on a volume basis are considered permissible since the volume of the gill tissue of *Mytilus edulis* in osmotically adapted individuals is the same in different salinities. LANGE (1968) believes that the discrepancies between the data calculated from isolated tissues and those obtained from whole mussels can be explained in this way.

A critical evaluation of the various claims would require more detailed information on state of acclimation, temperature, size of gill pieces, topography and morphology of gill area tested, techniques of gill piece removal, oxygen and carbon dioxide levels in test media, and degree of water movement during the test, than is available.

*Causes of salinity effects on respiratory rates.* A critical discussion of possible causal relations between salinity stress and changes in respiratory rates has been presented by POTTS and PARRY (1964). Although many osmoregulating aquatic invertebrates respond to subnormal salinities with an increase in respiratory rate, the hypothesis (e.g. SCHLIEPER, 1929, 1930, 1935, 1958) that this is due to increased energy demands for active ion transport cannot claim general applicability for the following reasons: (i) Changes in metabolic rate are, in most cases, much too large to be attributable to energy expenditure for ion- and osmoregulation alone; (ii) in several cases, increase in metabolic rates caused by reduced salinities is not confined to tissues which are expected to perform osmotic work; (iii) the large changes in respiratory rates imply very low efficiencies of the ion transport system, whereas experiments with isolated tissues reveal high efficiencies; (iv) respiratory rates of some aquatic animals are lower in subnormal salinities, increase in supranormal salinities, or are not measurably affected by salinity stress.

It appears that no single hypothesis can account for the salinity effects on metabolic rates reported in literature. Salinity may influence metabolic rates in multiple ways, e.g. via stimulation or diminution of locomotory activity (e.g. GROSS, 1957a; McFARLAND and PICKENS, 1965; DUNCAN and KLEKOWSKI, 1967); increase or decrease of water or salt contents of fluids of body cavities and cells; changes in internal ion ratios; and interference with neuromuscular, hormonal or enzymatic mechanisms. Immediate temporary elevation of oxygen consumption following salinity change may result from peripheral osmotic stimulations, and increased over-all alertness to counteract physiological stress.

Although freshwater-living invertebrates must expend more energy for regulatory work near their body surfaces than brackish-water or marine invertebrates, they probably require less energy for internal cell regulation. In most cells, ion transport is primarily concerned with sodium excretion against an electrochemical gradient. Freshwater invertebrates have lower sodium concentrations in their blood, hence sodium influx into their cells is reduced and less energy required for cellular replication. For ion regulation of heart muscle cells, the freshwater lamelli-branch *Anodonta cygnaea*, for example, appears to expend less than one tenth of the energy required by its marine counterpart *Mytilus edulis* (POTTS and PARRY, 1964).

*Rate of growth.* In marine and brackish-water invertebrates, growth rates vary with age, physiological state and environmental conditions; among the latter,

nutrition, temperature, salinity and water quality are usually of primary importance. While an impressive amount of information exists on the effects of temperature on growth rates (Chapter 3.31), relatively little is known about salinity effects.

In most euryhaline invertebrates, growth is restricted to significantly narrower salinity ranges than is survival. Under laboratory conditions, a few aquatic invertebrates attain maximum growth rates in salinity levels which are lower or higher than those of natural waters in which they maintain maximum population densities. Knowledge of such possible discrepancies, and of population genetical gradients in growth rates, may be of importance in mass cultivation for scientific or commercial purposes. Selection of salinity conditions and of genotypes which afford fastest growth could improve our present potential for providing aquatic 'laboratory organisms', nutrients for secondary and tertiary 'producers', and—last not least—more food for man. In aquacultural projects (Volume III), for which fast growth and maximum efficiency of food conversion into body substance is the primary objective, controlled changes in salinity may bring about better results. Studies concerned with salinity effects on growth rates are also of considerable theoretical interest as they are closely related to regulation of water and salt, permeability, active transport and other basic physiological phenomena at the organismic, tissue, cellular or molecular levels.

An example of faster growth under laboratory conditions, at salinities below those recorded in the natural habitat, is the budding rate (production of additional polyps) in the marine colonial hydroid *Clava multicornis*. Representatives of a *C. multicornis* population, which lives near Helgoland (southern North Sea) at a salinity of about 32‰, have been cultivated under controlled temperature, salinity and food conditions in the laboratory. The rate of polyp production per colony (within a wide temperature range) attains maximum values near 24‰S; it decreases in the order 32‰ > 16‰ > 40‰S (KINNE and PAFFENHÖFER, 1966). An example of faster growth at salinities above those in the natural habitat is the brackish-water colonial hydroid *Cordylophora caspia*. Representatives of a *C. caspia* population, which lives in the Kiel Canal ('Nord-Ostsee-Kanal'; West Germany) at salinities between 5‰ and 10‰, show (at 10° and 20° C) maximum growth rates (length of stolons and number of hydranths per colony) at 15‰S (KINNE, 1956b, 1958a).

Salinity has been reported to exert significant effects on rates of growth and development in larval stages of decapod crustacean crabs. In *Sesarma cinereum*, length of zoeal life is prolonged by a reduction in salinity; in essence, the megalops stage follows this trend (COSTLOW and co-authors, 1960). Comparable, if not quite as pronounced, effects have been observed in larvae of *Panopeus herbstii* (COSTLOW and co-authors, 1962). Rate of larval development of the off-shore crab *Hepatus epheliticus* is similar at 30‰ and 35‰S; at 25‰S, considerably more time is required for the zoea to attain the megalops stage, and at 20‰S the zoea are unable to complete their development to megalops (COSTLOW and BOOKHOUT, 1962). In *Callinectes sapidus*, duration of the megalops stage increases with an increase in salinity from 20‰ to 40‰ at 15° C but not at other test temperatures (COSTLOW, 1967). In his 1967 paper, COSTLOW presents the hypothesis that survival and duration of the megalops stage of *Callinectes sapidus* in the natural environment are

directly associated with the time of hatching, the time at which the megalops stage is reached in relation to seasonal changes in water temperatures, and the salinity in which the final zoeal moult occurs. He further assumes that the delay of metamorphosis in waters of high salinity and low temperature may have contributed to the occurrence of *C. sapidus* in the estuaries along a major portion of the Atlantic and Gulf coasts of the USA. In larvae of the land crab *Cardisoma guanhumi*, maintained in 24 different combinations of salinity and temperature from the time of hatching, duration of the 5 zoeal stages and 1 megalops stage is similar in 20‰ to 40‰S, but at 15‰ and 45‰S a longer period of time is required for complete development. Increments in body size of crabs during the first 7 postlarval moults are similar in 5‰ to 35‰S (25° C), but in fresh water, increase in size at moulting is reduced. Although there exists no apparent relationship between moulting frequency and salinities between 5‰ and 35‰, intermoult duration decreases in crabs maintained in fresh water (COSTLOW and BOOKHOUT, 1968).

COSTLOW and co-authors (1966) estimated the relationship between salinity, temperature and duration of larval stages in the decapod crab *Rhithropanopeus harrisi* by the fitting of a response surface (BOX and YOUNG, 1955; COSTLOW and co-authors, 1960, 1962; Chapter 12), where the response was taken to be

$$Y = \text{arc sine} \sqrt{(\text{duration in days})}$$

The functional form fitted was fully quadratic in salinity and temperature. The fit of a quadratic function in salinity and temperature to the variables requires 5 partial regression coefficients plus a constant, where each coefficient is associated with the linear and quadratic effects of salinity ( $S$ ,  $S^2$ ), the linear and quadratic effects of temperature ( $T$ ,  $T^2$ ), and the interaction between the linear components ( $T \times S$ ). Effects significant at the 10 to 20% level are designated as 'some effects', those beyond the 5% level as 'marked effects'. The square root of the sum of squares due to regression, including all effects, is designated as 'over-all correlation'; it gives a measure of perfectness of fit. The results of the statistical analysis are summarized in Table 4-53. Plotting the contours of duration of larval stages required compromises in computing. As shown by Fig. 4-102, the effect of salinity, as well as the interaction between salinity and temperature, is significant, even

Table 4-53

*Rhithropanopeus harrisi*. Results of statistical analysis of rate of larval development as a function of salinity and temperature (After COSTLOW, J. D., Jr., BOOKHOUT, C. G. and MONROE, R. (1966; modified) Studies on the larval development of the crab, *Rhithropanopeus harrisi* GOULD. I. The effect of salinity and temperature on larval development. *Physiol. Zool.*, **39**, 81-100. Copyright 1966 by the University of Chicago.

Dependent variable	Marked effects	Some effects	Over-all* correlation
Days from hatch to megalops	$T, T^2, S^2, (T \times S)$		0.986
Days from megalops to crab	$T, T^2, S^2, (T \times S)$	$S$	0.984
Days from hatch to crab	$T, T^2, S^2, (T \times S)$	$S$	0.996

\*Significant at 1% level

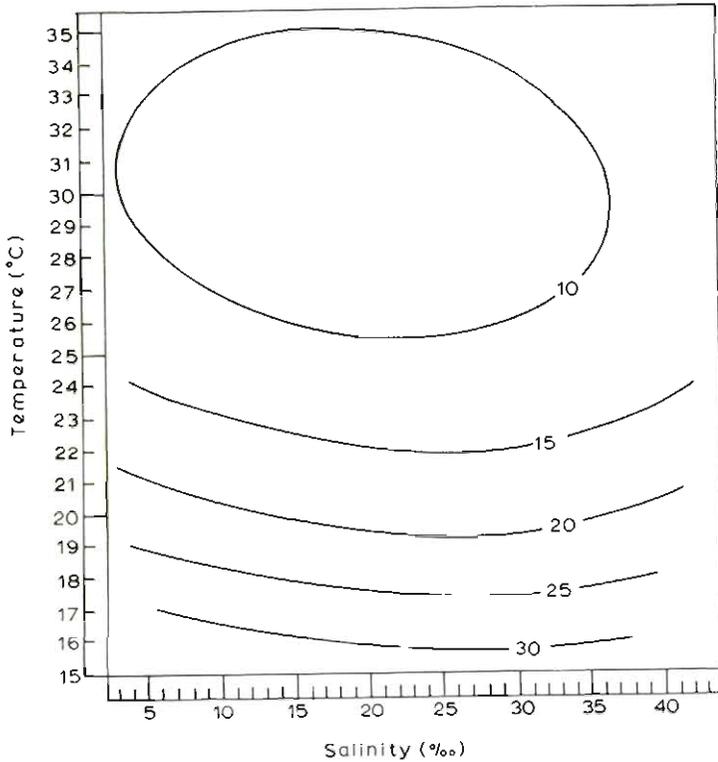


Fig. 4-102: *Rhithropanopeus harrisi*. Estimation of days required for development of all four zoeal stages; based on fitting a response surface to durations observed in 24 combinations of salinity and temperature. (After COSTLOW, J. D., JR., BOOKHOUT, C. G. and MONROE, R. 1966; redrawn.) Studies on the larval development of the crab, *Rhithropanopeus harrisi* GOULD. I. I. The effect of salinity and temperature on larval development. *Physiol. Zool.*, **39**, 81-100. Copyright 1966 by the University of Chicago

though the duration of the 4 zoeal stages is affected, to a considerable extent, by temperature alone. Within a salinity range of approximately 10‰ to 30‰, the minimum duration for zoeal development spans the temperature range from about 25.5° to 35° C. At lower and higher salinities, however, completion of zoeal development within the 10-day period becomes more dependent upon a narrower range of temperatures. Even at the lower temperatures, the increased period of zoeal development is dependent upon salinity. For example, at 20‰S, zoeae complete development to the megalops in about 15 days when maintained at 22° C; whereas in 3‰S and 22° C, duration of the 4 zoeal stages approximates more closely the 20-day contour. Fig. 4-103 illustrates the duration of the megalops stage of *R. harrisi*. The contour representing the minimum time for development of the megalops stage, 4 days, is confined to salinities below 27‰. As shown in Fig. 4-104, the projected duration of all larval stages of *R. harrisi*, from hatching to the first crab, presents a pattern similar to that of the megalops. In low and high salinities, complete development to the crab within the minimum time would require higher temperatures than comparable rates of development in the middle range of salinities. The number of larval stages of *R. harrisi* (4 zoeal stages plus 1 megalops stage) is consistent in all salinity-temperature combinations used.

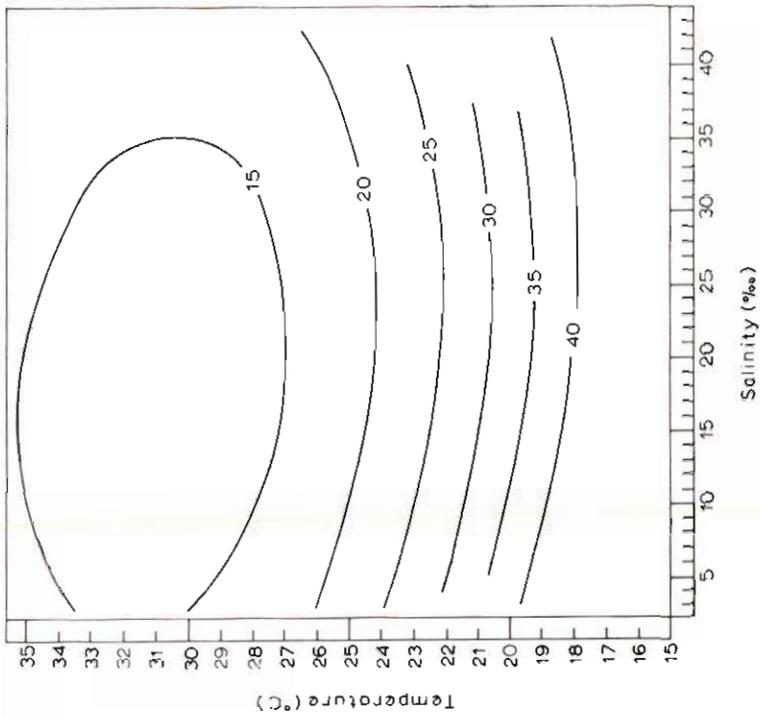


Fig. 4-104: *Rithropanopeus harrisi*. Estimation of days required for complete larval development from hatching to first crab stage; based on fitting a response surface to durations observed in 24 combinations of salinity and temperature. See Fig. 102. (After COSTLOW and co-authors, 1966; redrawn.)

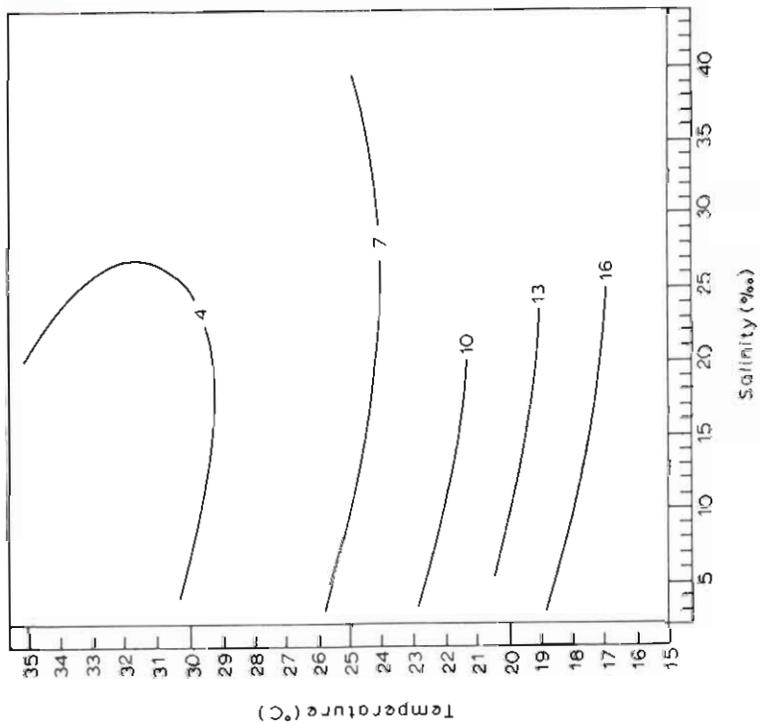


Fig. 4-103: *Rithropanopeus harrisi*. Estimation of days required for development of megalops; based on fitting a response surface to durations observed in 24 combinations of salinity and temperature. See Fig. 102. (After COSTLOW and co-authors, 1966; redrawn.)

Larvae of the mussel *Mytilus edulis* grow at rates equivalent to 70% or more of the maximum rates possible only in salinities from 25‰ to 35‰ at 15° C, and in salinities from 20‰ to 35‰ at 20° C (Table 4-54). The effects of salinity and temperature become related significantly as the limits of tolerance of either factor are approached (BRENKO and CALABRESE, 1969). Embryos of the coot clam *Mulinia lateralis* develop satisfactorily (at rates equivalent to 70% or more of maximum rates) in salinities from 22.5‰ to 30‰ at 25° C (optimum: 27.5‰S); however, a few embryos may develop normally in salinities as low as 15‰ and as high as 37.5‰. The larvae of *Mulinia lateralis* grow satisfactorily from 20‰ to 30‰S (32.5‰) and attain maximum growth rates in 25‰S (CALABRESE, 1969). In the oyster *Crassostrea gigas*, the formation of the larval shell is retarded in suboptimal salinities (FUJIYA, 1970). Effects of salinity on growth and development have also been demonstrated in turbellarians, the American lobster *Homarus americanus*, amphipods (references in: KINNE, 1964a) and several species of molluscs (e.g. DAVIS, 1958; WILBUR and YONGE, 1964).

Table 4-54

*Mytilus edulis*. Percentage increase in mean length of larvae at different combinations of salinity and temperature (After BRENKO and CALABRESE, 1969; modified)

Salinity (‰)	Temperature (°C)					
	5	10	15	20	25	30
15	2.6	12.0	44.2	64.4	11.2	0.0
20	8.9	33.6	66.5	80.5	31.1	0.0
25	20.6	45.3	81.5	96.7	64.6	0.0
30	19.8	50.5	83.9	98.8	64.8	0.0
35	14.5	41.9	76.8	86.8	49.2	0.0
40	8.0	29.5	59.1	53.6	23.8	0.0

GILCHRIST (1960) studied growth in three races of *Artemia salina* (La Palme, France; Arzeu, Algeria; San Diego, USA) at 25° C in 35‰ and 140‰S. The bisexual San Diego race reveals significant differences in growth rates in the two salinities; females grow much, males somewhat, slower in the higher salinity. In contrast, the La Palme race, which consists of parthenogenetic females, exhibits only insignificant variations in growth rates in 35‰ or 140‰S. This example illustrates that different populations or races of a given species may have different salinity requirements for growth. In *A. salina* from the Great Salt Lake in Utah (USA), growth rates have been examined in different combinations of salinity (5‰, 15‰, 32‰, 70‰S) and temperature (10°, 15°, 20°, 30° C) by VON HENTIG (1970), who fed his cultures with *Dunaliella tertiolecta*. Growth rates increase with increasing salinity up to 32‰, then decline somewhat in 70‰; in regard to temperature, growth rates increase up to 20° C and decrease in 30° C. The optimum condition of 32‰S and 20° C pertains only to growing subadults and adults; larvae grow best in 15‰S and at 30° C. Time to maturity depends primarily on temperature; within the range tolerated, salinity is of little importance.

In a few freshwater-living invertebrates, growth rates have been recorded under conditions of low salinity. While detailed studies have not come to the reviewer's attention, scattered information suggests that growth rates do not change significantly in very low salinities (1‰ to 3‰) but become severely retarded in salinities above 3‰ (3‰ to 8‰). Reports claiming increased growth rates in 1‰ to 2‰S, compared to those in fresh water, require confirmation. KINNE (unpublished) exposed sections of egg batches containing developing eggs of the freshwater-living gastropod *Lymnaea stagnalis* to different salinities (fresh water, 3‰, 6‰, 9‰S) and, after hatching, recorded the growth rates, at a temperature of 22° C, throughout the following 10 months. The snails were fed primarily on leaves of the garden lettuce *Lactuca sativa*. Growth rates, expressed as length and width of the snails' shells, proved to be similar in fresh water and 3‰S (average shell length after 9 months:  $30.0 \pm 2.2$  mm) but were reduced significantly in 6‰S (average shell length after 9 months:  $23.8 \pm 2.4$  mm; mortality in 6‰S was considerably higher than in fresh water or 3‰S). Maximum shell width after 9 months was  $13.4 \pm 1.2$  mm in fresh water,  $12.8 \pm 1.3$  mm in 3‰S, and  $10.1 \pm 1.5$  in 6‰S. The differences in shell shape are not statistically significant. In 9‰S, all young snails died within 17 days.

There is great need for detailed analyses of the effects of different salinity conditions on growth rates of marine and brackish-water invertebrates.

*Metabolic water and salt regulation.* Metabolic regulation counteracting undesired biological consequences of salinity variations may be considered under three headings: ion regulation, volume regulation, and osmoregulation. The study of the forces responsible for movements of ions and molecules across the borders of living systems still poses many unsolved problems. A large school of thought favours the idea that active transport (net flux of ions or molecules against the gradient) is based primarily on special properties of the cell membrane (membrane theory of cell permeability). Another school of thought, represented, for example, by NASSONOW and his associates (e.g. NASSONOW and AISENBERG, 1937; NASSONOW, 1938, 1939; NASSONOW and ALEXANDROW, 1943) and TROSHIN (1953a, b, 1958), holds that the permeability of the cell depends on the sorption activity of the living matter as a whole, but not on a 'hypothetical semipermeable membrane' (sorption theory of cell permeability). Whether the external permeability boundary is considered to be the cell membrane or the cell protoplasm as a whole, the fact remains that the permeating matter passes, or is actively transported, across boundaries of specifically organized living ultrastructures.

Ion, volume and osmoregulation are closely related, interdependent aspects of water and salt exchange between organism and environment. They can be employed simultaneously by a given individual and, in certain situations, may defeat attempts at conceptual separation. However, methodological differences, introduced by investigators, make it desirable to treat these three aspects separately.

In this section, attention is focused on quantitative differences in regulatory capacities. The physiological mechanisms of water and salt regulation employed by marine and brackish-water organisms will be dealt with in Volume II of this Treatise. The mechanisms have recently been discussed by POTTS and PARRY (1964), CROGHAN and co-authors (1965), DEHNEL (1966), KING (1966), QUINN and LANE

(1966), BURTON (1967), DALL (1967), KERLEY and PRITCHARD (1967), MANTEL (1967), SMITH (1967) and others.

The capacity for metabolic water and salt regulation varies with a number of endogenous (genetic constitution, neuro-endocrine control, hormones, age, body size, physiological state) and exogenous (hydrochemical properties of the surrounding water, temperature, nutrition, light, hydrostatic pressure, etc.) factors. Comparable developmental stages of one and the same species may exhibit different regulatory capacities due to differences in environmental history (state of adaptation; p. 893) and ecotype selection, resulting in interpopulational gradients of performance.

The literature concerned with capacities for ion, volume and osmoregulation in aquatic invertebrates has increased in recent years to such an extent that an exhaustive documentation would easily fill one or two volumes. Restrictions must therefore be made and general trends, that have become apparent, illustrated by referring to selected examples. Reviews on aspects of ion, volume and osmoregulation have been published by DUVAL (1924, 1925), SCHLIEPER (1929, 1930, 1935, 1955, 1964), BEADLE (1931, 1957), BETHE (1934), HARNISCH (1935, 1951), KROGH (1939), ROBERTSON (1949, 1953, 1954, 1957a, 1960, 1964), POTTS (1954), BROWN and DANIELLI (1955), VON BUDDENBROCK (1956), BLACK (1957), REMANE and SCHLIEPER (1958), TROSHIN (1958), ANDERSEN and USSING (1960), BROWN and STEIN (1960), NICOL (1960), SHAW (1960b), PROSSER and BROWN (1961), LOCKWOOD (1962), KINNE (1963a, b, 1964a, 1967b), POTTS and PARRY (1964), FOGG (1965), SCHOFFENIELS (1967), OGLESBY (1969a), FLORKIN and SCHEER (1969).

*Ion regulation.* Ion regulation may be defined as the capacity of an organism to build up and maintain specific ionic gradients between cell fluids, body cavity fluids and external medium. In this definition, the term 'cell fluids' refers to intra- and intercellular liquids, and the term 'body cavity fluids' to blood, lymph or other liquids of body cavities. Ion regulation comprises active physiological processes which require biologically useful energy. It has, presumably, a longer evolutionary history than volume or osmoregulation. All living cells possess some capacity for ion regulation.

Ionic gradients and the degree of ion regulation can be determined by comparing an analysis of one body fluid sample with that of another sample after it has been dialyzed against sea water across a collodion membrane permeable to water and salt but not to protein. Deviations from ionic equilibrium are probable only if ion concentrations in the original body fluids differ from those of sea water or dialyzed plasma by the following percentages: Na 0.6, K 2.6, Ca 1.5, Mg 1.8, Cl 1.1, SO<sub>4</sub> 1.2 (ROBERTSON, 1953, 1964).

Among protozoans, not much is known about ion regulation. In the marine ciliate *Uronema filificum*, the ionic composition has been determined by KEHLENBECK and co-authors (1965); the concentration gradients of K, Na and Cl between cell interior and environment are similar as in other marine invertebrates. The contractile vacuole of protozoans may be responsible for active Na extrusion (CHAPMAN-ANDRESEN and DICK, 1962; MARSHALL, 1966; DUNHAM and STONER, 1967). K is actively accumulated or passively maintained (CONNER, 1967). The

euryhaline marine ciliate *Miamiensis avidus*, a facultative parasite of sea-horses, was maintained axenically in a special medium (filtered sea water, lactalbumin hydrolysate solution, calf serum) and examined after exposure to different salinities (KANESHIRO and co-authors, 1969). In a 100‰ sea-water culture medium, *M. avidus* had the following ion concentrations (mM/Kg cells): 87.9 Na, 73.7 K, 3.7 Ca, 28.5 Mg, 60.8 Cl. Internal Na, Ca, Mg and Cl was lower, K higher, than in the ambient medium; Na and Cl changed with changes in salinity.

Coelenterates exhibit rather low capacities of ion regulation; however, the mesogloal fluid of *Aurelia flavidula* medusae contains considerably reduced levels of  $\text{SO}_4$ , and reveals a compensatory increase in Cl. Medusae of several other species were also reported to contain less  $\text{SO}_4$  than the surrounding sea water (MACALLUM, 1903; KOJIZUMI and HOSOI, 1936). These authors found rather high K concentrations, but this may have been caused, according to POTTS and PARRY (1964), by the presence of cells in the mesogloal jelly. In *Hydra (Pelmatohydra) oligactis*, uptake of radio-active ions  $^{24}\text{Na}$ ,  $^{82}\text{Br}$  and  $^{42}\text{K}$  has been investigated by LILLY (1955); all three ions are maintained at higher internal levels. The ratio of internal to external concentration has been determined for Na and Br. Internal Na is maintained at a steady level, with external concentrations varying from 5.4 mM/l to approximately 0.20 mM/l; internal Br decreases parallel to external Br from 2.5 to 0.05 mM/l.

Among the sipunculids, the osmoconformer *Themiste dyscritum* has an apparent ion deficit in the coelomic fluid, as indicated by low internal Cl concentrations relative to external levels; this deficit is most marked in worms exposed to low salinities, and may be made up by small molecular weight organic molecules (OGLESBY, 1968a). Species of *Phascolosoma* have been reported to maintain higher K and lower Mg and  $\text{SO}_4$  levels. However, the various ionic analyses of coelomic fluids of sipunculids (DUVAL, 1924; BETHE and BERGER, 1931; BIALASCEWICZ, 1933; STEINBACH, 1940; ROBERTSON, 1953; KAMEMOTO and LARSON, 1964) have produced such different results that generalizations are at present not possible; the capacities of sipunculids for ion regulation appear to be less pronounced than in molluscs or crustaceans.

Many molluscs concentrate K and Ca (Table 4-55). The blood of *Mytilus edulis*, for example, contains 135‰ K (100‰ = normal K concentration in sea water). Most molluscs examined to date dispel  $\text{SO}_4$ ; however, *Mytilus galloprovincialis* accumulates  $\text{SO}_4$  up to 120%. Na and Cl are more or less in equilibrium with the ambient sea water, except in cephalopods which tend to expel Na and to accumulate Cl. In contrast to crustaceans, molluscs do not reduce their Mg level significantly (lowest recorded Mg concentration: 96.5‰ in *Mytilus galloprovincialis*). *Buccinum undatum*, *Archidoris pseudoargus* and *Eledone cirrosa* accumulate Mg (Table 4-55; BETHE, 1929; BETHE and BERGER, 1931; ROBERTSON, 1949, 1953, 1964). POTTS and PARRY (1964) consider the resistance to, or preference for, Mg unusual and suggest that it may be a characteristic of marine molluscs. The highest capacity for ion regulation among molluscs is exhibited by the cephalopods. *Loligo forbesi* accumulates K up to 215‰. The progressive increase of the blood Na level in the series *Septia officinalis*, *Loligo forbesi*, *Eledone cirrosa* is paralleled by an increase in Ca, Mg and  $\text{SO}_4$ , as well as by a decrease in Cl, while the total ion concentration of the blood plasma reveals isosmotic equilibrium with the ambient sea

Table 4-55

Ionic constituents of blood plasma of marine molluscs. Ion concentrations are expressed as percentages of concentrations in dialyzed plasma (prosobranchs and cephalopods) or in sea water (other groups) (Data from ROBERTSON, 1949, 1953; after ROBERTSON, 1964; modified)

Invertebrates	Na	K	Ca	Mg	Cl	SO <sub>4</sub>	Plasma protein (g/l)	Total ion concentrations (% of sea-water values)
<b>Gastropods</b>								
<b>Prosobranchs</b>								
<i>Buccinum undatum</i>	97	142	104	103	100	90	25.3	99
<i>Neptunea antiqua</i>	101	114	102	101	101	98	24.1	100
<b>Opisthobranchs</b>								
<i>Pleurobranchus membranaceus</i>	100	117	112	99	100	102	0.3	100
<i>Archidoris pseudoargus</i>	99	128	132	107	100	96	0.4	100
<b>Bivalves</b>								
<b>Lamellibranchs</b>								
<i>Mytilus edulis</i>	100	135	100	100	101	98	0.3	100
<i>M. galloprovincialis</i>	101	121	107	97	99	120	0.8	99
<i>Pecten marinus</i>	100	130	103	97	100	97	—	100
<i>Ostrea edulis</i>	100	129	101	102	100	100	0.2	100
<i>Ensis ensis</i>	99	155	108	99	99	87	—	99
<i>Mya arenaria</i>	101	107	107	99	100	101	—	100
<b>Cephalopods</b>								
<i>Sepia officinalis</i>	93	205	91	98	105	22	109	98
<i>Eledone cirrosa</i>	97	152	107	103	102	77	105	100
<i>Loligo forbesi</i>	95	219	102	102	104	29	150	99

water. These relationships have been interpreted on the basis of the ideal laws of solutions (ROBERTSON, 1949, 1953).

The considerable capacity of cephalopods for regulating the ionic composition of their body cavity fluids (blood, lymph, coelom, eye fluids, etc.) is of importance for achieving buoyancy (POTTS and PARRY, 1964; ROBERTSON, 1964). Oceanic squid of the family Cranchiidae, for example, have large coelomic spaces filled with a slightly acid (pH 5.2) fluid, which contains about 480 mg-ions  $\text{NH}_4$  and 80 mg-ions Na; although the coelomic fluid is practically isosmotic with the surrounding sea water, it has a lower density, bringing about buoyancy equilibrium (DENTON and co-authors, 1958; DENTON, 1960). Also in the cranchiid genera *Verrilliteuthis*, *Galiteuthis* and *Helicocranchia* the weight of body tissues is counter-balanced by large amounts of coelomic fluid with a density lower than that of sea water. Again, the low density results from high concentrations of  $\text{NH}_4$  ions; ionic equilibrium is maintained by very high concentrations of Cl. At the low pH of the coelomic fluid (5.2),  $\text{NH}_4$  probably diffuses in from the blood or is secreted from the kidneys or parts of the coelomic epithelium (DENTON and co-authors, 1958; ROBERTSON, 1964).

The fluid excreted by the renal tubules has been analyzed in the cephalopods *Eledone cirrosa* and *Sepia officinalis* (Table 4-56). Renal sac fluid has a low protein content (1/100 or less that of the plasma) and is practically isosmotic with the blood plasma. In the renal sac fluid, concentrations of almost all major ions differ considerably from those of the blood plasma or the plasma ultrafiltrate. *Eledone cirrosa* re-absorbs K, Ca, Mg and Cl; it secretes Na and  $\text{SO}_4$ . In *Octopus hongkong-*

Table 4-56

Ionic constituents (mg/g water) of blood plasma and renal sac fluid of the cephalopod molluscans *Eledone cirrosa* and *Sepia officinalis* (Based on data by ROBERTSON, 1949, 1953)

	Na	K	Ca	Mg	Cl	$\text{SO}_4$	mg-ions/ kg water (total)
<i>Eledone cirrosa</i>							
Plasma	10.26	0.581	0.466	1.318	18.92	1.983	1081
Renal sac fluid	10.41	0.522	0.405	1.218	18.35	2.705	1073
Fluid as % plasma	101.0	90.0	87.0	92.0	97.0	136.0	99
Plasma ultrafiltrate* as % plasma	99.0	99.0	92.0	98.0	101.0	102.0	100
Sea water	10.43	0.378	0.399	1.258	18.80	2.624	1082
<i>Sepia officinalis</i>							
Plasma	10.58	0.931	0.434	1.383	20.87	0.47	1145
Renal sac fluid	8.35	0.465	0.302	0.936	20.85	1.01	1166
Fluid as % plasma	79.0	50.0	70.0	68.0	100.0	215.0	102
Plasma ultrafiltrate* as % plasma	98.0	98.0	84.0	96.0	102.0	105.0	100
Sea water	11.31	0.409	0.432	1.364	20.38	2.845	1174

\*Calculated from dialysis experiments, using the mean Donnan ratio, except in the case of Ca.

*ensis* the renal organs excrete daily the equivalent of about 138% of the blood volume or 29% of the extracellular fluid volume (MARTIN, 1957; MARTIN and co-authors, 1958). In *Sepia officinalis* minimum daily urine output amounts to 13% of the volume of extracellular fluids (ROBERTSON, 1953).

Annelids tend to retain high K concentrations. Their truly marine representatives, however, have only small potentials for ion regulation. In the polychaete *Aphrodite aculeata*, ionic composition of the almost protein-free coelomic fluid is very similar to that of the ambient sea water. Species of the genera *Amphitrite*, *Glycera* and *Arenicola* accumulate K; the two latter have reduced SO<sub>4</sub> levels (BIALASCEWICZ, 1933; SMITH *in*: COLE, 1940; ROBERTSON, 1949, 1953). The marine polychaete's capacity for ion regulation rarely exceeds 10% (POTTS and PARRY, 1964). *Marphysa gravelyi*, a brackish-water eunicid, regulates Na, K and Cl, and maintains fairly constant ratios of Na : Cl, K : Cl, K : Na and NaCl : KCl over salinities ranging from 9‰ to 26‰ (Tables 4-57, 4-58; KRISHNAMOORTHY, 1963; KRISHNAMOORTHY and KRISHNASWAMY, 1965, 1966b). Experiments and discussions on fluxes and active transport of Cl in nereid species have been presented by OGLESBY (1965b).

Crustaceans, especially the larger forms, have been shown to exhibit considerable capacities for ion regulation (e.g. WEBB, 1940; ROBERTSON, 1957a, 1960); many accumulate K, but in some, e.g. *Homarus gammarus*, this ion is found in concentrations as low as in sea water. In general, Mg and SO<sub>4</sub> are kept at considerably lower levels than in sea water. Species known to exhibit rather low levels of

Table 4-57

Blood chloride regulation in the euryhaline polychaete *Marphysa gravelyi*. Method of SENDROY, as modified by ROBERTSON and WEBB (1939). 27.5° ± 0.5° C. Chloride levels are higher in hypo-osmotic and lower in hyper-osmotic salinities (After KRISHNAMOORTHY, 1963; modified)

Salinity (‰)	Blood chloride after 24-hr exposure to test salinities		
	(g/l)	Standard error	Number of measurements
5.7	9.6	±0.005	3
8.5	10.7	±0.016	3
10.6	12.8	±0.004	8
14.6	14.4	±0.005	8
15.3	11.9	±0.004	12
16.6	13.9	±0.002	12
16.2	10.8	±0.006	8
18.4	14.1	Nil	4
19.5	14.8	±0.012	8
21.6	15.4	±0.003	12
23.0	14.1	±0.003	8
25.9	16.0	±0.006	12

Table 4-58

Ion regulation in the polychaete *Marphysa gravelyi* in different salinities. Zeiss flame photometer determinations (After KRISHNAMOORTHY and KRISHNASWAMY, 1966b; modified)

Salinity (‰)	Body fluid concentrations (mM/l)					
	Cl	Na	K	Ion ratios		
				Na:Cl	K:Cl	K:Na
9	301	150	28	1:2	1:11	1:5
11	358	135	24	1:3	1:15	1:5
16	305	90	18	1:3	1:17	1:5
26	464	163	33	1:3	1:14	1:5

locomotory activity (e.g. *Lithodes maia*, *Hyas coarctatus*, *Maia squinado*, *Dromia vulgaris*) appear to be characterized by higher blood-Mg levels than more active ones (e.g. *Carcinus maenas*, *Portunus puber*, *Pachygrapsus marmoratus*, *Nephrops norvegicus*); for details consult ROBERTSON (1953) and section *Activity* (p. 945) of the present subchapter. Most marine crustaceans tested have high Ca values. If exposed to brackish water, several crustaceans tend to maintain ionic ratios similar to those in sea water. The euryhaline amphipod *Corophium volutator* maintains, over a range of salinities from 1‰ to 35‰, blood Na, K, Ca and Cl more concentrated, but Mg less concentrated, than in the ambient medium. Its body surface permeability to ions (silver-staining technique) is confined to certain ventral patches and the gill (McLUSKY, 1968b). In the copepod *Tisbe reticulata*, internal K is regulated in diluted sea water but Na is not controlled (BATTAGLIA and BRYAN, 1964).

In sea water, *Carcinus maenas* elevates Na, Ca and Cl, but reduces Mg and SO<sub>4</sub>; in brackish water (16‰S), it also accumulates K against the gradient to the surrounding medium (SECK, 1957). LOCKWOOD and RIEGEL (1969) made measurements of the concentrations of Na, Ca and Mg in blood and urine of *C. maenas* after transfer to 50% or 150% sea water. Mg is concentrated in the urine by a secretory process when the crabs are in 100% sea water or in 150% sea water. There is evidence that the secretion rate declines in 50% sea water or in 100% Mg-free sea water, but no evidence for active withdrawal of Mg from the urine. A comparison of Mg excretion by *C. maenas* and *Pachygrapsus crassipes* shows that Mg is conserved more effectively in dilute media by *C. maenas* than by *P. crassipes*.

LOCKWOOD and ANDREWS (1969) followed Na fluxes of individual *Gammarus duebeni*, which moulted in sea water, for at least 6 days, at daily intervals from the morning after the moult. On the first morning, Na influx from sea water amounted to 15.1 μM/individual/hr; by the tenth day after the moult it had declined to 1.7 μM/individual/hr. Na influx from 10 mM/l NaCl plus sucrose solution isotonic with sea water declines from 4.48 μM/individual/hr to 0.14 μM/individual/hr in intermoult *G. duebeni*. Thionine inhibits over 90% of the influx from 10 mM/l NaCl plus isotonic sucrose on the first day following the moult; this fact, together

with other evidence, suggests that the major part of the Na influx from this medium is due to active uptake. The rate of active Na uptake is comparable to, or faster than, the rate of uptake by individuals acclimated to fresh water. The Na influx occurs primarily across the body surface. LOCKWOOD and ANDREWS suggest that the high level of Na uptake is associated with the water uptake which occurs at moult. While, in some crustaceans, much of the fluid taken up at moulting can be attributed to the drinking and subsequent re-absorption of ambient medium,

'the drinking rate of freshly moulted *Gammarus* is totally inadequate to explain the amount of sodium taken up. A drinking rate of over 400  $\mu\text{l/hr}$  would be required to account for the thionine-inhibited portion of the sodium influx. This is nearly six times the total volume of the animal. The observed drinking rate, as measured with *Amaranth*, is less than 1  $\mu\text{l/hr}$ ' (LOCKWOOD and ANDREWS, 1969, p. 602).

Table 4-59

Ionic composition of blood plasma of decapod and stomatopod crustaceans (After ROBERTSON, 1953; modified)

Crustaceans	Ion concentrations in blood plasma as percentage of concentration in dialyzed plasma						Protein (mg)	H <sub>2</sub> O (ml)
	Na	K	Ca	Mg	Cl	SO <sub>4</sub>		
STOMATOPODA								
<i>Squilla mantis</i>	111	129	108	32	101	82	65	916
DECAPODA								
<i>Eupagurus bernhardus</i>	105	130	137	49	96	135	69	926
<i>E. prideauxi</i>	102	156	126	76	98	129	80	916
<i>Dromia vulgaris</i>	97	120	84	99	103	53	37	947
<i>Hyas araneus</i>	102	132	106	93	102	104	29	952
<i>Maia squinado</i>	100	125	122	81	102	66	53	931
<i>Portunus depurator</i>	105	134	111	47	97	78	37	951
<i>P. puber</i>	110	147	120	41	101	83	54	936
<i>Pachygrapsus marmoratus</i>	94	95	92	24	87	46	35	951

Analysis of the pooled blood plasma from four female *Squilla mantis* reveals regulatory capacities of the same type and degree as found in a number of other decapod crustaceans: accumulation of cations except Mg (which is markedly reduced) and lowered SO<sub>4</sub> values (Table 4-59). *Eupagurus bernhardus* and *E. prideauxi* accumulate considerable quantities of SO<sub>4</sub>. *Dromia vulgaris* has very low SO<sub>4</sub> values combined with high Mg and very low Ca concentrations. The spider crabs *Hyas araneus* and *Maia squinado* maintain high Mg values, compared to *Portunus depurator*, *P. puber* and *Pachygrapsus marmoratus*. Interestingly, *P. marmoratus* maintains all ions determined below equilibrium concentrations; its Mg and SO<sub>4</sub> concentrations are extremely low (ROBERTSON, 1953).

In the crabs *Hemigrapsus nudus* and *H. oregonensis*, concentrations of Na, K, Ca and Mg of blood and urine have been measured at 8 salinities (6 to 175‰ sea

water) and 3 temperatures (5°, 15° and 25° C), both in summer and in winter (DEHNEL and CAREFOOT, 1965; DEHNEL, 1966, 1967). In 6 to 75% sea water, blood Na, K and Ca are considerably hypertonic to ambient media concentrations. In 100 to 175% sea water, ion concentrations approach isotonicity. Blood Mg, however, is regulated at a hypotonic level (about one-third of medium concentration) in all test salinities above 12% sea water. The test temperatures employed exert no consistent influence on blood and urine concentrations of Na, K or Ca in either season; however, increased temperatures appear to impair Mg regulation. Seasonal differences in the capacity to control Na and K were also inconsistent and revealed no general trend; blood Mg concentrations are almost identical in summer and winter; yet, in low salinities, blood Ca is higher in winter than in summer. Major gradients are maintained between cations of muscle and blood. Na and Ca are higher, K and Mg lower, in the blood than in the muscle cells. Muscle cations are hypotonic to ambient medium concentrations, 'with minor exceptions' (DEHNEL, 1967, p. 547). Muscle Cl is maintained rather constant; it is hypotonic to the blood, as well as to the external salinities employed. Changes in muscle water, relative to changes in test salinities, suggest movement of water between blood and muscle, while maintenance of a constant blood water content is indicative of variations in filtration rate of the antennary gland.

McFARLAND (1963) determined ion concentrations in blood serum and muscles of two euryhaline and two stenohaline shrimps. In the euryhaline *Penaeus setiferus* and *P. aztecus*, and in the stenohaline *Trachypeneus similis*, serum ions account for about 95% of the serum osmoconcentration, in the stenohaline *Siconina dorsalis* for only 84%. Muscle K concentrations are highest in the two euryhaline forms, intermediate in *T. similis*, and lowest in *S. dorsalis*. Muscle Ca and Mg are maintained at fairly constant levels in *P. setiferus* and *P. aztecus* in brackish and sea water, but Na, K and Cl tend to increase with salinity; at salinities above that of sea water muscle K decreases; all other ions mentioned remain at about the same level as in sea water. Ratios of muscle cations to serum cations are higher in the euryhaline than in the stenohaline shrimps; the difference is attributed primarily to decrease in muscle K in the stenohaline forms.

In the mantis shrimp *Squilla empusa*, serum cations and Cl account for 95% of the serum osmoconcentration in sea water, but for only 67% in 12‰ to 13‰ S (LEE and McFARLAND, 1962). The balance is made up, in part, by non-protein nitrogenous compounds, most probably amino acids. With decreasing salinities, concentrations of serum Na, K, Ca, Mg and Cl decrease; however, below 60% sea water, Na, Cl and particularly Ca tend to remain constant. Muscle Na and Cl decline with decreases in environment and serum concentrations; in contrast, K remains constant while Ca and Mg show slight tendencies to increase.

Active ion transport in crustaceans is subject to intraspecific (interpopulational) differences and individual adjustments. In the copepod *Tisbe reticulata*, exchange rates for <sup>42</sup>K and <sup>137</sup>Ca are higher in the *violacea* form than in the *trifasciata* form. In regard to <sup>42</sup>K, interpopulational differences between these two polymorphic forms are greater than between three different geographical populations of *T. furcata*. The form *violacea* favours lower salinities and higher temperatures and is more euryplastic than *trifasciata*. This finding indicates that polymorphism can be associated with quantitative differences in metabolic regulation, and that such

differences may be related to habitat conditions (BATTAGLIA and BRYAN, 1964; BATTAGLIA, 1967). Individuals from a Baltic Sea (about 13‰ to 18‰S) population of *Carcinus maenas* regulate blood Na (and total blood osmoconcentration) in low salinities more effectively than those of a North Sea (about 32‰S) population (Fig. 4-105). These interpopulational differences appear to consist of a genetic and a non-genetic component, since cross acclimation lessens (but does not eliminate) the divergencies (THEEDE, 1969a). Individual adjustments (non-genetic adaptation; p. 928) in regulatory capacities have also been reported for *Callinectes sapidus* (ANDERSON and PROSSER, 1953).

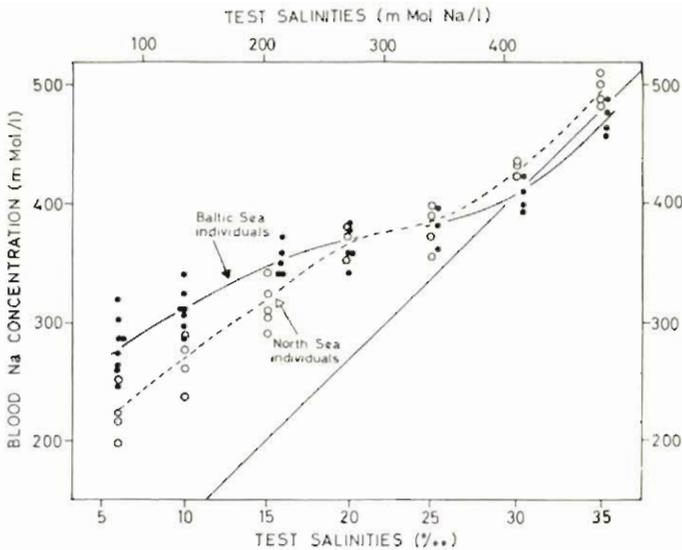


Fig. 4-105: Intraspecific (interpopulational) differences in the capacity for sodium regulation in the crab *Carcinus maenas*. Individuals from the Baltic Sea (13–18‰S) regulate more effectively in low salinities than those from the North Sea (32‰S). Individual measurements, made 3 days after transfer from 15‰ or 30‰S (stabilizing media) into the various test salinities; 16.5° C. (After THEEDE, 1969a; modified.)

Decapod crustaceans regulate their ionic composition via gills, gut and antennary (maxillary) glands; to a lesser degree, via urinary bladder and possibly other organs or tissues. The activity of the regulatory sites varies in different species and depends on the ionic gradients between cell fluids and body cavity fluids, and those between body cavity fluids and external medium. In reduced salinities, gills (lamellar epithelium) and, to a lesser extent, gill chamber (branchia epithelium lining) represent primary sites of active ion uptake. The gut may serve as site for ion uptake from the swallowed ambient medium, or from food in low salinities, and as site of water re-absorption in high salinities. Antennary glands regulate specific blood ions (e.g. Mg), particularly in hyperosmotic media. 'Kidneys' may support hypertonic regulation in low salinities (e.g. K re-absorption in tubules) and hypotonic regulation in high salinities (e.g. Na and Ca excretion via urine). The urinary bladder may participate in Mg regulation and re-absorb glucose (e.g. in *Pachy-*

*grapsus crassipes*). Extravascular 'salt pools' have been proposed (HUKUDA, 1932; GROSS, 1958) to account for Na and K balances and act as ion reservoirs in crabs under fluctuating salinity stress (ROBERTSON, 1949, 1953; PROSSER and co-authors, 1955; BURGER, 1957; GROSS, 1958, 1967; GREEN and co-authors, 1959; RIEGEL and LOCKWOOD, 1961; LOCKWOOD, 1962; DEHNEL and STONE, 1964; POTTS and PARRY, 1964; DEHNEL and CAREFOOT, 1965; GROSS and CAPEN, 1966; and others). In the land crab *Gecarcinus lateralis*, COPELAND (1968) found a salt-absorbing tissue in the respiratory lamellae of the gills in the form of a highly interdigitated epithelium. The folds of the epithelium are supplied with mitochondria, forming 'mitochondrial pumps'. The intercellular spaces observed between the folds satisfy the morphological requirements for the model system of water transport, based on the theory of standing osmotic gradients (DIAMOND, 1962, 1965; DIAMOND and TORMEY, 1966). Most of the regulatory tissue of the *G. lateralis* gill is localized in the three most posterior gills, which rest on the pericardial sac. COPELAND has suggested, therefore, that the pericardial sac transfers ground water to the gills for salt and water absorption.

Owing to a high protein content, passive equilibrium between blood plasma and ambient medium across the gills would result in higher concentration of cations and lower concentration of anions in the plasma, as well as in a much higher Ca content because of the formation of a Ca-protein complex (ROBERTSON, 1953). Apparently, most of the internal K is held electrostatically by non-diffusible organic ions, organic phosphates and protein, and low internal Na levels are maintained by active extrusion of Na ions. On the basis of this hypothesis, put forward by USSING (1949, 1953) and HODGKIN (1951), cellular K stands in Donnan equilibrium with the outside K. In *Eriocheir sinensis* the Donnan ratios ( $[K_i]/[K_o]$ ,  $[Cl_o]/[Cl_i]=r$ ) are 18.4 and 3.21 respectively, in *Carcinus maenas* 8.8 and 10.5, and in *Nephrops norvegicus* 20.6 and 9.39. The theoretical requirements are approximated only in *Carcinus maenas*.

'It seems that in *Eriocheir* and *Nephrops* active uptake of K by a metabolic process must be postulated, since the Donnan equilibrium is inadequate to explain the ratios, and the binding of large amounts of internal K in unionized complexes is very improbable' (ROBERTSON 1957a, p. 243).

Echinoderms are poor ion regulators. Body cavity fluids of representatives of all classes tested are more similar to sea water than those of any other phylum. The only significant differences appear to be a slightly higher K and a higher H concentration. *Echinus esculentus* and *Holothuria tubulosa* have ionic ratios in their body cavity fluids so similar to that of the surrounding medium that the system must be close to equilibrium (SHAW, 1960b). In the sea-star *Asterias rubens*, the ionic composition of the general body cavity fluid conforms closely to that of the external medium, both in sea and brackish water (Table 4-60); while in the ambulacral fluid, K is accumulated to about 160% of the external concentration over a wide range of salinities (BINYON, 1962). Members of the genus *Holothuria* concentrate K and Mg by about 3%, those of *Marthasterias* accumulate K by 11%, but slightly reduce Mg (POTTS and PARRY, 1964). Ionic concentrations in cells of echinoderm blood, muscle and body wall, however, may differ clearly from those of the surrounding sea water; the same holds for the ionic composition of

Table 4-60

*Asterias rubens*. Proportions of major ions (mM/l) in the body cavity fluid and ambient sea water of 31‰S or brackish water of about 16‰S (After COLE, 1940; SECK, 1957; REMANE and SCHLIEPER, 1958; modified)

Medium	Na	K	Ca	Mg	Cl	SO <sub>4</sub>
31‰ S	417	9.10	9.41	50.1	483.0	30.3
Body cavity fluid	412	9.56	9.31	50.0	488.0	30.1
16‰ S	215	4.98	5.56	24.05	252.8	13.08
Body cavity fluid	216	5.40	5.60	24.22	255.0	13.05

echinoderm eggs. Unfertilized sea-urchin eggs contain about 20 times more K and 9 times less Na than sea water (COLE, 1940; ROBERTSON, 1949, 1953; ROTHSCHILD and BARNES, 1953).

In aquatic insects, a considerable amount of research has been devoted to ion regulation. Two examples must suffice here. STOBART (1959, 1960) studied steady-state exchange and net transport of Na in freshwater-living 4th instar larvae of the mosquito *Aedes aegypti* by means of flame photometry and <sup>22</sup>Na. Steady-state exchange between larvae and external medium can be increased about 6 times by feeding, even though there is no difference between the Na levels of fed and starved larvae. About 90% of the exchange occurs through the anal papillae. Net transport by Na-deficient larvae is more rapid in fed (ca 50 mM/l/hr) than in starved (ca 10 mM/l/hr) individuals. Net Na transport is reduced quite abruptly when the normal Na level in the haemolymph is re-attained; the rapid control deserves further investigation. The aquatic larvae of the dipteran insect *Ephydra cinerea* can take up <sup>22</sup>Na and <sup>86</sup>Rb against concentration gradients (NEMENZ, 1960b). In ligated individuals, excretion of <sup>22</sup>Na and water is impaired. In ambient media containing NaCl and CaCl<sub>2</sub>, cuticula permeability for electrolytes is significantly reduced (presumably due to the Ca ions). Permeability for D<sub>2</sub>O remains independent of the ionic composition of the ambient medium during the first 48 hrs; however, after 96 hrs it varies parallel to electrolyte permeability. Addition of MgCl<sub>2</sub> leads to increased permeability.

The capacity for ion regulation has also been assessed by exposing marine and brackish-water living invertebrates to artificial sea water, or to brackish water, of varying ionic compositions (BERGER, 1929; BETHE, 1929). In *Mytilus edulis*, blood and tissue chlorides rise and fall proportionately to changes in the external medium (KROGH, 1938, 1939); a similarly poor ion regulator is the holothurian *Caudina chilensis* (KOIZUMI, 1932). Examples of powerful ion regulators are the amphipod *Gammarus duebeni* (BEADLE and CRAGG, 1940a; LOCKWOOD and ANDREWS, 1969) and the crabs *Eriocheir sinensis* (SCHOLLES, 1933), *Carcinus maenas* (WEBB, 1940), *Ocyropsis albicans* (FLEMISTER and FLEMISTER, 1951), *Pachygrapsus crassipes* (PROSSER and co-authors, 1955), *Uca pugnax*, *U. pugilator* (GREEN and co-authors, 1959) and *Coenobita clypeatus* (GROSS and HOLLAND, 1960).

In view of the many papers published on ion regulation in marine and brackish invertebrates, it is surprising how little we know about physiological and ecological effects of natural waters of deviating ionic composition. From the information available, it appears that (i) small deviations are ecologically unimportant; (ii) significant changes cause reduced capacities for growth and reproduction and change environmental resistance, e.g. to thermal stress; (iii) extreme deviations lead to metabolic disturbances and increased mortality. In general, euryhaline organisms tend to be less affected by ionic deviations than stenohaline ones.

Changes in ionic composition of extracellular fluids may affect tension capacities of muscle cells. Extracellular variations in Na concentration appear to be of particular importance in this respect. The role of Ca in muscle performance is well documented for mammals and several invertebrates; Ca seems to represent a principal link between excitation and contraction (SANDOW, 1965); it may be accumulated actively in muscle cells (HASSELBACH and MAKINOSE, 1961), suggesting a regulatory function of the sarcoplasmic reticulum (WEBER and co-authors, 1964). Assessments of the effects of monovalent cations on the Ca-accumulating capacity of the cardiac sarcoplasmic reticulum (PALMER and POSEY, 1967) revealed that Na and, to a lesser degree, Li (but not K) reduce the amount of muscle Ca. Reduction of Ca binding by Na is not due to inhibition of uptake but to a rapid release of bound Ca. The amount of Ca released by Na does not appear to be enough to explain contraction, on the basis of Na influx into the muscle, but may be important in regulation of muscle tension.

In extremely low salinities, ion regulation may be affected significantly by the ion contents of the food consumed. Unfortunately, only very few investigations have been devoted so far to this important aspect. In long-term rearing and breeding experiments, the importance of ions (single and in combination) taken up with the food ought to be analyzed. In the amphipod *Gammarus duebeni*, survival rates in running distilled water increase markedly if salt-containing food is offered; the same is true for the isopod *Sphaeroma hookeri* if exposed to running water of extremely low salinity (own unpublished results). The importance of Ca and Fe taken up with the food has been demonstrated in aquatic larvae of the insect *Chironomus thummi* (STRENZKE and NEUMANN, 1960; NEUMANN, 1961b, 1962).

Ionic analyses of body fluids are subject to various errors, and many must be viewed with reservations because of the limitations of the methods employed. Inorganic constituents of body fluids are usually considered to be ions behaving as they would in normal aqueous solutions of comparable concentrations; however, in body fluids, unknown and presumably variable amounts may be bound to organic molecules. As pointed out by STEINBACH (1940) and DUBUISSON (1954), and stressed by ROBERTSON (1957a), intracellular cations may not be evenly dispersed but topographically related to intracellular structures: in *Nephrops norvegicus*, for example, liquid pressed from muscles has the same Cl level as the muscle itself (on a water-content basis), but contains only 74 to 80% of the Na, K and acid-soluble P and less than 10% of the Ca and Mg. This finding suggests that most of the Ca and Mg is bound to structural proteins not present in the soluble proteins of the liquid. Ions most difficult to analyze accurately are Ca, Mg and SO<sub>4</sub>, while measurements of Cl concentration are probably the most reliable. Large differences in ionic composition of body fluids may be found in recently handled

specimens (e.g. LEE and McFARLAND, 1962). Considering these difficulties and the relatively few marine invertebrates studied, the following conclusions may be drawn: (i) the ionic composition of body fluids of aquatic invertebrates differs from that of the ambient medium, even under conditions of isosmoticity; (ii) the capacities of aquatic invertebrates for ion regulation vary considerably; major ions are accumulated against the gradient by some, but dispelled by others; (iii) in spite of such variation, taxonomically related invertebrates often show similar regulatory potentials; (iv) the potential for ion regulation tends to increase in the series echinoderms, coelenterates, sipunculids, annelids, decapod crustaceans; molluscs exhibit considerable variations (low capacities in some lamellibranchs to pronounced capacities in cephalopods).

Ion regulation occurs essentially at two levels: between cell fluids and body cavity fluids, and between body cavity fluids and external medium. Most marine invertebrates tested show differences in ion ratios between cell fluids and blood. Non-growing cells maintain a quasi steady state in the ratios of ions continuously passing in and out; growing cells increase the incoming proportions. On the whole, the similarities in ionic ratios of body fluids among marine invertebrates are more impressive than the differences. This fact and the similar ionic ratios in body fluids and ocean water have caused speculations as to the marine origin of life and other evolutionary aspects, including the origin of vertebrates in fresh water. For a discussion on this problem, consult PEARSE and GUNTER (1957).

Considering the evolution of ion regulation, the first ion to be accumulated was, presumably, K; the first ions to be actively excreted, Na, Mg and  $\text{SO}_4$ . Ion regulation preceded osmoregulation and evolved very early. All recent isosmotic marine invertebrates (osmoconformers) are capable of some degree of ion regulation. In fact, active ion transport is a fundamental biological process, a basic characteristic of all living things. Evolutionary elaborations of active ion transport provided the basis for the development of specific organs for ion absorption and excretion and for the multitude of osmoregulatory mechanisms found today. Most of our present-day marine invertebrates still accumulate K; they collect H and Cl ions, keep Na and Cl low, and tend to exclude Mg and  $\text{SO}_4$ . Numerous marine invertebrates exhibit pH values in their blood which are 0.5 to 1 pH units below those of the ambient sea water (NICOL, 1960).

Little is known about gradients and dynamics of exchange in regard to trace elements (Table 4-2). A trace element of considerable biological importance is copper. It plays an important role in enzyme systems and respiratory pigments of numerous marine invertebrates. Crustaceans appear to take up most of the Cu required from the ambient medium via their gills (ZUCKERKANDL, 1960; KERRUT and co-authors, 1961; WIESER, 1965a, b, 1966, 1967). According to WIESER (1967), in marine crustaceans, the water flow maintained by ciliary or muscular mechanisms can be considered sufficient to provide several orders of magnitude more Cu than required; food probably plays only a minor role in supplying Cu. In contrast, terrestrial isopods must rely heavily on their food as Cu source (possibly in symbiosis with Cu-concentrating and liberating micro-organisms). In cephalopods also, the main Cu source appears to be the food consumed (GHIRETTI and VIOLANTE, 1964; DECLEIR and co-authors, 1970). In freshly hatched *Sepia officinalis*, the amount of body Cu decreases quickly. It is, possibly, excreted with the yolk

remains and must, subsequently, be secured from food substances. Mobilization of protein and copper from yolk into blood may account for the presence of haemocyanin in the blood of *S. officinalis* embryos (DECLER and co-authors, 1970). According to DUDNIKO and MIKHREEV (1964), at water temperatures between 20° and 22° C, a concentration of 4 mg/l Cu ions killed all individuals of *Dreissena polymorpha* examined within 24 hrs; at a concentration of 1 mg/l, within 48 hrs. In contrast, LUKANIN (1964) reports that, at temperatures below 22.5° C, more than 8000 mg CuSO<sub>4</sub> per litre are required to kill the total test population of *D. polymorpha*. Consequently, LUKANIN doubts the feasibility of using Cu ions to combat adult *D. polymorpha* which tend to settle in water pipes and hence may cause damage. It seems necessary to point out that the physiological effects of aqueous Cu solutions may depend on the degree of chemical 'complexation'. According to STEEMANN NIELSEN and WIUM-ANDERSEN (1970), the affinity of Cu to diethyl-dithiocarbamate is much higher than to the organic matter which complexes Cu in nature. Consequently, it is not possible to distinguish the two forms of Cu during analysis. In the centres of upwelling, ocean waters become suitable for plankton growth only after the addition of a chelator. This suggests that a large part of the Cu found in the subsurface waters of the oceans is present in ionic form. Cu in ionic form is very poisonous to unicellular algae at concentrations usually found in natural waters (STEEMANN NIELSEN and WIUM-ANDERSEN, 1970).

*Volume regulation.* A number of euryhaline invertebrates possess the capacity to regulate their body volume. They endure and re-adjust deformations in shape due to sudden changes in osmotic gradients between internal and external media. Sudden changes in osmotic gradients lead to distortions in the steady-state balance of the continuous in and outflow of water and salts. Severe distortions may cause significant alterations in body volume. In volume regulators these are followed by re-adjustments, involving changes in excretion or uptake of water or salts which finally lead to a new steady-state balance. Such re-adjustments usually take minutes, hours or days (Fig. 4-106).

Most orthostenohaline marine invertebrates lack the ability to regulate their body volume. If salinities fall or rise appreciably, these volume conformers swell or shrink, due to passive exchange of water or salts. The deformations endured in body volume remain and, if considerable, lead to death unless normal salinity conditions are restored. Since all marine invertebrates are, to some extent, permeable to water and salts, the volume changes induced by salinity variations are always less than those in a perfect osmometer. Volume conformers are, for example, several sipunculids, marine polychaetes, most coelenterates, molluscs and echinoderms. Also eggs of many marine invertebrates, especially those of annelids and echinoderms, lack abilities for volume regulation. Their membranes have low permeabilities for salt. In short-term experiments, rapid gain or loss of water results in swelling or shrinking curves which parallel those calculated on the basis of gas laws. In an unfertilized sea-urchin egg, inwardly and outwardly directed water movements are proportional in quantity to the egg's surface area and to the difference in osmoconcentration of internal and external media. Transferred into water of about 7‰S, sea-urchin eggs swell rapidly and finally burst. Eggs of the polychaete *Marphysa gravelyi*, isolated from the jelly, show, over longer periods of

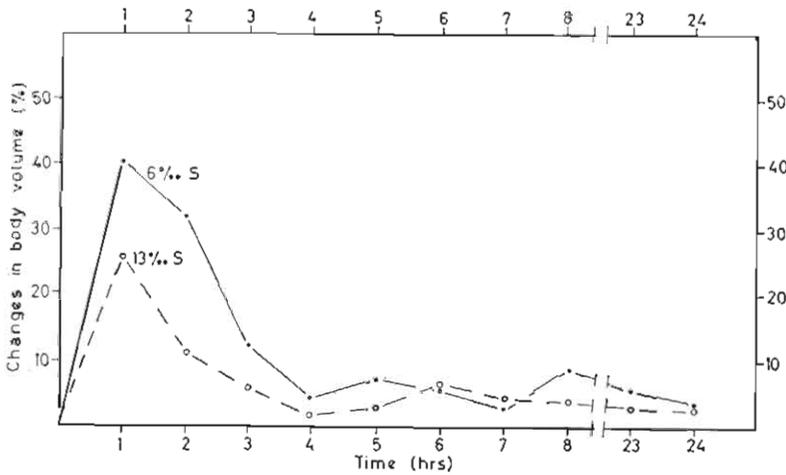


Fig. 4-106: Body volume regulation in the polychaete *Marphysa gravelyi* following transfer from undiluted sea water into blood hypo-osmotic media of 6‰ and 13‰ S respectively. Each point is the mean of 10 determinations. 29.5°C. (Based on data by KRISHNAMOORTHY and KRISHNASWAMY, 1968c.)

time, passive volume adjustments (KRISHNAMOORTHY, 1951). During their development, eggs of the echinoderm *Strongylocentrotus lividus* absorb large amounts of salts, indicating the beginning of effective ion regulation in the growing embryo.

More specific information on volume regulators seems in order. When exposed to slowly changing salinities, several euryhaline protozoans are able to regulate their volume. The major regulatory device is assumed to be their contractile vacuole. Thus, in the euryhaline marine ciliate *Miamiensis avidus*, the contractile vacuole output is related to external osmolarity. In ambient concentrations exceeding 100‰ sea water, vacuole output decreases; in diluted sea water, it increases. These, and other, results by KANESHIRO and co-authors (1969) indicate that the contractile vacuole of *M. avidus* regulates cell volume by expelling the passively entering water at salinity-dependent rates. However, protozoans without contractile vacuoles may also be capable of volume regulation.

Among multicellular aquatic invertebrates, a capacity for volume regulation has been reported, for example, in the sipunculids *Phascolosoma japonicum*, *Themiste zosterocolum*, *T. dyscritum* (KOLLER, 1939; GROSS, 1954; OGLESBY, 1968a), the turbellarian *Procerodes ulvae* (PANTIN, 1931b; WEIL and PANTIN, 1931; BEADLE, 1934), the polychaetes *Marphysa gravelyi* (Fig. 4-107; KRISHNAMOORTHY, 1951; KRISHNAMOORTHY and KRISHNASWAMY, 1966c), *Nereis diversicolor* (SCHLIPPER, 1929; BEADLE, 1931, 1937; ELLIS, 1937, 1939; JØRGENSEN and DALES, 1957; BOGUCKI and WOJTCZAK, 1964), *N. virens* (TOPPING and FULLER, 1942; JØRGENSEN and DALES, 1957), *N. limnicola* (SMITH, 1957, 1963, 1964a), the leech *Hirudo medicinalis* (BOROFFKA, 1968), and the decapod crabs *Carcinus maenas* (NAGEL, 1934; BETHE and co-authors, 1935) and *Pachygrapsus crassipes* (GROSS and MARSHALL, 1960).

The question whether sipunculid worms are capable of regulating their body volume after salinity changes has been a matter of some controversy (OGLESBY, 1968a). Reports dealing with about ten different species (QUINTON, 1900; SCHÜCKING, 1902; DEKHUYZEN, 1921a, b; HARMS and DRAGENDORFF, 1933; BETHE, 1934; ADOLPH, 1936; KOLLER, 1939; GROSS, 1954; KAMEMOTO and LARSON, 1964; KAMEMOTO and NITTA, 1964; KARANDEEVA, 1964; FLOREY, 1966; VIRKAR, 1966) are largely inconclusive; some provide no data and only state that the worms do or do not regulate their body volume after transfer into a different salinity (OGLESBY, 1969a). While ADOLPH (1936) and VIRKAR (1966) could find no evidence for volume regulation in *Phascolopsis gouldii*, KOLLER (1939) and GROSS (1954) reported that this species, as well as *Phascolosoma japonicum* and *Themiste zostericum*, can regulate its water content if the salinity changes are not very great. In *Themiste dyscritum*, volume regulation is restricted to individuals acclimated to high salinities and to salinity changes which are not excessive (OGLESBY, 1968a); water content depends strongly upon salinity; the worms accumulate large amounts of water osmotically after transfer into reduced salinities.

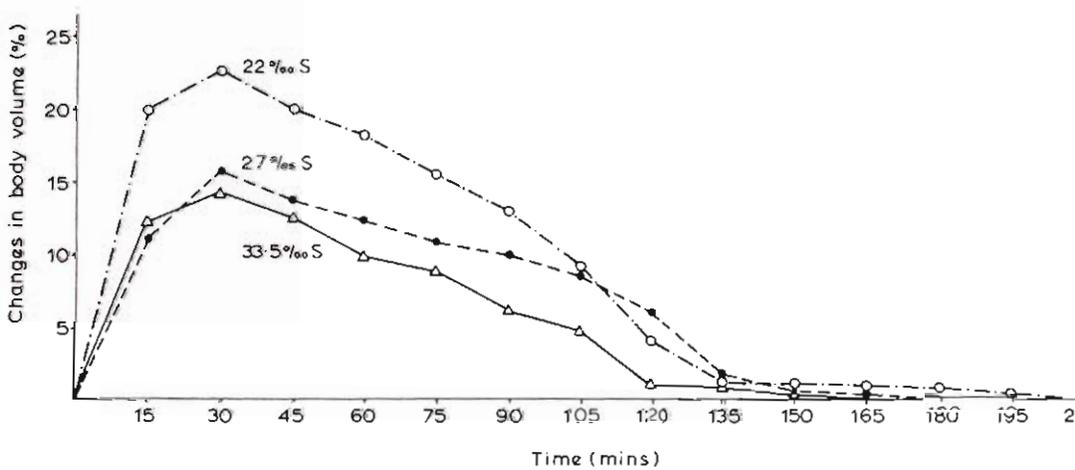


Fig. 4-107: Volume regulation in larvae of the polychaete *Marphysa graveleyi* exposed to different reduced salinities. (After KRISHNAMOORTHY, 1951; modified.)

OGLESBY'S (1968a) paper on *Themiste dyscritum* provides an example for investigating the capacity of volume regulation. He performed two experiments.

In the first experiment the worms were initially acclimated to 98‰ sea water (100‰ sea water = 560 mMCl) for more than 1 week. Six individuals were then transferred directly to each of 6 salinity levels: 49, 80, 89, 98 (controls), 111 and 139‰ sea water. Body-weight changes were recorded for 4 to 5 days, after which the worms were returned to 98‰ sea water. During the experiment, the test media were changed each day. The results are illustrated in Fig. 4-108. As in similar transfers with polychaetes (e.g. OGLESBY, 1965a, b, 1968b) and other sipunculids (KOLLER, 1939; GROSS, 1954; VIRKAR, 1966), after transfer an immediate gain or loss of water occurs which is proportional to the magnitude of the salinity change.

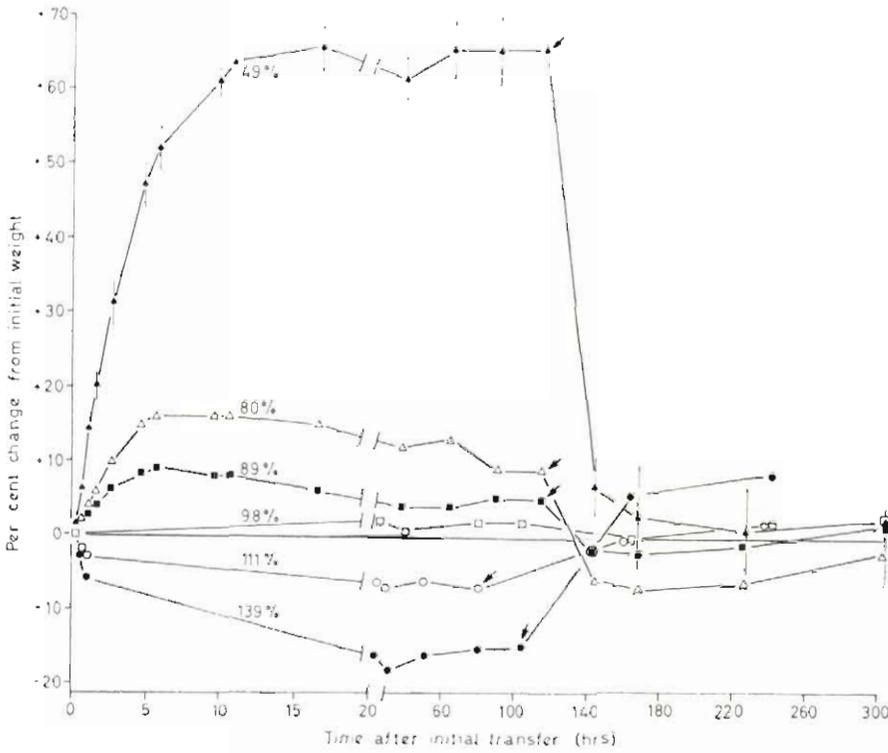


Fig. 4-108: Time course of body weight changes in the sipunculid worm *Themiste dyscritum* after transfers from 98% sea water to the salinities indicated. N=6 in all cases. Arrows: return of worms to 98% sea water). Note change in time scale after 20 hrs. Vertical lines: standard deviation (indicated for one curve only but representative of the amount of variability encountered in all curves). (After OGLESBY, 1968a; modified.)

Variations in body volume (weight) by controls are slight. After initial water gain, worms transferred to 80 and 89% sea water begin to lose weight again and gradually approach their initial weights. This fact is interpreted as evidence of volume regulation. There is no volume regulation by worms transferred to 49% sea water, nor, apparently, in those transferred to supranormal salinities. Subsequent to their return to 98% sea water, all worms 'undershoot' or 'overshoot' their initial weight in 98% sea water, except those transferred from 49% sea water.

In the second experiment, *Themiste dyscritum* was exposed to a series of small transfer steps, each of about 10% sea water. Beginning with 80 worms in 99% sea water, 70 were transferred to 90% sea water and 10 left in the higher salinity as controls. Of the 70 in 90% sea water, 60 were transferred after 1 week to 76% sea water, 10 remaining in 90% sea water as controls. This procedure was continued progressively at weekly intervals until the last 10 worms were transferred to 29% sea water. All 80 worms were weighed throughout the experiment at the same times. The results were analyzed by computer (Fig. 4-109) and each curve corrected for weight changes relative to controls. Body weight of controls and experimentals increases gradually during the first 2 weeks (due to handling?); thereafter it tends

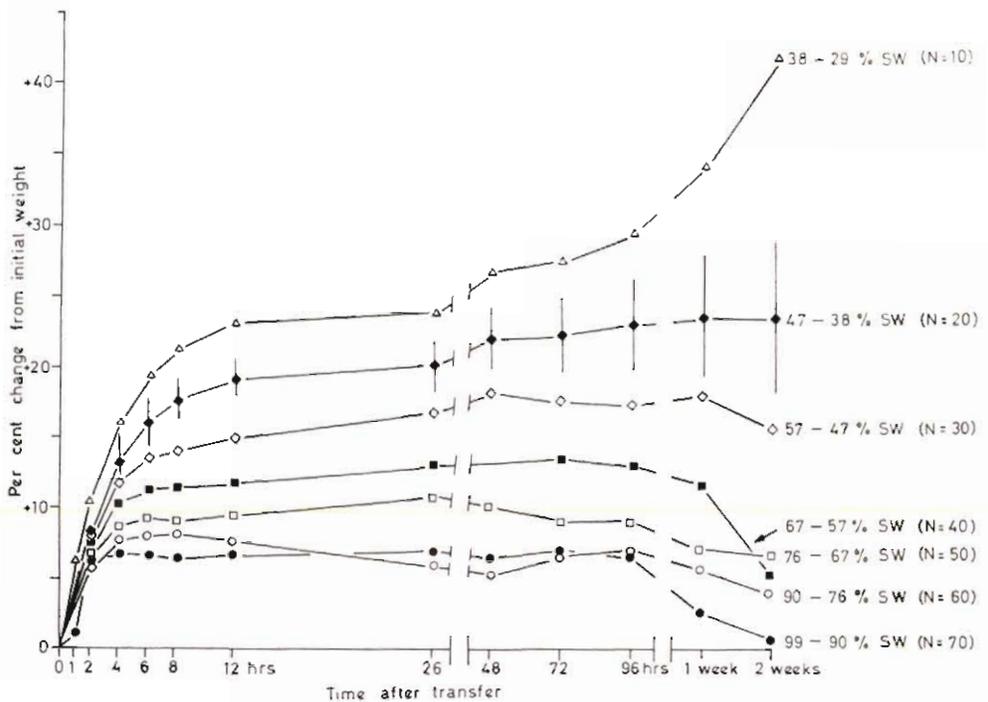


Fig. 4-109: Time course of body weight changes in *Themiste dyscritum* after transfers (steps of approximately 10% sea water). Vertical lines: standard deviation (indicated for one curve only; see legend to Fig. 4-108). SW = sea water. Note change in time scale after 26 and after 96 hrs. (After OGLESBY, 1968a; modified.)

to decrease, possibly due to starvation (TOWLE and GIESE, 1966). The curves indicate that there may have been some volume regulation by the worms transferred within the salinity range 99 to 67% sea water, becoming apparent only after a week or more in some cases. As in the first transfer experiment there was much individual variation in amount and time course of volume regulation. Worms transferred within the salinity range 67 to 29% sea water either remain stable after initial weight gain or continue to gain weight to the end of the experiment. The lower the salinity, the greater the amount of water taken up initially and the less the subsequent degree of volume regulation. These results show that, even when transfers involve only small changes in salinity, the capacity for volume regulation is restricted to the sipunculid worms exposed to high salinities. Apparently, *T. dyscritum* is incapable of volume regulation when kept in sub-normal salinities, regardless of the magnitude of the transfer. Volume regulation is possible only in worms adapted to normal habitat salinities and only when the imposed salinity changes are not excessive.

In other sipunculid worms, KOLLER (1939), GROSS (1954) and KAMEMOTO and NITTA (1964) have shown that body volume can only be regulated if there is no interference with nephridial function. Removal of nephridia (KOLLER), or ligation of nephridiopores and anus (GROSS; KAMEMOTO and NITTA) abolishes the capacity for volume regulation, while anal ligation alone (KAMEMOTO and NITTA) has no

negative effect. These reports suggest that the nephridia of sipunculids are most important to their limited capacity for volume regulation, by eliminating, as urine, at least some excess water taken in osmotically in subnormal salinities. However, in *Themiste dyscritum*, nephridial contents are little different in concentration from the coelomic fluid (OGLESBY, 1968a).

The triclad turbellarian worm *Procerodes (Gunda) ulvae* lives in Devonshire (Great Britain) estuaries, which are characterized by considerable daily salinity fluctuations. It is most abundant about halfway between high and low tide levels. If the turbellarians are exposed to distilled water or soft tap water, they rapidly increase in volume and finally burst. If exposed to natural hard stream water, or water to which calcium chloride has been added, their volume increases to about 70% and, after a while, begins to decrease somewhat (Fig. 4-110). Under these

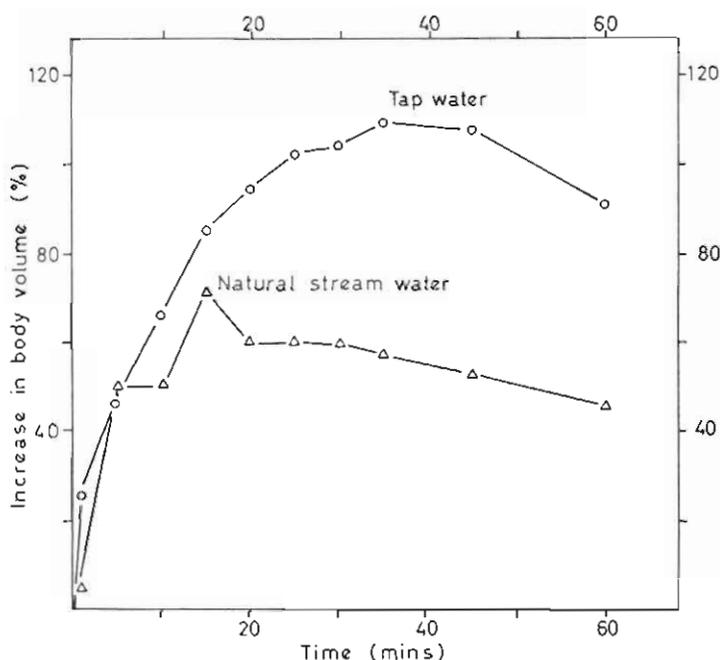


Fig. 4-110: Volume regulation in the turbellarian *Procerodes ulvae* exposed to tap water or natural stream water. (After WEIL and PANTIN, 1931; modified.)

conditions survival is possible for several days (WEIL and PANTIN, 1931). The regulatory devices involved include changes in membrane permeability, related to endogenous (acclimation) and exogenous (calcium content) factors. Increase in external calcium concentration reduces membrane permeability. Excess water is taken up and later slowly removed by the gut epithelium (Fig. 4-111). Part of this water seems to be stored in gut cells during the low salinity phase (PANTIN, 1931a, b).

If specimens of the euryhaline polychaete worm *Nereis diversicolor* are transferred into subnormal salinities, their body volume begins to increase; shortly thereafter, urine flow from nephridia is augmented and, as a result, body volume

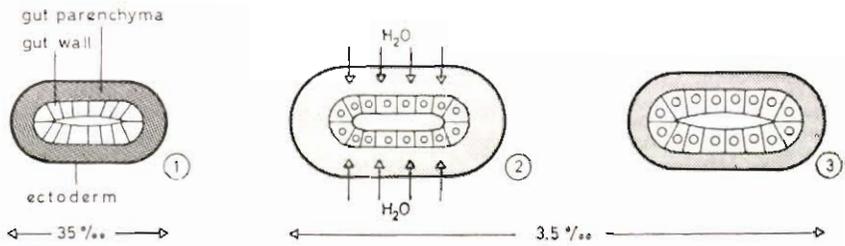


Fig. 4-111: Volume regulation in the intertidal turbellarian *Procerodes ulvae*. Schematic body cross sections. (1) Condition during life in undiluted sea water of about 35‰ S. (2) A few hours after transfer into 3.5‰ S; H<sub>2</sub>O has entered through the ectodermal surface layer and caused considerable swelling of the gut parenchyma; gut wall cells begin to collect excessive H<sub>2</sub>O in intracellular vacuoles. (3) About 12 hrs after transfer; gut wall cells have removed most of the H<sub>2</sub>O, bringing about a decrease in body volume. (After BEADLE, 1934; modified.)

decreases again (BEADLE, 1937). Reduced salinity causes, at the same time, increased salt loss, which is subsequently compensated for by increased intensities of active salt uptake (FRETTER, 1955; JØRGENSEN and DALES, 1957). Stabilization of blood osmoconcentration to the new steady-state gradient between internal and external media is completed far in advance of volume stabilization (BEADLE, 1937; JØRGENSEN and DALES, 1957). In very low salinities, *N. diversicolor* may be able to re-absorb some salts in its nephridial tubules and thus to produce a urine which is hypo-osmotic to the ambient medium (POTTS and PARRY, 1964; OGLESBY, 1965b). Upon transfer into reduced salinities, volume (weight) increase is much less, and initial volume more rapidly approached in *Nereis diversicolor* than in *N. virens*. This difference is probably a consequence of the lower body surface permeability of *N. diversicolor* (JØRGENSEN and DALES, 1957). The nephridia possibly assist in volume regulation (as in the estuarine fanworm *Sabella pavonina*; EWER and EWER, 1943). In Indian polychaetes, KRISHNAN (1952) found that the nephridia of *Lycastis indica*, which inhabits waters of very low salinities, are larger and better vascularized than those of *Perinereis nuntia* which inhabits marine waters. *Nereis limnicola*, *Nereis (Neanthes) succinea* and *Nereis vexillosa*, exposed by OGLESBY (1965b) to subnormal salinities, do not regain their original body weight, even after 48 to 72 hrs. Variation of body water content with salinity is less marked in *N. limnicola* and *N. diversicolor* than in the poorer volume regulators *N. succinea* and *N. vexillosa*.

Increase in body volume due to osmotic water uptake is, of course, always combined with increase in body weight; however, weight increase is not always paralleled by measurable volume increase. Some hard-shelled aquatic invertebrates exhibit osmotic water uptake and weight increase in hypo-osmotic media, but their hard outer surfaces restrict changes in total body volume (usually measured, within short periods of time, by the displacement method).

*Osmoregulation.* Osmoregulation may be defined as the capacity of an organism to establish and maintain specific osmotic gradients between cell fluids, body cavity fluids and ambient medium; it requires metabolic energy. Changes in

salinity tend to deform osmotic steady-state gradients temporarily or permanently. If salinities decrease significantly, for example, additional water enters the organism and more salts are lost via diffusion. In order to re-approach the original osmotic gradient, water must be expelled and salts replaced. The intensity of these regulatory processes tends to increase with the osmotic gradient between organism and environment; if the gradient surpasses the organism's regulatory potential, osmocontrol breaks down and, ultimately, death follows.

In habitats with short-term rhythmic salinity variations, such as estuaries, maximum osmotic equilibrium between organism and environment may never be attained. Changes in osmoconcentration of body cavity fluids, and especially of cell fluids, must be assumed to be out of phase (up to several hours; depending on the organisms involved and temperature) with salinity fluctuations. Consequently, changes in internal osmoconcentration will hardly ever reflect the lower or upper extremes of tidal salinity variations.

Aquatic invertebrates exhibit different capacities for osmoregulation based on genetic properties. These differences may reveal important insights into the long-term salinity history of the organism involved and its phylogenetic relationships. Within one and the same species, differences in osmoregulative capacities may vary with the life-cycle stage considered, physiological state (non-genetic adaptation, nutrition, health) and environmental stress. Among the environmental factors, time course of salinity change, temperature, water movement, pressure, dissolved gases, light and food are of primary importance.

Most oceanic invertebrates exhibit no, or very limited, potentials for osmoregulation. As long as they remain in their natural environment, they have no osmoregulatory problems. If transferred into significantly suboceanic salinities, they gain water, swell and after seconds, minutes or hours suffer lethal osmotic damages; conversely, if transferred into supra-oceanic salinities, they lose water and shrink. These forms are referred to as osmoconformers; they are poikilosmotic or osmolabile. In some oceanic invertebrates, osmotic water uptake in subnormal salinities is limited by concomitant fast salt loss, resulting in reduced rates of water uptake and thus providing a certain means of compensation. Even though their outer membranes are readily permeable to water or salt, or both, osmoconformers are capable of some degree of ion regulation. While the osmoconcentration of their body fluids closely parallels that of the ambient medium, if tested over a range of salinities, their body cavity fluids and especially their cell fluids tend to remain slightly hyperosmotic as long as the test individuals survive. Osmoconformers are by no means restricted to life in the open oceans; several have succeeded to establish themselves in coastal waters.

Examples of osmoconformers studied experimentally are: several protozoans and coelenterates (e.g. KROGH, 1939), the sipunculid *Themiste dyscritum* (OGLESBY, 1968a), the polychaetes *Perinereis cultrifera*, *Nereis pelagica*, *Arenicola marina*, *Sabellaria paronina* (e.g. SCHLIEPER, 1929; KROGH, 1939), the lamellibranch *Mytilus edulis* (e.g. REMANE and SCHLIEPER, 1958), the chiton *Sypharochiton pelliserpentis* (BOYLE, 1969), the crustaceans *Maia squinado*, *Hyas araneus*, *Cancer pagurus* (e.g. POTTS and PARRY, 1964), *Elminius modestus*, *Balanus balanoides*, *B. crenatus*, *B. improvisus*, *B. balanus*, *Chthamalus stellatus* (FOSTER, 1969c) and the holothurian *Caudina chilensis* (KOIZUMI, 1932, 1935). Osmoconformers are

usually, but not necessarily, stenohaline. Some tolerate appreciable changes in external and internal osmoconcentration and may thus be rather euryhaline, e.g. the polychaete *Arenicola marina* (SCHLIEFER, 1929), and the sipunculid *Themiste dyscritum* (OGLESBY, 1968a).

Aquatic invertebrates with pronounced potentials for osmoregulation are referred to as osmoregulators. The vast majority of osmoregulators inhabit waters with (fluctuating) sub- or supra-oceanic salinities. Most osmoregulators tend to maintain significantly hyperosmotic body fluids in reduced salinities, but become poikilosmotic in higher ambient salt concentrations. Over much of their poikilosmotic range, these osmoregulators maintain—more or less strictly parallel to salinity variations—measurable hyperosmoticity; it is wrong, therefore, to claim (as has been done in many papers and text books) that they are isosmotic in higher salinities (REMMERT, 1969). Complete isosmoticity is probably attained only after breakdown of the osmoregulatory mechanism. Osmoregulators which exhibit significant hyperosmoticity in reduced salinities but poikilosmoticity in higher salinities are called hyperosmotic regulators (see also p. 868). A smaller group of osmoregulators tends to maintain significant hyperosmoticity in reduced salinities as well as hypo-osmoticity in elevated salinities. These forms are called hyper-hypo-osmotic regulators (see also p. 868). Examples of hyper-hypo-osmotic regulators

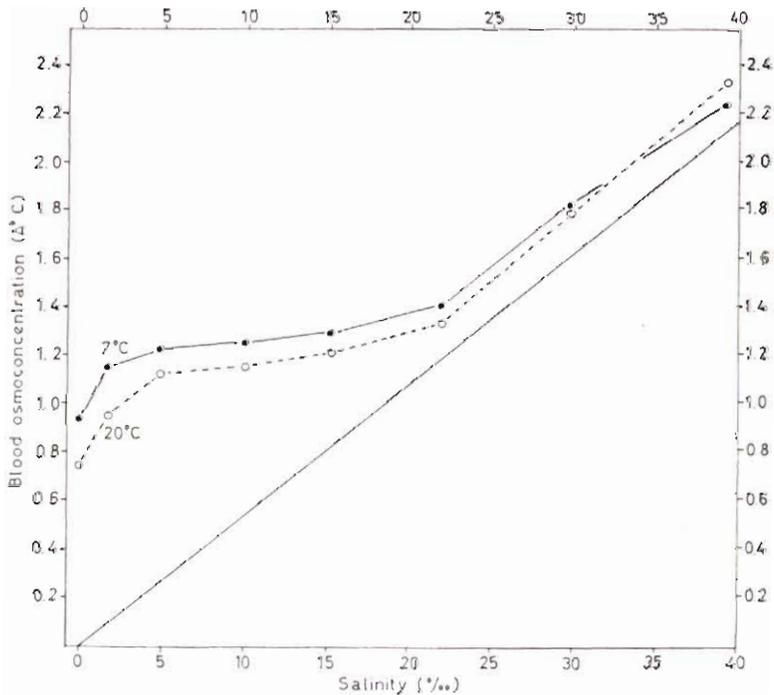


Fig. 4-112: Capacity for osmoregulation in the amphipod *Gammarus duebeni* as a function of salinity and temperature. All test individuals were raised in the respective salinities and exposed to 7° or 20° C for at least 40 days prior to measurements. Each point represents the mean value of at least 8 freezing-point determinations on 8 different individuals. (After KINNE, 1952b; modified.)

are shore shrimps, brine shrimps, semiterrestrial and terrestrial crabs; but also polychaetes such as *Marphysa gravelyi* (KRISHNAMOORTHY and KRISHNASWAMY, 1966b) and the isopod *Cyathura polita* at low temperatures (SEGAL and BURBANCK, 1963). The most potent hyper-hypo-osmotic regulators are found among euryhaline aquatic larvae of dipteran insects (p. 921).

Osmoconformers and osmoregulators do not represent clearly distinguishable groups but two opposite ends of a series of differences in capacities for osmoregulation.

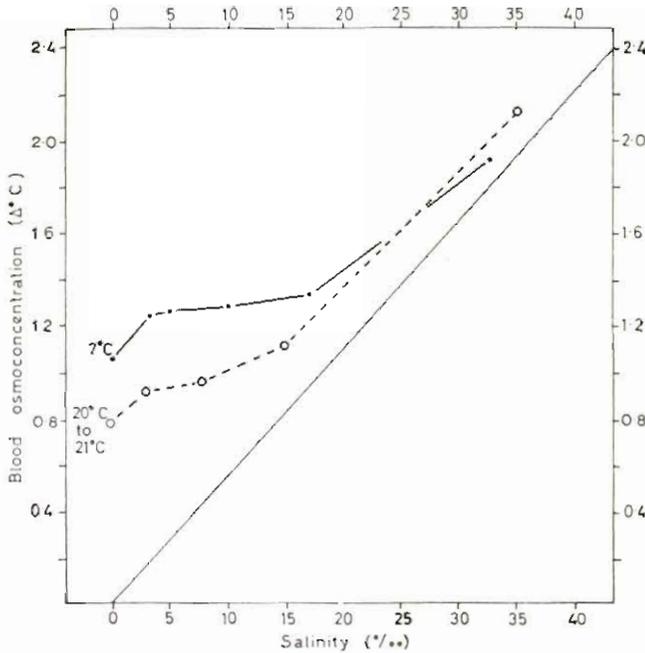


Fig. 4-113: Capacity for osmoregulation in the decapod crab *Rhithropanopeus harrisi* as a function of salinity and temperature. Winter crabs, maintained at 7°C, were exposed to test salinities for at least 27 days; summer crabs, kept at 20° to 21°C, for at least 14 days. Each point represents the mean of 10 freezing-point determinations on 10 different individuals (except in fresh water and 2‰S at 20° to 21°C where up to 60% of the test individuals died during the experiments). (After KINNE and ROTTHAUWE, 1952; modified.)

tion. As has been pointed out already, even one and the same individual may be a conformer in one part of its salinity range but a regulator in another. The amphipod *Gammarus duebeni*, for example, hyperregulates its blood up to about 23‰S but conforms in higher ambient concentrations (Fig. 4-112); the decapod crab *Rhithropanopeus harrisi* regulates up to 17‰S but is poikilosmotic above 20‰S (Fig. 4-113); the shrimp *Crangon crangon* hyperregulates up to about 20‰S, is isosmotic near 27‰S, hyporegulates in 30‰ and 32‰S, and conforms (remaining hypo-osmotic) in still higher salinities (Fig. 4-114). The marine mite *Halacarus basteri basteri*, reared on blotting paper moistened with artificial sea water, hyper-

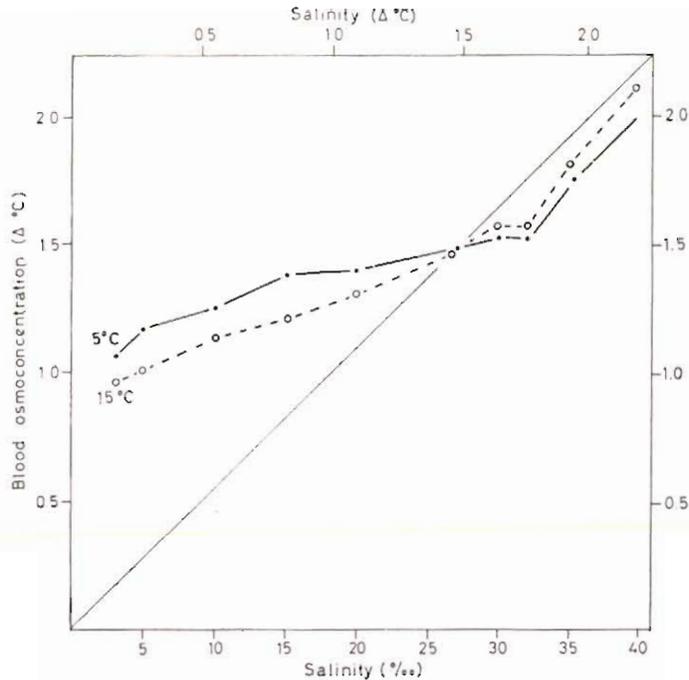


Fig. 4-114: Capacity for osmoregulation in the shrimp *Crangon crangon* as a function of salinity and temperature. Each point represents the mean value of at least 20 freezing-point determinations of the blood fluid. (After FLÜGEL, 1963; modified.)

regulates its body cavity fluids in salinities from 3.5‰ to 25‰, remains homeo-osmotic between 25‰ and 45‰, and conforms above 45‰; these results were obtained by KIRCHNER (1969) on adult mites, starved for at least 8 days, from Kiel Bay (western Baltic Sea) and Helgoland (southern North Sea) after 1 week's acclimation to different salinity levels and at temperatures of 9° or 12° C.

Early ontogenetic unicellular stages (egg, spermatozoon, zygote) or oligocellular stages (cleavage phases, blastula, gastrula) of most, if not all, marine invertebrates appear to lack potentials for effective osmoregulation and tend to conform to their osmotic environment unless protected by membranes, slime, jelly, etc., providing them with extremely low permeabilities to water and salt.

The osmoregulative potentials of decapod larvae have been considered by KALBER and COSTLOW (1968) and KALBER (1970) on the basis of haemolymph osmoconcentrations of developmental stages exposed to different salinities. The zoeae of the spider crab *Libinia emarginata*, which is stenohaline in the adult stage, are unable to osmoregulate for some time after hatching, but then acquire the capacity to regulate during a large part of their planktonic life before 'reverting' to the adult pattern in the late megalopa. Such temporary shift from osmoconformer to osmoregulator during the life cycle reveals insights into the evolutionary history of the species and its present-day ecological potential to occupy waters with changing salinities. The stenohaline sublittoral crab *Hepatus epheliticus* is an efficient osmo-

regulator throughout its entire larval existence. The littoral estuarine crab *Callinectes sapidus* hyperregulates as newly hatched larva and as adult. The zoeae, however, are osmoconformers during the middle part of their development; they recover hyperregulation within about 48 hrs and retain it to adulthood. The zoeae of the mud crab *Rhithropanopeus harrisi* are effective hyperregulators at hatching. As the first zoeal moult approaches, they begin to hyperregulate against salinities as high as 40‰, thus creating an inward water flux which leads to body volume increase at ecdysis. During the 5th day of zoeal life, the larvae become osmoconformers for at least 12 hrs. During this period, osmoregulation must be accomplished at the cellular level (cell interior versus haemolymph). Just before the moult to the megalopa, the zoea larvae again become capable of intensive hyperregulation and, at the same time, of slight hyporegulation. In the land crab *Cardisoma guanhumi*, daily assessments of the osmoregulative capacity from hatching to the end of larval development revealed that the larvae are able to hyperregulate against 10‰S and to hyporegulate against 40‰S during their first day of life. Hyperregulation becomes more pronounced until the day preceding the second moult, at which time the larvae keep their haemolymph osmoconcentration significantly above that of 30‰S. At the time of the second moult, the larvae begin to hyporegulate against salinities as low as 15‰ and, in some cases, even lower. During the intermoult period of zoeal stages 3, 4 and 5, the larvae hyperregulate in 10‰S but become isosmotic, or even slightly hypo-osmotic to this salinity for 24 hrs or less following the moult. *Cardisoma guanhumi* larvae are nearly isosmotic in salinities equivalent to those found well up in estuaries during the latter 60% of their larval existence. As far as indicated in the respective studies, the decapod larvae investigated were maintained and tested at normal temperatures; the larvae of *C. guanhumi*, for example, were maintained at 25° C and tested at 23° to 25° C (KALBER and COSTLOW, 1968; see also COSTLOW and co-authors, 1960, 1962, 1966; KALBER and COSTLOW, 1966; KALBER, 1970).

While total osmoconcentration of body cavity fluids results primarily from inorganic ions, that of cell fluids depends on both inorganic and organic constituents. Unfortunately, intracellular osmoconcentration has received far less attention than that of the fluids of body cavities. In the polychaete *Marphysa graveleyi*, intracellular regulation may involve quantitative changes in amino acids (KRISHNA-MOORTHY and KRISHNASWAMY, 1965). Megalops and first stage crabs of the decapod *Rhithropanopeus harrisi* reared in 10 different combinations of salinity and temperature were blotted alive on filter paper and their free amino acids extracted. Amino-acid composition (aspartic acid, glycine, lysine, alanine) and concentration varied in the various salinity/temperature combinations (COSTLOW and SASTRY, 1966). It has been further suggested that osmotically active particles of unspecified chemical nature can be exchanged between cells and coelomic fluid, altering osmoconcentration and composition of the latter during stress (GROSS, 1954). Our present knowledge on such intra- versus extracellular aspects of osmoregulation in marine invertebrates does not yet allow us to draw definite conclusions. Since there can be no doubt that osmoregulation is ultimately a cell physiological problem, more information on intracellular processes of regulation is urgently required. The possibility of metabolic water production as a means of osmoregulation deserves special attention.

Marine invertebrates may have appreciable quantities of protein in their blood plasma, a fact which complicates the interpretation of differences in total osmoconcentration between sea water and blood plasma (owing to Donnan effects produced by the indiffusibility of proteins and formation of calcium-protein complexes). Although blood-protein concentrations may reach 80 g/l in decapod crustaceans and exceed 100 g/l in cephalopod molluscs, the Donnan ratio does not seem to exceed 1.03 and only 10 to 20% of the calcium is present in the form of a calcium proteinate (ROBERTSON, 1949, 1953, 1957a). In general, cnidarians, annelids and echinoderms contain less blood-protein than crustaceans and cephalopods. In the euryhaline polychaete *Marphysa gravelyi*, total contents of free amino acids in the coelomic fluid vary over a salinity range from 6.7‰ to 29.2‰ from 10 µg/ml to 32 µg/ml and may assist in body cavity fluid osmoregulation (KRISHNAMOORTHY and KRISHNASWAMY, 1965). In the blood of aquatic Trichoptera larvae (*Limnephilus affinis*), increase in the non-electrolyte fraction may be due to mobilization of amino acids from a protein reservoir (SUTCLIFFE, 1961a). A significant rise in blood-protein and a shift towards ureotelism occurs in the crayfish *Orconectes rusticus* when under osmotic stress (SHARMA, 1968). In the sipunculids, coelomic-fluid concentrations of several organic (and nitrogenous) compounds, such as proteins, sugars, amino acids, ammonia and urea have been determined (DELAUNAY, 1912, 1913, 1926, 1931; DAMBOVICEANU, 1926; KISCH, 1929; FLORKIN, 1936; WILBER, 1948; SETON and WILBER, 1949; ROBERTSON, 1953; TRAVIS, 1960; TOWLE and GIESE, 1966; VIRKAR, 1966). As pointed out by OGLESBY (1968a, b), in all cases the reported levels were rather low (0.1 to 5 mM) and it appears that these compounds do not contribute significantly to the total osmoconcentration of the coelomic fluid. The levels of some compounds vary with nutritional and reproductive states of the sipunculids (KISCH, 1929; TOWLE and GIESE, 1966). Definite proof for an active role of organic compounds of the coelomic fluid in osmoregulative processes is still lacking.

STEPHENS (1960a, b, 1962a, b, c, 1963, 1964) and STEPHENS and SCHINSKE (1961) have demonstrated that a number of marine invertebrates are capable of removing glucose and amino acids from dilute solutions in the surrounding sea water. In the malidanid worm *Clymenella torquata* (STEPHENS, 1962a, b, 1963), measurements were made of the rate of uptake of amino acids and compared with the concentrations at which these compounds occurred in the habitat. The results suggest that the uptake process might contribute significantly to the nutrition of these worms. According to STEPHENS (1964), both *Nereis limnicola* and *N. succinea* are capable of removing glycine from dilute ambient solutions at intermediate and high salinities; uptake declines rapidly at chlorosities of less than 200 meq./l. The salinity at which glycine uptake declines, agrees closely with estimates of the point of onset of osmoregulation and of chloride regulation in the two worms. Considering the documented ability of marine invertebrates to remove amino acids from ambient media and the failure to demonstrate this for limnic invertebrates, STEPHENS (1964) suggests that the processes of osmoregulation and glycine uptake are incompatible. In *N. limnicola* and *N. succinea*, glycine uptake is an exponential function of wet weight; it is linear with time for periods of at least 1 hr, and appears to take place across the body wall, without the necessary participation of the gut. In *N. limnicola*, adaptation of the physiological system mediating glycine uptake

to a change in salinity extends over more than 14 days. According to STEPHENS (1963), *Clymenella torquata* is able to accumulate lysine, valine, glycine and phenylalanine. Evidence for uptake of amino acids directly across the body wall has also been obtained in *Neanthes arenaceodentata* (REISH and STEPHENS, 1969). Autoradiography suggests intake across the general body surface in other marine invertebrates also (FERGUSON, 1967; FONTAINE and CHIA, 1968; LITTLE and GUPTA, 1968; SOUTHWARD and SOUTHWARD, 1968). The nutritional significance of amino-acid uptake in marine invertebrates, however, remains to be established unequivocally (STEPHENS, 1967, 1968).

Osmoregulators often exhibit significant inter- and intraspecific differences in their capacities for osmoregulation. Interspecific differences may occur even in closely related species of the same genus. Thus among *Gammarus* species, the potential for hyperosmotic regulation increases in the order *Gammarus locusta*, *G. salinus*, *G. duebeni*, *G. pulex*. Pronounced intraspecific differences can be found in successive life-cycles stages, e.g. egg, embryo, larva, subadult, adult. Typically, the osmoregulatory potential is minimal in eggs, develops in embryos and comes to full power in larvae, subadults or adults (consult p. 909 for further details). A recent example of intraspecific (interpopulational) differences in the capacity for osmoregulation among adult individuals has been provided by THEEDE (1969a). Adults of the decapod crab *Carcinus maenas* from the Baltic Sea (about 13‰ to 18‰S) and the North Sea (about 32‰S) clearly exhibit different regulatory potentials (Fig. 4-115). Such interpopulational differences may result from geographic or gene flow isolations, selections and individual adjustments (non-genetic

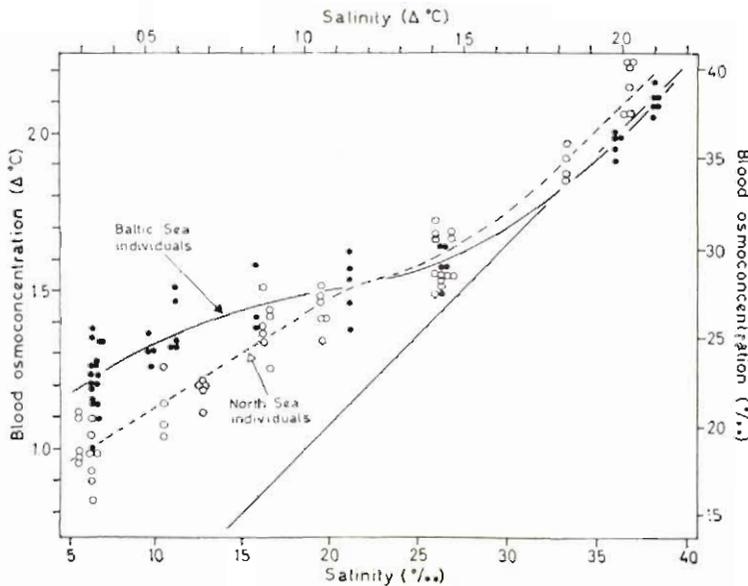


Fig. 4-115: Intraspecific (interpopulational) differences in capacity for osmoregulation of crabs *Carcinus maenas* from the Baltic Sea ( $\sim 13\text{‰}$  to  $18\text{‰}$ S) and the North Sea ( $\sim 32\text{‰}$ S). Individual measurements of blood osmoconcentration made 3 days after transfer from  $15\text{‰}$  or  $30\text{‰}$ S (stabilizing salinities) to the various test salinities;  $16.5^\circ\text{C}$ . (After THEEDE, 1969a; modified.)

adaptation). Determinations of blood osmoconcentration in large numbers of apparently identical specimens of the ocypodid crab *Australoplax tridentata* reveal considerable individual variability (BARNES, 1968b). Pronounced individual variability in blood osmoconcentration and in the osmoregulative potential appears to be a rather widespread phenomenon; it represents an important prerequisite for establishing performance gradients within the distributional area of a given species. For further examples of interpopulational differences in osmoregulative capacity and related problems consult SEGAL and BURBANCK (1963), BATTAGLIA (1967), BURBANCK (1967), MUUS (1967b) and SEGAL (1967).

Inter- or intraspecific differences in osmoregulative capacities reveal themselves under salinity stress rather than in normal salinities. The normal body cavity fluid osmoconcentration may, in fact, be quite similar; but the low or high critical salinities at which the regulatory mechanism begins to fail or to break down, often differ and usually show close relationships to the prevailing limiting habitat salinities. In salinities equivalent to, or somewhat below, 30 to 40% sea water, the polychaetes *Nereis limnicola*, *Laeonereis culveri*, *Nereis (Neanthes) succinea* (OGLESBY, 1965a), *Nereis diversicolor* (ZENKEVITCH, 1938; KARPEVICH and OSADČICH, 1952; SMITH, 1955b; HOHENDORF, 1963) and *Perinereis cultrifera* (ZENKEVITCH, 1938) maintain quite comparable osmoconcentrations in their coelomic fluids. However, these species differ markedly in regard to the lower critical salinity at which their coelomic fluid concentration begins to decline rapidly (Table 4-61); *Nereis diversicolor* and *Nereis (Neanthes) succinea* exhibit considerable intraspecific differences in representatives of populations from different parts of their geographic range. In salinities above 30 to 40% sea water, the body cavity fluids of all species listed in Table 4-61 are close to isosmoticity with

Table 4-61

Approximate lower critical salinities at which coelomic fluid concentrations of euryhaline polychaetes begin to decline rapidly, indicating the beginning of breakdown of osmoregulation (After various authors from OGLESBY, 1965a; modified)

Polychaete species	Critical lower salinity	
	% sea water	mMCl/l
<i>Nereis limnicola</i>	1	2-4
<i>Laeonereis culveri</i>	<2	<10
<i>Nereis diversicolor</i>		
from Northern Europe	3-6	15-30
from Kiel (Germany)	6-10	30-50
from Azov and Caspian Seas	10-11	50-60
from Black Sea	10-18	50-100
<i>Nereis (Neanthes) succinea</i>		
from San Francisco Bay (California, USA)	6-10	30-50
from Alligator Harbor (Florida, USA)	18	100
<i>Perinereis cultrifera</i>	45	250

the ambient medium. There are no evident differences between measurements conducted by melting-point and chloride-titration methods, indicating that non-electrolytes do not contribute significantly to total coelom osmoconcentration, and that chloride concentration varies parallel to total osmoconcentration, i.e. chloride is not regulated independently (OGLESBY, 1965a). In *Nereis diversicolor*, exposed to salinities between 0.5‰ and 35‰, non-electrolytes constitute between 3.3 and 8.2% of the total osmotically active particles in the coelomic fluid (HOHENDORF, 1963). Greater proportions of non-electrolytes, largely free amino acids, are found within the cells of euryhaline worms (JEUNIAUX and co-authors, 1961), the crayfish *Astacus astacus* (DUCHATEAU-BOSSON and FLORKIN, 1961) and the sea-star *Asterias rubens* (JEUNIAUX and co-authors, 1962); they may play a role in intracellular osmoregulation.

With respect to habitat salinities, osmoregulators may be subdivided into euryhaline, holeuryhaline and oligohaline regulators (see also p. 867). Marine euryhaline osmoregulators can regulate in waters of reduced, increased or strongly fluctuating salinities, but require more salt than is available in pure fresh water. Holeuryhaline osmoregulators can regulate in salinities ranging from that of pure fresh water to that of full strength sea water or higher. Oligohaline osmoregulators are able to regulate in pure fresh water but their regulatory mechanisms collapse in salinities exceeding 5‰ to 8‰.

Euryhaline osmoregulators inhabit, in most cases, coastal areas. Examples of fairly well investigated euryhaline osmoregulators are: (i) the polychaetes *Nereis diversicolor* (SCHLIEPER, 1929, 1930; BEADLE, 1937; ZENKEVITCH, 1938; BOGUCKI, 1954, 1963; FRETTER, 1955; SMITH, 1955a, b, c, 1956, 1964b; JØRGENSEN and DALES, 1957; BRYAN, 1963; HOHENDORF, 1963; BOGUCKI and WOJTCZAK, 1964) and *Nereis (lighti) limnicola* (SMITH, 1957, 1959, 1963, 1964a; STEPHENS, 1964; OGLESBY, 1965a, b); (ii) the crustaceans *Carcinus maenas* (FREDERIQ, 1904; DUVAL, 1925; BETHE, 1929; SCHLIEPER, 1929; MAGARIA, 1931; PANTIN, 1931c; BIALASCEWICZ, 1933; SCHOLLES, 1933; SCHWABE, 1933; NAGEL, 1934; BETHE and co-authors, 1935; HUF, 1936; ROBERTSON, 1937, 1949, 1957a; WEBB, 1940; SHAW, 1955c, d, 1958a, b, 1961a; SECK, 1957; RIEGEL and LOCKWOOD, 1961; FLÜGEL, 1963; THEEDE, 1969a; LUCU and co-authors, 1970), *Pachygrapsus crassipes* (BAUMBERGER and OLMSTED, 1928; JONES, 1941; HIATT, 1948; GROSS, 1955, 1957a, 1958, 1959; PROSSER and co-authors, 1955; GROSS and MARSHALL, 1960; GROSS and CAPEN, 1966; RUDY, 1966), *Hemigrapsus nudus* (BAUMBERGER and OLMSTED, 1928; DEHNEL, 1962, 1966, 1967; DEHNEL and STONE, 1964; DEHNEL and CAREFOOT, 1965), *Rhithropanopeus harrisi* (JONES, 1941; KINNE and ROTT-HAUWE, 1952; COSTLOW and SASTRY, 1966; SMITH, 1967), *Palaemonetes varians*, *Palaemon serratus*, *Palaemon squilla*, *Penaeus indicus*, *Penaeus carinatus*, *Penaeus setiferus*, *Penaeus aztecus*, *Metapenaeus dobsoni*, *Metapenaeus monoceros* (PANIKKAR, 1939, 1940a, b, 1941a, 1950, 1968; PANIKKAR and VISWANATHAN, 1948), *Crangon crangon* (BROEKEMA, 1941; FLÜGEL, 1960, 1963; WILLIAMS, 1960; MCFARLAND, 1963), *Gammarus locusta*, *G. obtusatus*, *G. duebeni*, *G. oceanicus*, *Marinogammarus finmarchicus* (e.g. BEADLE and CRAGG, 1940a, b; KINNE, 1952b; LOCKWOOD, 1961; SHAW and SUTCLIFFE, 1961; WERNTZ, 1963) and *Artemia salina* (MARTIN and WILBUR, 1921; MEDWEDEWA, 1927; PLATTNER, 1955; CROGHAN, 1958a, b, c, d, e; COPELAND, 1966, 1967).

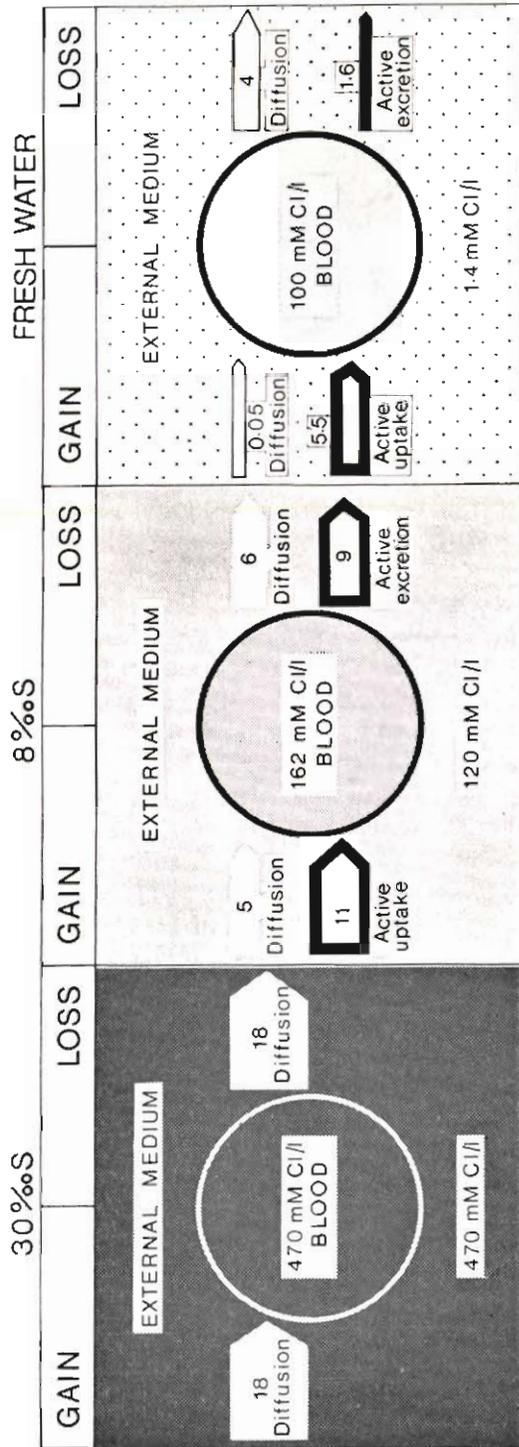


Fig. 4-116: Osmoregulation in the euryhaline polychaete *Nereis diversicolor*. Diagram illustrating approximate chloride fluxes at 24° to 25° C in 30‰ S, 8‰ S and fresh water respectively. Cl changes are indicated by arrows and expressed in  $\mu\text{M/g/hr}$ . (Based on data by Jørgensen and Dales, 1957, as interpreted by Potts and Parry, 1964; original.)

Two of these examples, *Nereis diversicolor* and *Carcinus maenas*, are referred to here in some detail; for more complete accounts consult POTTS and PARRY (1964) and pp. 868–870 of this subchapter.

Exchanges of sodium between *Nereis diversicolor* and its ambient medium have been investigated by FRETTER (1955), those of chloride by JØRGENSEN and DALES (1957). From these papers, and the review by POTTS and PARRY (1964), the following general picture emerges. *N. diversicolor* is poikilosmotic in 35‰S and somewhat higher salinities, but hyperosmotic in suboceanic salinities. Upon transfer to low salinities it takes up water by osmosis and loses salts via diffusion; at first, rates of water uptake exceed those of excretion and body volume increases; but as the blood becomes diluted, water uptake decreases and eventually is exceeded by urine flow so that the volume begins to re-approach its original level. In 30‰S, exchange rates of sodium are high ( $10.9 \mu\text{M/g/hr}$ ; ca 4% of body sodium/hr) and those of chloride even higher ( $18.2 \mu\text{M/g/hr}$ ). In 8‰S, passive sodium efflux is 3.5, passive influx 2.6 and urine loss  $4.4 \mu\text{M/g/hr}$ ; if the urine were blood isosmotic, the rate of urine production would be 2.8% body water/hr. In higher salinities, sodium and chloride fluxes are about proportional to external concentrations. The chloride fluxes in 30‰S, 8‰S and fresh water are illustrated in Fig. 4-116. With decreasing salinities, blood Cl concentration and diffusion rates decrease; active uptake and excretion via urine attain maximum values in 8‰S.

*Carcinus maenas* is able to live in diluted sea water because it can maintain its blood osmoconcentration significantly higher than that of the ambient medium, and because its tissues continue to function even when the blood osmoconcentration decreases to the equivalent of only 60% sea water. While the majority of marine crustaceans can concentrate potassium and calcium against the gradient,

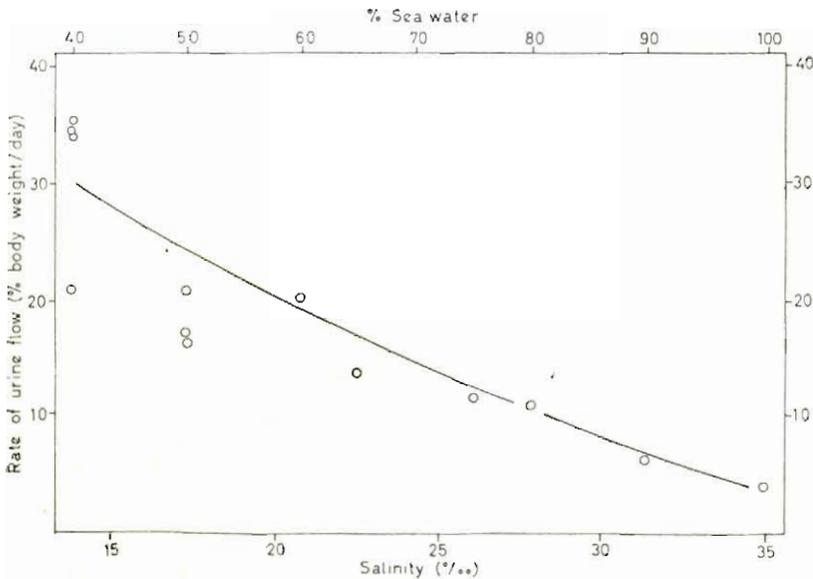


Fig. 4-117: Rate of urine flow in the euryhaline crab *Carcinus maenas* as a function of salinity. Temperature not specified. (After SHAW, 1961a; modified.)

## 4.31. SALINITY—INVERTEBRATES (O. KINNE)

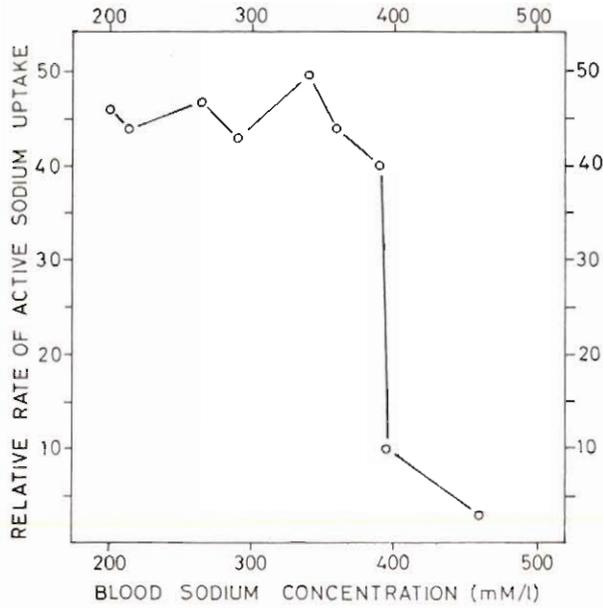


Fig. 4-118: Rate of active sodium uptake (arbitrary units) in the crab *Carcinus maenas* as a function of blood sodium concentration. (After SHAW, 1961a; modified.)

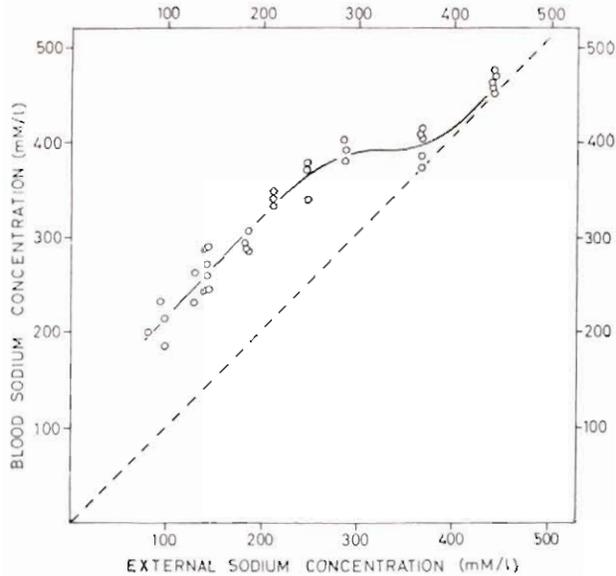


Fig. 4-119: Blood sodium concentration in the crab *Carcinus maenas* as a function of the sodium concentration of the external medium. (After SHAW, 1961a; modified.)

*C. maenas* can, in addition, also accumulate sodium and chloride; it further appears to be less permeable to water and salts than are marine crabs (SHAW 1961a; POTTS and PARRY, 1964). The relation between salinity and rate of urine flow is illustrated in Fig. 4-117. The rate of active sodium uptake rises sharply when the blood sodium concentration decreases below 400 mM/Na/l (Fig. 4-118); at the critical level, a 5% decrease is sufficient for full activation of the ion transport system; further decline in external Na leads to parallel decrease in blood sodium (Fig. 4-119). The sodium fluxes of *C. maenas* are summarized in Fig. 4-120. Blood sodium concentration and rates of sodium diffusion into and out of *C. maenas* decrease with decreasing salinity. Active sodium uptake amounts to 8 mM/kg/hr both in 17‰ and 13‰S. Sodium loss via urine increases from 0.7 mM/kg/hr in 33‰S to 3.3 mM/kg/hr in 17‰S and to 3.8 mM/kg/hr in 13‰S.

Holeuryhaline osmoregulators are few in number. A typical example is the wool-handled crab *Eriocheir sinensis* (BERGER, 1931; SCHOLLES, 1933; SCHWABE, 1933; SCHLIEPER, 1935; KROGH, 1939; KOCH and co-authors, 1953, 1954; KOCH and EVANS, 1956a, b, c; SHAW, 1961b; DE LEERSNYDER, 1967). Our present knowledge on osmoregulation in *Eriocheir sinensis* (p. 870) does not yet allow us to draw an adequate picture of water and salt balances in this physiologically most interesting crab.

Oligohaline osmoregulators live, in most cases, in fresh water. They are direct or indirect (via terrestrial forms) descendants of ocean-living invertebrates and exhibit pronounced capacities for hyperosmotic regulation (p. 871). In freshwater invertebrates, the osmoconcentration of body cavity fluids is about 50 mOsm/l in ciliates, hydrozoans and lamellibranchs, 100 to 300 mOsm/l in the majority of forms and 300 to 650 mOsm/l in decapods and some insects; as in euryhaline forms, it varies with temperature (tends to increase at subnormal temperatures), season and physiological state. Similar to the situation in brackish water, the most important variables in the osmoregulation of freshwater invertebrates are permeability to water and salts, concentration of salts in the urine, rate of urine loss and rate of active salt uptake. For further details the reader is referred to POTTS and PARRY (1964).

A recent example of the regulative capacity of an oligohaline osmoregulator has been provided by BOROFFKA (1968) who used the freshwater-living leech *Hirudo medicinalis*, kept at about 20°C, as test organism. Individuals maintained in fresh water have a blood osmolarity of 202 mOsm/l, a blood sodium level of 125 mM/l, a blood chloride level of 36 mM/l and a blood potassium level (NICHOLLS and KUFFLER, 1964) of 4 mM/l. After exposure to increasing salinity levels for 2 to 12 weeks, blood osmolarity and concentrations of sodium and chloride increase (Figs 4-121, 4-122, 4-123). In freshwater and more or less isosmotic salinity levels, *H. medicinalis* excretes a strongly blood hypo-osmotic urine. In individuals acclimated to hyperosmotic media, urine osmoconcentration is considerably higher, but always remains hypo-osmotic to the blood. Chloride and sodium are excreted in equivalent amounts, and account practically for the total urine osmoconcentration. In salinities above 30‰ sea water, urine chloride concentration exceeds blood chloride concentration (Fig. 4-123). Rate of urine flow amounts to 3 to 6  $\mu$ l/hr/cm<sup>2</sup> body surface in fresh water; after 8 weeks acclimation, it is less than half that in 10‰ sea water, and so low in 40‰ sea water that it can no longer

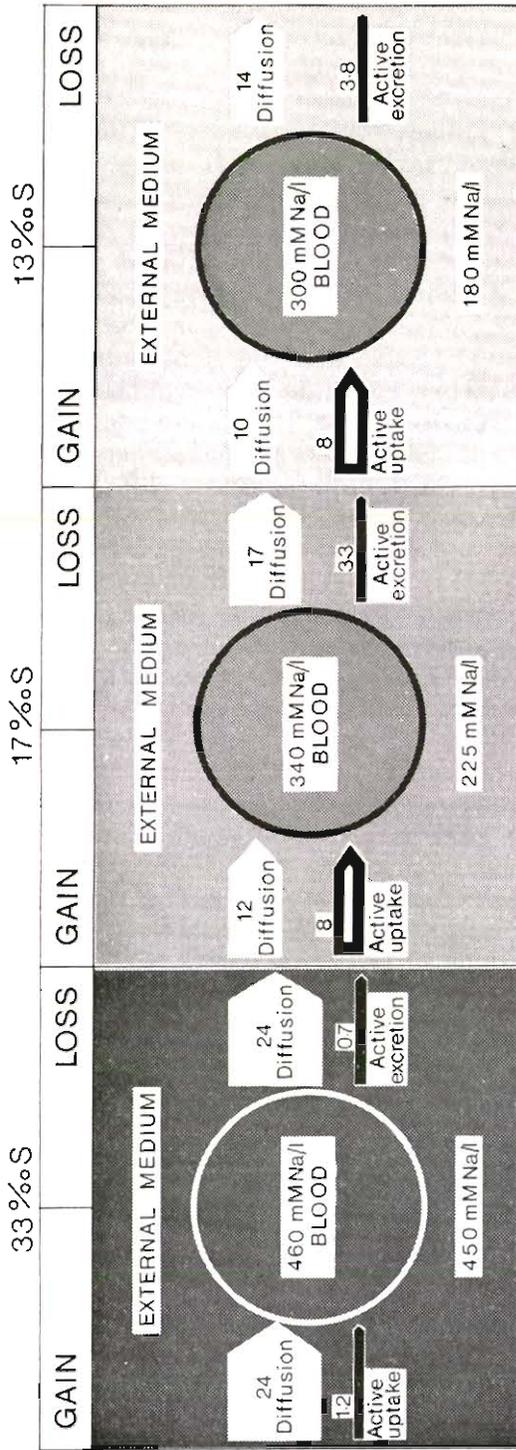


Fig. 4-120: Osmoregulation in *Carcinus maenas*. Diagram illustrating approximate sodium fluxes in 33‰, 17‰ and 13‰ respectively. Temperature not specified. Na changes are indicated by arrows and expressed in mM/kg/hr. (Based on data by SHAW, 1961a, as interpreted by POTTS and PARRY, 1964; original.)

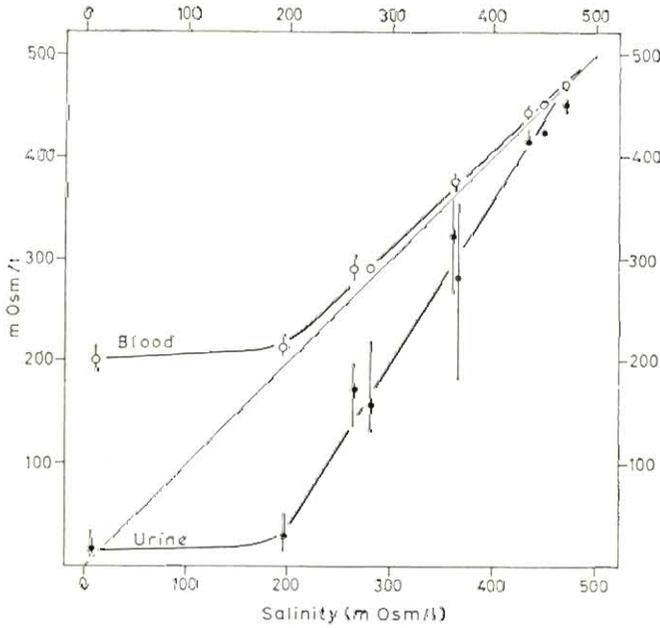


Fig. 4-121: Osmoconcentration of blood and urine (final urine) as function of salinity (expressed as mOsm/l) in the leech *Hirudo medicinalis*. Vertical lines: variability of average values (calculated from 2 to 3 single measurements, performed on a total of, usually, 6 individuals). About 20° C. (After BOROFFKA, 1968; modified.)

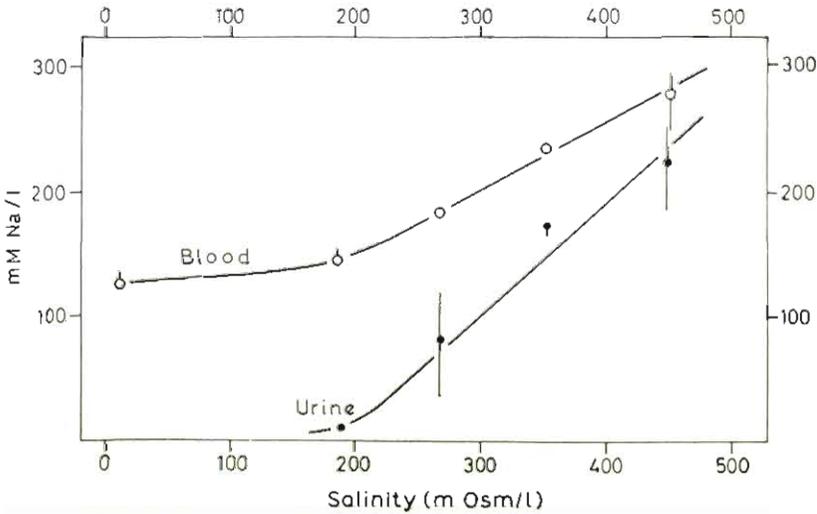


Fig. 4-122: Sodium concentration in blood and urine of *Hirudo medicinalis* as function of salinity (mOsm/l); see also legend to Fig. 4-121. (After BOROFFKA, 1968; modified.)

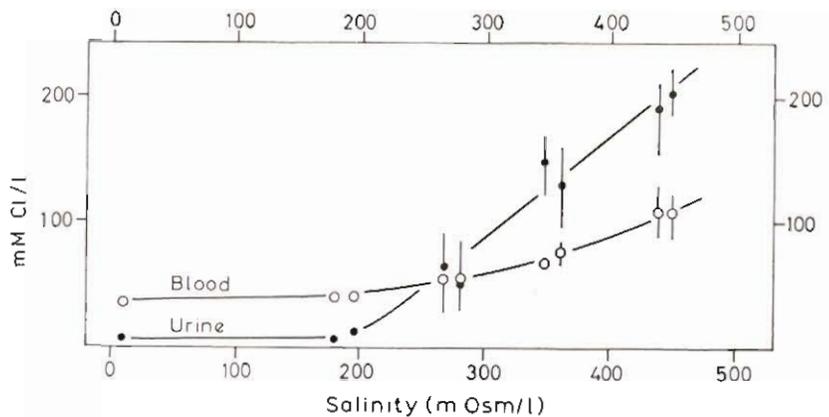


Fig. 4-123: Chloride concentration of blood and urine of *Hirudo medicinalis* as function of salinity (mOsm/l); see also legend to Fig. 4-121. (After BOROFFKA, 1968; modified.)

be measured precisely by direct cannulation (Table 4-62). According to BOROFFKA and co-authors (1970), primary urine is probably formed in two steps in the canaliculi of all nephridial lobes: (i) filtration through endothelial pores into the connective tissue; (ii) secretion by nephridial cells into the canaliculi.

Several authors have attempted to assess the capacity for osmoregulation of marine and brackish-water invertebrates only on the basis of their occurrence in waters with different salinity regimes. Such procedure may easily lead to wrong conclusions since euryhalinity in the field is not necessarily the result of effective regulation, but can be based on low surface permeability and/or high tissue tolerance to reduced or increased salinities. A certain measure of osmotic independence may also be facilitated by behaviour. Barnacles, for example, close their shells when exposed to adverse osmotic conditions (e.g. BARNES and BARNES, 1957; FOSTER, 1969a, c) and semiterrestrial crabs collect and store water and select

Table 4-62

Calculated renal salt excretion (final urine) in the freshwater living leech *Hirudo medicinalis* after 2 to 12 weeks exposure to the salinity levels indicated (about 20° C). Approximate average values. Individual measurement variation about  $\pm 30\%$  (After BOROFFKA, 1968; modified)

Salinity	Urine flow ( $\mu\text{l/hr/cm}^2$ body surface)	Urine sodium (mM/l)	Urine chloride (mM/l)	Urine osmocon- centration (mOsm/l)	Renal excretion ( $10^{-3}\mu\text{M/hr/cm}^2$ )		
					sodium	Cl	osmotically active substances
Fresh water	4.6	6	6	15	28	28	69
10% sea water	1.6	6	6	18	10	10	29
20% sea water	1.2	8	8	28	10	10	34
30% sea water	0.5	72	62	150	33	29	70

water pools with preferred salinities (e.g. GROSS, 1957b; GROSS and HOLLAND, 1960; BLISS, 1968; see also p. 925).

A number of investigations have been conducted on osmoregulation in aquatic larvae of insects. Larvae of *Aedes aegypti* have been studied by WIGGLESWORTH (1933, 1938), RAMSAY (1950, 1951, 1953) and STOBART (1960), of *Aedes detritus* by BEADLE (1939), of *Sialis lutaria* by BEADLE and SHAW (1950) and SHAW (1955a, b), of *Corethra plumicornis* by SCHALLER (1949), of *Limnephilus affinis*, *L. stigma* and *Anabolia nervosa* by SUTCLIFFE (1961a, b), and of *Chironomus thummi thummi*, *C. halophilus* and *C. salinarius* by NEUMANN (1961a, b). TREHERNE (1954) examined larvae of the coleopteran genus *Helodes*, SCHOFFENIELS (1950) larvae of the odonate genera *Aeschna* and *Libellula*. Most larvae of aquatic insects possess considerable capacities of osmoregulation (Tables 4-63, 4-64). When kept in salty media, many exhibit remarkable powers for hypo-osmotic regulation. In *Aedes aegypti* and *Sialis lutaria*, haemolymph osmoconcentration rises with increasing salinity, so that the haemolymph remains hyperosmotic to the ambient medium. Regulation of haemolymph salt concentration begins to break down when the salinity approaches a level roughly equivalent to the normal total osmoconcentration of the haemolymph (about 170 mM NaCl/l) and the larvae die when the salinity increases beyond that level. External osmoconcentrations exceeding 170 mM NaCl/l are also fatal to larvae of *Corethra plumicornis*. In fact, in the majority of euryhaline freshwater insect larvae, external concentrations above equivalents of 30

Table 4-63

Blood osmoconcentration in aquatic larvae of dipterans in different salinities. Approximations. The values for *Ephydra cinerea* larvae are about as high as those of the brine shrimp *Artemia salina*; they are the highest ever reported for an insect (Based on data from various authors)

Salinity (‰)	Species	Blood osmo- concentration		Author
		% NaCl	Δ° C	
0.2	<i>Chironomus thummi</i> <i>thummi</i>	0.65	0.38	NEUMANN (1961a)
	<i>Aedes aegypti</i>	0.82	0.48	WIGGLESWORTH (1938)
	<i>Culex pipiens</i>	0.82	0.48	" "
	<i>Ephydra cinerea</i>	2.40	1.40	NEMENZ (1960a)
5	<i>Chironomus halophilus</i>	0.77	0.45	NEUMANN (1961a)
	<i>Aedes detritus</i>	0.85	0.49	BEADLE (1939)
	<i>Chironomus salinarius</i>	1.08	0.63	NEUMANN (1961a)
33	<i>Ephydra strenzkei</i>	0.91	0.53	NEUMANN (1961a)
	<i>Ephydra riparia</i>	0.96	0.56	{ BEYER (1940) SUTCLIFFE (1960)
	<i>Ephydra cinerea</i>	2.57	1.50	NEMENZ (1960a)
	<i>Clunio marinus</i>	1.15	0.67	" "
	<i>Coelopa frigida</i>	1.18	0.68	SUTCLIFFE (1960)
	<i>Cricotopus vitripennis</i>	1.24	0.72	" "
	<i>Chironomus salinarius</i>	1.81	1.06	NEUMANN (1961a)

Table 4-64

Salinity ranges and corresponding variations in blood-osmoconcentration of aquatic larvae of dipterans. Averaged maximum values (After NEUMANN 1961a; modified)

Salinity range (‰)	Species	Maximum variations in blood osmoconcentration		Author
		% NaCl	$\Delta^{\circ}\text{C}$	
0.1-8	<i>Chironomus thummi</i> <i>thummi</i>	0.65-0.77	0.38-0.45	NEUMANN (1961a)
0.1-10	<i>Aedes aegypti</i>	0.82-0.95	0.45-0.56	WIGGLESWORTH (1938)
	<i>Culex pipiens</i>	0.82-0.95	0.45-0.56	“ ”
0.1-20	<i>Chironomus halophilus</i>	0.77-1.61	0.45-0.94	NEUMANN (1961a)
0.1-65	<i>Aedes detritus</i>	0.85-1.40	0.48-0.82	BEADLE (1939)
1.0-50	<i>Chironomus salinarius</i>	1.08-2.33	0.63-1.36	NEUMANN (1961a)
6.5 > 100	<i>Ephydra riparia</i>	0.76-1.15	0.44-0.67	{ BEYER (1940)
	<i>Ephydra strenzkei</i>	0.76-1.15	0.44-0.67	{ NEUMANN (1961a)

to 50% sea water cause death. However, larvae of the dipteran *Haliella casperi* and *Ephydra macellaria* have been found alive—as have larvae of two unknown dipteran species—in brine waters of roughly 8 times the concentration of normal sea water (CASPERS, 1952; REMANE and SCHLIEPER, 1958). In the Great Salt Lake of Utah (USA), larvae of *Ephydra cinerea* continue to osmoregulate if external salt concentrations rise to more than 32% by weight (250 atm); the osmotic pressure of this haemolymph is about 20 atm (NEMENZ, 1960a). Larvae of *Aedes detritus* can osmoregulate in salinities more than twice as high as that of normal sea water, with their haemolymph remaining hypo-osmotic.

Intermediate capacities are exhibited by larvae of the trichopteran *Limnephilus affinis*, which occur in both fresh and brackish-water habitats of N.W. Europe. SUTCLIFFE'S (1961a) study revealed that *L. affinis* larvae can tolerate salt concentrations up to at least 75% sea water and survive for short periods in 85% sea water. Their body wall is highly permeable to water, but relatively impermeable to sodium and chloride. Most of the sodium and chloride is taken up via the mouth. Sodium and chloride levels of the haemolymph are regulated intensively and maintained strongly hypo-osmotic against steep concentration gradients. Chloride concentration in the rectal fluid can be at least 3 times higher than that in the haemolymph, and slightly higher than in the external medium. In salinities higher than the equivalent of about 200 mM NaCl/l, water balance is maintained by keeping the haemolymph approximately isosmotic with the ambient medium. This is, in part, achieved by increasing the non-electrolyte fraction of the haemolymph. A small quantity of osmotically free water is available to replace osmotic water loss, it is obtained by drinking salt water and subsequent salt extrusion in the rectum.

Larvae of the freshwater trichopterans *Limnephilus stigma* and *Anabolia nervosa* cannot survive in external salt concentrations above about 60 mM NaCl/l (SUTCLIFFE, 1961b). Haemolymph osmoconcentration increases with salinity and is

slightly hyperosmotic, indicating the absence of adequate hypo-osmotic regulation. When the haemolymph chloride concentration is raised above the normal level, the Malpighian tubule-rectal system produces fluid with a chloride concentration hypertonic to the haemolymph; the system is highly sensitive to changes in the haemolymph chloride level.

The failure of many freshwater invertebrates to penetrate into brackish or marine waters, exceeding in osmoconcentration the equivalent of their blood fluids, may be related to their inability to increase the amino acid content of muscle cells (RAMSAY, 1954). In the salt tolerant *Limnephilus affinis*, osmoconcentration of cell fluids probably can also be raised by increasing the non-electrolyte fraction, as in its haemolymph (SUTCLIFFE, 1961a). Low haemolymph salt concentrations appear advantageous for keeping cellular salt levels low, high haemolymph total osmoconcentrations, at the same time, for preventing excessive water loss. In addition, a general increase in cellular tolerances to high osmotic pressures 'may be a common feature of salt-water insects' (SUTCLIFFE, 1961a, p. 516). Larvae of *Aedes detritus* survive, and even pupate, at treble haemolymph osmotic pressures following penetration of non-electrolyte glycerol (BEADLE, 1939), and death of the freshwater crab *Potamon niloticus* in salt water may be due, in part, to increased penetration of sodium ions into the interior of muscle fibres (SHAW, 1959a).

The considerable osmotic independence observed in the aquatic larvae of dipterans is largely due to very low body surface permeability, active ion uptake (anal papillae), ion excretion (Malpighian tubules), and water and/or salt reabsorption (rectum). In *Aedes detritus*, *E. riparia* and *C. vitripennis*, which do not possess functional anal papillae, intake of salt water through the gut is likely to occur; preliminary measurements reveal that *E. riparia* is able to produce a rectal fluid which is much more concentrated than the ambient medium; a similar, if less pronounced, ability has been demonstrated in larvae of *Coelopa frigida* and *Aedes detritus* (SUTCLIFFE, 1960). The substrate-living larvae of the genus *Chironomus*—which have a reduced tracheal system and haemoglobin in their blood—possess body surfaces highly permeable to oxygen, and also to water and salts (HARNISCH, 1935, 1951; KOCH, 1938; HAAS, 1957). Among the dipteran larvae examined, representatives of the genus *Chironomus* exhibit the lowest osmoregulatory potentials (Tables 4-63, 4-64), presumably because of their high permeability; their regulatory mechanisms appear to be largely the same as in the more homo-osmotic representatives (NEUMANN, 1961a).

The capacity for osmoregulation depends on the time course of the salinity change. A number of euryhaline aquatic invertebrates have been shown to exhibit higher capacities upon gradual changes from normal to extreme salinities (step-wise transfer or slow salinity variation), than upon sudden changes (direct transfer from normal to extreme salinity). An example is the cyclopoid crab *Macrophthalmus setosus* (BARNES, 1968a). For ecological considerations, it is important to know the osmoregulative capacities under conditions of sudden, as well as gradual, salinity changes. The final results may not always be the same, since sudden changes can impair the regulatory devices, or result in lethal injuries, while gradual changes may cause neither impairments nor death.

The capacity for osmoregulation is also a function of temperature (Chapter 3). Comprehensive investigations, employing sufficient numbers of diverse test tem-

peratures and salinities, or of defined environmental fluctuations, are still lacking. In general, maximum regulation can be expected only in normal or optimum temperature ranges of the test organisms. Most of the euryhaline invertebrates hitherto examined exhibit greater osmoregulative capacities in the lower than in the upper part of their normal temperature ranges. Thus the amphipod *Gammarus duebeni* maintains a higher total blood osmoconcentration in reduced salinities at 7° C than at 20° C (Fig. 4-112; KINNE, 1952b); the crab *Rhithropanopeus harrisi* exhibits more effective hyperregulation at 7° C than at 20° to 21° C (Fig. 4-113; KINNE and ROTTHAUWE, 1952); the crab *Carcinus maenas* and the shrimp *Crangon crangon* hyperregulate more successfully at 5° than at 15° C (Fig. 4-114; FLÜGEL, 1959, 1960, 1963). In salinities above 25‰ to 30‰, *Crangon crangon* also hyporegulates more effectively at 5° than at 15° C; a certain tendency for maintaining lower total blood osmoconcentrations in blood hyperosmotic salinities at lower test temperatures is indicated also in *Gammarus duebeni* and *Rhithropanopeus harrisi*.

The crabs *Hemigrapsus oregonensis* and *H. nudus*, when measured at a series of different experimental temperatures and salinities, increase their blood osmoconcentrations significantly with decreasing temperatures (DEHNEL and STONE, 1964). The same situation is found with regard to seasonal differences. In salinities below that of sea water, *Hemigrapsus oregonensis* and *H. nudus* have consistently higher blood osmoconcentrations in winter than in summer; in salinities above that of sea water, winter individuals are able to maintain lower blood osmoconcentrations than summer crabs (DEHNEL, 1962). The isopod *Cyathura polita* exhibits, in 50‰ sea water, maximum hyperregulation at 5° C; its regulatory capacity decreases in 22° C and still more in 32° C. If exposed to river water, there are no significant differences at 5° or 22° C, but 32° C causes, initially, a reduction in total blood osmoconcentration. In 125‰ sea water, osmoregulation is again most efficient at 5° C, resulting in a surprising degree of hyporegulation, while at 22° and 32° C, *C. polita* becomes more or less isosmotic. The isopods had been collected in the field in 0.5‰ to 1.0‰S at 22° to 23° C and maintained in 25‰ sea water for at least 24 hrs previous to the experiments; the test individuals, therefore were not stabilized—as most others referred to above—but examined while adjusting to the new conditions (SEGAL and BURBANCK, 1963; see also FRANKENBERG and BURBANCK, 1960). Larvae of the dipteran *Ephydra cinerea* are, at 3° C, capable of maintaining their blood osmoconcentration fairly constant over salinities ranging from that of distilled water to some 300‰S. This outstanding osmoregulative capacity decreases somewhat at higher temperatures. At 21° C, blood osmoconcentration remains the same ( $\Delta^\circ$  C 1.8 to 1.9) in the highest test salinities, but decreases ( $\Delta^\circ$  C about 1.4) in medium test salinities and further ( $\Delta^\circ$  C about 1.1) in distilled water. Ligated larvae have reduced capacities for osmoregulation; the effect of ligation is accentuated by the high test temperatures (NEMENZ, 1960a).

From the experimental results referred to in the preceding two paragraphs, it appears that temperature decrease towards the lower end of the tolerable temperature range leads to increases of blood osmoconcentration over the salinity range of hyperosmotic regulation and to small or no decreases of blood osmoconcentration over the range of poikilosmoticity (respectively the range of hypo-osmotic regu-

lation). In other words, the degree of homoco-osmosis (osmotic independence) of the euryhaline invertebrates tested tends to increase with decreasing tolerable temperatures. Beyond the lower and upper tolerable thermal limits, the functioning of osmoregulative processes becomes impaired, resulting in decreased osmotic gradients and finally isosmosis. In *Crangon crangon*, for example, the lower thermal limit seems to lie somewhat below 2° C; at this temperature hyper- and hypo-osmoregulation become considerably less efficient than at 5° or 15° C (FLÜGEL, 1963).

The physiological basis for these beneficial effects of relatively low temperatures on the osmoregulative capacity of invertebrates under salinity stress is unknown. VERWEY'S (1957) pertinent considerations were largely based on BROEKEMA'S (1941) work on *Crangon crangon*, which has been superceded with regard to temperature effects on the osmoregulative potential by the different results of FLÜGEL (1959, 1960, 1963). Temperature increase is bound to augment the intensity of water and salt exchanges between organism and environment. It appears reasonable to assume that, at higher temperatures, passive water and salt exchanges accelerate more rapidly with temperature than active transport. Such 'thermal disharmonization' would deform steady-state exchanges and tend to decrease osmotic gradients between body fluids and external media. Even more pronounced disharmonizations may be expected to occur at or beyond the lower and upper critical temperatures, leading finally to a complete breakdown of regulatory processes.

The capacity for osmoregulation may be supported by behaviour, especially in more complex invertebrates such as decapod crabs. *Pachygrapsus crassipes* selects suitable salinities if given a choice (GROSS, 1957b); *Coenobita perlatus* varies the frequency with which it visits water pools of different salinities as well as the time spent in or outside such pools (GROSS and HOLLAND, 1960); *Birgus latro* moistens its respiratory membranes with the help of its appendages and drinks water from small sources (GROSS, 1955), and *Cardisoma carnifex* drinks water of different salinities from small shallow puddles and absorbs water from sand dampened with fresh or sea water, thus regaining water lost by evaporation and lowering its blood osmoconcentration towards the normal level (DEHNEL and CAREFOOT, 1965; GROSS and co-authors, 1966). *Coenobita perlatus* habitually migrates to the sea at night in order to replenish the water supply in its shell (SEURAT, 1904); it also visits brackish water for the same end (GROSS, 1964b). *Coenobita brevimanus* can fill its shell reservoir from small water puddles (4 cm<sup>2</sup> in area and 1 cm deep); like *Birgus latro*, it does not depend on the sea for its source of water. *C. brevimanus* can thrive on a damp substrate in the absence of surface water for more than 2 weeks. GROSS (1964b) suggests that these three species represent three evolutionary steps away from the ocean toward life on land (*C. perlatus* → *C. brevimanus* → *B. latro*). Behaviour supporting osmoregulation has also been observed in the terrestrial crab *Gecarcinus lateralis* (GROSS, 1963b). It can regain water lost by evaporation or exposure to high salinities from sand dampened with fresh water. If placed on sand dampened with sea water it will, unless other water sources are available, dehydrate and die, probably because of dried respiratory membranes. There is evidence for functional water reservoirs in *G. lateralis*. Most terrestrial crabs occupy burrows with mud or water at the bottom (e.g. HERREID and GIFFORD, 1963).

Temporary reduction in osmotic stress via behavioural means has also been reported for certain osmoconformers. The barnacles *Balanus crenatus*, *B. balanoides*, *B. improvisus*, *B. balanus*, *Elminius modestus* and *Chthamalus stellatus* can, over hours or even days, evade extreme salinities by closing their opercular valves (BELIAEV, 1949; FOSTER, 1969a, c; see also BORSUK and KREPS, 1929 and NEWMAN, 1967). The chitons *Chiton tuberculatus* (AREY and CROZIER, 1919) and *Sypharochiton pelliserpentis* (BOYLE, 1969) and numerous other molluscs clamp down tightly to the substrate, close their shells or release protecting slime on severe osmotic stress. The more dilute the test medium, the more rapid and complete the clamping down in *S. pelliserpentis*. The resulting retardation of osmotic adjustment required and the considerable degree of tolerance to body fluid dilution are sufficient to ensure survival for periods of 10 hrs; thus the range of salinity variations recorded in the field (14‰ to 45‰S) suggests that exposure to osmotic extremes is not likely to limit this chiton in its exploitation of littoral habitats (BOYLE, 1969).

Calculations concerning the amount of thermodynamic work involved in osmoregulation indicate that it amounts only to a very small fraction of the total energy cost of metabolism, estimated from rates of oxygen consumption. In the mollusc *Anodonta cygnea*, calculations of minimum thermodynamic work performed in osmoregulation give a value of about 1.2% of the total metabolic energy (ROBERTSON, 1964). In the polychaete *Nereis diversicolor*, the energy required for osmoregulation varies from 0.2% of the total metabolic energy in 7‰S (20% sea water) to about 2.5% in fresh water (POTTS and PARRY, 1964). The energy requirements for chloride regulation in different salinities are listed in Table 4-65. In the crab *Carcinus maenas*, the energy required for osmoregulation in 14‰S (40% sea water) amounts to 0.0024 cal/g/hr (assuming a temperature of 15° C; SHAW, 1961a; POTTS and PARRY, 1964). Since *C. maenas*, in 15‰S at 15° C, consumes about 141 mg/O<sub>2</sub>/hr (SCHWABE, 1933), which is equivalent to about 0.4 cal/g/hr, osmoregulation requires 0.6% of the total metabolic energy cost.

Table 4-65

Energy requirements for chloride regulation of the polychaete *Nereis diversicolor* in different salinities at 25° C (Calculated from data by JØRGENSEN and DALES, 1957; after POTTS and PARRY, 1964; modified)

External medium Salinity	Chloride concentration (mM Cl/l)	Body fluid (mM Cl/l)	Active influx ( $\mu$ M Cl/g/hr)	Energy for maintenance of active influx (cal/g/hr)
7‰ (20% sea water)	110	162	10.85	0.00177
3.5‰ (10% sea water)	55	140	7.9	0.0033
fresh water (0% sea water)	0	100	5.5	0.0127

*Metabolic efficiency.* Changes in salinity may affect not only rates but also efficiencies of metabolism. This has been demonstrated for the euryhaline fish *Cyprinodon macularius* (KINNE, 1960; Chapter 4.32) and seems to hold also for euryhaline aquatic invertebrates. Depending on the salinity conditions, a given amount of food may be converted into different amounts of body substance and energy for biological processes. For a proper assessment of energy budgets of invertebrates living in different salinity regimes, we must learn more about salinity influences on metabolic efficiencies.

REEVE (1963a) demonstrated that metabolic efficiency varies as a function of salinity in young brine shrimp *Artemia salina*. Brine shrimps were collected in the Great Salt Lake (Utah, USA) and fed with cultures of the alga *Phaeodactylum tricorutum*. Efficiency of growth (increase in body weight divided by weight of food consumed per unit time) reaches a peak in 35‰S (Fig. 4-124). The apparent efficiency maximum in salt concentrations corresponding to the salinity of normal sea water provides further evidence that *A. salina* tolerates brine waters rather than prefers them, in the sense of finding optimum osmotic conditions there. REEVE believes that the decrease in growth efficiency in sub- and supra-oceanic salinities may be due to increased proportions of assimilated food being appropriated for osmotic work and/or to the increasing cost of enzymatic energy liberations under osmotic stress. In view of the rather low percentage of metabolic energy required for osmoregulation (p. 926), progressive difficulties in energy liberations appear to represent the more likely reason for decreased efficiencies in external salinities.

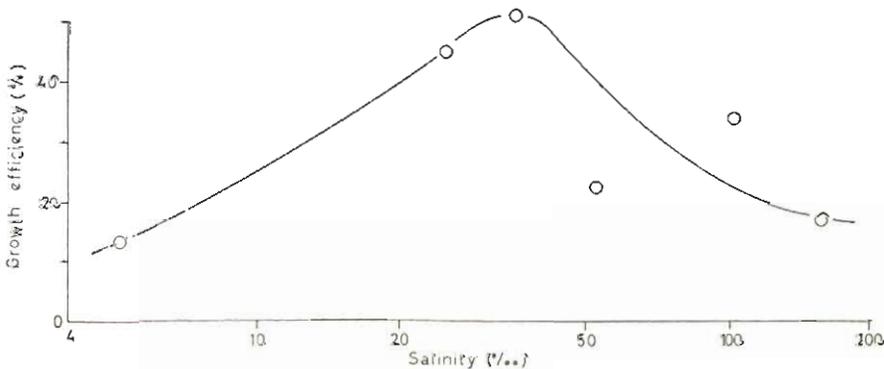


Fig. 4-124: Efficiency of growth as a function of salinity in young brine shrimps *Artemia salina*. (After REEVE, 1963a; modified.)

A study of metabolic efficiencies in developing *Artemia salina* embryos reveals that very high and very low salinities represent a physiological burden which manifests itself in increased energy expenditures (BIOLOGISCHE ANSTALT HELGOLAND, 1968, 1969; VON HENTIG, 1970; PANDIAN, 1970). With increasing salinity and decreasing temperature, VON HENTIG (1970) recorded increasing calorific requirement for the embryonic development of *A. salina* (Table 4-66). The increasing calorific requirements are met by augmented consumption of reserve fats, proteins and carbohydrates. The calories of fats and proteins consumed rise more markedly than those of carbohydrates; fats become the most important

Table 4-66

Energy expenditure during embryonic development of *Artemia salina* exposed to different combinations of salinity and temperature. Given are average values for the consumption of fats, proteins, and carbohydrates in percentage amounts of the gastrula values and in calories provided by each class of substances per embryo. The initial average calorific values per gastrula are: 0.005540 cal for fats, 0.005865 cal for proteins, and 0.002685 cal for carbohydrates (After VON HENTIG, 1970; modified.)

Salinity (‰)	Temperature (°C)	Fats		Proteins		Carbohydrates	
		(%)	(cal)	(%)	(cal)	(%)	(cal)
15	10	25.75	·001430	21.15	·001240	38.00	·000982
	15	23.35	·001300	17.00	·001000	33.75	·000918
	20	16.10	·000894	15.35	·000895	31.40	·000845
	30	14.75	·000822	15.85	·000925	29.65	·000794
32	10	31.50	·001745	26.10	·001535	40.80	·001100
	15	29.60	·001550	23.30	·001368	38.60	·001040
	20	24.15	·001345	22.90	·001340	37.35	·001004
	30	22.50	·001255	23.15	·001362	35.60	·000955
70	10	38.50	·002130	31.75	·001860	44.05	·001240
	15	36.40	·002020	30.00	·001763	43.30	·001165
	20	31.90	·001770	29.55	·001735	41.85	·001125
	30	28.65	·001590	29.75	·001745	39.95	·001065

source of biologically useful energy. Throughout the embryonic development, carbohydrate consumption is greatest by weight, but in terms of calorific values becomes progressively less significant as energy expenditure increases. Energy expenditure is, in part, a function of the duration of embryonic development. KHMELEVA (1967) studied the energy budget for the complete life cycle of *A. salina*. She found the energy expenditure (cal per individuum) to be 2.7 for growth, 2.4 for moulting, 16.3 for reproduction and 38.5 for routine metabolism.

In genetically identical colonies of the brackish-water living hydroid *Cordylophora caspia*, the speed of digestion increases in the order 16.7‰ > 30‰ > fresh water (KINNE, 1958a). As a euryhaline sedentary animal, *C. caspia* would certainly lend itself to detailed studies concerning possible salinity influences on metabolic efficiencies.

*Non-genetic capacity adaptation.* Quantitative aspects of performance may be modified significantly by non-genetic capacity adaptation (acclimation, acclimatization). Consequently, knowledge on the state of acclimation (environmental history) is required before the performance of individuals, exposed to different salinity conditions, can be properly assessed. The concept of non-genetic capacity adaptation has been considered in Chapters 3.31 and 12.

Unfortunately, the literature on non-genetic capacity adaptations to salinity is still scanty and refers almost exclusively to different constant salinity levels; next

to nothing is known about acclimation of marine and brackish-water invertebrates to fluctuations in salinity or to variations in solute composition. Acclimations to different salinity levels involve primarily quantitative adjustments in water and salt balances, and in respiratory rates. The most ancient type of non-genetic capacity adaptation to salinity appears to be over-all tissue acclimation in osmoconformers lacking specific organs for effective regulation. Osmoregulators employ specialized regulatory organs such as gills, gut and excretory glands, which then tend increasingly to represent primary sites of salinity acclimation. Acclimation to salinity affects not only the rate of metabolism but also its economy (KINNE, 1964a, c).

In the time course of non-genetic capacity adaptation to salinity variations, three phases may be distinguished (KINNE, 1964c; see also Chapter 3.31, p. 474): immediate response, stabilization, and the new steady state.

The immediate response begins seconds or minutes after a significant salinity change and frequently involves over- or undershoots in performance, e.g. in locomotory activity, metabolic rate, body volume, or water and salt exchanges. Immediate responses may also manifest themselves in intense muscle contractions (or relaxations), secretion of slime or jelly, changes in quantity and quality of free amino acids and changes in colour, as well as in behaviour. It is unknown whether such immediate responses represent an integral part of the process of non-genetic adaptation proper in all cases.

The phase of stabilization usually lasts hours, days or weeks. When the fresh-water-living leech *Hirudo medicinalis* is transferred into 14‰S at about 20° C, stabilization of blood osmoconcentration is attained within a few hours; stabilization of the body volume, however, takes some 2 to 4 weeks (BOROFFKA, 1968). In the crab *Hemigrapsus oregonensis*, stabilization of blood osmoconcentration was followed by DEHNEL (1962) after transfer into salinities ranging from 6‰ to 175‰ normal sea water. In summer crabs, stabilization was studied at 15° C (Fig. 4-125), in winter crabs at 5° C (Fig. 4-126). Both test temperatures approximate seasonal habitat conditions. Changes in blood osmoconcentration are rapid; about one half of the total change occurs within the first 3 hrs. In the summer crabs exposed to salinity levels from 6‰ to 100‰, sea water, stabilization is completed after 24 hrs; while in 125‰ and 150‰ sea water, stabilization is still uncompleted after 24 hrs. All winter crabs complete stabilization within 24 hrs, except in 175‰ sea water. Summer and winter crabs are hyperosmotic to all test salinities. Similar time courses of stabilization of blood osmoconcentration have been obtained for *Hemigrapsus nudus* (DEHNEL, 1962).

In *Hemigrapsus oregonensis* and *H. nudus*, urine osmoconcentration falls in diluted and rises in concentrated, ambient media at rates directly related to osmotic gradients between body cavity fluids and environment, subject to seasonal adaptation and experimental temperature; the major changes occur within 48 hrs (DEHNEL and STOSSE, 1964). SCHWABE (1933) exposed Mediterranean decapods (habitat salinity about 42‰) to 51‰ and 25‰S. Upon transfer into 51‰S, the blood of the stenohaline osmoconformer *Maia verrucosa* becomes rapidly isosmotic, the crabs collapse and, if turned on their backs, fail to re-assume the normal position. However, after about 1 hr, *M. verrucosa* begins to recover and to regain strength. Transfer into 25‰S leads to slower changes of blood osmoconcentration

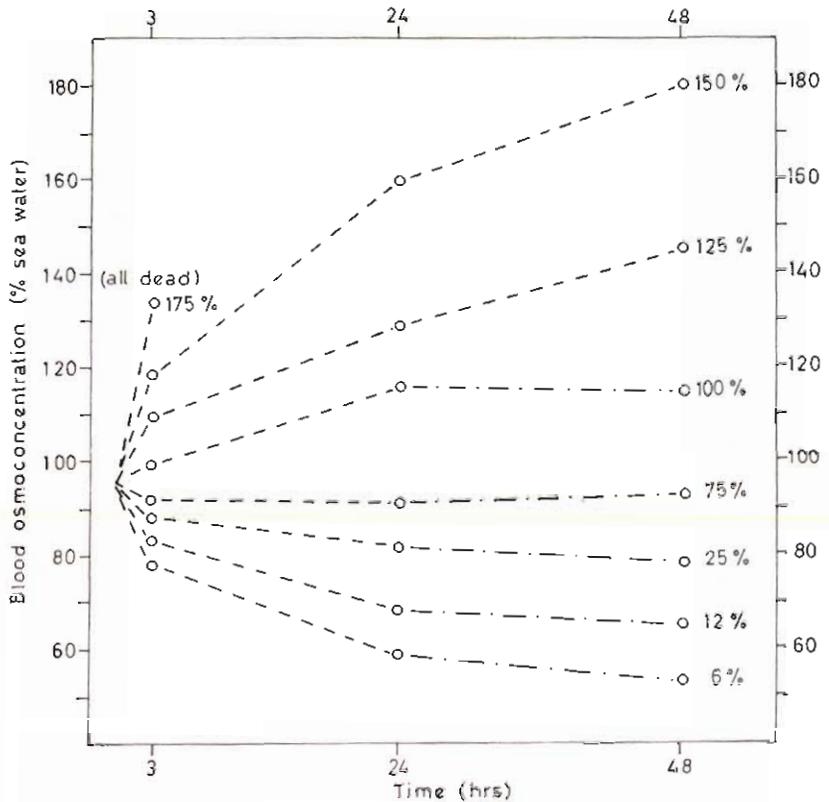


Fig. 4-125: Stabilization of blood osmoconcentration in the crab *Hemigrapsus oregonensis* after sudden changes in salinity. Summer crabs, tested at 15° C. Each point represents the mean of 10 to 15 individuals. Values for blood osmoconcentration and salinity (at each curve) are given in percent of normal sea water. Dash-dot lines indicate new steady state (completed stabilization). (After DEHNEL, 1962; modified.)

(isosmosis is reached after 24 to 32 hrs), but at the same time to progressively irreversible damage, demonstrating lack of appropriate capacities for non-genetic adaptation to 25‰ S; the crabs begin to die after 15 hrs.

In *Carcinus maenas* transferred from 25.9‰ S ( $\Delta^{\circ}C = 1.4$ ) to 11.8‰ S ( $\Delta^{\circ}C = 0.63$ ), blood osmoconcentration decreases from 1.75  $\Delta^{\circ}C$  to 1.3  $\Delta^{\circ}C$  in 26 hrs and then remains constant (DUVAL, 1925). According to GROSS (1963a, b), measurable acclimation of *Hemigrapsus oregonensis* after transfer into about 51‰ S requires more than 5 days, strong acclimation 22 days. Freshwater-living crayfish *Astacus astacus*, transferred into blood isosmotic brackish water (15‰ S), increase their blood osmoconcentration, rapidly at first, then more slowly, and complete stabilization after about 12 days; concomitant decrease in oxygen consumption settles after 20 to 30 days at a new level, equivalent to 60% of the original metabolic rate (HERRMANN, 1931; SCHWABE, 1933).

The lamellibranch *Mytilus edulis* has a higher metabolic rate in the Baltic Sea (15‰ S) than in the North Sea (30‰ S); if North Sea individuals are transferred to

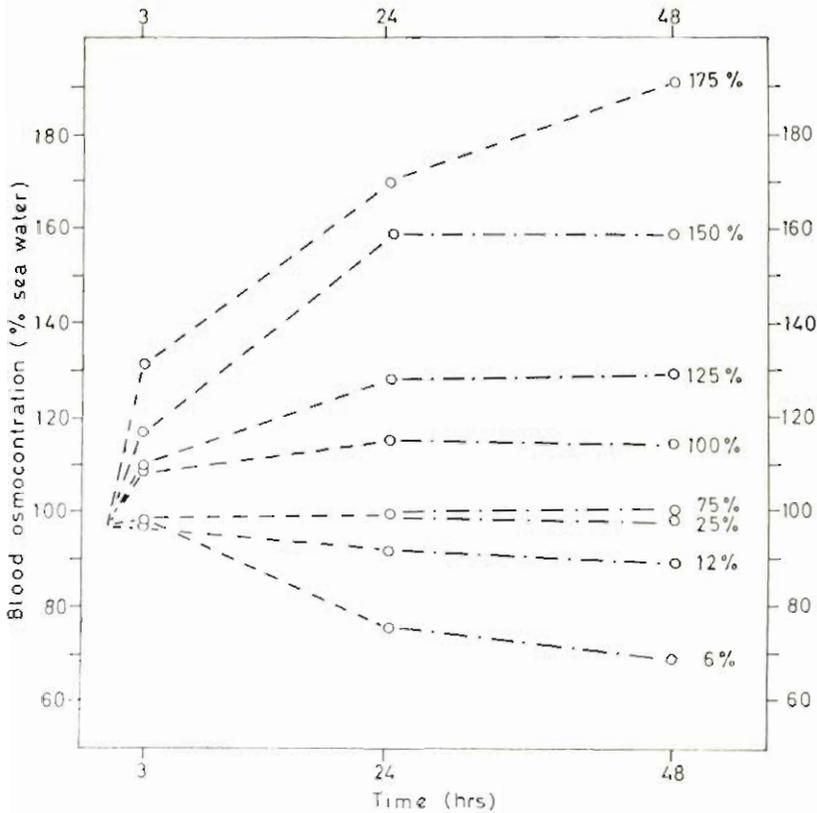


Fig. 4-126: Stabilization of blood osmoconcentration in the crab *Hemigrapsus oregonensis* after sudden changes in salinity. Winter crabs, tested at 5° C. See also legend to Fig. 4-125. (After DEHNEL, 1962; modified.)

Baltic Sea water, tissue respiration increases 20% within a few hours; further increase is slow, and stabilization is attained only after 4 to 7 weeks (SCHLIEFER, 1955).

From the information available, the following conclusions may be drawn: (i) The time course of stabilization varies with the function studied, the metabolic rate of the tested organism and the degree of the salinity changes, as well as with temperature and season. (ii) The rate of stabilizing processes tends to increase with metabolic rate and temperature. (iii) Maximum percentages of the total change occur within the first portion of the stabilization period. (iv) The absolute amount of adjustment achieved per unit time tends to increase with the difference in salinity (as long as the critical salinity limits are not surpassed).

The new steady state of performance after a defined change in salinity has been studied in only very few cases. Comprehensive accounts are lacking. In the brine shrimp *Artemia salina*, the new rate of oxygen consumption is different in males and females; after complete acclimation to 35‰ and 140‰S, oxygen consumption is proportional to the 0.662 power of dry weight in females (3.4 to 7.6 mm long) in

both media (GILCHRIST, 1956); males (3.3 to 7.3 mm long), however, show progressive differences in the two media with increasing body length, their oxygen consumption is proportional to the 0.883 power of dry weight in 35‰S, but to the 0.624 power in 140‰S. The higher respiratory rate in 35‰S is presumably related to the larger surface area of the second male antennae in that salinity (GILCHRIST, 1958).

Complete acclimation of freshwater crayfish *Astacus astacus* to increased salinity results in a reduction of the osmotic gradient between body fluids and external medium, decrease in urine output by half in 8‰S, and the production of negligible amounts of urine in 15‰ to 20‰S (HERRMANN, 1931). In the crab *Callinectes sapidus*, the breakpoint of the blood-medium curve occurs at lower salinities in individuals collected in dilute sea water than in specimens collected in full-strength sea water; after acclimation of crabs from dilute sea water to full-strength sea water, the breakpoint shifts towards higher salinities (ANDERSON and PROSSER, 1953). The crab *Hemigrapsus oregonensis* exhibits a greater capacity for osmoregulation in high salinities after acclimation for more than 20 days to about 51‰S than individuals previously kept at about 34‰S; this non-genetic adaptation occurs after both sudden and gradual salinity changes (GROSS, 1963a).

KRISHNAMOORTHY and VENKATRAMIAH (1969) studied myosin ATPase activity in the decapod *Scylla serrata*. The crabs, which inhabit the Krishna Estuary (India; average salinity: 23‰), were acclimated at 29° C to 33‰ and 8.3‰S, respectively and the flexor muscles of the legs selected for study. The pH specificity and thermostability of the myosin ATPase vary as a function of acclimation salinity. Enzyme from 23‰S crabs reveals two pH maxima, one at pH 7.0, the other at pH 9.0. Upon adaptation to 33‰S, the peak at pH 7.0 shifts to 6.0; upon adaptation to 8.3‰S, the peak disappears (Fig. 4-127). Enzyme of 23‰S crabs shows maximum activity at 30° C, of 33‰S crabs at 38° C, of 8.3‰S at 24° C (Fig. 4-128). These changes are assumed to be due to non-genetic capacity adaptation to salinity at the molecular level. The ecophysiological significance of the salinity-dependent variations in myosin ATPase activity must be sought in the muscular efficiency of the crab. The enzyme underlies quantitative changes in the liberation of terminal phosphate bond energy rather than qualitative shifts. Of course, myosin ATPase activity cannot be considered the sole criterion for estimating muscular efficiency; the latter depends largely on levels of energy storage, fatigue, physical components and relaxing factors (EBASHI and ENDO, 1969). According to KRISHNAMOORTHY and VENKATRAMIAH (1969), *S. serrata* acclimates simultaneously under natural conditions in the estuary, both to higher salinity and temperature, and adjusts its ATPase activity, probably by changing the synthetic pattern of the myosin molecule. The increased thermostability of the enzyme, resulting from adaptation to supranormal salinities, may be due to changes in activation energy of enzyme catalysis (see also KRISHNAMOORTHY and VENKATRAMIAH, 1971).

*Genetic capacity adaptation.* Genetic capacity adaptations, i.e. genetically controlled adjustments in performance of organisms inhabiting waters with different salinity conditions, are likely to be involved in the interpopulational or interspecific differences referred to repeatedly in this subchapter. The present status of our pertinent knowledge does not allow statements beyond those already made.

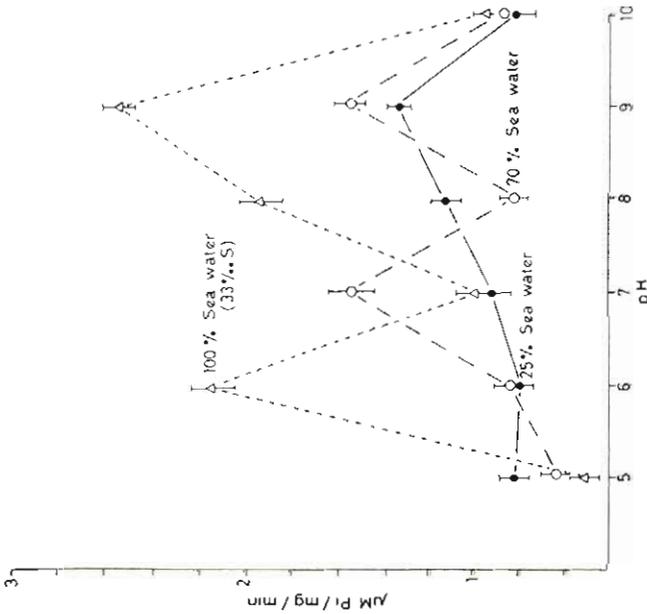


Fig. 4-127: *Scylla serrata*. Profile pH curves of myosin ATPase activity of the flexor muscle of crabs adapted to three different salinities. Each point gives the mean value and standard deviation of 6 determinations on different groups of pooled tissue. Pi: inorganic phosphorous. Assay conditions: 0.1 mM CaCl<sub>2</sub>; 0.5 mM ATP; 37° C. Habitat medium: 70% sea water. (After KRISHNAMOORTHY and VENKATRAMIAH, 1969; modified.)

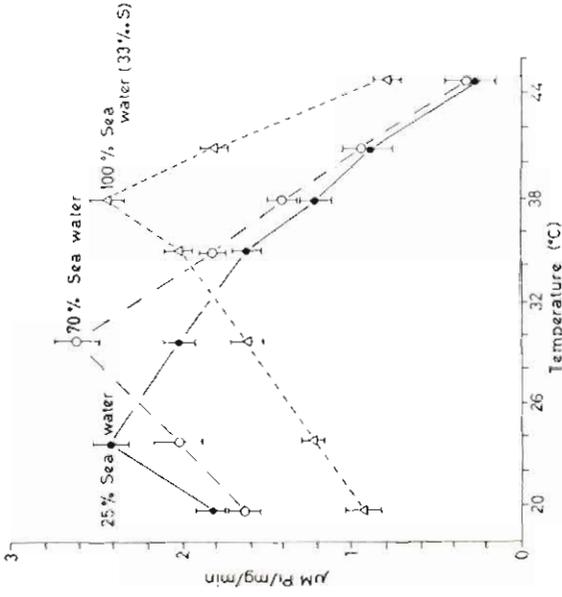


Fig. 4-128: *Scylla serrata*. Thermostability of myosin ATPase activity of the flexor muscle of crabs adapted to three different salinities. Each point indicates the mean value and standard deviation of 6 determinations on different groups of pooled tissue. Pi: inorganic phosphorous. Assay conditions: 0.1 mM CaCl<sub>2</sub>; 0.5 mM ATP; pH 9.0. (After KRISHNAMOORTHY and VENKATRAMIAH, 1969; modified.)

### Activity

The degree and kind of organismic activity depends upon numerous internal and external parameters; among the latter, salinity (both in regard to total osmoconcentration and ionic composition) may be of importance, next to light (Chapter 2), temperature (Chapter 3), pressure (Chapter 8), dissolved gases (Chapter 9), and other abiotic environmental factors, as well as to biotic aspects, such as population density, food and behaviour.

*Locomotion and work performed.* Upon sudden variations in salinity, aquatic invertebrates may exhibit quantitative and qualitative changes in locomotion and work performed such as boring, burrowing, tube building, water propulsion or feeding.

BROEKHUYSEN (1941) placed representatives of six intertidal gastropod species in a large petri dish partly filled with sea water; he then increased or decreased the salinity by gradually adding either concentrated sea water, or distilled water. This was continued until all 10 individuals of each experiment had ceased crawling. At this point the salinity was determined by means of titration. The results of these simple, but revealing experiments are illustrated in Fig. 4-129. Except for *Oxystele tigrina*, the salinity ranges decrease parallel to the habitat height occupied by the respective species on the shore (see Fig. 4-86).

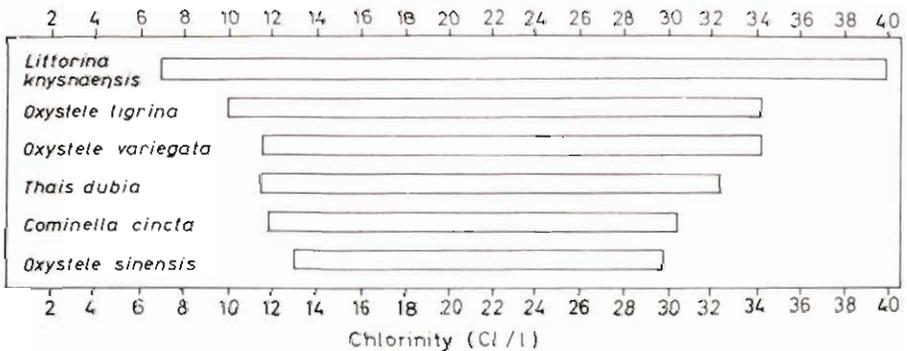


Fig. 4-129: Salinity ranges (in g Cl/l) within which crawling of the six intertidal gastropods indicated is possible. (After BROEKHUYSEN, 1941; modified.)

The euryhaline prosobranch snail *Potamopyrgus jenkinsi*, which inhabits fresh-water lakes, rivers, estuaries and brackish-water pools, changes its locomotory activity in different salinities (DUNCAN, 1966). Fig. 4-130 illustrates rates of locomotion of individuals from fresh-water and brackish-water habitats, after acclimation to the test salinities. *P. jenkinsi* shows maximum locomotory rates in the middle part of the salinity range; snails from fresh water move fastest in 18‰ S, those from brackish water in 22‰ S.

If exposed to different conditions of salinity and temperature, the flatworm *Stylochus ellipticus* reveals differences in rates of locomotion and of 'righting' (LANDERS and TONER, 1962). *S. ellipticus* is a predator of oysters (LOOSANOFF, 1956) and one of the most abundant marine polyclads along the Atlantic and Gulf

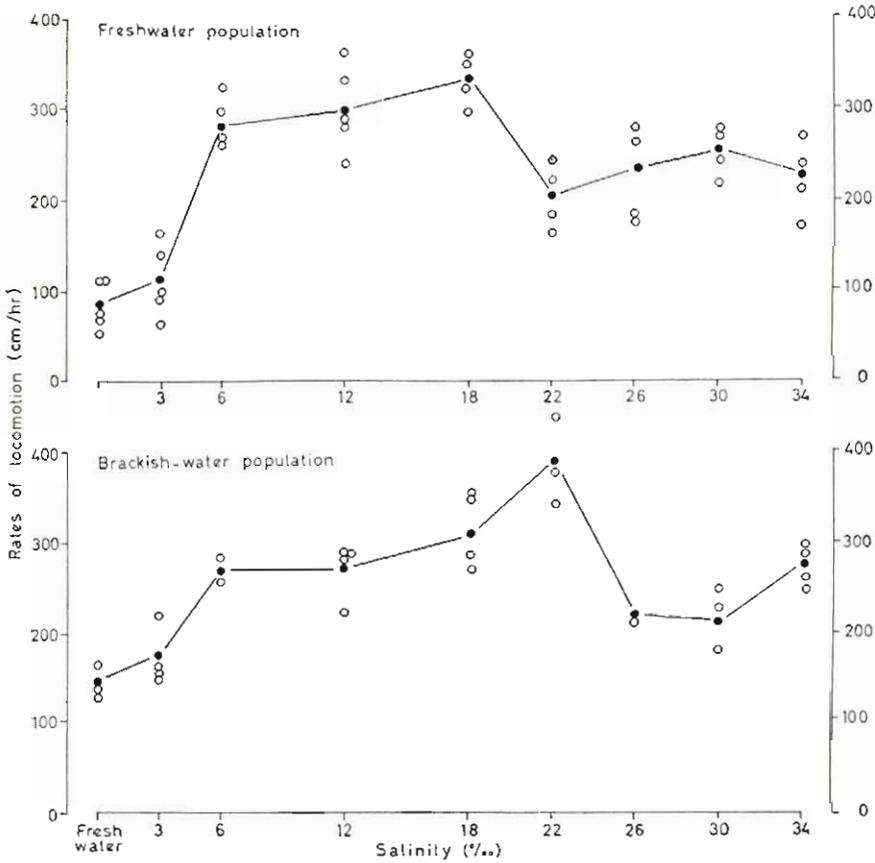


Fig. 4-130: Locomotory rates of the snail *Potamopyrgus jenkinsi* from fresh water (Jeziorak, Poland) and from brackish water (Zalew Wiślany, Poland) after long-term exposure to different constant salinities at 18° to 20° C. White circles: mean of 3 measurements on 1 snail; black circles: means of 5 different snails. (After DUNCAN, 1966; modified.)

coasts of the United States (HYMAN, 1940). In laboratory tests, the flatworm exhibits some locomotory activity in all combinations of salinity and temperature offered. When the levels of salinity and temperature are progressively reduced, the depressing effects of these two factors apparently begin to critically re-inforce each other, with the result that rates of locomotion slow down. Righting times (time spans required by a worm to return to normal position after being turned ventral side up) were determined frequently in each test salinity; however, more observations were made in the lower salinities (in which individual response variations were largest) than in higher salinities. Worms of 10 to 18 mm length, from Milford Harbor (Connecticut, USA; habitat salinities: ca 26‰ to 28‰, temperatures: -1° to ca 25° C), were transferred directly into test salinities at 18° to 22° C. Fig. 4-131 reveals that average righting time remains close to 12 secs in salinities ranging from 7.5‰ to 27‰; in 5‰S, righting time increases to 22 secs, in 2.5‰S to 37 secs.

*Marphysa gravelyi*, a common polychaete of brackish waters of Madras (India), which are characterized by intensive salinity fluctuations, responds to abrupt salinity stress by changes in spontaneous muscle activity (KRISHNAMOORTHY and KRISHNASWAMY, 1963). Whole worms exhibit spontaneous muscle activity in sea water dilutions ranging from 20 to 70‰, while muscle preparations are active only from 20 to 50‰; maximum activity is displayed in 30‰ sea water. Similar results were obtained on *Arenicola* species (WELLS and LEDINGHAM, 1940). The results reported on *Marphysa gravelyi* make further experiments desirable (avoidance of shock reactions, differentiation between effects of total osmoconcentration and important ions, such as Na, K, Ca and Mg).

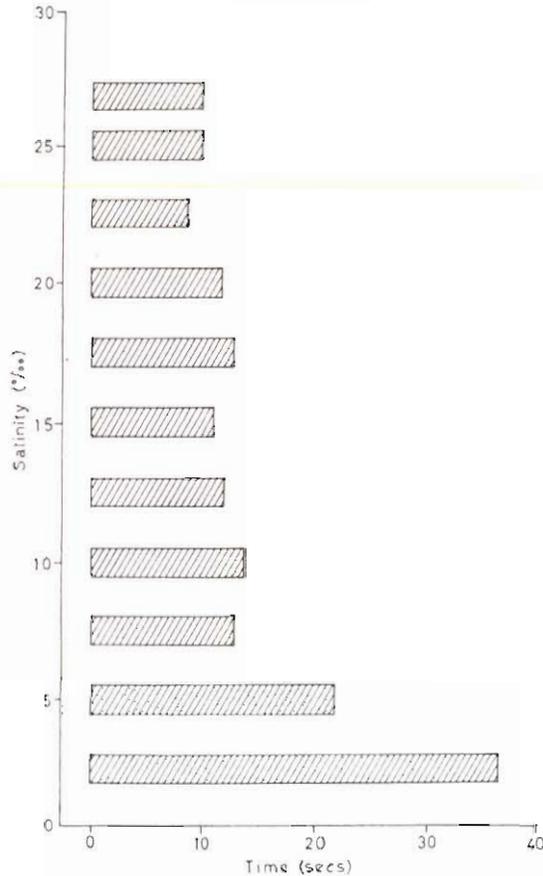


Fig. 4-131: Average righting time of the flatworm *Stylochus ellipticus* after direct transfer into different salinities at 18° to 20°C. (After LANDERS and TONER, 1962; modified.)

In the wood-boring isopods *Limnoria tripunctata*, *L. lignorum* and *L. quadripunctata*, the average daily burrowing rate is affected by salinity (REISH and HETHERINGTON, 1969). All three species exhibit maximum burrowing activities at a chlorinity of 17.5‰; at the same time, they reveal distinct interspecific differences (Fig. 4-132).

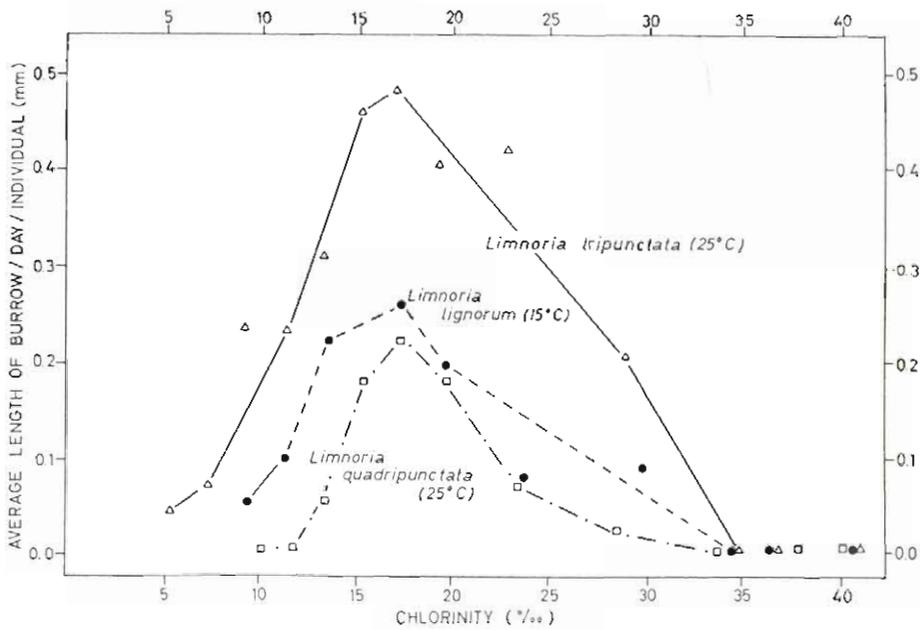


Fig. 4-132: Average daily burrowing rate of three wood-boring isopods of the genus *Limnoria* at different chlorinities. (After REISH and HETHERINGTON, 1969; modified.)

Tube-building activities in relation to salinity have been investigated by NEFF (1969) in the serpulid worms *Hydroides brachyacantha* and *Eupomatus dianthus*. If carefully removed from their tubes, consisting of a mixture of crystalline calcium carbonate and a mucopolysaccharide matrix material, many serpulids begin to secrete concretions of calcium carbonate. *H. brachyacantha* and *E. dianthus* fail to produce concretions in salinities below about 20‰. Above 20‰S, the rate of concrete secretion increases with increasing salinity and environmental calcium concentration.

The intensity of water propulsion as a function of salinity has been studied by NAGABHUSHANAM and SAROJINI (1965b) in the lamellibranch *Branchidontes recurvus*. Employing the neutral-red technique, these authors demonstrated that, in 18‰S at 26°C, *B. recurvus* removes, within 1 hr, about 50% of the neutral red added. With a lowering of salinity, the rate of water propulsion decreases (Table 4-67). Quite similar results have been obtained with the lamellibranch *Mulinia lateralis* (NAGABHUSHANAM and SAROJINI, 1965a). Water propulsion in lamellibranchs depends largely upon the activity of their ciliary epithelium. Hence the studies referred to under the heading *Salinity tolerance at the subindividual level* (p. 836) should be consulted; see also WINTER (1969).

In the barnacles *Balanus balanoides* and *Elminius modestus* (habitat salinity 32‰ to 34‰), cirral activity decreases slightly, both in sub- and supranormal salinities (Fig. 4-133). There is no cirral beating below 17‰S nor above 53‰S (FOSTER, 1969c).

Table 4-67

Relative rates of water propulsion in the mussel *Branchi-dontes recurvus* after transfer into test salinities for a few hours; 26° C (After NAGABHUSHANAM and SAROJINI, 1965b; modified)

Salinity (‰)	Average percentages of neutral red removed per individual within the periods indicated			
	15 mins	30 mins	45 mins	60 mins
18	15	28	38	51
14	10	21	30	38
10	4	9	16	25
6	2	3	5	8

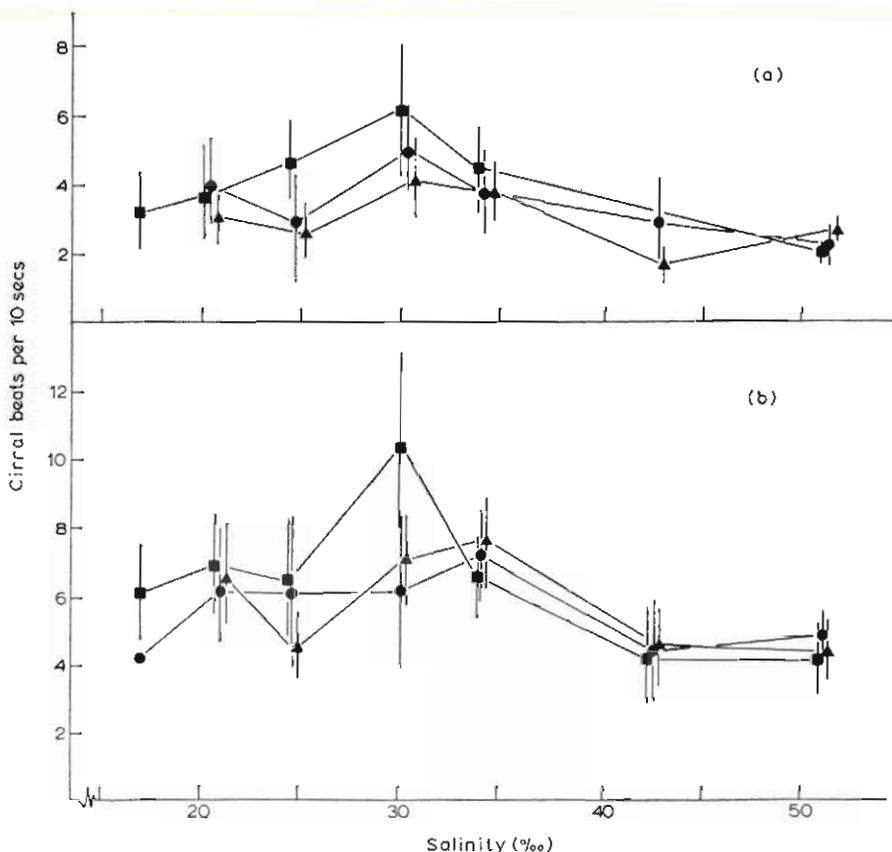


Fig. 4-133: Cirral activity in the barnacles *Balanus balanoides* (a) and *Elminius modestus* (b) following continuous submersion in the salinities indicated; circles: after 1 day, triangles: after 2 days, squares: after 3 days. Means for 10 individuals. Vertical bars: standard deviation. 15° C. (After FOSTER, 1969c; redrawn.) By permission of The Royal Society.

The activity of tentacles and oral muscles of the euryhaline hydroid *Cordylophora caspia* changes with salinity. Genetically identical and environmentally fully stabilized colonies were fed with oligochaete worms (*Enchytraeus albidus*) of defined size, and the time measured which elapsed between first contact and complete disappearance of the worm in the fed hydranth's gastral cavity. At 13° C, average feeding time amounts to 13.0 mins in 16.7‰S, 16.1 mins in 30‰S and 21.8 mins in fresh water (KINNE, 1958a).

The formation of byssal threads in the lamellibranchs *Modiolus demissus* and *Mytilus edulis* (calculated as number of threads/individual/hr) may be influenced by variations in salinity. According to VAN WINKLE (1970), *Modiolus demissus* did not form threads in sea water without calcium or magnesium, and low-salinity (16‰ to 20‰S) acclimated mussels adapted more rapidly to 32‰S than high-salinity (32‰ to 34‰S) acclimated mussels to 16‰S. In VAN WINKLE's experiments, *Mytilus edulis* formed no threads in 16‰S, although it is capable of producing byssal threads in the laboratory in this salinity (GLAUS, 1968); in 32‰S, thread formation varied from 0.25 to 0.60 threads/mussel/hr. According to GLAUS (1968), thread production is greater at 31.3‰S than at 15.9‰ or 46.3‰S. REISH and AYERS (1968) reported a sharp decrease in thread formation by *Mytilus edulis* between 25.3‰ and 28.9‰S.

Changes in feeding activity as a function of salinity have been reported for two boring snails, *Polinices heros* and *P. duplicata* which are predators of the clam *Mya arenaria* (HANKS, 1952). *P. heros* inhabits primarily waters with high and fairly constant salinities along the open coast, while *P. duplicata* is an inhabitant of estuaries, bays and harbours with reduced and varying salinities. HANKS conducted his feeding experiments at water temperatures between 14° and 18° C. In a salinity of 32‰, *P. heros* feeds at a slightly higher rate than *P. duplicata*. However, in 25‰S, both snails consume similar numbers of clams per 10 days (Table 4-68). Whilst *P. heros* exhibits a decrease in feeding activity with a lowering of salinity from 32‰ to 25‰, *P. duplicata* maintains similar feeding activities at 32‰ and 25‰S. With further lowering of salinity, *P. heros* reduces its feeding rate much more than *P. duplicata*. *P. heros* stops feeding in 10‰S, *P. duplicata* in 6‰S. Feeding rates are also influenced by salinity and temperature in the marine prosobranch gastropods *Eupleura caudata* and *Urosalpinx cinerea* which are among the most serious predators of the Eastern oyster *Crassostrea virginica* (MANZI, 1970). In fact, the damage inflicted by these drills on oyster beds is estimated to amount to millions of dollars per annum (e.g. GALTSOFF and co-authors, 1937). MANZI recorded feeding rates of the two gastropods at 12 salinity-temperature combinations as the mean number of oyster spat consumed per drill per 10-day trial. 12.5‰S is near the lower limit for feeding activity. Feeding rates increase with each increase in salinity and temperature; maximum rates were measured at the highest salinity (26.5‰) and temperature (25° C) tested. At all salinity-temperature combinations, *U. cinerea* consumed more oyster spat than did *E. caudata*.

*Reduction of contact with adverse salinities.* Reduction of contact with adverse salinities can be brought about by secretion of mucus, jelly or similar protective substances, closure of shells, retreat into burrows, muscle contraction, or withdrawal of sensitive body parts. As the invertebrate concerned must feed,

Table 4-68

Feeding activity of the snails *Polinices heros* and *P. duplicata* as a function of salinity. Feeding rate is expressed as number of *Mya arenaria* consumed per snail per 10 days, 14° to 18° C (After HANKS, 1952; modified)

Salinity (‰)	<i>Polinices heros</i>			<i>Polinices duplicata</i>				
	No. of snails	Feeding period (days)	No. of clams con- sumed	Feeding rate	No. of snails	Feeding period (days)	No. of clams con- sumed	Feeding rate
32	6	8.5	27	5.3	6	8.5	23	4.5
25	3	7	10	4.7	6	7.5	21	4.7
18	9	7	10	1.6	9	7	14	2.3
14	6	7	1	0.2	6	7	7	1.7
12	6	14	3	0.4			No data	
10	6	14	0	0.0	12	7	10	1.2
8					3	14	2	0.5
6			No feeding		6	14	0	0.0

exchange gases and defecate, the period of contact reduction is limited.

Reduction of contact with adverse ambient media may be exemplified by closure of opercular valves in cirripedes. When placed in such low salinities that cirral activity is inhibited, *Elminius modestus*, *Balanus balanoides*, *B. crenatus*, *B. improvisus*, *B. balanus* and *Chthamalus stellatus* close their opercular valves, with the result that the osmoconcentration of mantle cavity fluid and blood is maintained for some time hyperosmotic to the diluted external medium (FOSTER, 1969c).

*Elminius modestus*, immersed abruptly in media of sub- or supranormal salinities at 15° C, revealed the following responses. In 25‰ and 50‰ sea water (Menai Straits, U.K.; 32‰ to 34‰S), specimens initially maintain their cirral activity; blood osmoconcentration falls, within the first hour, to a value corresponding to about 80‰ sea water. Thereafter, the valves are closed and the decrease is more gradual (Fig. 4-134a). In 25‰ sea water, critical osmotic damages occur after 30 hrs; in 50‰ sea water, the blood becomes nearly isosmotic in 5 days, during which time some of the specimens resume cirral activity. In 140‰ sea water (no valve closure), near isosmoticity is reached in 10 hrs, in 200‰ sea water (valve closure) in about 50 hrs (Fig. 4-134b). FOSTER's results indicate that, while there is no permanent control, severe short-term osmotic stress can be reduced significantly by temporary valve closure.

Comparable cases of reduced contact due to shell closure have been reported in the molluscs *Mytilus edulis* (CRONKIN and KROGH, 1938), *Patella vulgata* (ARNOLD, 1957), *Scrobicularia plana* (FREEMAN and RIGLER, 1957), *Acmaea limulata* (SEGAL and DEHNEL, 1962), *Littorina* spp. (AVENS and SLEIGH, 1965), *Siphonaria pectinata* (MCALISTER and FISHER, 1968), and in other marine invertebrates.

*Transformation into resistant resting stages.* During periods of adverse environmental conditions, a number of aquatic invertebrates transform into resting stages, such as cysts, spores, gemmulae and menonts. These are generally much more resistant to environmental stress than active life-cycle stages (p. 825). Some invertebrates regularly form resting stages in the course of their life cycle, others only under exceptionally severe conditions.

Several authors have suggested that, in addition to temperature and nutrition, salinity may act as stimulator for transformation into resting stages. There is some evidence that this may be the case, for example, in euryhaline protozoans, sponges, hydrozoans and tardigrades. However, detailed analyses have not come to the reviewer's attention.

*Selection of more favourable conditions.* Selection of more favourable conditions has been demonstrated in salinity preference experiments conducted on the interstitial copepod *Parastenocaris vicesima* (JANSSON, 1967). Among the salinities offered (0.1‰ to 10‰S), most *P. vicesima* choose 0.1‰, 0.2‰, 0.5‰ or 2.5‰S, indicating a preference for low salinities between 0.1‰ and 2.5‰. This choice is, according to JANSSON, in general agreement with distributional records in the natural habitat. Even though further cases of selection of more favourable salinity conditions by aquatic invertebrates have been reported, no comprehensive studies appear to be available as yet.

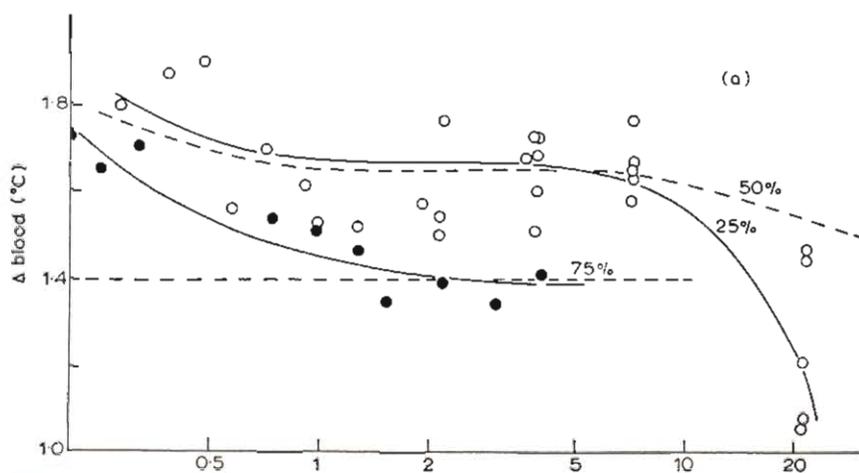


Fig. 4-134(a): *Elminius modestus*. Closure of opercular valves reduces the osmotic stress due to rapid salinity change. Abrupt transfer into 75% ( $\Delta = 1.4^\circ\text{C}$ , ●), 50% ( $\Delta = 0.9^\circ\text{C}$ ) and 25% ( $\Delta = 0.45^\circ\text{C}$ , ○) sea water. Horizontal broken line: isosmoticity in 75% sea water. Abscissa: hours. The barnacles closed their valves in 50% and 25% sea water. Individual data; eye-fitted curves.  $15^\circ\text{C}$ . (After FOSTER, 1969c; redrawn.) By permission of The Royal Society.

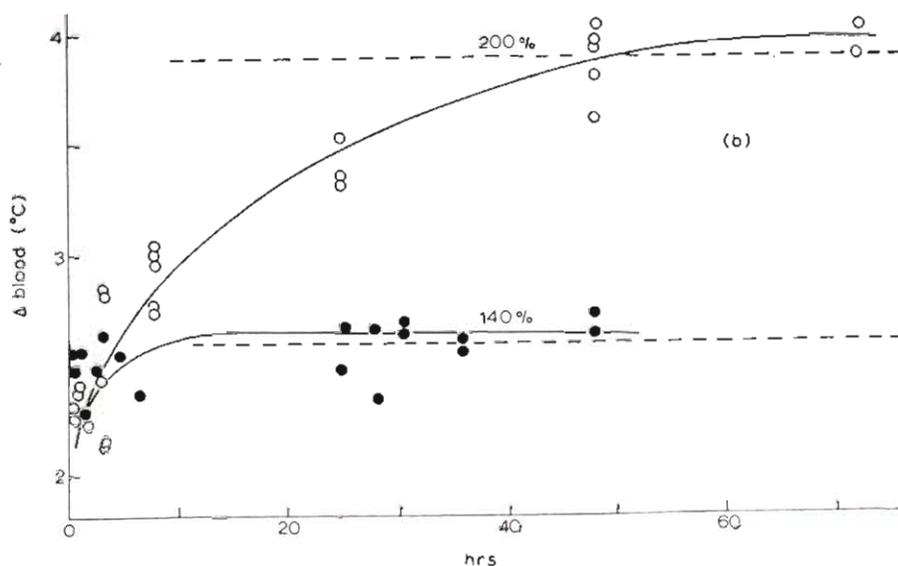


Fig. 4-134(b): *Elminius modestus*. Closure of opercular valves reduces the osmotic stress due to rapid salinity change. Abrupt transfer into 140% ( $\Delta = 2.6^\circ\text{C}$ , ●) and 200% ( $\Delta = 3.9^\circ\text{C}$ , ○) sea water. Horizontal broken lines: isosmoticity. The barnacles closed their valves in 200% sea water. Individual data; eye-fitted curves.  $15^\circ\text{C}$ . (After FOSTER, 1969c; redrawn.) By permission of The Royal Society.

*Direct salinity effects on motility.* Salinity may possibly exert direct effects on the motility of aquatic invertebrates, which rely on blood movement or sea-water transfer (into and out of certain body parts) for locomotion.

In numerous molluscs, for example, body parts are extended slowly by blood influx and relaxed quickly by retractor muscles (RUSSELL-HUNTER, 1968; RUSSELL-HUNTER and RUSSELL-HUNTER, 1969). Naticids exhibit a great capacity for pedal expansion, an important prerequisite for their locomotory and predatory activities. This capacity is based on water uptake into internal sinuses (analogous in ontology to nephridia rather than to coelomoducts, or elaborations of pedal mucous gland lumina), thus providing a hydraulic skeleton of variable volume. A *Polinices duplicata* weighing 46 g in contracted condition, takes in 124 ml sea water when fully expanding to a weight of 170 g (RUSSELL-HUNTER and RUSSELL-HUNTER, 1969). Of the sea water taken up during expansion, about 90% enters the pedal water-sinus system, about 5 to 7% circulates rapidly through the mantle cavity, and about 2% is superficial water on the snail's surfaces. There is no direct exchange between sinus water and blood and, in fully expanded snails, little or no exchange between sinuses and ambient sea water; labelling showed that 49 to 71% of the pedal sea water remains unexchanged after 72 hrs (RUSSELL-HUNTER and APLEY, 1969). Nevertheless, it may be assumed that sudden salinity changes can directly interfere with the locomotory activities of such invertebrates. It would certainly be worthwhile to put this assumption to a critical test.

*Density and viscosity.* Changes in salinity lead to respective changes in density and viscosity of the ambient medium. These may be of importance in regard to movement and maintenance of position in planktonic invertebrates. Variations in density can effect the amount of energy which must be expended for migrating and positioning. Even minor density changes can interfere with movements, diurnal migrations and other activities of plankton communities.

The density of the protoplasm of most marine invertebrates, hitherto studied in this respect, ranges between 1.0400 and 1.0500. This range lies slightly above the density of sea water (1.0281 at 10° C and 35‰ S; 1.0323 at -2° C and 40‰ S).

In planktonic organisms not counteracting the constant pull of gravity by locomotion, maintenance of a given depth is possible only if they are not heavier than sea water, or if they 'ride' on upwardly directed water currents. Many planktonic invertebrates migrate actively to suitable water depths. Frequently, they perform diurnal vertical migrations whereby changes in environmental factors (e.g. light, temperature, salinity, nutrition) act as synchronizers. Our pertinent knowledge has recently been discussed by RUDJAKOV (1970), who points out that, within the 24-hr rhythm, downward movements may be attributed entirely to passive sinking—a fact which suggests that the diurnal vertical migrations are in essence the result of rhythmic alternations between phases of high and low locomotory activity. The phase of high activity results in active upward movements, while the phase of low activity causes passive sinking to greater depths. Since the degree of activity is subject to modification due to intensity changes in light, temperature, salinity, pressure and food supply, the total resulting activity pattern may be very complex.

While many marine protozoans are somewhat heavier than sea water (e.g. NICOL, 1960), the flagellate *Noctiluca miliaris* is lighter, due to the presence of body salts of lower specific gravity than sodium chloride. When taken from sea water with a specific gravity of 1.024 and tested in diluted media, *N. miliaris* just floats in water of a specific gravity of 1.014 (DAVIS, 1953).

Among the few marine invertebrates which have an over-all specific gravity less than that of the surrounding water are siphonophores, such as species of the genera *Physalia* and *Veella*, which have gas-filled floating pneumatophores; pelagic cephalopods, such as species of *Nautilus* and *Spirula* with chambered, air-containing shells; and the planktonic snail *Glaucus* sp., which is said to contain intestinal gases (NICOL, 1960).

In view of recent evidence, related to the fact that osmoconcentration and ionic composition of body cavity fluids and cell fluids may change measurably due to mechanical stress (handling, contact with nets, aquaria walls, etc.), new measurements on plasmatic densities and ion ratios of plankton organisms appear desirable.

*Ionic composition.* Ionic composition of ambient media and body fluids may affect the level of organismic activity. This has been suggested or demonstrated, especially for decapod crustaceans.

Increase of ambient magnesium over three times the normal value leads to

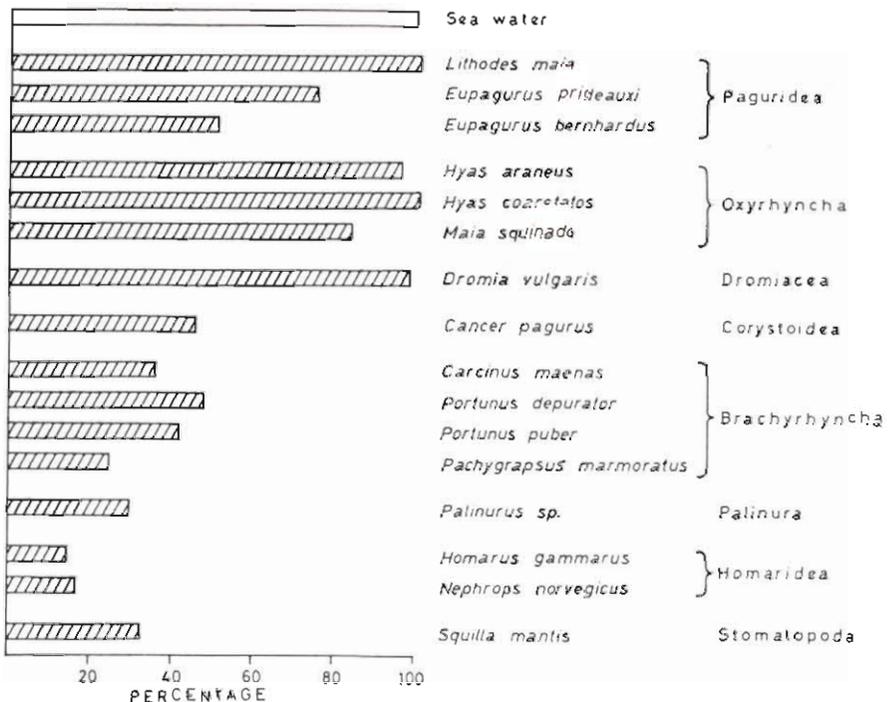


Fig. 4-135: Comparison of percentage magnesium values in sea water and in 16 different crustacean species (blood plasma) on a mg/g water basis. (After ROBERTSON, 1953; modified.)

parallel increases in magnesium blood concentration of *Carcinus maenas*, causing lessening of muscular tone and impairment of normal reflexes (BETHE, 1929).

ROBERTSON (1949, 1953) compared the magnesium concentrations in the blood of 16 crustaceans (Fig. 4-135). Species with low levels of locomotory activity, like *Lithodes maia*, *Hyas araneus*, *H. coarctatos*, *Maia squinado* and *Dromia vulgaris*, exhibit the highest magnesium concentrations (84 to 101% of the magnesium concentration in sea water). On the other hand, *Eupagurus prideauxi* and *E. bernhardus* move about more actively and have correspondingly lower magnesium concentrations in their blood. The remaining species, except *Cancer pagurus*, are all more active and have magnesium concentrations less than half that in sea water. While *C. pagurus* usually shows little locomotory activity in aquaria, it can move quite quickly. Recalling the fact that excess magnesium ions in the form of magnesium chloride or magnesium sulphate solutions are used to narcotize marine invertebrates, ROBERTSON (1953) assumes that reduction in magnesium and increase in locomotory activity are causally related.

Further experimental evidence seems to support ROBERTSON's view. Thus the locomotory activity of several penaeidcan shrimps is inversely correlated to their respective blood serum magnesium levels (McFARLAND, 1963). Perfusion of isolated walking legs of *Carcinus maenas* with a fluid containing 1.5 to 2 times as much magnesium as the blood depresses neuromuscular transmission (KATZ, 1936), while perfusion with a fluid containing only 5 to 20% of the blood magnesium concentration enhances muscular responses (BOARDMAN and COLLIER, 1946). Inverse relations between magnesium concentration in the perfusing fluid and response to nerve stimulation have also been reported in other decapods (WATERMAN, 1941).

Other ions, as well as the quantitative balance between different ions, may also influence the degree of locomotory activity (ROBERTSON, 1953). Reduction of the blood calcium concentration leads to similar results in *C. maenas* as increase of magnesium; if, on the other hand, blood plasma calcium is increased by exposing the crabs to calcium-enriched sea water, excitability increases markedly (BETHE, 1929). Hence the balance between magnesium and calcium ions is probably important for locomotory performance; the ratio of the equivalents of calcium/magnesium ranges from 0.19 to 0.31 in crustaceans with relatively low activities (*Lithodes maia*, *Hyas araneus*, *H. coarctatos*, *Maia squinado* and *Dromia vulgaris*) to 0.39 to 2.0 in the remaining crustaceans listed in Fig. 4-135.

In molluscs, magnesium is maintained at a uniformly high level and calcium does not vary much, although it is usually slightly higher than in sea water. The most variable cation is potassium. Variations in body fluid potassium levels affect neuromuscular responses; moderate increases in potassium ions stimulate locomotory activity (WELLS, 1928; ROSS and PANTIN, 1940; ROBERTSON, 1953). In various marine invertebrates, increased potassium concentrations in sea water cause augmentations in rhythmic activities, similar to those resulting from increased calcium levels (BETHE, 1927). These results have led ROBERTSON (1953) to suggest that the more pronounced muscular activity among cephalopods, compared to that of gastropods and lamellibranchs—although based primarily on considerable structural differences—may be at least enhanced by their higher blood potassium concentrations.

*(c) Reproduction*

The salinity range within which a euryhaline invertebrate is able to reproduce is usually much narrower than that permitting growth of individuals. In general, salinity affects rates and modes of reproduction less obviously than light (Chapter 2) or temperature (Chapter 3). Salinity is also of less importance as a diurnal or seasonal timing or co-ordinating stimulus for gonad growth, gamete maturation, gamete release, or migrations and gatherings associated with reproductive activities; this is probably related to the fact that rhythmic salinity variations are usually less pronounced and less regular than variations in intensities of light or temperature.

*Salinity effects on reproduction in the sea*

Salinity may affect decisively reproduction in areas where it underlies pronounced changes (e.g. in estuaries) or considerable gradients (e.g. in the Baltic Sea). Changes in salinity have been shown to modify rates of reproduction and to bring about a shift from sexual to asexual reproduction or vice versa. Extensive salinity fluctuations or extremely low salinities may cause the number of benthic invertebrate species with pelagic larvae to decrease, and the number of species with non-pelagic larvae to increase. Invertebrates which release their offspring at advanced stages of development, or provide some kind of brood protection (resistant egg membranes or gelatinous coverings, brood pouches, egg-care in tubes, burrows, nests, etc.) appear to enjoy ecological advantages in rough osmotic climates.

In the Baltic Sea, with its decreasing salinities from west to northeast, salinity may become of paramount importance as a limiting factor for reproduction. Reduced reproductive capacities down to complete sterility due to low salinities have been reported for several Baltic Sea invertebrates; examples are the coelenterate scyphozoan *Lucernaria quadricornis* and the sea-star *Asterias rubens* (REMANE, 1940). In the eastern Baltic Sea, the echinoderms *Asterias rubens* and *Ophiura albida* become sterile and maintain their stocks only by larval reinforcements from saltier waters (BRATTSTRÖM, 1941). Medusae of the coelenterate *Aurelia aurita* can still produce viable germ cells in salinities below 6‰, but the scyphistoma stage apparently does not develop (SEGERSTRÅLE, 1957). In the northern Baltic Sea, the viviparous nemertean *Prostoma obscurum* is still capable of reproduction in salinities between 3‰ and 4‰ at temperatures below 1° to 2° C (LASSIG, 1964).

The Kiel Canal ('Nord-Ostsee-Kanal'), which connects the North Sea and Baltic Sea is another example of a habitat with a pronounced salinity gradient. In this canal, the colonial hydroid *Laomedea loveni* exhibits changes in its reproductive potential (numbers of gonophores per colony and of eggs per gonophore) which appear to be directly related to salinity (KINNE, 1955c; see also SCHÜTZ and KINNE, 1955; SCHÜTZ, 1969).

HYNES (1954) has reported that, in England, the euryhaline amphipod *Gammarus duebeni* lays more eggs in brackish water than in fresh water (Table 4-69). In most other areas of its geographic distribution, *G. duebeni* does not occur in fresh water at all or, if it temporarily enters freshwater habitats, loses completely its potential for reproduction.

Table 4-69

*Gammarus duebeni*. Number of unhatched marsupium eggs per female. The females of different body lengths were collected in brackish and fresh waters, respectively, on the Isle of Man, Great Britain (After HYNES, 1954; modified)

Habitat	Size group of female (mm)	Number females examined	Number of marsupium eggs		mean and standard deviation
			max.	min.	
Brackish water (Ganseay beach)	7-8	3	11	5	7.33 ± 1.87
	8-9	20	20	3	11.50 ± 0.78
	9-10	20	20	10	14.60 ± 0.61
	10-11	20	26	10	20.75 ± 1.05
	11-12	20	34	11	23.85 ± 1.63
	12-13	9	37	9	29.33 ± 2.96
Fresh water (Port Erin stream)	8-9	6	13	6	10.17 ± 1.26
	9-10	20	18	4	12.35 ± 0.81
	10-11	20	26	10	17.10 ± 0.84
	11-12	20	28	14	20.65 ± 0.88
	12-13	20	35	16	24.05 ± 1.26
	13-14	4	44	22	34.00 ± 4.98

Reduced rates of reproduction have also been reported in freshwater invertebrates penetrating into brackish water, although there is little critically analyzed information available. The freshwater sponge *Ephydatia fluviatilis*, for example, loses, in brackish water, its potential for asexual reproduction by gemmulae, and the snail *Theodoxus fluviatilis* produces smaller egg capsules containing fewer eggs (55 to 80) than in fresh water (more than 100); for references consult REMANE and SCHLIEPER (1958).

Salinity variations may also modify time and length of the breeding season. Unfortunately, the reports available are based solely on descriptive field observations which do not allow a critical analysis of the extent to which the changes observed are a direct function of salinity; in most cases, the modifications in breeding seasons appear to be influenced significantly by other environmental factors, especially by light, temperature and the quantity and quality of food available.

#### *Salinity effects on reproduction in the laboratory*

In the laboratory, salinity effects on reproduction of aquatic invertebrates have been investigated only in a few cases. No comprehensive studies have been conducted yet. Salinity-induced prolongation or shortening of embryonic development can lead to the addition or omission of structural units or developmental stages.

In the brackish-water living colonial hydroid *Cordylophora caspia*, rates of asexual reproduction have been shown to be a function of salinity. Single primary

Table 4-70

*Cordylophora caspia*. Rate of asexual reproduction (increase in number of hydranths per colony). Freshly settled primary polyps obtained from colonies collected in the habitat (Kiel Canal, West Germany; about 5‰S, 16°-17° C) were allowed to develop into new colonies after gradual transfer into 6 different salinities. Test temperature about 16° C; ah: average number of hydranths, based on 5 to 7 individuals in each case; sd: standard deviation (After KINNE, 1956b; modified)

Age of developing colony (days)	Fresh water		2.0‰S		5.0‰S		10.0‰S		16.7‰S		30.0‰S	
	ah	sd	ah	sd	ah	sd	ah	sd	ah	sd	ah	sd
1	1.0	0.0	1.0	0.0	1.0	0.0	1.0	0.0	1.0	0.0	1.0	0.0
6	1.0	0.0	1.0	0.0	1.0	0.0	1.3	0.2	1.0	0.0	1.0	0.0
12	0.8	0.1	1.0	0.0	1.0	0.0	1.6	0.4	1.8	0.4	1.5	0.2
20	1.1	0.1	1.4	0.5	1.6	0.9	3.2	0.9	3.5	1.4	2.0	1.6
30	1.2	0.5	2.2	0.7	3.8	1.3	6.8	0.9	10.2	2.2	(5.0)	—
40	2.0	1.7	4.2	1.9	9.8	2.3	15.5	3.2	20.2	1.4	(8.3)	—
50	3.4	2.4	7.9	2.8	14.2	3.2	24.2	3.8	36.0	4.2	—	—

polyps obtained from three female and three male colonies were transferred into different salinities and subsequently allowed to develop into colonies at about 16° C. The resulting data are listed in Table 4-70. Rates of hydranth budding increase in the order fresh water, 2.0‰, 5.0‰, 10.0‰, 16.7‰ and then decline steeply in 30.0‰S.

In the marine colonial hydroid *Clava multicornis*, maintained at 12° and 17° C, doubling times of polyp numbers per colony increase in the order 40‰, 16‰, 32‰, 24‰S (KINNE and PAFFENHÖFER, 1966).

Asexual reproduction (strobilation) in polyps of the coelenterate *Chrysaora quinquecirrha* maintained at 19.7‰S could be initiated within 7 days by elevating the salinity to 24.7‰ (temperature: 'winter conditions'; Chesapeake Bay, Maryland, USA). Ephyrae were released within 10 days. The same responses were observed in experiments conducted during the summer (CARGO and SCHULTZ, 1967).

Salinity may affect fission and regeneration processes in actinians. In *Diaudumene luciae*, the fastest rate of longitudinal fission was observed in slightly reduced salinities (MIYAWAKI, 1951). In *Anthopleura stellula*, increase of salinity beyond habitat conditions causes interruption of transverse fission; dividing anemones lose their body constrictions (SCHMIDT, 1970). Transversely cut cerianthids complete oral disc regeneration more quickly in diluted sea water than in normal habitat salinities (COTRONEI, 1924). In contrast, LOUIS (1960) found no salinity influence on rates of longitudinal fission in *Anemonia sulcata*. SCHMIDT (1970) assumes that salinity variations affect fission processes indirectly, through supporting or reducing the biological effects of (unknown) fission stimulating substances. The most important factor inducing fission in *A. stellula* seems to be the accumulation of stimulatory substances in the ambient water.

In several freshwater ciliates, cell division rates tend to increase if the salinity is slightly augmented. Maximum rates were observed near 1‰S. In higher salinities (3‰ to 4‰), cell division rates decrease considerably (Ax and Ax, 1960).

There are also some scattered reports on salinity effects on sexual reproduction of marine and brackish-water invertebrates. The brackish-water hydroid *Cordylophora caspia* forms, at 17° to 20° C, gonophores (organs of sexual reproduction) in salinities ranging from fresh water (about 0.4‰) to 30‰. Maximum gonophore production is limited to salinities between 5‰ and 15‰. Size and number of gonophores per polyp as well as size and number of eggs per gonophore are subject to changes: in fresh water and in 30‰S, not more than 1 gonophore per secondary polyp is formed which is small and usually contains only 2 to 3 eggs; in 5‰S up to 4 gonophores develop containing on an average 9 large eggs (Fig. 4-136). Extreme salinities suppress sexual reproduction more severely than asexual reproduction (KINNE, 1956b, c, 1958a).

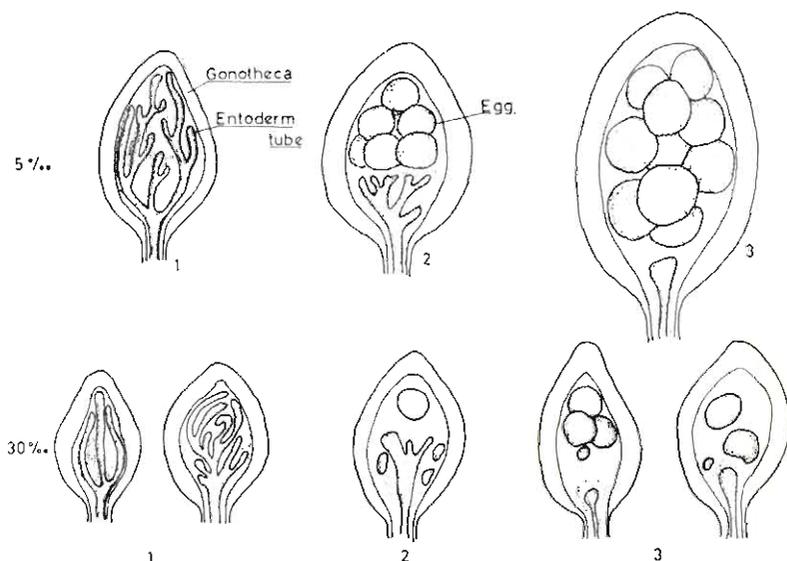


Fig. 4-136: Reduction of reproductive capacity in the brackish-water hydroid *Cordylophora caspia* due to supranormal salinity. Shown are corresponding developmental stages (1, 2, 3) of female gonophores in 5‰ and 30‰S. In 30‰S, gonophores are smaller and produce smaller and fewer eggs than in 5‰S. 19° to 20° C. (After KINNE, 1956b; modified.)

At 12° and 17° C, marine hydroids *Clava multicornis* from Helgoland (southern North Sea) produce gonophores in 16‰, 24‰, 32‰ and 40‰S. Although the data available are insufficient for a detailed analysis, it was possible to show that salinity and temperature ranges are narrower for sexual than for asexual reproduction; number and size of gonophores tend to increase with increasing food supply; they also depend on food quality (KINNE and PAFFENHÖFER, 1966).

Females of the amphipod *Gammarus duebeni* (13 to 14 mm total length) produce per oviposition, at 18° to 20° C, an average of 18 eggs in 2‰S, 27 eggs in 10‰S and 17 eggs in 30‰S. The approximate percentage survival of marsupial eggs also

varies with the rearing salinity and temperature (Table 4-71). Incubation periods (time spans between fertilization and hatching) show no significant differences in salinities ranging from 2‰ to 30‰, when examined at 5° to 6° C. However, at temperatures above 8° C, a progressive retardation occurs in both 2‰ and 30‰S, relative to values obtained in 10‰S (KINNE 1952c, 1953a, b, 1959; see also DENNERT and co-authors, 1969). According to BROEKHUYSEN (1936), the lower limiting salinity for embryonic development in the crab *Carcinus maenas* is about 20‰ at 16.3° C but 26‰ at 10° C.

Table 4-71

Reproductive potential of *Gammarus duebeni* females of 13 to 14 mm body length in different combinations of salinity and temperature. All test individuals were born and raised under the conditions indicated; 8° to 15° C: temperatures paralleled seasonal habitat fluctuations, without attaining minimum or maximum field values. Average values of 14 to 18 individuals in each case (After KINNE, 1953a; modified)

Salinity (‰)	Number of eggs per oviposition at		Approximate percentage survival of marsupial eggs at		
	8°–15° C	18°–20° C	8° C	16° C	20° C
2	39	18	85–90	60	0
10	52	27	85–95	85–95	50–80
30	36	17	85	50–60	0

Although the brine shrimp *Artemia salina* thrives in its natural habitat in salinities up to 150‰, its embryonic development proceeds faster and with higher hatching percentages in normal sea water. The minimum amount of water required for completion of embryonic development and for successful hatching can be obtained by the cysts only in salinities below 90‰ (BIOLOGISCHE ANSTALT HELGOLAND, 1968; VON HENTIG, 1970). *A. salina* females release (i) eggs with dark, hard shells which do not develop immediately; (ii) less pigmented, thin-shelled eggs which continue their development without interruption; (iii) pale, unfertilized eggs, unable to develop; or (iv) freshly hatched nauplii (e.g., VON HENTIG, 1970). While it is tempting to assume that the kind of sexual products released depend on the environmental factors effective before or during reproduction, conclusive pertinent evidence is lacking. VON HENTIG points out that, in his material (Great Salt Lake, Utah, USA), no relationship between salinity or temperature conditions and the production of cysts could be established; hard-shelled and soft-shelled eggs, as well as nauplii, were released under identical laboratory conditions. Only at 7‰S and 10° C did the females produce exclusively nauplii; it seems possible that the availability of dissolved oxygen is of importance. The number of eggs per brood depends on nutritional conditions (DUTRIEU, 1960; REEVE, 1963b; D'AGOSTINO and PROVASOLI, 1968; PROVASOLI and co-authors, 1970).

In *Artemia salina*, the rate of reproduction increases with the quantity and quality of food offered. Under comparable conditions, experiments in 15‰, 35‰ and 100‰S revealed maximum reproductive rates in 15‰S, but no significant

differences in 35‰ or 100‰S (GROSCH, 1962). The number of offspring per brood varied between 65 and 149; the total number of offspring per female, between 186 and 387. Similar results have been obtained by D'AGOSTINO and PROVOSOLI (1968), who cultivated their *A. salina* in diaxenic media. Within the range of salinities tested (5‰ to 200‰S), maximum reproduction rates were found, however, in 60‰S. Field data by GILCHRIST (1956) indicate a decrease in reproduction rates at very high salinities (in 115‰S, 72% of the females examined carried eggs; in 140‰S, 49%; in 160‰S, 15%). In laboratory experiments (VON HENTIG, 1970) carried out in salinities ranging from 15‰ to 70‰S, the average number of offspring per brood increased with salinity. In 70‰S, a brood consisted on an average of 110 eggs at 10° C, 118 at 15° C, 148 at 20° C and 143 at 30° C (Table 4-72).

In *Artemia salina* and *Tigriopus japonicus* fed on algae, fertility stops after a few aseptic generations. In amphigonic and parthenogenetic *A. salina* subjected to low-salinity stress, fertility was restored after addition of milligram concentrations of yeast and liver extract. In *T. japonicus* and *Daphnia magna*, fertility of aseptic cultures was re-established by adding vitamin mixtures to the algae plus crustacean medium. The vitamins act directly on the algae by increasing their nutritional value for the crustaceans cultivated (PROVASOLI and co-authors, 1970). These results indicate that studies devoted to the analysis of salinity effects upon reproduction may yield misleading or unsatisfactory results unless the specific nutritional requirements of the test organism are carefully considered.

The eggs of most marine invertebrates require considerable amounts of water for completion of embryonic development and hatching. In the European lobster *Homarus gammarus*, for example, a single egg (3.69 mg wet weight) requires as much as 4.88 mg water for successful embryogenesis (PANDIAN, 1970). Salinity variations may interfere with such requirements and affect development as well as the hatching process. A simple osmotic hatching mechanism, as proposed by several earlier students of water and salt exchanges in aquatic eggs, is inadequate to explain the events and time course of hatching in the *H. gammarus* egg. Immediately after release, the egg imbibes 6% of the total amount of water required; during subsequent development, 85%; the rest (9%) is supplied by metabolic water. Rates of water and salt uptake during embryonic development are essentially parallel. PANDIAN assumes that imbibition of water by developing marine demersal eggs assists in (i) osmotic hatching; (ii) floating of the hatched larva by means of reducing its specific gravity; (iii) quickly adjusting larval body temperatures to environmental fluctuations.

Within the normal temperature range, oyster (scientific name not given) spermatozoa were active in salinities ranging from about 5‰ to 40‰; sperm life was longest near 23‰S. Ontogenetic development proceeded normally to the first swimming stage in salinities ranging from 14.5‰ to 39‰; below this range, eggs developed to some extent, but no swimming larvae were obtained (CLARK, 1935). In the oyster *Crassostrea gigas*, spawning is inhibited when the salinity falls below 27‰. Salinities between 23‰ and 28‰ provide optimum conditions for fertilization and embryonic development. The salinity range which allows embryonic development is wider towards the lower than towards the higher part of the tolerated temperature range (FUJIXA, 1970).

The American oyster *Crassostrea virginica* from Long Island Sound (USA)

Table 4-72

Salinity effects on reproductive rates of *Artemia salina* from Great Salt Lake, Utah, USA. Each value represents the average for 7 females. Food: *Dunaliella tertiolecta* (After von HENTIG, 1970; modified)

Salinity (‰)	Temperature (°C)	Time to first copulation (days)	Intervals between successive broods (days)	Average number of progeny per brood	Average number of broods per female	Average total number of offspring per female	nauplii (%)
15	10	—	—	—	—	—	—
	15	—	—	—	—	—	—
	20	12	7	124	2.4	283	65
	30	7	3.5-4	108	2.5	270	88.5
32	10	63	—	—	—	—	—
	15	22	11	74	2.8	207	78
	20	13	7	132	3.0	396	69.2
	30	8	4	130	3.6	470	71.2
70	10	61	26	110	1.0	110	100
	15	23	12-13	118	2.8	330	92
	20	14	7.5-8	148	2.8	428	76.5
	30	9	4-4.5	143	3.4	473	61

matures gonads and spawns at  $27.5 \pm 1\text{‰}$ S. Eggs do not develop at  $10\text{‰}$ S and it has not been possible to rear straight-hinge larvae from such eggs to setting size. It is uncertain yet, how much these limiting salinities may be affected by the salinity at which the parent oysters develop gonads and spawn. Very few eggs yield straight-hinge larvae at  $12.5\text{‰}$ S; but larvae reared to the straight-hinge stage at  $27.5\text{‰}$ S survive and grow at approximately normal rates when kept at  $12.5\text{‰}$ S and  $30^{\circ}$  C. Interestingly, larvae reared to setting size at  $27.5\text{‰}$ S can successfully complete metamorphosis in salinities as low as  $9\text{‰}$  or  $10\text{‰}$  (CALABRESE and DAVIS, 1970).

The oyster drilling gastropods *Eupleura caudata* and *Urosalpinx cinerea* do not deposit egg capsules at salinities near  $15\text{‰}$  or lower. In  $20\text{‰}$ S, *E. caudata* deposits a few egg capsules, while *U. cinerea* deposits none ( $15^{\circ}$  C). In  $26.5\text{‰}$ S, both drills produce egg capsules at all temperatures tested ( $15^{\circ}$ ,  $20^{\circ}$ ,  $25^{\circ}$  C). The number of capsules deposited increases in both drills with each increase in test salinity ( $15\text{‰}$ ,  $20\text{‰}$ ,  $26.5\text{‰}$ ) and temperature (MANZI, 1970). These results indicate that the effects of salinity and temperature on reproduction of the oyster drills are interrelated. In contrast to oviposition, the number of eggs per capsule does not vary with salinity and temperature. MANZI believes that the increased reproductive rate at higher salinities and temperatures may be the result of a generally increased metabolic rate affecting both ripening of ova and production of egg capsules.

Brief periods of air exposure (desiccation) may, in some intertidal invertebrates, act as stimulus for gamete release. Even the scallop *Pecten maximus* can be conditioned in the laboratory to release gametes at times other than its normal spawning season by taking it out of water for approximately 2 hrs; spawning then occurs within 2 to 4 hrs after re-immersion. At  $15^{\circ}$  C, laboratory cultured *P. maximus* develops ripe gametes practically throughout the year (GRUFFYDD and BEAUMONT, 1970).

Salinity may affect reproductive processes also via variations in sex ratio. In the euryhaline *Gammarus duebeni*, for example, a salinity of  $30\text{‰}$  tends to shift the ratio of female to male offspring in favour of the males (KINNE, 1952a). A detailed analysis of sex-determining factors by BULNHEIM (1969) has revealed that salinity affects the sex ratio indirectly. In the Elbe estuary (Germany), up to about 25% of the *G. duebeni* females turned out to be infested by the microsporidian *Octospora effeminans*. Microsporidian-infested *G. duebeni* females produce practically only daughters. In experiments conducted in  $2\text{‰}$ ,  $10\text{‰}$ ,  $20\text{‰}$  and  $30\text{‰}$ S, *G. duebeni* females lay eggs free from microsporidians in  $30\text{‰}$ S; these eggs differentiate into females or males according to genetic and environmental (photoperiod) conditions. Consequently, the complex sex-determination mechanism of *G. duebeni* becomes salinity dependent, due to the different salinity tolerances of host and parasite (see also BULNHEIM, 1966, 1967). The archiannelid *Dinophilus gyrociliatus* deposits egg capsules which contain two kinds of eggs: large ones (under normal conditions giving rise to females) and small ones (giving rise to males). The ratio large eggs: small eggs, and hence the sex ratio of the offspring, is influenced (i) by environmental factors such as salinity, ionic composition of the sea water and nutrition, and (ii) by genetic factors (genotype of mother, but not father). Under constant environmental and genetic conditions, the sex ratio is very stable (TRAUT, 1969).

Field observations in the Baltic Sea suggest that sex ratios of copepods are modified by subnormal salinities (ACKEFORS, 1969a).

(d) *Distribution*

In the open oceans, salinity appears to exert little influence on the distribution of invertebrates, except for areas with significant salinity stratifications. In coastal waters, however, salinity may be of considerable importance, and, in habitats with pronounced salinity gradients—such as estuaries, canals, lagoons—or in areas with significantly reduced salt concentrations, become an ecological master factor governing, to a large extent, horizontal and vertical distributions of a variety of marine, brackish and limnic invertebrates.

Organismic distributions depend upon multidimensional factor combinations. Of primary importance are genetic background, time, and abiotic as well as biotic environmental factors. There exists a considerable number of papers which report salinity effects on invertebrate distributions. However, most reports represent incidental observations or descriptions of specific situations. Since salinity may influence a multitude of organismic functions and structures, and since our knowledge of the underlying mechanisms is still inadequate, a comprehensive assessment of the role of salinity in invertebrate distributions is not yet possible. Only in regard to phylogenetical transgressions of originally oceanic invertebrates into fresh, brackish, hypersaline and brine waters has a number of hypotheses and theories been advanced (for examples consult pp. 867-872).

*Horizontal distributions*

BARY (1959, 1963) has suggested correlations between the distribution of pelagic invertebrates in the Atlantic Ocean and certain temperature and salinity conditions of near-surface water bodies. On the basis of his data he constructed temperature-salinity-plankton (tsp) correlation diagrams. Each tsp diagram is concerned with a brief period of time; short-term changes and seasonal fluctuations resulting in shifts of 'fronts' or mixing patterns may be detected by comparing a series of diagrams. The planktonic species in question (mainly copepods) occur regularly only where conditions are favourable. They may be carried by water movements into other ocean areas, but they continue to thrive only so long as the same water body is present. If water bodies mix, the presence of a species depends on the ecological properties of the mixture.

The correlations between plankton distribution and temperature-salinity values do not appear to depend always directly upon these two environmental factors. BARY (1963) assumes that other (still unknown) properties of the respective water bodies may represent the primary regulators of the planktonic distributions considered.

Relationships between hydrological factors (particularly temperature and salinity) and horizontal invertebrate distributions have been studied by numerous authors, e.g. GORBUNOV (1934, 1937), DERJUGIN (1936), GURJANOVA (1939, 1944), USHAKOV (1940, 1945), HESSE and co-authors (1951), BLACKER (1957), GOLIKOV (1960, 1968), KOBJAROVA (1960), MILEIKOVSKY (1960, 1966, 1968, 1970a, b), NESIS (1960) and GRAINGER (1963). The possibility of employing planktonic organisms

as indicators of water bodies (and vice versa) results from the fact that plankton forms tend to remain closely associated with water qualities which allowed the population to establish itself. According to GOLIKOV (1968), long-living benthic invertebrates without pelagic life-cycle stages depend more upon long-term hydrological conditions in their distribution than other marine organisms. Thus they provide good indicators of current systems and the nature and origin of oceanic water masses.

Salinity effects on horizontal distributions are well documented in estuaries and related habitats with pronounced salinity gradients. In the Columbia River estuary (USA), HAERTEL and OSTERBERG (1967) distinguished three major groups of plankton organisms: the first group enters the estuary from the ocean and remains associated with salty waters, the second group is indigenous to the estuary and associated with brackish waters, and the third group immigrates or is carried in from freshwater habitats and remains associated with freshwater masses in the upper estuary. The intermediate, indigenous brackish-water group is characterized by much larger numbers of individuals and smaller numbers of species than the adjacent marine or limnic groups. Increase in individual numbers and decrease in species numbers is, in general, indicative of stress habitats with increased environmental fluctuations and extreme intensities of environmental factors. Table 4-73 illustrates the horizontal distributions of aquatic invertebrates as a function of the salinity range and the season in the Columbia River estuary. Some of the species collected in certain seasons only may have been present throughout the year; the salinity ranges given are conservative estimates (lower limits of marine species are based on bottom salinities, upper limits of limnic species on surface salinities). Comparable results have been reported for other estuaries.

In the estuary of the River Elbe (Germany), KÜHL and MANN (1967) reported 3 general situations in regard to the horizontal distributions of planktonic invertebrates: (i) regular short-term variations in the species, present in a given area, caused by tides; (ii) irregular variations (sometimes lasting up to several days), caused by changes in weather and wind; (iii) long-term variations caused by different amounts of fresh water discharged by the Elbe into the North Sea. While the estuarine area occupied by the different plankton organisms depends primarily on the salinity gradient, seasonal appearance is influenced predominantly by temperature. The number of species and of individuals per plankton sample collected between the light ship 'Elbe I' and the town of Glückstadt show certain regularities which are correlated to the salinity gradient (GIERE, 1968). Using the species-diversity index 'd' of GLEASON (1922)

$$d = \frac{S - 1}{\ln N}$$

where  $S$  = number of species and  $N$  = number of individuals, GIERE comes to the conclusion that the numbers of species and individuals are not inversely correlated in the zooplankton of the Elbe estuary, but both decrease towards the inner estuary parts, obviously due to the decreasing salinity (Fig. 4-137). The species-diversity index decreases fairly continuously with decreasing salinity. The species dominance (HULBERT, 1963) changes largely inversely to the diversity curve. The increase of dominance values with decreasing salinity is caused by the concomi-







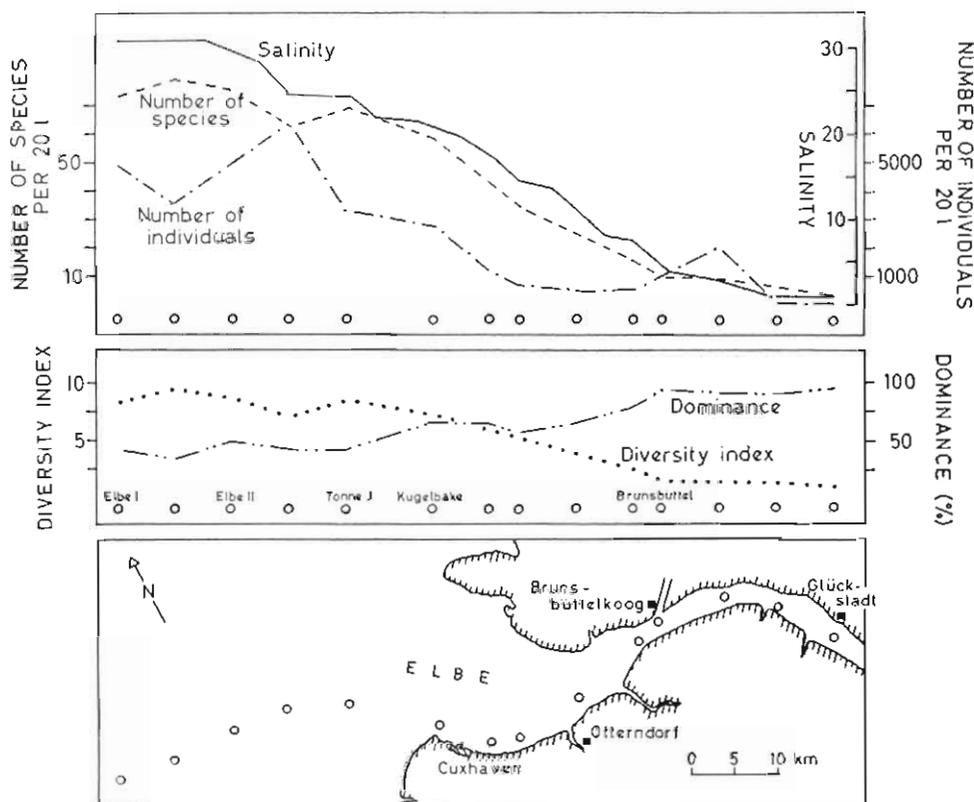


Fig. 4-137: Number of species and individuals of zooplankton per 20 l habitat water as a function of the salinity gradient in the Elbe estuary (Germany). Dominance and diversity indexes are given in the middle section of the graph. Open circles: stations. (After GIERE, 1968; modified.)

tant decrease in marine zooplankton species. Possible shiftings in the general salinity regime of the Elbe estuary due to seasonal, tidal or climatic variations are illustrated in Fig. 4-138.

As pointed out on page 822, numerous classifications have been proposed which attempt to generalize distributional salinity ranges of aquatic organisms. While the classifications suggested may be suitable for characterizing distributional ranges in specific areas with considerable salinity gradients or fluctuations (estuaries, canals, lagoons, semi-enclosed or enclosed sea areas), they can hardly claim general applicability. The most useful classifications appear to be those with few subdivisions and maximum flexibility. In regard to estuarine zones, Table 4-74 attempts to reduce the number of subdivisions and terms proposed to a few basic categories (see also Fig. 4-73). In this Table, different life-cycle stages of one and the same organism may belong to different categories, and adults of one and the same species may occur in more than one category as migrator or visitor. 'Horo-halini-cum' is a new term designating the limiting salinity range (ecophysiological barrier) of 5‰ to 8‰ (p. 827). Of course, even such a simplified classification can hardly be

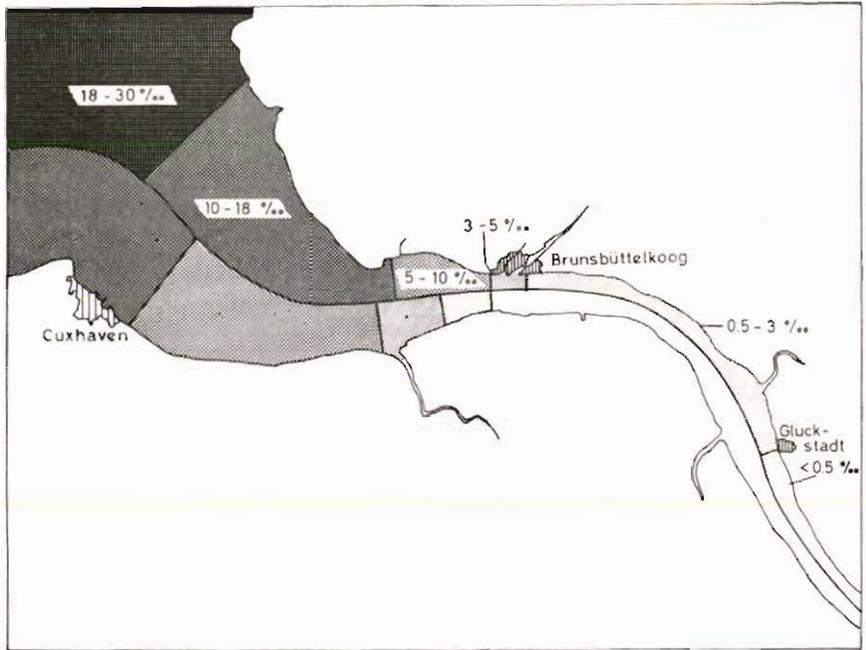


Fig. 4-138: Possible shiftings in the general salinity regime of the Elbe estuary (Germany) due to seasonal, tidal or climatic variations. Looking seaward, maximum ranges are illustrated right, minimum ranges left of the imaginary mid-line of the estuary. (After CASPERS, 1959a, 1968; modified.)

more than a general guide, since the distributional limits of planktonic and benthonic invertebrates depend on a variety of factors and factor combinations, rather than on salinity alone.

For inland brackish waters, HEEREBOUT (1970) presented a classification which incorporates both average chlorinities and the extent of variations in chlorinity. HEEREBOUT exemplifies relationships between faunistic distributions and salinity patterns in 19 brackish inland waters of the southwest Netherlands and concludes that, in general, a decrease in average chlorinity has the same effect on the fauna as an increase in the degree of chlorinity variation. As a result of the absence of tides, salinity fluctuations are less rapid in inland brackish waters than in estuaries. However, the differences between the minimum and maximum salinities attained can be more pronounced in brackish lakes than in estuaries.

In estuaries in which the ratio of width to depth is sufficiently large, the rotation of the earth (Coriolis force) affects directional aspects of tidal water exchanges and lateral variations in salinity. There is a tendency for the inward-flowing sea water and the outward-flowing river water to be displaced to their respective right sides. Consequently, the water on the right of an observer looking seaward may be lower in salinity than the water to his left (e.g. BOWDEN, 1967; PRITCHARD, 1967). PRITCHARD (1952a, b), for example, found the salinity of the James River (USA) to be on an average 1‰ higher on the left than on the right side. Such differences may influence organismic distributions. GIÈRE (1968) reports differences in zoo-

Table 4-74

Estuarine zones, their salinity ranges, and the salinity relations of estuarine organisms. Limnic euryhaline and marine euryhaline organisms overlap (broken lines) in the horohaliniticum (Original)

Zone	Salinity range (‰)	Salinity relations of organisms					
		limnic oligostenohaline	limnic	limnic	limnic	limnic euryhaline	limnic euryhaline
River	<0.5 limneticum						
Upper estuary	0.5-5 oligohaliniticum						
Inner estuary	5-8 horohaliniticum*						
Middle estuary	8-18 mesohaliniticum						
Lower estuary	18-30 polyhaliniticum						
Sea	30-40 thalassicum						

\* From horos (Greek): limit or boundary line

————— increasing degree of euryhalinity —————>

limnic  
euryhaline  
euryhaline  
(endemic  
estuarine)  
hol-  
eury-  
haline

limnic

oligohaline

limnic  
oligostenohaline

5-8 horohaliniticum\*

8-18 mesohaliniticum

18-30 polyhaliniticum

30-40 thalassicum

limnic

oligohaline

limnic  
oligostenohaline

5-8 horohaliniticum\*

8-18 mesohaliniticum

18-30 polyhaliniticum

30-40 thalassicum

limnic

oligohaline

limnic  
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5-8 horohaliniticum\*

8-18 mesohaliniticum

18-30 polyhaliniticum

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5-8 horohaliniticum\*

8-18 mesohaliniticum

18-30 polyhaliniticum

30-40 thalassicum

plankton distribution on the left (southern) and right (northern) sides of the Elbe estuary (Germany), which are apparently correlated to differences in salinity (Fig. 4-139). On 5 stations (1-5; total distance about 15 km) salinity is higher on the left side (wide-spaced hatching) of the Elbe estuary than on the right side (narrow-spaced hatching). Accordingly, marine forms show, on an average, higher abundance on the left side (nauplii of *Acartia* and *Temora* species, larvae of polychaetes and lamellibranchs, *Noctiluca miliaris* and total micro-zooplankton), while nauplii of limnic euryhaline *Eurytemora* species are more abundant on the right side of the estuary.

In the estuary of the River Ythan (Scotland) the distribution of the amphipod *Corophium volutator* is controlled by a critical lower salinity of 2‰ (McLUSKY, 1968a). In areas with salinities between 2‰ and 5‰, *C. volutator* is present but in reduced numbers. Breeding occurs only in salinities exceeding 7.5‰. In areas with salinities above 5‰, distribution and abundance are controlled by the nature of

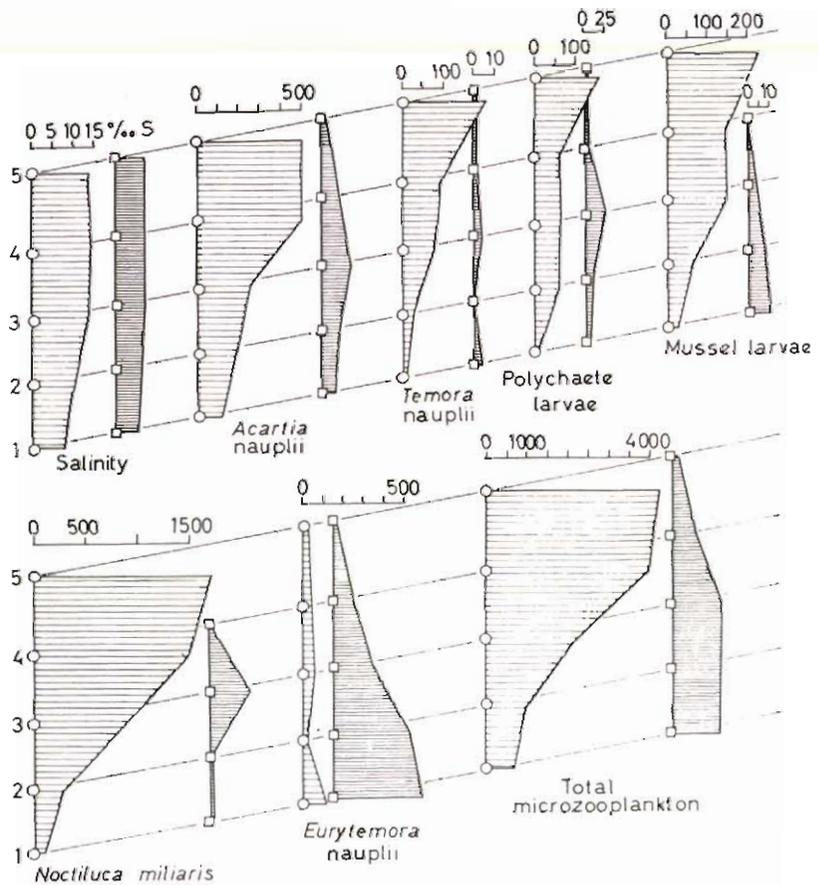


Fig. 4-139: Salinity and zooplankton distribution (individuals per 20 l) in parallel samples taken on the left and right sides respectively of the Elbe estuary (Germany). Left side: wide-spaced hatching; right side: narrow-spaced hatching. Stations 1 to 5 lie between Otterndorf and Cuxhaven; see Fig. 4-137. (After GIERE, 1968; modified.)

Table 4-75

Approximate sediment salinities (‰) at 7 stations in the Pocasset River estuary, Massachusetts, USA (After SANDERS and co-authors, 1965; modified)

Station	Mean salinity	Magnitude of salinity change during tidal cycle	Maximum rate of salinity change per hour
7	30	0.7	0.6
6		fresh water spring	
5	27	0.5	0.2
4	23	1.8	0.8
3	21	1.4	0.7
2	17	3.0	0.8
1	7	9.5	5.5

the substrate, but where the salinity decreases below 5‰, effects of salinity override substrate influences. These findings exemplify two important ecological aspects: (i) The total distributional area of a population may be made up of reproductive centres and peripheral sterile areas which must be continuously repopulated (recruitment from reproductive centres). (ii) For a given organism and in a given estuary, salinity may be a master factor controlling distribution within a quite specific intensity range only; outside that critical range, its importance decreases to that of a secondary, tertiary, etc. environmental entity while other factors (in the present example, the type of substrate) take over primary distributional control.

In the estuary of the Pocasset River (Massachusetts, USA), the salinity regime has a marked effect on the distribution of the benthonic fauna (SANDERS and co-

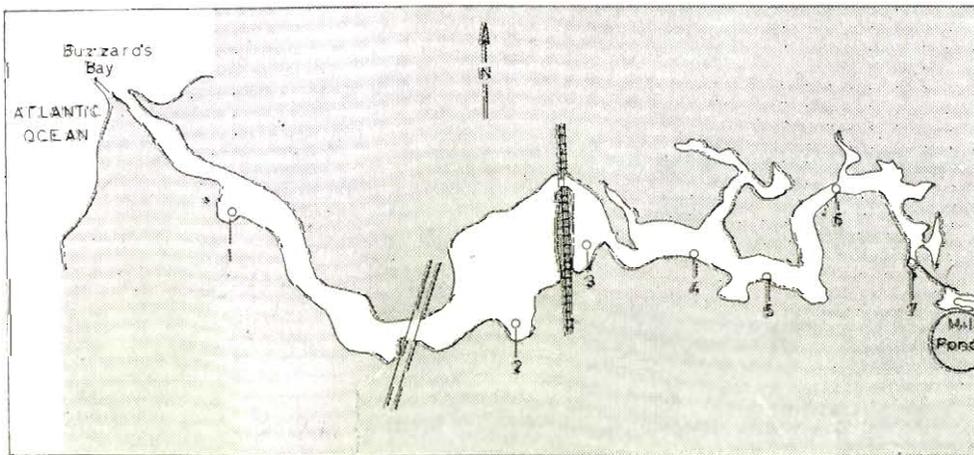


Fig. 4-140: Pocasset River (USA) estuary with stations. Straight line distance between estuary mouth and Mill Pond is approximately 2.2 km. (After SANDERS and co-authors, 1965; modified.)

authors, 1965). The epifauna (living on the sediment surface) is subjected to extreme and rapid salinity variations; it is poorly represented, particularly in the upper part of the estuary. The infauna (living in the sediment) makes up the vast majority of the estuarine fauna. Due to the latent period required to establish equal salinities in and outside the sediment after rapid salinity fluctuations (see also p. 830), the salinities in the sediment are more stable and the infauna is subject to a reduced salinity stress. Infauna and epifauna elements with equal salinity tolerances may therefore exhibit different distributional salinity limits along the length of the estuary. At sediment salinities (Table 4-75) above 19‰ to 22‰, marine forms predominate. Fig. 4-140 illustrates the location of the Pocasset River stations, Fig. 4-141 the number of marine, brackish and limnic benthos species

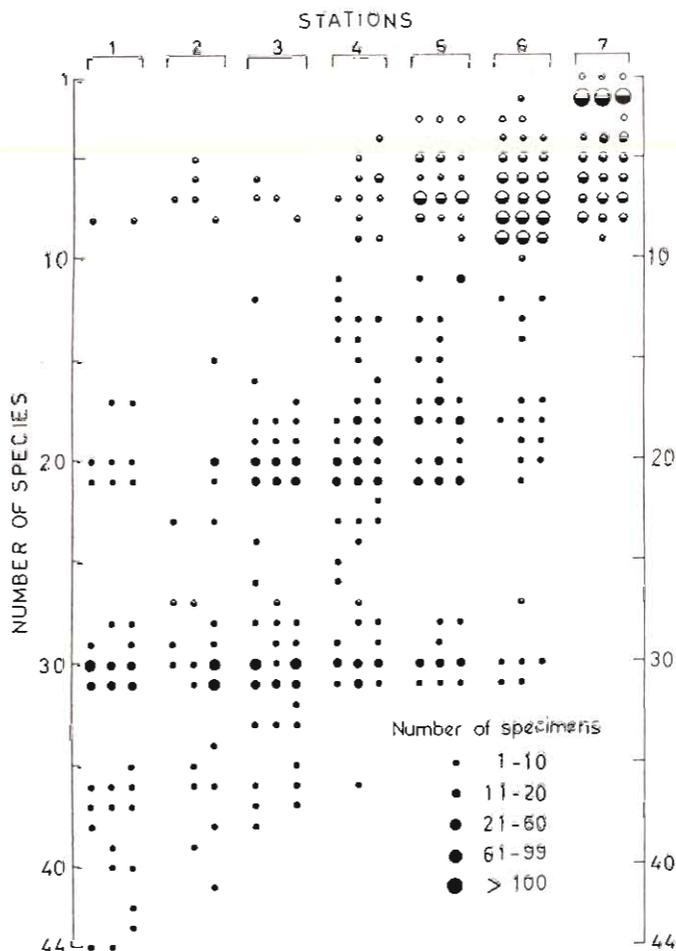


Fig. 4-141: Horizontal distribution of 44 species, separated into marine (filled circles), brackish (half-filled) and limnic (open circles) species at the stations illustrated in Fig. 4-140. The presence and abundance (number of specimens) is indicated. (After SANDERS and co-authors, 1965; modified.)

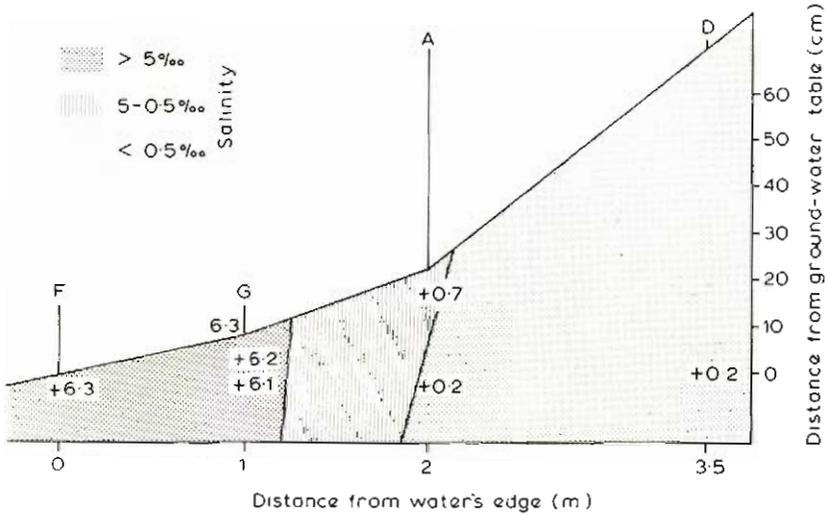


Fig. 4-142: Salinities on a beach near the Askö Laboratory (Swedish Marine Station in the Baltic Sea) in June, 1966. Each plus sign indicates a measurement. (After JANSSON, 1967; modified.)

recorded at these stations. Marine species dominate at stations 1 to 4; station 5 lies in a zone of transition; stations 6 and 7 are characterized by brackish-water species. Limnic species occur—in low individual abundance—only at stations 5 to 7.

A detailed distributional study, based on combined investigations in the field and in the laboratory (KINNE, 1956d, 1957b, d), has been conducted by JANSSON (1967). JANSSON investigated the horizontal distribution of the mesopsammic

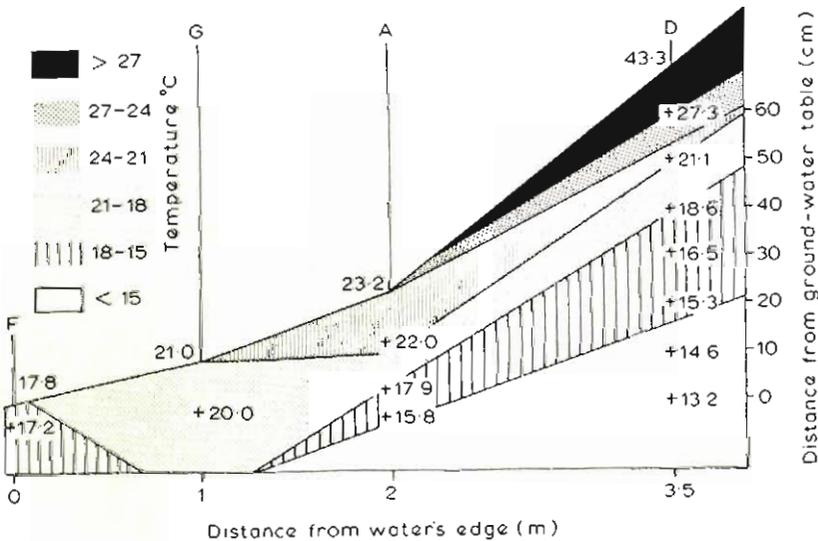


Fig. 4-143: Temperature on a beach near Askö in June, 1966. (After JANSSON, 1967; modified.)

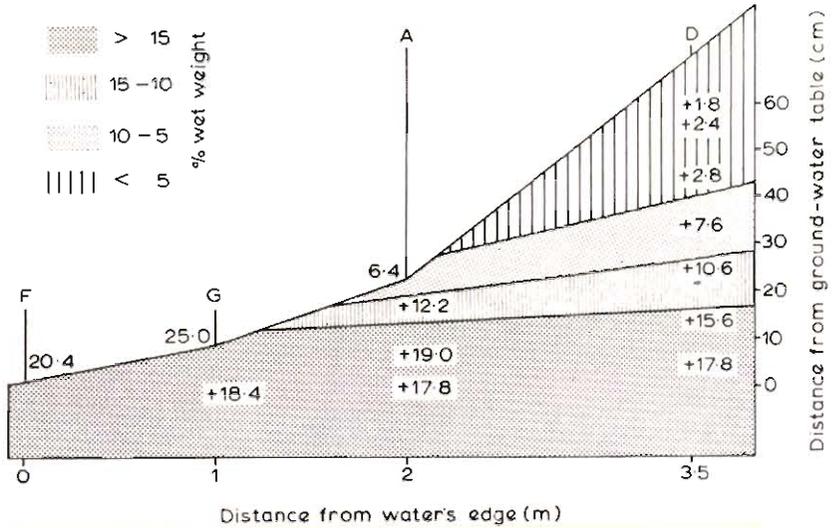


Fig. 4-144: Amounts of interstitial water on a beach near Askö in June, 1966. (After JANSSON, 1967; modified.)

copepod *Parastenocaris vicesima* in a sandy beach near Askö (Sweden) as a function of salinity (Fig. 4-142), temperature (Fig. 4-143), interstitial water content (Fig. 4-144), oxygen availability (Fig. 4-145), grain size (Fig. 4-146) and organic matter (Fig. 4-147) at 4 successive stations, and related his findings to the results of tolerance and preference experiments performed under controlled environmental conditions in the laboratory. The 4 sampling stations F, G, A, D are indicated in all the figures. The salinity gradient (Fig. 4-142) is steep, and fresh water is encountered already at Station A in the deeper sand layers (0.2‰S). Temperatures

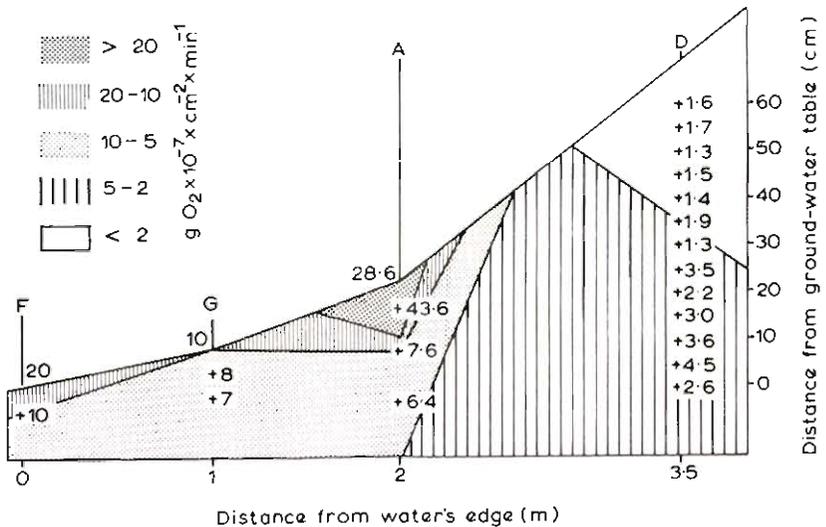


Fig. 4-145: Availability of oxygen on a beach near Askö in June, 1966. (After JANSSON, 1967; modified.)

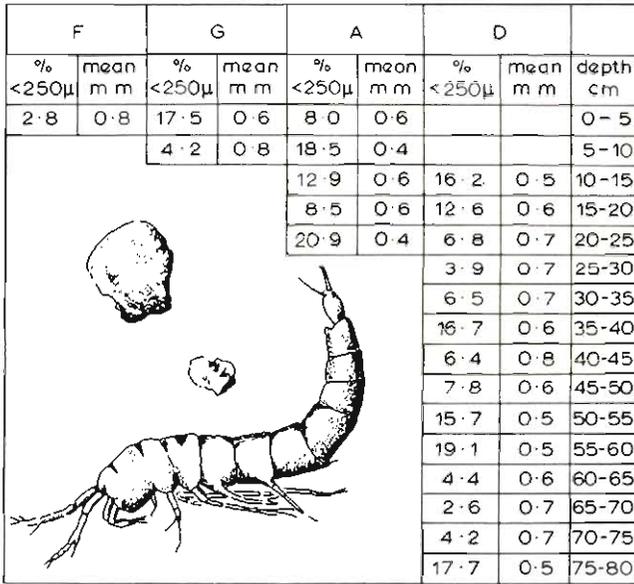


Fig. 4-146: Grain size distribution on a beach near Askö in June, 1966. The left columns under each of the four stations (F, G, A, D) indicate the percentage of the total sample containing grains with diameters less than 250 $\mu$  (After JANSSON, 1967; redrawn.)

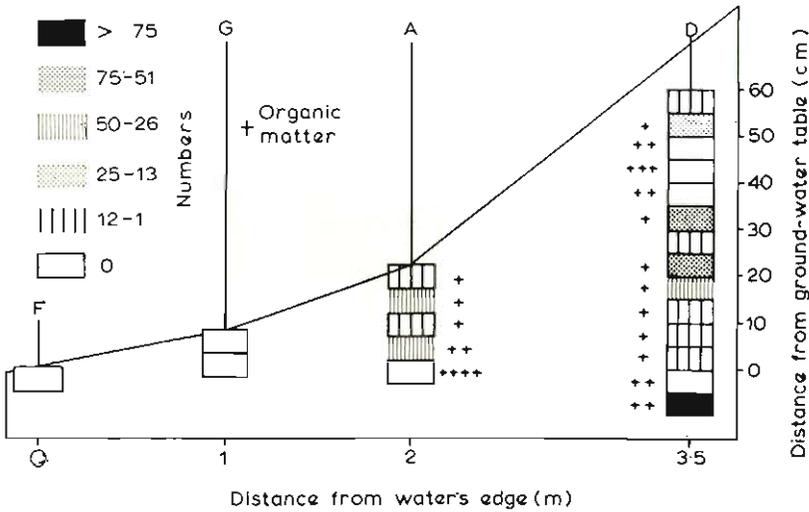


Fig. 4-147: Relative amounts of organic matter (plus signs) and individual numbers of the copepod *Parastenocaris vicesimu* per sample. (After JANSSON, 1967; modified.)

(Fig. 4-143) reach maximum values on the dry sand surface at Station D of  $43.3^{\circ}\text{C}$ ; however, they fall rapidly with increasing sand depth (decreasing distance from ground-water table) and reach a value of  $13.2^{\circ}\text{C}$  at 0 cm. Near the beach surface, temperatures also decrease considerably with decreasing distance from the water's edge. The great vertical range of the temperature interval  $21^{\circ}$  to  $18^{\circ}\text{C}$  near station G is probably due to a specific combination between sun inclination and heat conduction. Interstitial water content (Fig. 4-144), i.e. the amount of water contained between the sand grains (expressed as per cent wet weight), reveals a few anomalies, which are due to irregularities in grain size distribution (JANSSON, 1966). In general, the amount of interstitial water decreases progressively with increasing distance from the water's edge and from the ground-water level. Oxygen availability (Fig. 4-145) is rather low in most parts of the beach, especially in the upper sand layers of Station D. The higher values at the foreshore surface are caused by wave action (especially at Station A). Grain size distribution (Fig. 4-146), plotted in terms of mean values, reveals a quite homogenous picture throughout all the Stations (0.4-0.8 mm grain diameter); if cumulative curves of each individual sample are compared, however, clear differences—especially in regard to smaller grains—become apparent. Relative amounts of organic matter (Fig. 4-147) were estimated in samples, employing a scale from zero to + + + +, where the 4 plus signs indicate samples in which 50% of the total sample volume is detritus. The organic matter consists mostly of floccular, half-decomposed, filamentous algae, especially *Cladophora* sp. with large amounts of epiphytic diatoms (mostly *Epithemia* sp.). Fig. 4-147 also gives the average numbers of *Parastenocaris vicesima* individuals collected per Station (rectangles). Field distributions, measurements of environmental field parameters and laboratory experiments suggest strongly a positive correlation between the horizontal distribution of the copepod *Parastenocaris vicesima* and salinity. The absence of the copepod at Stations F and G is due to salinities above 5‰. For a complete assessment of the factors governing the horizontal distribution of *P. vicesima* it is also necessary to know the local weather conditions effective previous to field observations.

Seasonal changes in distributional patterns due to salinity have been suggested or claimed in several cases. It may suffice here to refer to a recent paper by HUGHES (1969), who investigated the responses of both postlarvae and juveniles of the pink shrimp *Penaeus duorarum* to changes in salinity. HUGHES exposed his shrimp to salinity changes, similar to those occurring with changing tides in their natural inshore environment (off Florida, USA), in a constant-current apparatus. Juvenile shrimp are almost invariably positively rheotactic; however, with a decrease in salinity, the sign of the response is reversed, resulting in active downstream swimming, which often gives way to passive drifting. Under low light conditions, postlarvae move about actively in the water column; unable to withstand even slow water currents, they are easily displaced; with a decrease in salinity they sink to the bottom or remain low in the water column, where they can better maintain their position. Responses of postlarvae at a discontinuity barrier between bodies of water differing in salinity indicate their ability to perceive differences as small as 1‰S. There exists an apparent 'aversion' to penetrating such a barrier into water of lower salinity. If comparable responses are elicited *in situ* during flood tides, juveniles would swim against the current in an offshore

direction, while postlarvae, by being active in the water column, would be displaced shoreward. Following the decrease in salinity which accompanies ebb tide, the juveniles would swim (or be passively displaced) with the water current, again in offshore direction, and postlarvae would sink low in the water column or settle on the substrate where they are better able to resist displacement. Such responses could explain the distributional patterns found on the spawning grounds of the pink shrimp off southern Florida, approximately 60 to 100 miles (96 to 160 km) S.E. of the Everglades. The early postlarval stages (total length 0.8-1.4 cm) arrive in the estuary and remain until they reach a total length of approximately 7.0 to 10.0 cm; at this length, they return to deeper waters as juveniles or sub-adults. Sampling data reveal that the arriving postlarvae are collected predominantly from night flood tides while juveniles are taken primarily on the night ebb tides (TABB and co-authors, 1962; HUGHES, 1969). A similar situation has been reported for the brown shrimp *Penaeus aztecus* in Louisiana (USA) estuaries (ST. AMANT and co-authors, 1966). Also other shrimp species are known to undertake seasonal movements into and out of inshore waters which appear to be facilitated by selective use of tidal currents and hence may be salinity (as well as temperature) dependent (VERWEY, 1958, 1960; STIEVE, 1961; PANIKKAR, 1968).

#### *Vertical distributions*

Variations in vertical distributions are of particular importance in planktonic organisms. Sufficiently strong salinity stratifications may affect the distribution of plankton in the water column. However, salinity can also influence the vertical distribution of substrate-living invertebrates, especially in forms which are not fixed to certain depths by the lengths of their food-collecting or respiratory organs.

Planktonic organisms have been reported to aggregate at salinity and density interfaces (haloclines) in the sea (e.g. NELSON, 1928; CARRIKER, 1951; HANSEN, 1951; BANSE, 1955, 1956a, 1959; GILLBRICHT, 1955; BLACKBURN, 1956; DELLA CROCE and SERTORIO, 1959; SCHWARZ, 1961; BARHAM, 1963). Experimental evidence (HARDER, 1952, 1954, 1957; LANCE, 1962) suggests that many planktonic forms can perceive haloclines and exhibit characteristic distributional responses. HARDER (1968) points out that density interfaces may be preferred sites for certain marine planktonic invertebrates. Of the various planktonic representatives examined (Table 4-76), only polychaete larvae and young mysids did not respond to the vertical discontinuities in density, and larvae of the mollusc *Limacina retroversa* avoided it. Most forms introduced into HARDER's device (Fig. 4-148) accumulate on both the upper and lower surfaces of the thin salinity interface. A few forms aggregate almost exclusively at the interface (e.g. veliger larvae of *Littorina* sp.); others occupy the whole test cylinder but exhibit higher population densities near the interface (e.g. several copepods; single individuals penetrate freely through the halocline). Larvae of *Teredo diegensis* avoid the upper, less saline portion of the test cylinder when its salinity is reduced to 50‰ sea water, while they show random distribution in the control cylinder, except for a slight accumulation near the lighted water surface (Fig. 4-149).

In a series of experiments, HARDER (1968) determined the minimum salinity gradients to which a number of zooplankton forms respond (Table 4-77). The gradients required vary with the test species and range between 0.23S‰ in

Table 4-76

Responses (accumulation, avoidance or no reaction) of planktonic invertebrates to density discontinuities (After HARDER, 1968; modified)

Invertebrates	Responses to discontinuity layers
Protozoa	
<i>Noctiluca</i> sp.	accumulation?
<i>Gymnodinium</i> sp.	accumulation?
<i>Tintinnopsis</i> sp.	accumulation
Ctenophora	
<i>Pleurobrachia pileus</i>	accumulation
Chaetognatha	
<i>Sagitta</i> sp.	accumulation
Polychaeta	
larvae of undetermined species	no reaction
Copepoda	
<i>Acartia clausi</i>	accumulation
<i>Clausocalanus arcuicornis</i>	accumulation
<i>Corycaeus anglicus</i>	accumulation
<i>Corycaeus</i> sp.	accumulation
<i>Euterpina acutifrons</i>	accumulation
<i>Eurytemora hirundo</i>	accumulation
<i>Oithona nana</i>	accumulation
<i>Oithona similis</i>	accumulation
<i>Temora longicornis</i>	accumulation
<i>Tigriopus californicus</i>	accumulation
Amphipoda	
<i>Themisto abyssorum</i>	accumulation
Cirripedia (nauplii)	
<i>Pollicipes polymerus</i>	accumulation
<i>Balanus tintinnabulum</i>	accumulation
Mysidacea	
Young 'mysids'	no reaction
Mollusca	
<i>Limacina retroversa</i>	avoidance
<i>Teredo diegensis</i> , larvae	accumulation
<i>Littorina</i> sp., veliger larvae	accumulation
<i>Haminea</i> sp., larvae	accumulation
Appendicularia	
<i>Oikopleura labradoriensis</i>	accumulation?

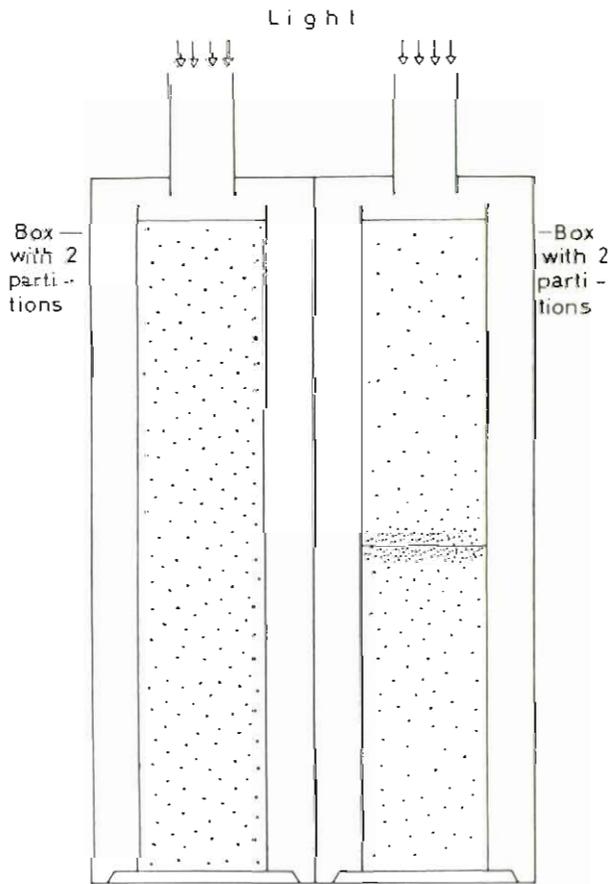


Fig. 4-148: HARDEE's device for testing the responses of plankton organisms to haloclines (vertical discontinuities in salinity). A partitioned box holds two glass cylinders, each with a capacity of 2 l. The control cylinder (left) contains a water column of homogenous salinity and plankton organisms exhibiting random distribution; in the test cylinder (right) lighter water, with a lower salinity, "rides" on heavier, saltier water and the planktons tend to accumulate both on the upper and lower surfaces of the salinity interface. Upon illumination from the side, the interface shows up as a thin line on a screen behind the cylinder and organismic distributions can be recorded photographically. (After HARDEE, 1968; modified.)

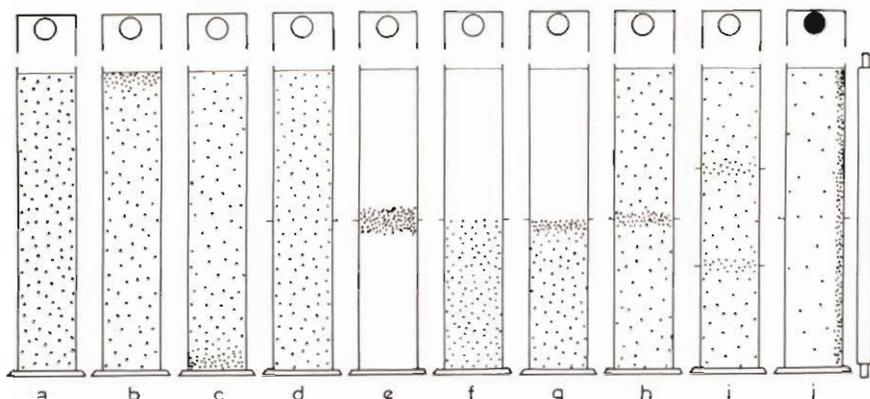


Fig. 4-149: Distributional responses of zooplankton forms in test cylinders without (a-c) and with (d-j) vertical salinity gradients; a-i are illuminated from above or receive no light; j is illuminated from the side. (After HARDER, 1968; redrawn.)

*Eurytemora hirundo* and 16.0S‰ in *Artemia salina* and *Trigriopus californicus*. In another series of experiments, HARDER found that larvae of the bivalve *Teredo diegensis* are distributed more or less randomly above and below a halocline with a gradient of 3.65S‰ or less; a gradient of 4.15S‰ causes a slight accumulation on either side of the interface, and a gradient of 5.19S‰ a marked accumulation above the interface. Representatives of copepod genera typical of coastal waters respond to a gradient of 0.54S‰. Thermoclines have the same effects as haloclines, suggesting that changes in density represent the primary controlling factor. HARDER tested this suggestion by establishing salinity gradients with and without density gradients (addition of sugar to one of the layers) and found it supported by his results.

It remains to be seen to what extent HARDER's experimental results can be applied for interpreting vertical plankton distributions in the sea. The device used

Table 4-77

Minimum salinity gradients at the interface, eliciting responses of the zooplankton species listed (After HARDER, 1968; modified)

Species	Minimum salinity gradient (‰)	Response relative to interface
<i>Eurytemora hirundo</i>	0.23	accumulation
<i>Temora longicornis</i>	3.63	accumulation
<i>Pollicipes polymurus</i>	0.70	accumulation
<i>Artemia salina</i>	16.0	accumulation
<i>Trigriopus californicus</i>	16.0	accumulation
<i>Themisto abyssorum</i>	8.20	accumulation
<i>Teredo diegensis</i>	3.65	accumulation
<i>Limacina retroversa</i>	8.73	avoidance
Various copepod species	0.54	accumulation

by him (or similar, preferably larger, set ups) may provide useful details as to the role of the salinity factor for the distribution of planktonic organisms. In addition, experiments in small 'model oceans' with controllable gradients of salinity and other important ecological factors should be attempted. They are likely to provide new impetus and long needed progress towards a better understanding of the factors controlling vertical distributions.

In oceans and coastal waters, one would expect to find salinity imposed vertical distribution gradients of plankton forms, only if the salinity gradients persist at least for hours or days, and if water movements are reasonably slow. In the vast majority of papers dealing with vertical distributions in the sea, light, temperature, hydrostatic pressure and availability of food have been shown or suggested to be of greater importance as controlling factors than salinity.

The role of some external factors in vertical migrations of marine animals has been reviewed by VERWEY (1966). He comes to the conclusion that vertical migrations are based on a simple system of physical or chemical factors. Changes in light intensity, temperature, salinity, water movement and other factors may initiate vertical movements, whereas directional components such as gravity, pressure and light facilitate orientation. Locomotory activity is governed by 'unstable', orientation by 'stable' environmental components. In this system, the effects of unstable factors are influenced by those of the stable ones. Despite the simplicity of the underlying system, the resulting phenomena of vertical migration reveal considerable diversity, presumably due to the complex interrelationships between the unstable environmental factors *per se* and their biological consequences.

In intertidal invertebrates, the upper distributional ranges are affected by salinity and desiccation (evaporation, rainfall), together with temperature and biotic limiting factors. Motile forms, such as the limpet *Patella vulgata*, may adjust their distributional area individually to changes in salinity, desiccation and temperature stress (LEWIS, 1954; DAVIES, 1969). Invertebrates firmly cemented to the substrate, such as the barnacle *Balanus balanoides*, must suffer the full impact of adverse environmental conditions at their settling site. Variations in vertical distributions of barnacles are related, initially, to environmental conditions effective during larval settlement; later, to the survival potentials of the settled barnacles. *B. balanoides* settles at levels higher than those at which it eventually survives (FOSTER, 1969a). The 'wastage' at high levels is the result of long emersion periods. Even if the newly settled cyprids survive to moult, they grow more slowly at high shore levels because of the restricted times for feeding and defecation, and the increased environmental stress. Slow growth reduces the advantage of size-correlated increase in desiccation tolerance.

In barnacle species occupying upper or lower levels of the intertidal, biochemical differences in desiccation tolerance may be of degree rather than of kind; their vertical separation appears to be affected to a large extent by competition and factors related to cyprid settlement (BARNES and BARNES, 1964). For a more complete discussion of aspects of distribution among barnacles consult FOSTER (1969a).

Salinity dependent or salinity controlled horizontal and vertical distributions of aquatic invertebrates have been reported in numerous other papers. It may suffice here to list the following examples: SCHLIENZ (1923), FISCHER-PIETTE

(1931), REMANE (1933, 1934, 1940, 1950, 1955, 1959, 1963), EKMAN (1935, 1953), CAUDRI (1939), SVERDRUP and co-authors (1942), ALLEE and co-authors (1949), GUNTER (1950, 1961), SEGERSTRÅLE (1951a, b, 1953, 1957, 1969), PURASJOKI (1953), ANDREWARTHA and BIRCH (1954), SCHÜTZ and KINNE (1955), SMITH (1955a, c, 1956), FORSMAN (1956), DARLINGTON (1957), HEDGPETH (1957), CASPERS (1958, 1959a, b), MOORE (1958), REMANE and SCHLIEPER (1958), ODUM (1959), COOPER (1961), GLOVER (1961), NEUMANN (1961a, 1962), WELLS (1961), DEHNEL (1962), DUNBAR (1963), HOHENDORF (1963), ZENKEVITCH (1963), FRIEDRICH (1965), LASSIG (1965), OGLESBY (1965a, b), RIEMANN (1966), DYBERN (1967), KÜHL (1967), KÜHL and MANN (1967), LAUFF (1967), MUUS (1967a), NAYLOR and HAAHTELA (1967), THIEL (1968), ACKEFORS (1969a, b), DENNERT and co-authors (1969), DORNHEIM (1969), GORDON (1969), SCHÜTZ (1969), SCHULZ (1969), VERNBERG and VERNBERG (1970).

#### *Endogenous properties*

While many marine ecologists have sought to understand distributions 'wholly in terms of the environment', in the final analysis, the responses of individuals and populations to the sea around them are 'determined by the peculiarities of their internal mechanisms' (WALFORD, 1963, p. 109). KINNE (1963b) provided examples among macrocrustaceans, which illustrate how functional and structural properties of the species involved can explain major differences in their over-all distributions. On the basis of their osmoregulatory capacities, more than 50 species could be placed into four groups inhabiting waters of different salinities. BATTAGLIA and BRYAN (1964) compared the capacities for ionic and osmotic regulation in harpacticoid copepods of the genus *Tisbe* in relation to polymorphism and geographic distribution; the homozygote forms *violacea* and *trifasciata* show different abilities to exist in diluted sea water. These two genotypes exhibit, at the same time, significantly different rates of uptake of  $^{22}\text{Na}$ ,  $^{42}\text{K}$  and  $^{137}\text{Cs}$ , which seem to be related to their respective potentials for inhabiting waters with modified salinities (see also BATTAGLIA, 1967, 1970). BARNES (1967) found parallels between the capacity for osmoregulation and the distribution in waters with different salinities in five Australian grapsoid crabs. The abilities of hyperosmoregulation decrease in the order *Paracleistostoma mcneilli*, *Australoplax tridentata*, *Mictyris longicarpus*, *Macrophthalmus setosus* and *M. crassipes*; this order corresponds with that obtained by listing these species according to the degree of their distributional penetration of the Brisbane River (Australia), with the exception of the position of *Mictyris longicarpus*. In other cases, capacities for osmoregulation and distributional limits seem to be less congruent.

Parallelism of osmoregulative capacity and salinity limits in the field suggests that the intensities of other environmental factors are within the tolerance range for population survival; in such cases, salinity most likely represents the primary limiting environmental entity. Regulative capacities exceeding actual distributional salinity limits suggest the presence of other primary limiting factors (e.g. substratum, food, temperature).

For a number of marine bivalve species, SCHLIEPER and KOWALSKI (1956), SCHLIEPER (1958, 1966), SCHLIEPER and co-authors (1960, 1967), RESHÖFT (1961), VERNBERG and co-authors (1963) and THEEDE (1965a) have demonstrated close

relations between distribution and cellular tolerance to difference salinities (see also p. 836). The degree of cellular tolerance is considered a species- (or population) specific endogenous property.

Genetic aspects of benthos distributions, controlled or influenced by salinity, have been discussed by BATTAGLIA (1967), with special reference to inter- and intra-specific selection, adaptive polymorphism, genetic structure of populations and geographic differentiation in physiological characteristics. It is likely that more knowledge on such aspects will add profoundly to our understanding of salinity influenced distributions of invertebrates inhabiting coastal waters with rough osmotic and ionic climates.

Among planktonic invertebrates, feeding habits of co-existing forms often appear to represent a master factor in vertical (sometimes also in horizontal) distributions. Preferred feeding depths, feeding times and nutritional components available tend, in these cases, to be of greater importance than light, temperature or salinity. Marine planktonic copepods, for example, exhibit a step-like pattern in their vertical distributions, both in migrating and non-migrating species, which is primarily related to their feeding habits (VINOGRADOV, 1956; GEINRIKH, 1957; VINOGRADOV and VORONINA, 1964; ZALKINA, 1970). Large populations of copepod species with similar feeding habits can co-exist only if they occupy different (in space and time) water layers. The degree of mutual exclusion from the centres of maximum abundance increases with decreasing food supply (VINOGRADOV, 1956, 1968; VINOGRADOV and VORONINA, 1964; see also VINOGRADOV and co-authors, 1970).

### (3) Structural Responses

Sub- or supranormal salinities and extensive fluctuations in osmoconcentration and ionic composition may, in various ways, affect structural properties of aquatic invertebrates. In general, functional and structural responses to salinity appear to be interrelated in a similar way as pointed out with respect to temperature (Chapter 3.31). Structural responses to salinity variations are based ultimately upon differences in metabolism, affecting development, differentiation and relative growth of body parts (KINNE, 1958a; 1964a). In lower invertebrates, the primary sites for structural responses to salinity seem to be the external and internal (e.g. intestinal) body surfaces, in higher invertebrates, also organs involved in ion, volume and osmoregulation.

#### (a) Size

Both sub- and supranormal salinities tend to cause reductions in final body size. Thus, in the gastropod genus *Neritina*, dwarfs have been observed in the lowest and highest salinities encountered over the distributional range of the species concerned (METCALF, 1930; ANDREWS, 1940).

Numerous examples are available to illustrate reductions in final size, in distributional areas of marine or brackish-water invertebrates with significantly lowered salinities. Such 'brackish-water pauperization' often goes hand in hand with a reduction in over-all vitality. However, ROMANE (1934) reports cases in which

body size reduction did not apparently reduce the vitality of the population involved. He stresses the similarity between the phenomenon of size reduction in low salinity and Bergmann's rule, according to which final size of homoiothermal animals (and often of poikilothermal ones also) tends to be smaller in warm and larger in cold climates (REMANE and SCHLIEPER, 1958; see also Chapter 3.32). Numerous examples and several exceptions of brackish-water pauperization, particularly in cnidarians, crustaceans, molluscs and echinoderms, can be found in METCALF (1930), REMANE (1934, 1940), PICARD and LEROCH (1949), BOETTGER (1950), PEARSE and GUNTER (1957), SEGERSTRÅLE (1957), MOORE (1958), REMANE and SCHLIEPER (1958) and LAUFF (1967). A detailed evaluation of the pertinent field data is difficult, since various other factors, in particular temperature and food, and genetic differences between populations, may considerably influence the situation (KINNE, 1964a). The picture is even more complex with respect to fresh-water organisms penetrating into brackish water (e.g. REMANE, 1950).

In laboratory experiments, final colony size of *Cordylophora caspia* has been shown to be a function of salinity. Total colony length reaches a maximum in 15‰ to 17‰S and decreases both in lower and in higher salinities (KINNE, 1956b, 1958a). A similar reduction of final size in sub- and supranormal salinities occurs in *Gammarus duebeni* (Table 4-78), and presumably also in *Artemia salina*. The ctenophore *Pleurobrachia pileus* remains smaller in 45‰S than in a normal salinity of about 32‰ (GREVE, 1969). In the suboptimal salinities of the middle and eastern Baltic Sea, *P. pileus* becomes more delicate and easily disintegrates after fixation in formalin (MIELCK and KÜNNE, 1935).

Table 4-78

Final body length in the amphipod *Gammarus duebeni* as a function of salinity. Averages based on 30 specimens in each case; maxima represent individual data. Annual temperature fluctuations similar to those in the habitat. All individuals were born and raised in the salinities indicated (After KINNE, 1959; modified)

Salinity (‰)	Averages final body length (mm)		Maximum final body length (mm)	
	♀♀	♂♂	♀	♂
2	14.8	21.2	15.4	21.9
10	15.2	22.3	18.4	24.0
30	14.7	22.0	15.5	22.7

#### (b) External Structures

Externally visible structural responses to salinity stress include changes in dermal differentiations, degree of calcification, pigmentation, meristic characters, body

shape and body appendages. In extreme cases, salinity stress may—possibly in combination with other factors such as temperature and nutrition—cause growth patterns in laboratory experiments which are so abnormal that they can only be referred to as monstrosities.

In general, it is difficult, if not impossible, to establish convincing evidence of direct salinity influences on organismic structures, solely on the basis of field observations, as numerous other factors may interfere. Under controlled laboratory conditions, on the other hand, structural modifications may develop which hardly show up in the field (and are thus of little or no ecological importance) because they are linked with critical reductions in survival rates and in the capacity for intra- or interspecific competition. Combined field and laboratory studies are required here, as in most other cases, for adequate analyses. Our present knowledge on externally visible structural responses to salinity is still very limited, and where such responses have been documented, we are largely unable to interpret their ecological significance.

In several brackish-water crustaceans, size and number of dermal differentiations, such as spines and chetae, tend to increase in species which inhabit waters with increasingly reduced salinities; this holds, for example, for the series *Gammarus locusta* > *G. oceanicus* > *G. salinus* > *G. zaddachi*. Within one and the same species, however, KINNE (1954b) could not demonstrate such structural variations in breeding experiments on *Gammarus oceanicus*, *G. salinus*, *G. zaddachi* and *G. duebeni*; the same is true of other crustacean species which have been exposed to different salinities (e.g. HÖFKEN, 1937; SPOONER, 1947). Oligochaetes may either increase or decrease their number of chetae with decreasing salinity (HAGEN, 1954). Polychaetes *Fabricia sabella* of similar body length have on their thorax 8 to 9 uncini chetae in water of 7‰ to 10‰S, but 9 to 12 in 34‰S (BANSE, 1956b).

The degree of calcification of body cases, exoskeletons or shells, may decrease with decreasing salinities. In the ectoproctan *Membranipora crustulenta*, for example, calcification of the body case is usually less pronounced in subnormal than in normal salinities (BORG, 1931, 1936). Various molluscs have been claimed to produce thinner shells in reduced salinities, for example, *Mya arenaria* (NEWCOMBE and KESSLER, 1936) and *Macoma baltica* (LEVANDER in: REMANE and SCHLIEPER, 1958, p. 43); the latter two authors quote further examples of reduced calcification in low salinities, which are assumed to be related to salinity variations.

The degree of pigmentation of body surfaces and shells can be modified by salinity. The gastropod *Neritina virginea* deposits less shell pigment in supranormal salinities, resulting in a more brilliant light reflection, and the gastropod *Littorina littorea* exhibits brighter colours in subnormal salinities (ANDREWS, 1940; see also COMFORT, 1951). Various other invertebrates show colour variations which have been claimed to be related to habitat salinity. However, the information at hand is, in most cases, insufficient for a critical evaluation, as modifications in pigmentation may be caused by a variety of environmental factors, including light, temperature and nutrition, as well as by genetic properties. Cases of genetic polychromatism which may be related to salinity variations have been reported for species of the copepod genus *Tisbe* by BATTAGLIA (1957, 1967) and for the colonial ascidian *Botryllus schlosseri* by SABBADIN (1959).

Reports which claim quantitative or qualitative changes in meristic characters

(i.e. in serial morphological units such as segments) due to salinity variations do not yet provide convincing evidence. It is tempting, however, to suggest the possibility of a certain parallelism to changes in vertebrae and fin rays observed in fishes (Chapters 3.32, 4.32).

Changes in body shape, which are, or may be, related to salinity variations, have been reported, particularly in coelenterates and molluscs.

Among the coelenterates, salinity has been shown to influence the shape of colonies and of single hydranths in the hydroid *Cordylophora caspia* (KINNE, 1956b, 1957a, c, 1958a). In a series of laboratory experiments, individual hydranths (from the 'Nord-Ostsee-Kanal', Federal Republic of Germany) with identical genetic backgrounds have been exposed to different constant salinities and allowed to regenerate to new (secondary) colonies. The typical shapes of the colonies obtained in fresh water, 15‰ and 30‰S are illustrated in Fig. 4-150. In fresh water, 70 to

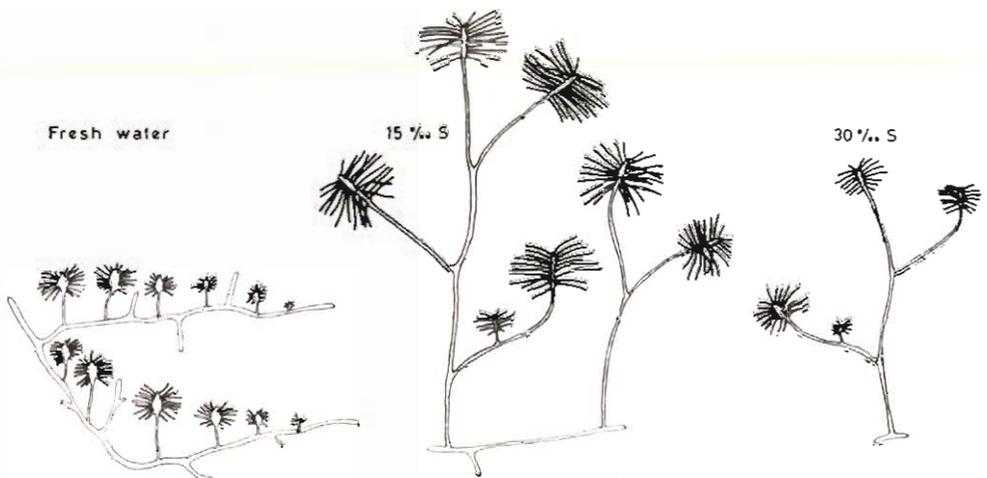


Fig. 4-150: Shape of *Cordylophora caspia* colonies cultivated in three different salinities; typical examples. All three colonies were obtained from genetically identical hydranths. 20° C. (After KINNE, 1958a; modified.)

90% of the total length of the colonies consists of stolons which are firmly attached to the bottom of the culture vessel; from these stolons arise single, unbranched hydranths. In 15‰S, the colonies consist of 10 to 20% stolons, in 30‰S of 0 to 14%. In 15‰ and 30‰S, the colonies are branched and their long hydrocauli carry small elongated hydranths.

Also the hydranths of *Cordylophora caspia* themselves reveal characteristic changes (Fig. 4-151). In fresh water, they are shortest and widest and carry, on an average, 33 tentacles at 10° C and 22 at 20° C. In 15‰S, the hydranths are much longer and narrower and carry 38 tentacles at 10° C, and 31 at 20° C. In 30‰S, the hydranths are somewhat smaller than in fresh water at 10° C, but larger at 20° C; they are narrower than in 15‰S and carry 27 tentacles at 10° C and 23 at 20° C (Table 4-79). While hydranth length reaches a maximum in 15‰S, hydranth width decreases continuously with increasing salinity. Comparable results have

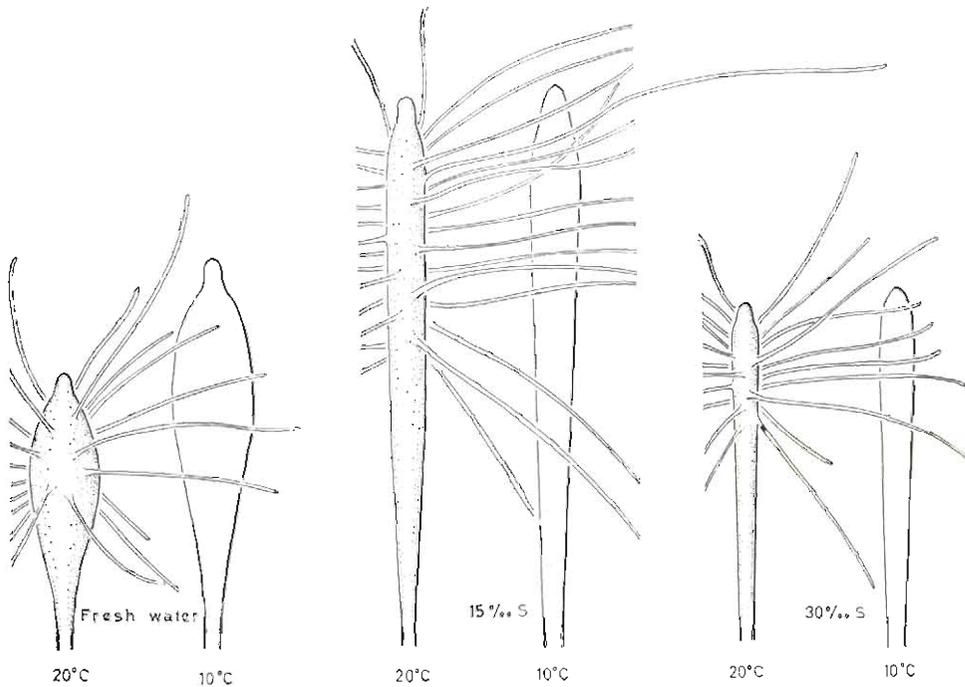


Fig. 4-151: Shape of *Cordylophora caspia* hydranths from genetically identical colonies cultivated in three different salinities at 10° and 20° C; typical examples. Tentacles shown only on 20° C hydranths; on the right sides in full length (in 15‰ S only 1 tentacle is drawn in full length). (After KINNE, 1958a; modified.)

Table 4-79

*Cordylophora caspia*. Length, width and tentacle number of fully grown hydranths from genetically identical colonies. The colonies were grown under the different conditions of salinity and temperature indicated. Average values, based on 25 measurements from 5 different colonies in each case. The differences between values obtained in 15‰ S and fresh water, and those between 15‰ and 30‰ S are, in all cases, statistically significant (After KINNE, 1958a; modified)

Salinity (‰)	Temperature (°C)	Hydranth dimensions (mm)		Number of tentacles per hydranth
		length	width	
Fresh water	10	3.00	0.64	33
	20	2.10	0.46	22
15	10	4.40	0.42	38
	20	4.32	0.27	31
30	10	2.78	0.28	27
	20	2.62	0.18	23

been obtained on *C. caspia* from the lower region of the River Warnow (German Democratic Republic) by GOSSELCK (1969). GOSSELCK studied populations from two habitats with different salinity regimes (Kabutzenhof, ca 5‰ to 7‰S; Petribrücke, ca 1‰ to 3‰S) and one aquarium population kept under laboratory conditions in 14‰S for 3 years. He transferred representatives of these populations to different constant salinities (0‰, 2‰, 6‰, 10‰, 16‰, 24‰, 30‰S; at identical but not stated temperatures) and obtained for hydranth length and width the curves illustrated in Figs 4-152 and 4-153. Different populations of *C. caspia* may

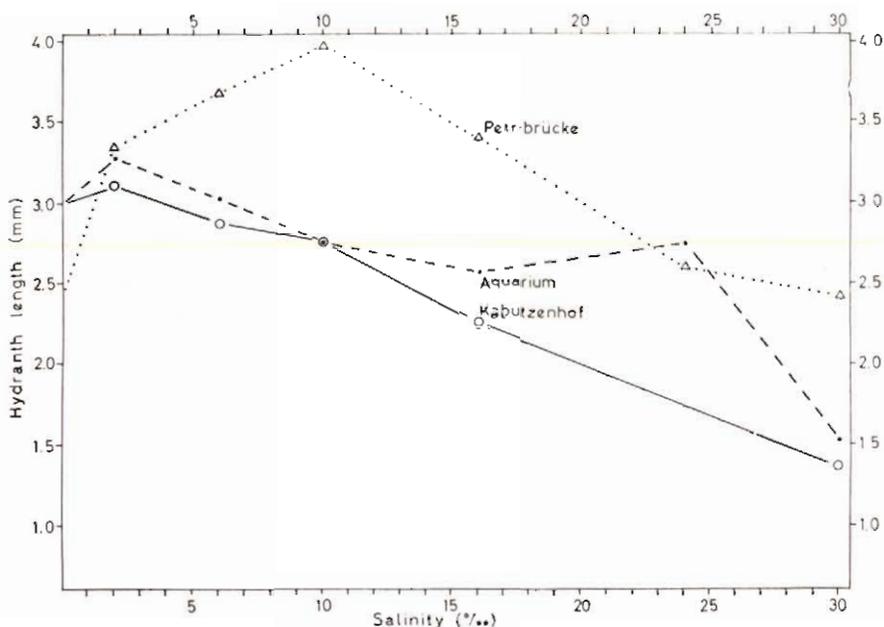


Fig. 4-152: *Cordylophora caspia*. Hydranth length as a function of salinity. Temperature conditions not stated. Salinity history: 'Aquarium' cultures were kept for 3 years under laboratory conditions in 14‰S; 'Petribrücke' field salinities ca 1‰ to 3‰; 'Kabutzenhof' field salinities ca 5‰ to 7‰S. (After GOSSELCK 1969; modified.)

reveal different responses to salinity; the performance in the field (ecological potential) may not always be identical to that in the laboratory (physiological potential).

Length and width of the tentacles of *Cordylophora caspia* are more difficult to measure. However, in the material from the 'Nord-Ostsee-Kanal', these dimensions also reveal a relationship to the cultivation salinity: both at 10° and at 20° C, tentacle length attains maximum values in 15‰S; at 10° C, tentacles are longer in fresh water than in 30‰S; at 20° C, they are about equally long in these two salinities (KINNE, 1956b, 1958a).

The salinity-induced changes in hydranth shape, tentacle number per hydranth and tentacle dimensions lead to pronounced differences in the surface to volume ratio of the hydranths involved (Fig. 4-154). The surface-volume ratio increases with salinity and temperature. As the hydranths represent the sites of maximum

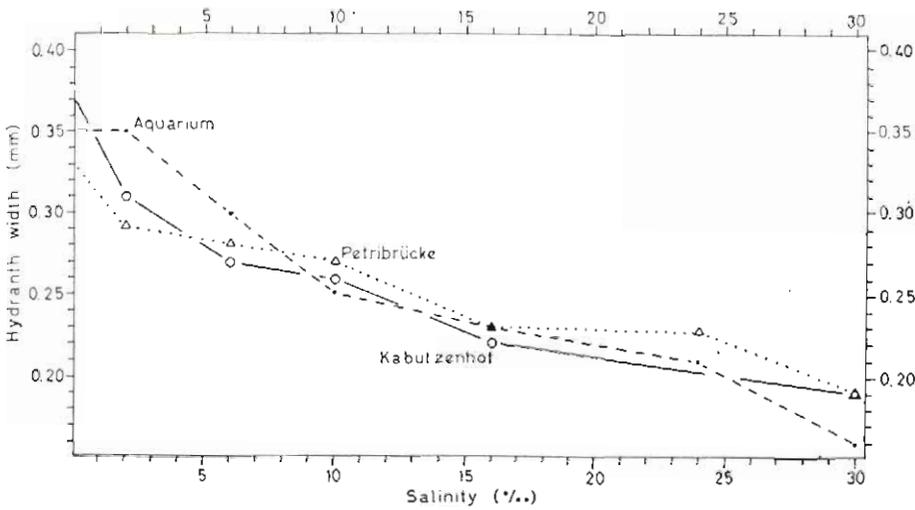


Fig. 4-153: *Cordylophora caspia*. Hydranth width as a function of salinity. For further details, consult legend to Fig. 4-152. (After GOSSELCK, 1969; modified.)

metabolic exchange between colony and ambient medium (hydrocauli and stolons are more or less isolated by a sheet of periderm), changes in their surface-volume ratio may affect metabolic and regulatory performance (KINNE, 1958a, b).

In regard to molluscs, a number of authors have claimed salinity-induced modifications in shell structure. In view of the importance for taxonomy of molluscan shell structures, such claims ought to be considered with special care. According to field observations, shells of the lamellibranch *Cardium edule*, from habitats with significantly increased salinities, reveal a series of structural changes. In very salty water, the shells tend to be thinner, more intensively coloured and of greater relative length than in habitats with normal or subnormal salinities; at the

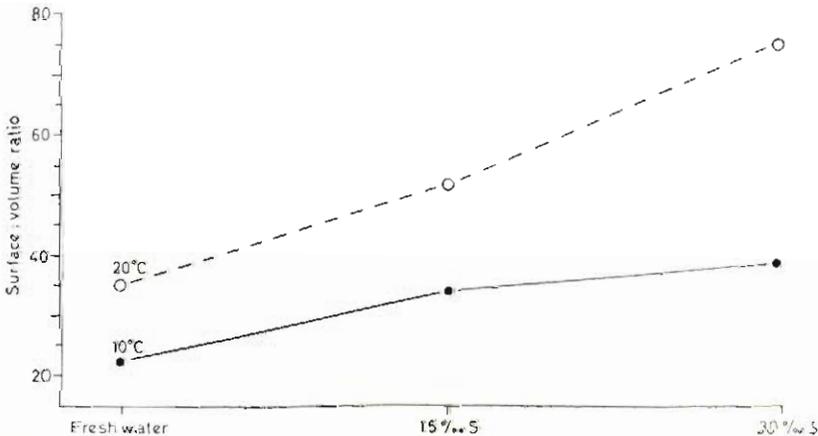


Fig. 4-154: *Cordylophora caspia*. Surface to volume ratio in hydranths of identical genotype grown in the different conditions of salinity and temperature indicated. (After KINNE, 1958a; modified.)

same time, the shells often have smaller beaks and reveal ribbing on their inner surface (BATESON, 1889). Apparently, the species investigated by BATESON was *C. lamarcki* (LAUCKNER, personal communication). In his recent study on the biology of *C. edule* and *C. lamarcki*, LAUCKNER (1971) comes to the conclusion that habitat salinities (4‰ to 30‰S) play a significantly lesser role in regard to variations in shell structure of the two species than the degree of exposure (water movement, grain size and motility of the sediment) and, possibly, water temperature and nutrition. In contrast, EISMA (1965), who compared average salinities in various habitats in the Netherlands (Zuiderzee, Wadden Sea, North Sea coast, Rhine-Meuse-Scheldt Estuary and some inland waters) to shell characteristics of *Cardium edule*, claims a close relationship between these two parameters. In the habitats where the cockles were sampled, mean chlorinities varied from less than 5‰ to 18‰. EISMA found the closest relation between average chlorinity and average number of ribs per valve (Fig. 4-155) and points out that comparison with

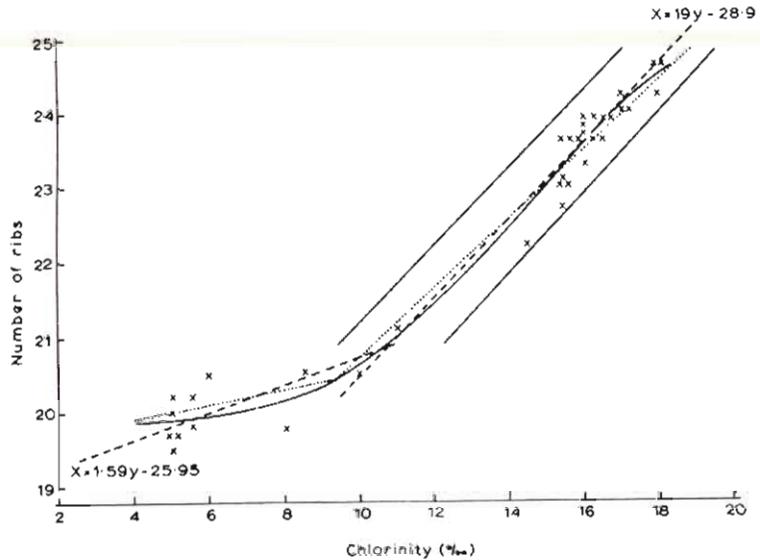


Fig. 4-155: *Cardium edule*. Relationship between average number of ribs per valve and average chlorinity. (After EISMA, 1965; modified.)

a few samples from coasts outside the Netherlands showed that this relationship 'is, most probably also valid for the other North Sea coasts, the Baltic and the Atlantic and Mediterranean coasts' (p. 536). From the average number of ribs, EISMA was able to determine the average habitat chlorinity with an accuracy of  $\pm 1.3\%$  ( $P=0.05$ ), when the average rib number was 20.9 or higher (the lower limit corresponding to 10.8‰ Cl); for still lower chlorinities he suggests the use of other indicators.

'The relations between average salinity and the average weight of 20 mm shells, the % *Cardium edule* var. *lamarcki* (distinguished by the relation between shell-width and ligament-length), the maximum age, and the average rate of growth are not as close as the relation between the average number of

ribs and the average salinity, but may serve as a check on other determinations. The relation between the average weight and average salinity can be used especially to estimate salinities lower than 10.8‰ Cl, but not enough reliable data were available to construct a good graph' (EISMA, 1965, pp. 536-537).

EISMA believes, with some reservation, that the relationships between shell shape and average salinity, established by him, can be used in the reconstruction of palaeo-environments and in field studies conducted in localities where the average salinity is not known. LAUCKNER's (1971) studies are based on a larger number of data than those of EISMA. They indicate that rib number in *Cardium edule* and *C. lamarcki* (from North Sea coasts of Norway, Denmark, Germany, and from Baltic Sea coasts of Denmark and Germany) tend to increase somewhat, with salinity, to a maximum value and then to decrease again. In *C. edule*, the maximum number of ribs (25-26) occurs in salinities close to 24‰ S (habitat salinity range: 10‰ to 30‰ S), in *C. lamarcki* (maximum rib number: 24-25) close to 14‰ S (salinity range: 4.5‰ to 30‰ S). As pointed out before, these variations in rib number may be controlled, according to LAUCKNER, primarily by the degree of exposure rather than by salinity.

Environmentally induced modifications in shell structure of molluscs must be based ultimately on changes in the shell-forming tissue. To the reviewer's knowledge, HOOP (1940) is the only author who has, up to now, attempted to analyze possible salinity effects on the mantle tissues of euryhaline molluscs. His results, which are dealt with briefly in the section *Internal Structures*, do not provide unequivocal evidence in favour of, or against, such an influence of salinity on the basis of histological findings. For general aspects of shell formation in molluscs consult WILBUR (1964).

Changes in body proportions due to salinity variations have been claimed to exist in a number of euryhaline crustaceans. However, the evidence presented is insufficient in all the cases that have come to the reviewer's attention, with the exception of ABONYI's (1915) observation that thorax and abdomen lengths, in their relations to total body length, vary as a function of salinity in *Artemia salina*.

Changes in body appendages (e.g. extremities, abdominal segments, gills) due to salinity stress have been demonstrated in the brine shrimp *Artemia salina* (SCHMANKEWITSCH, 1875, 1877; ABONYI, 1915; ARTOM, 1920; GAJEWSKI, 1922; GROSS, 1932; KUENEN, 1939; HESSE and DOFLEIN, 1943; GILCHRIST, 1960). Salinity affects the shape of body appendages, especially the phyllopods (ABONYI, 1915) and the caudal furca (ARTOM, 1920). Such structural adjustments to salinity conditions exist among genetically similar individuals, as well as among specimens with different chromosome numbers (p. 994). According to GROSS (1932), who investigated the relationship between polyploidy and structural variability, parthenogenetic and gametogenetic forms are morphologically identical, but high salinities cause a tendency towards polyploidy via automixis. GOLDSCHMIDT (1952) doubts, however, whether automixis may have played a significant role in the normal maturation process of the material studied by GROSS. In contrast to the above-named authors, BOND (1933) could not find significant structural differences

in *A. salina* from habitats with different salinities (near San Francisco, USA).

In aquatic mosquito larvae, anal papillae change their size and shape as a function of salinity (PAGAST, 1936; KOCH, 1938; WIGGLESWORTH, 1938; HARNISCH, 1943, 1951; STRENZKE, 1956; HAAS and STRENZKE, 1957; STRENZKE and NEUMANN, 1960). The thin-walled anal papillae serve as sites of ion uptake from the surrounding water. In larvae of *Chironomus thummi*, and of related species, the papillae become reduced in size with increasing salinity, but enlarge in moor water poor in ions.

KINNE (unpublished) reared the freshwater snail *Lymnaea stagnalis* (from fertilized eggs) in different constant salinities (fresh water, 3‰, 6‰, 9‰S; food: primarily leaves of *Lactuca sativa*) at different temperature levels. At 22° C, the majority of the test individuals exposed to fresh water and to 3‰S survived for at least one year; the 6‰S specimens died within 7 months, the 9‰ specimens within 17 days. While the ratio shell length to shell width did not reveal significant alterations in the different salinities, the 3‰ and 6‰S individuals began (after 1 to 3 and 2 to 5 months, respectively) to exhibit an apparently unusually large, freely extended 'penis' (one-third or more of total shell length). Only in some individuals was the expanded penis sometimes withdrawn for brief periods. The possible significance of this phenomenon, which was never observed in the freshwater series, is not known. The fact that the large extended penis shifts the ratio

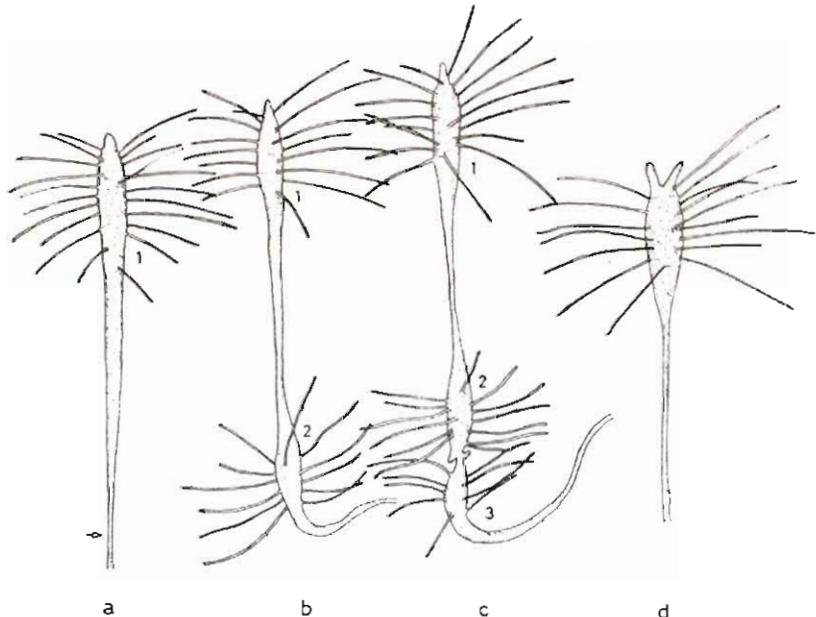


Fig. 4-156: *Cordylophora caspia*. Abnormalities in hydranth morphology due to supranormal salinity (24‰S). Hydranths begin to increase their length (a), until, near their base, a second (2), third (3), etc. hydranth differentiates. In this way, uni-axial hydranth aggregates are formed, in which the direction of the oral pole (mouth end) alternates 180°. Arrow: border between hydranth and hydrocaulus. (d) Abnormal hydranth with twin mouth. 16° to 17° C. (After KINNE, 1956b; modified.)

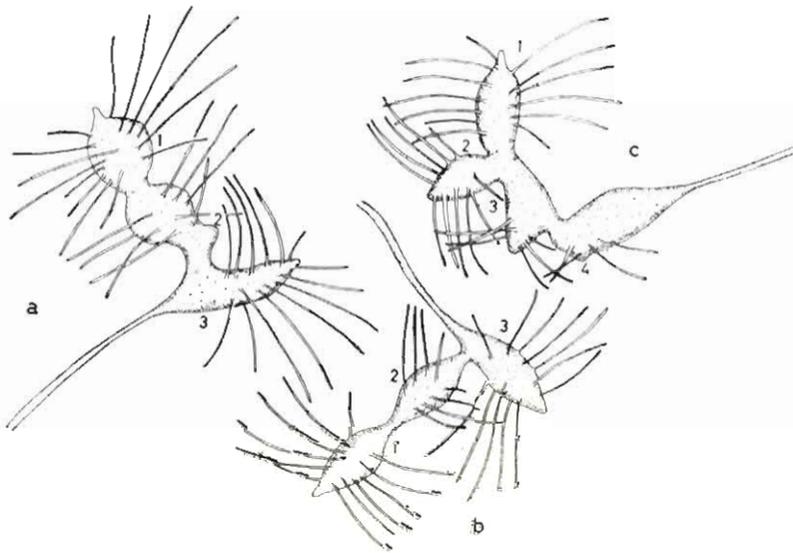


Fig. 4-157: *Cordylophora caspia*. Hydranth monstrosities in 24‰ S at 16° to 17° C. Multi-axial hydranth aggregates consisting of 3 to 4 fused hydranths. (After KINNE, 1956b; modified.)

soft-body-surface-area to soft-body-volume in favour of the former, suggests a possible relation to gaseous, salt or water exchanges between body and environment; however, parasitic infestation or microbial infection cannot be ruled out as possible causes for the enlargement and continued expansion.

Extreme salinities may, in laboratory tests, cause structural monstrosities. In *Cordylophora caspia*, supranormal salinities of 24‰ or 30‰ can cause a variety of monstrosities in older colonies. Most of the structural abnormalities observed have in common a severe reduction in stolon material, leading to the formation of uni- and multi-axial hydranth aggregates, large coenenchymal sacs and globular hydranth complexes without stolons or hydrocauli (Figs 4-156, 4-157, 4-158, 4-159). All these monstrosities continued to feed (oligochaete *Enchytraeus albidus*); they survived for months. A hydranth complex like the one illustrated in Fig. 4-159 changed, at a total age of 241 days into a stolon coil with 2 normal hydranths (Fig. 4-160); it had not been fed for the last 71 days. On the basis of available information, it is impossible to decide whether this structural normalization is related to the preceding starvation period. As the abnormalities were observed only in the highest salinities offered, there can hardly be any doubt that supranormal salinities are responsible for disturbing growth pattern and differentiation processes. However, the relatively high initial age of the test material and the nutrition (the colonies received only *Enchytraeus albidus*) may also have been of importance (KINNE, 1956b).

Structural abnormalities due to low salinities have been reported in Rotatoria (RENTZ, 1940) and Oligochaeta (HAGEN, 1954). In the oyster *Crassostrea gigas*, salinities below 23‰ and, especially, above 28‰ cause a marked tendency for the blastomeres to separate from each other (FUJITA, 1970).

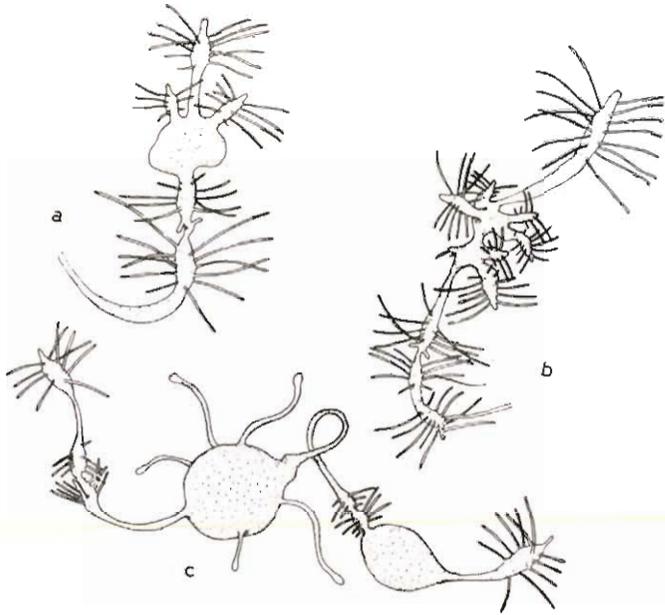


Fig. 4-158: *Cordylophora caspia*. Hydranth monstrosities in 24‰S at 16° to 17° C. Multi-axial hydranth aggregates (a, b) begin to grow large coenenchymal sacs (c). (After KINNE, 1956b; modified.)

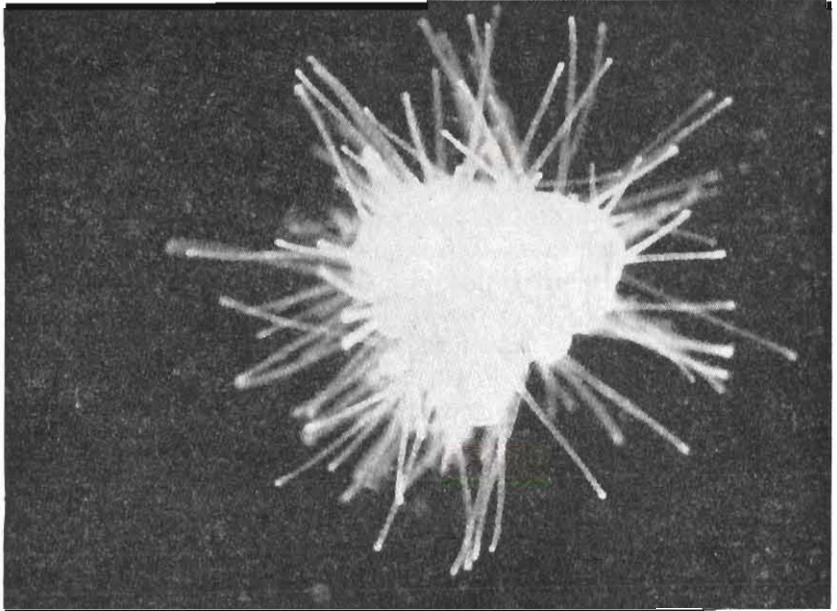


Fig. 4-159: *Cordylophora caspia*. Hydranth monstrosity in 24‰S at 16° to 17° C. Globular non-attached hydranth complex without stolons or hydrocauli. Photograph of living 'colony'. (After KINNE, 1956b; modified.)

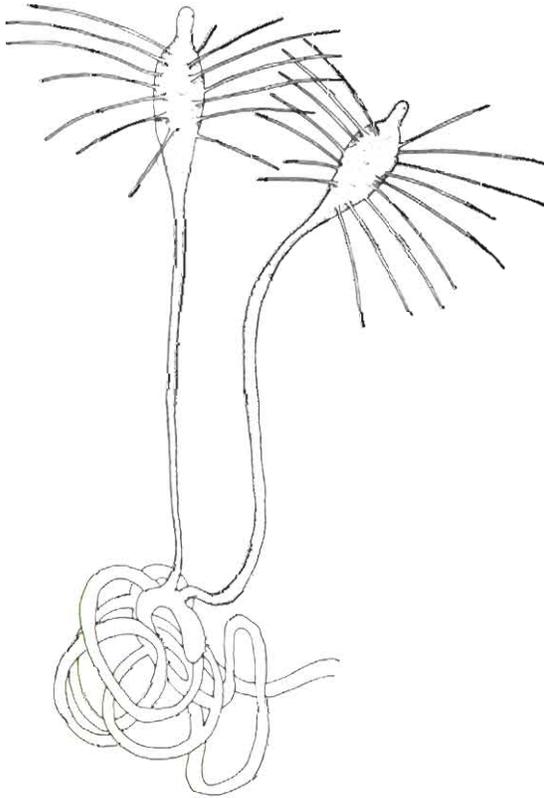


Fig. 4-160: *Cordylophora caspia*. These two normally built hydranths developed, after 71 days starvation, from a globular hydranth complex like the one illustrated in Fig. 4-159. 24‰S at 16° to 17° C. (After KINNE, 1956b; modified.)

### (c) Internal Structures

Long-term exposure to sub- or supranormal salinities may modify the size and shape of internal organs, dimensions and architecture of individual cells, size of nuclei, and, possibly, even secondary protoplasmic microstructures.

In crustaceans, size and shape of regulatory organs, such as gills, gut or antennal glands, have been reported to exhibit relationships, both in inter- and intraspecific comparisons, to salinity. However, the information at hand is scanty and frequently unconvincing. PEARSE (1929a, b) reported reduction in number and size of gills in some estuarine or freshwater crabs, in comparison to their salt-water living counterparts, and pointed out that those reductions lead to a decrease of total area through which exchange diffusion with the diluted medium occurs. According to SCHWABE (1933), nephridial canals are longer in the freshwater-living *Gammarus pulex* than in the brackish-marine *Gammarus locusta*. Nephridial canals have been shown, by PETERS (1935), to be more highly differentiated in the freshwater *Astacus astacus* than in the marine *Homarus gammarus*.

A number of papers consider structural adjustments in crustaceans to desiccation, air exposure and life on land. They focus on interspecific comparisons. During the phylogenetic process of terrestrialization, the crustacean gill undergoes several structural changes: (i) it receives additional support by sclerotization and ridges (VAN RABEN, 1934); (ii) its functional surfaces become reduced (PEARSE, 1929a, b, 1950; AYERS, 1938; GRAY, 1953); and (iii) provisions are made for continuous moistening of the surfaces. Species of *Uca* and *Ocypode* feature special respiratory openings between their third and fourth legs (EDNEY, 1960). In general, land isopods use the same structures for respiration as their aquatic ancestors, namely the pleopods. These show, however, definite adjustments to air breathing in more terrestrial species (MODLINGER, 1931); while the semiterrestrial Ligiidae and Trichoniscidae have unmodified pleopods, Oniscidae have the exopodites of their pleopods hollowed out below, and Porcellionidae and Armadillidiidae possess hollow tuft-like invaginations known as pseudotracheae, which facilitate respiration in air of reduced humidity. The most profound respiratory adjustments to land life are the vascular tufts and the vascularization of the gill chamber walls in species of *Ocypode*, *Coenobita* and *Birgus* (HARMS, 1932; VAN RABEN, 1934). Both are developments *de novo*. In terrestrial crabs, such as *Gecarcinus lateralis*, the pericardial sacs have become adjusted to function as sites of water storage. COPELAND (1968) suggests that the pericardial sac of *G. lateralis* transfers ground water to the gills for salt and water absorption, serves for water storage and assists—as a hydraulic—in shedding the old exoskeleton (see also BLISS, 1963 and BLISS and MANTEL, 1968). In species of *Oniscus* and other advanced land isopods, VERHOEFF (1917, 1920) demonstrated a series of water conducting channels, which run externally along both sides of the body from head to uropods, with cross channels on the pereion. This capillary system can pick up water from the substrate via the apposed uropods and conduct it to the respiratory surfaces on the pleopods. If no free water is available, regurgitated fluid may be conducted from the mouth to the pleopods to keep the respiratory surfaces moist (EDNEY, 1960). Some shore and land isopods are able to roll themselves into balls, e.g. species of *Sphaeroma*, *Armadillidium* and *Tolypeutes*. Such rolling helps to protect the softer, appendage-carrying subsurface from potential enemies and may also reduce water loss in dry

Table 4-80

*Cordylophora caspia*. Approximate number of ectoderm cells per hydranth body and per mm<sup>2</sup> hydranth body surface area. Genetically identical material, raised in the salinity-temperature combinations indicated (After KINNE, 1958a; modified)

Salinity (‰)	Approximate average number of ectoderm cells			
	per hydranth body		per mm <sup>2</sup> surface area	
	10° C	20° C	10° C	20° C
Fresh water	41,600	22,200	8,900	10,100
15	34,300	17,900	6,800	5,400
30	11,300	4,500	5,200	3,400

habitats; it is often accompanied by a relocation of eggs from the external brood pouch into internal brood sacs (HANSEN, 1905; KINNE, 1954c). For further information consult TERRESTRIAL ADAPTATIONS IN CRUSTACEA (1968).

In *Cordylophora caspia* from the 'Nord-Ostsee-Kanal' (Federal Republic of Germany), genetically identical hydranths, exposed for weeks to different salinities at 10° or 20° C, reveal significant differences in number of cells, dimensions of individual cells, and in size of nuclei and nematocysts (KINNE, 1958a). At 20° C, the approximate average cell number of a hydranth (ectoderm plus endoderm) is 40,000 in fresh water, 35,000 in 15‰S and 10,000 in 30‰S. Table 4-80 gives the number of ectoderm cells per hydranth body and per mm<sup>2</sup> hydranth body surface area for 6 combinations of salinity and temperature. In all cases, ectoderm cell number decreases with increasing salinity. There is no direct relationship between hydranth size and cell number, in the sense that large hydranths consist of more cells than small hydranths. Freshwater hydranths are smaller than 15‰S hydranths, but

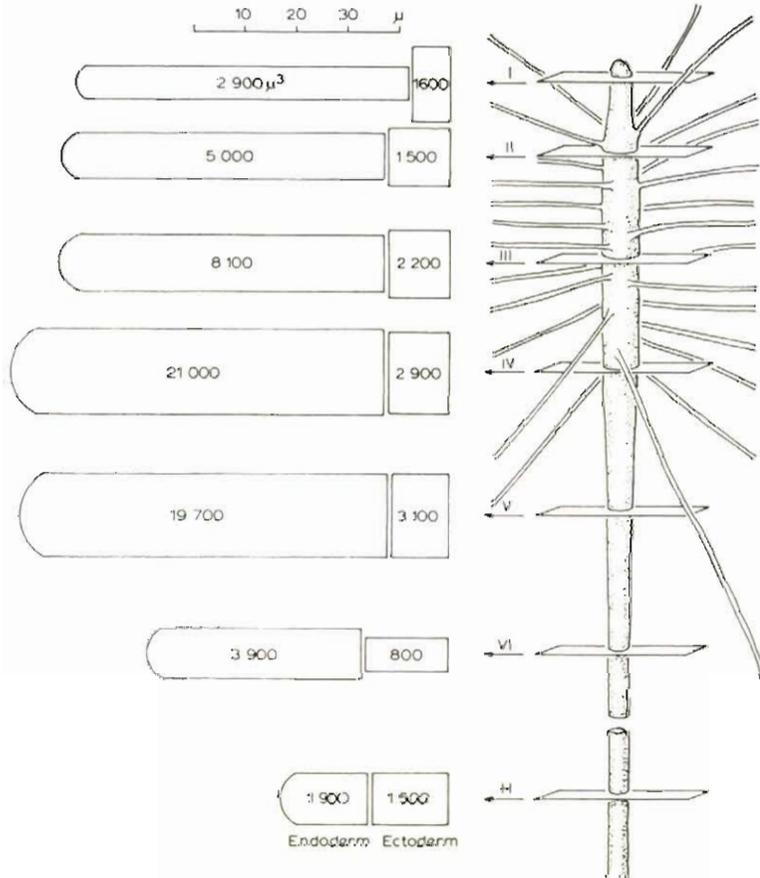


Fig. 4-161: *Cordylophora caspia* hydranth grown in 15‰S at 20° C. I to VI: regions of the hydranth body examined histologically; H: hydrocaulus. For each region, the typical height, width and volume of endo- and ectoderm cells are given; for cell height and width consult top scale. (After KINNE, 1958a; modified.)

they consist of considerably more cells. The changes in hydranth size and shape are primarily due to changes in cell dimensions.

Cell dimensions vary in different parts of the hydranth of *Cordylophora caspia*. In order to examine salinity-related differences in cell dimensions, six different hydranth regions and the hydrocaulus had to be investigated separately. Fig. 4-161 illustrates these different regions schematically in a hydranth grown in 15‰S at 20° C and gives the average height, width and volume for the ecto- and endoderm cells of each region. In hydranths grown at 20° C in different salinities, cell height decreases in regions I-V both in the ectoderm (Fig. 4-162) and in the endoderm (Fig. 4-163) with increasing salinity; the differences found in region VI and in the hydrocaulus are statistically insignificant. Cell width also shows pronounced changes; in the ectoderm, the cells grow wider with increasing salinity in regions I-V; in the endoderm they grow wider in regions III-V, but show little change in regions I and II. In summary, compared to their dimensions in an optimum salinity (15‰S), the cells of the main parts of the hydranth body become higher and narrower in a suboptimal salinity (fresh water) and lower and wider in a supra-optimal salinity (30‰S). This relation is illustrated in Fig. 4-164. Less pronounced but parallel salinity-dependent changes in cell dimensions occur at 10° C.

The surface to volume ratio of cells tends to increase somewhat with increasing salinity. The ratio free cell surface area (in ectoderm cells, the area in direct contact with the ambient medium, in endoderm cells, the area in direct contact with the enteron fluid) to cell volume has been determined for hydranth region IV (Table 4-81). It attains higher values in ectoderm than in endoderm cells and increases

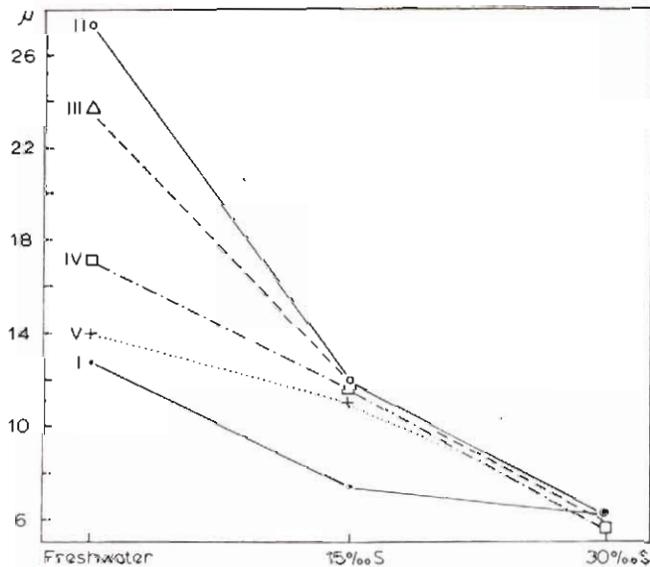


Fig. 4-162: *Cordylophora caspia* hydranths grown at 20° C in fresh water, 15‰ and 30‰S. Height of ectoderm cells in regions I to V (see Fig. 4-161). Genetically identical material. Each value represents the average of 70 measurements. (After KINNE, 1958a; modified.)

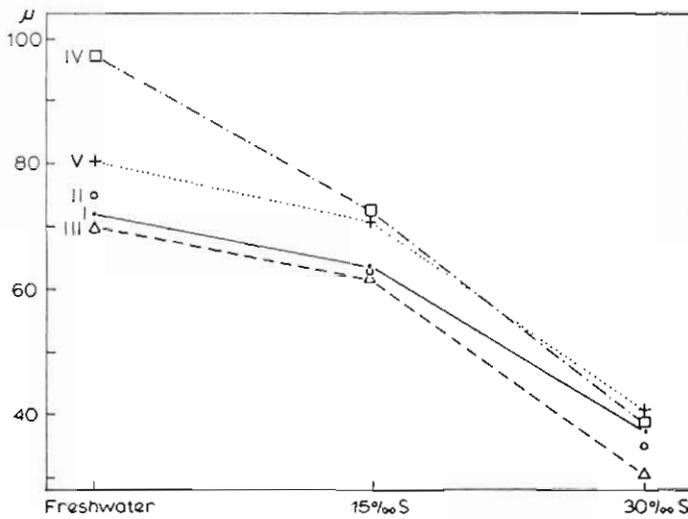


Fig. 4-163: *Cordylophora caspia* hydranths grown at 20° C in fresh water, 15‰ and 30‰ S. Height of endoderm cells in regions I to V. Genetically identical material. Each value represents the average of 70 measurements. (After KINNE, 1958a; modified.)

with increasing salinity. At 10° C the ratio is frequently smaller than at 20° C; this fact, however, is not evident from Table 4-81.

The diameter and volume of the nuclei increase with decreasing salinity, both in ectoderm and endoderm cells of the hydranth body (Table 4-82). In all test salinities, the nuclei are larger at 10° C than at 20° C. The volume relation nucleus: cell tends to increase with decreasing salinity in the ectoderm, but shows little change in the endoderm; at 10° C it is similar to, or larger than, at 20° C.

The length and width of the nematocysts of *Cordylophora caspia* change with salinity in the same way as the nucleus: they increase in suboptimal salinities and decrease in supra-optimal salinities (Table 4-83).

Table 4-81

*Cordylophora caspia*. Ratio free cell surface area to cell volume as a function of salinity in hydranth region IV. Genetically identical material, raised in the salinity-temperature combinations indicated. The average values presented are based on 70 measurements in each case (After KINNE, 1958a; modified)

Salinity (‰)	10° C		20° C	
	Ectoderm	Endoderm	Ectoderm	Endoderm
Fresh water	0.06	0.03	0.05	0.02
15	0.07	0.02	0.07	0.02
30	0.08	0.03	0.16	0.04

Table 4-82

*Cordylophora caspia*. Salinity effects on diameter and volume of nuclei and on the volume ratio nucleus: cell, at 20° C. Genetically identical material, raised in the salinities indicated. Each value is based on 70 individual measurements (After KINNE, 1958a; modified)

Hydranth region and Salinity (‰)	Nucleus diameter ( $\mu$ )*		Nucleus volume ( $\mu^3$ )		Volume ratio nucleus:cell	
	Ectoderm	Endoderm	Ectoderm	Endoderm	Ectoderm	Endoderm
<b>I Mouth region</b>						
Fresh water	5.12	3.46	70	22	0.03	0.01
15	5.09	3.26	69	18	0.04	0.01
30	4.56	3.09	50	16	0.03	0.01
<b>II Upper tentacle region</b>						
Fresh water	6.10	5.06	119	68	0.05	0.01
15	5.68	4.04	96	35	0.06	0.01
30	4.74	4.35	56	43	0.03	0.01
<b>III Middle tentacle region</b>						
Fresh water	6.19	6.17	125	124	0.05	0.02
15	5.45	5.25	85	76	0.04	0.01
30	4.85	4.98	60	65	0.03	0.01
<b>IV Lower tentacle region</b>						
Fresh water	5.94	5.77	110	101	0.09	0.01
15	5.26	5.12	76	70	0.03	0.003
30	4.76	4.90	56	62	0.02	0.004
<b>V Neck region</b>						
Fresh water	5.98	5.72	112	98	0.06	0.01
15	5.39	5.60	82	92	0.03	0.01
30	4.82	5.23	59	75	0.03	0.01
<b>VI Growth region</b>						
Fresh water	6.01	5.45	114	85	0.16	0.01
15	5.16	5.06	72	68	0.09	0.02
30	4.40	5.05	45	68	0.06	0.02
<b>Hydrocaulus</b>						
Fresh water	5.75	5.30	100	78	0.05	0.05
15	5.53	4.82	89	59	0.06	0.03
30	4.85	4.59	60	51	0.06	0.03

\*The increase in nucleus diameter with decreasing salinity is, in practically all cases, statistically significant for regions I-V ( $P \leq 0.01$ ) but not for

Table 4-83

*Cordylophora caspia*. Length and width of nematocysts from tentacles. Genetically identical material, raised in the salinity-temperature combinations indicated. Average values of 70 individual measurements.  $P$  = rounded off  $P$ -values (After KINNE, 1958a; modified)

Salinity (‰)	10° C				20° C			
	Length $\mu$	$P$	Width $\mu$	$P$	Length $\mu$	$P$	Width $\mu$	$P$
Fresh water	7.65		3.46		7.00		2.91	
15		0.008		0.02		0.009		0.01
	6.97		3.21		6.62		2.86	
		0.01		0.008		0.002		0.003
30	6.58		2.95		6.03		2.69	

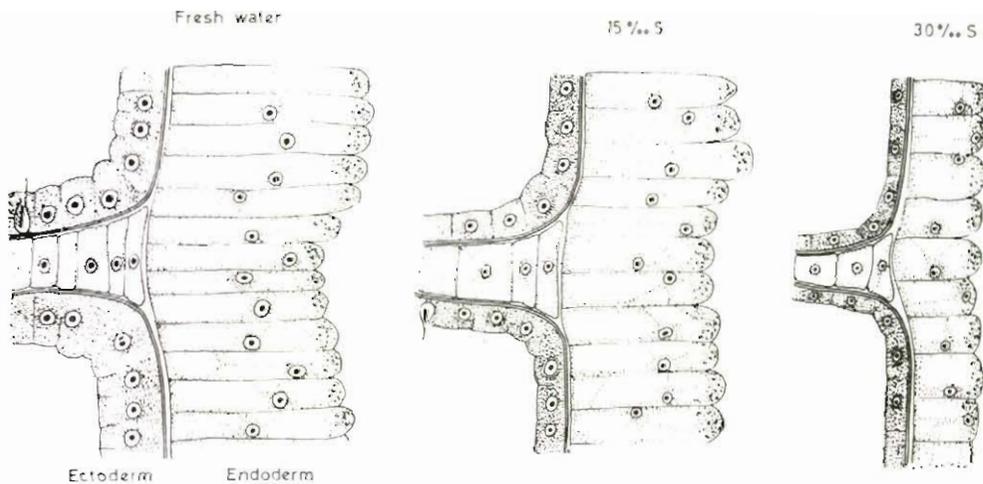


Fig. 4-164: *Cordylophora caspia*. Influence of salinity on cell dimensions at 20° C (hydranth region IV). Longitudinal sections. Genetically identical material. (After KINNE, 1958a; modified.)

A schematic summary of the most important structural consequences of salinity stress in *Cordylophora caspia* is presented in Fig. 4-165. Dimensions and numbers of cells determine shape and size of hydranths and these, in turn, largely determine shape and size of the colonies. The differences in cell dimensions and in nucleus size, together with parallel differences in colony growth rates, suggest alterations in cell metabolism. The columnar cells of the freshwater raised hydranths with their big nuclei indicate high metabolic activity. In higher invertebrates and vertebrates, columnar epithelia with large nuclei are known to occur in places where increased active transport (e.g. of water and/or salt) and other metabolic work is required. In *C. caspia*, increase of cell number per hydranth surface area, reduction of free cell surface area, increase of cell height and of nucleus size in fresh

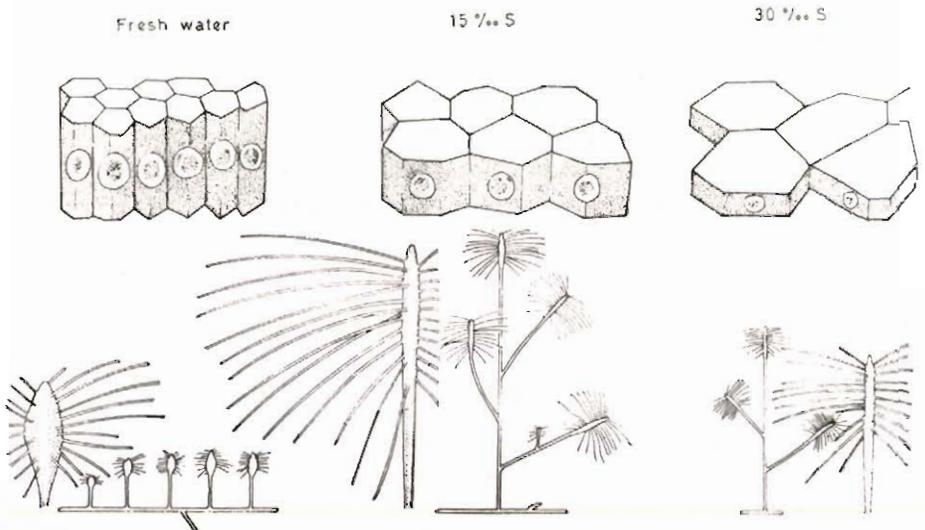


Fig. 4-165: *Cordylophora caspia*. Schematic illustration of the most important structural consequences of salinity stress. (After KINNE, 1958a; modified.)

water can be interpreted as structural adjustments to hypo-osmotic stress. In contrast, reduction in cell number per hydranth surface area, increase in free cell surface area, flattening of cells and decrease of nucleus size in 30‰S seem indicative of increased passive exchange diffusion and reduced cellular metabolism. It would be of interest to examine *C. caspia* cells under salinity stress for possible alterations in subcellular structures, as well as in regard to their biochemistry. More complete discussions of the results reported have been presented by KINNE (1956b, 1958a; see also KINNE, 1957a, 1958b).

HOOP (1940) investigated structural aspects of mantle tissues in euryhaline lamellibranchs from habitats with different salinity regimes. He used 88 *Mya arenaria*, 105 *Cardium edule*, 95 *Macoma baltica* and 142 *Mytilus edulis* from the North Sea (ca 32‰S), the Baltic Sea (ca 18‰S) and the Schwentine Estuary, Kiel Bay of the Baltic Sea (less than 10‰S). While Hoop could not find differences in lamellibranchs from the North Sea and the Baltic Sea, he reported that *Mya arenaria* and *Cardium edule* from the Schwentine Estuary have, on an average, a lower mantle epithelium than their counterparts from the North Sea and the Baltic Sea. In most individuals from the Schwentine, he found, furthermore, reduced mucus glands. In view of the pronounced individual differences recorded by Hoop, and the fact that the three habitats not only differ in regard to their average salinity, but also with respect to salinity fluctuations, temperature and other factors, his findings require confirmation.

In the brine shrimp *Artemia salina*, chromosome number may be related to salinity conditions. The fact that chromosome numbers differ in different forms or races of *A. salina* had already been noted by ARTOM (1911). The diploid chromosome number is 42: bisexual races are diploid; the polysomic, parthenogenetic races were found to be di-, tri-, tetra-, penta- and, possibly, even octoploid. GROSS (1932) has claimed that the tendency toward polyploidy (via automixis) increases in high

salinities (see also p. 983). LA MARCHE and co-authors (1969) compared chromosome preparations of various Californian (USA) races of *A. salina*. In San Francisco race no. 3 and in the Utah race, they found different chromosome numbers in different tissues; reproductive isolation of the different races could not be demonstrated unequivocally.



## 4. SALINITY

### 4.3 ANIMALS

#### 4.32 FISHES

F. G. T. HOLLIDAY

##### (1) Introduction

This subchapter emphasizes responses to salinity of whole fishes rather than physiological and biochemical responses of specific tissues. Changes in specific organs or tissues or, for example, in blood osmoconcentration are referred to, in general, as indicators of the responses of the whole fish; total rates of urine flow may be quoted, but the underlying glomerular and tubular mechanisms are not described. They will be treated, together with physiological and biochemical mechanisms and specific sites of water and salt regulation, in Volume II of this Treatise. In regard to structural responses, changes in tissues concerned with salinity regulation are, however, discussed.

Although most of the literature available refers to adult fishes, a good deal of emphasis will be placed on egg and larval stages. The responses to salinity are often different at these stages, and are frequently based on different mechanisms, than in the adult individual.

Many of the studies selected to exemplify typical responses to salinity variations are related to (i) the economic importance of fish which at some stage in their life histories are likely to be influenced by a change in salinity; (ii) the scientific importance of the information, especially if it provides at the same time convenient material for the assessment of commercial situations; (iii) the fact that the early vertebrates evolved in marine conditions (ROBERTSON, 1957; WHITE, 1958), while the teleosts evolved in fresh water (SMITH, 1932). Indications of these ancestries are found in present-day fishes.

##### (2) Functional Responses

###### (a) Tolerance

The ability to tolerate water of a particular salinity varies, amongst other things, with the stage of development of the fish. It has now been well established that the developing eggs and newly hatched larvae of some marine teleosts can tolerate extremely wide ranges of salinity. For example, in the laboratory, the eggs of the herring *Clupea harengus* can be fertilized, incubated and hatched in salinities ranging from 5.9‰ to 52.5‰ (HOLLIDAY and BLAXTER, 1960). BATTLE (1930) reared *Enchelyopus cimbrius* in salinities as high as 70‰. In nature, BARLOW (1958) found that *Cyprinodon macularius* was able to survive in salinities of up to 90‰, and RENFRO (1960) reported that the eggs of *Cyprinodon variegatus* would hatch in a salinity of 110‰. In the Black Sea, eggs of the flounder *Pleuronectes flesus* hatch

in rock pools with salinities as high as 50.2‰ (ZAITSEV, 1955). VON WESTERHAGEN (1970) examined the relationship between egg development and combined salinity and temperature conditions in *Gadus morhua*, *Pleuronectes flesus* and *Pleuronectes platessa*. Optimum conditions of development were: in *G. morhua* 20‰ to 33‰S and 4° to 8° C, in *P. flesus* 33‰S and 4° C, and in *P. platessa* 20‰S and 6° C. Salinity and temperature are interrelated, in that low salinities are tolerated best at optimum (or lower) temperatures.

Eggs of other teleost species develop in areas subject to rapid fluctuations in salinity, for example, Pacific salmon (*Oncorhynchus gorbusha* and *Oncorhynchus keta*) frequently spawn in the intertidal gravel; this is especially true in the streams of S.E. Alaska, where these fishes spawn in the intertidal zone even when freshwater spawning grounds are available (HELLE and co-authors, 1964). ROCKWELL (1956) showed that normal percentages of the eggs of *O. gorbusha* and *O. keta* were able to develop when the salinity during fertilization did not exceed 18‰; salinities above 24‰ reduced the rate of successful fertilizations, but even at a salinity of 30‰ fertilization was possible in some eggs. ROCKWELL suggested that the eggs were isosmotic with a salinity of about 12‰. He also showed that hatching was most successful in terms of percentage hatch, and length of time from fertilization to hatching, in salinities ranging from 6‰ to 24‰.

Changes in the ability to survive extreme salinities are linked with both age and size. The yolk sac larvae of many species are especially tolerant. HOLLIDAY (1965) reported an upper level of tolerance (defined as 50% of the larvae being able to survive and remain active for at least 24 hrs) for yolk sac larvae of *Clupea harengus*, *Pleuronectes platessa* and *Gadus callarias* of 60‰ to 65‰S. Tolerance to low salinities at this stage varied from 1.4‰ in *Clupea harengus* to 10‰ in *Gadus callarias*. CONTE and co-authors (1966) studied the changes in the ability to survive in water of high salinity in *Oncorhynchus kisutch*. The results of this work are summarized in Fig. 4-166 (a, b). The eggs of this species hatch in fresh water; the ability to survive in relatively high salinities begins very soon after the end of the period of yolk-sac absorption, thus preceding seaward migration of these juvenile stages by some 6 to 7 months; it persists beyond the end of the migration period, and in this respect differs from, for example, the steelhead trout *Salmo gairdnerii* (CONTE and WAGNER, 1965). The larger individuals of *O. kisutch* showed a greater ability to survive; size rather than age was the key factor in this respect.

KURATA (1959) and HOLLIDAY (1965) studied the effects of age on the survival in different salinities of larval and juvenile stages of 3 species of marine teleosts (Fig. 4-167). The reader is referred to the section on *Metabolism* (p. 1001) for a discussion of some of the regulatory processes that underlie this changing pattern of survival. Following abrupt transfer from sea water (32‰ to 34‰S) to water of a salinity of 50‰, the tissues of the yolk-sac larvae of *Clupea harengus* were able to tolerate for periods of 3 to 6 hrs an internal osmotic concentration equivalent to a salinity of 22.5‰ (normal level for body fluids is equivalent to about 12‰S). The yolk-sac larvae of *Pleuronectes platessa*, when similarly transferred, showed tissue tolerances up to 30‰S. In both fishes, regulation takes place within 24 hrs following the transfer, returning body fluids to concentrations equivalent to about 15‰S.

A primary cause of death in extreme salinities is the attainment of blood and body-fluid levels, which are not tolerated by the tissues. There is evidence that

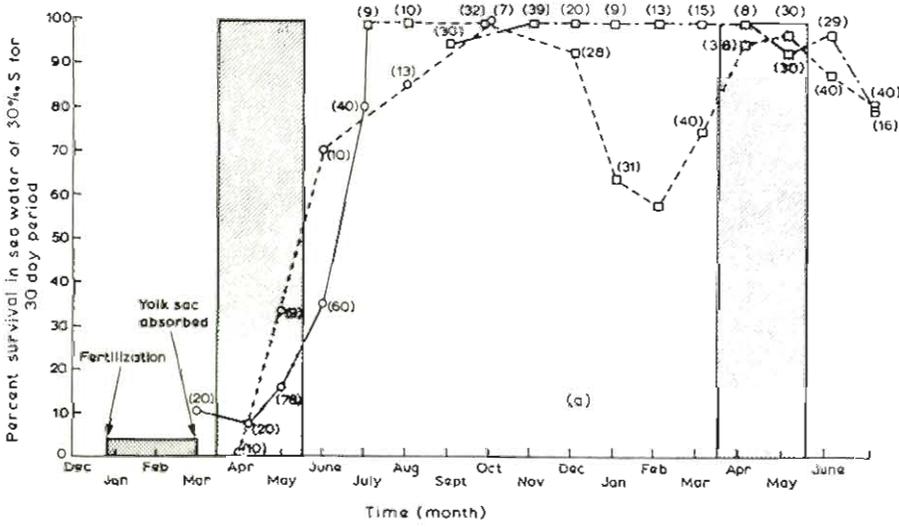


Fig. 4-166(a): Chronological development of sea-water adaptation by juvenile coho salmon *Oncorhynchus kisutch*, expressed as per cent survival. Responses of two different size classes: ○ 3-8 cm, □ 9-15 cm; ( ) total number of fish tested; brood year: ···· 1963, --- 1964, — 1965. Screened area (left, bottom); period of embryonic development; hatched areas: period of seaward migration. (After CONTE and co-authors, 1966; modified.)

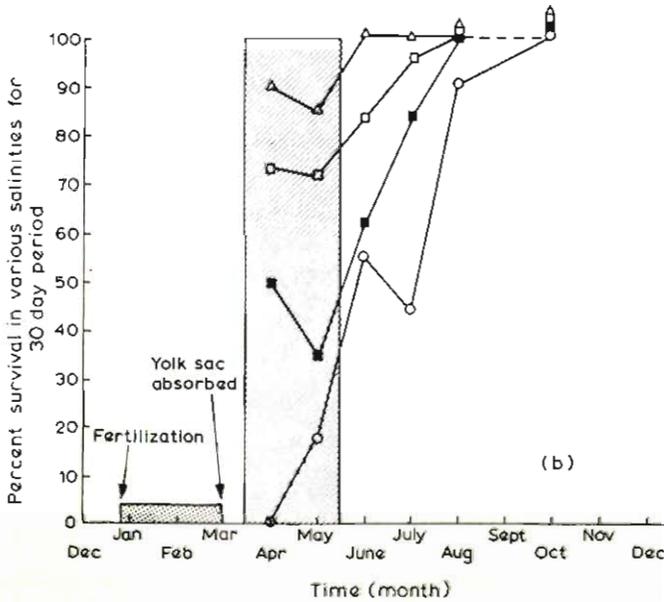


Fig. 4-166(b): Chronological development of sea-water adaptation by juvenile *Oncorhynchus kisutch*, expressed as per cent survival. Responses to different salinities: ○ 30‰, ■ 28‰, □ 26‰, △ 24‰. See also legend to Fig. 4-166(a). (After CONTE and co-authors, 1966; modified.)

the nervous system may be less able to tolerate internal changes in osmoconcentration than other systems. It is possible that the relatively undifferentiated cells of the embryo and early larva are more tolerant than the highly specialized tissues of the later larva and young fish.

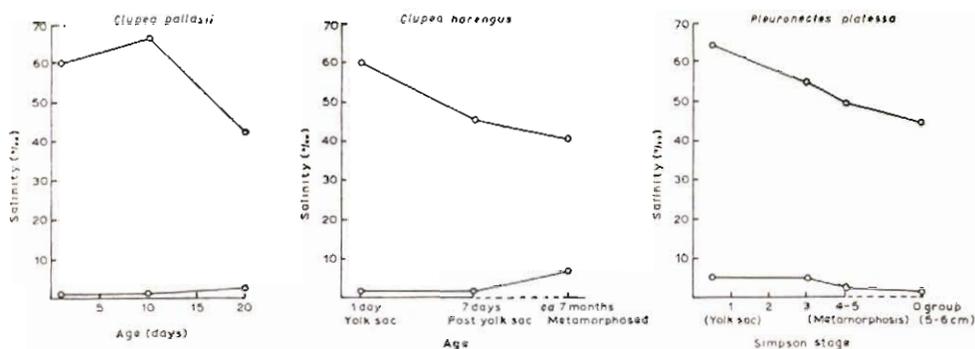


Fig. 4-167: The effects of age on salinity tolerance in *Clupea pallasii*, *C. harengus*, and *Pleuronectes platessa*. The experiments were based on the  $LD_{50}$  principle; the circles are the mean of 10 experiments with 10 larvae. The upper and lower lines represent the levels of tolerance to high and low salinities. (Left diagram after KURATA, 1959, the other two after HOLLIDAY, 1965; redrawn.)

Changing patterns of regulation, and changing abilities to tolerate, are both important factors in determining the ultimate limits of survival.

It is difficult to generalize on the question of the survival in different salinities of adult fishes. Clearly, fish such as *Lampetra fluviatilis*, *Salmo salar*, *Gasterosteus aculeatus* and *Anguilla anguilla* during the course of their adult life are able to tolerate both completely freshwater and completely marine conditions, although there is a change-over in regulatory patterns and tolerance capacities which coincides with and often precedes migrations from one medium to another (CONTE and co-authors, 1966). *Lampetra fluviatilis*, once the change-over following migration from sea water to fresh water has occurred, can no longer survive in sea water (MORRIS, 1956). This fish passes through different physiological conditions during its life history; hence it is difficult to find a simple definition of its tolerance to salinity applicable throughout its adult life. A number of lists have been compiled of species which are capable of surviving certain salinity changes at specific times during their life (e.g. GUNTER, 1938, 1942, 1956; SCHWARTZ, 1964; ALTMAN and DITTMER, 1966). The length of some of these lists (there are 107 species listed by ALTMAN and DITTMER) indicates the difficulty of assessing this aspect of fish tolerance. Survival is based on a combination of tissue tolerance, regulation and physiological state. Although the general patterns have been discussed repeatedly (reviews: BLACK, 1957; PROSSER and BROWN, 1965; PARRY, 1966), our present knowledge is based on relatively few species.

The highest salinity at which living adult fish (*Cyprinodon variegatus*) have been found under field conditions is 142.4‰ (SIMPSON and GUNTER, 1956).

Some measurements have been made on the rate at which fish respond physiologically to a change in salinity. In some instances, for example *Blennius pholis* (HOUSE, 1963) and *Fundulus heteroclitus* (POTTS and EVANS in: PARRY, 1966), a

response has been recorded after a few minutes; however, complete adaptation in terms of a stabilized blood concentration takes at least 1 hr in *Platichthys flesus* (MOTAIS, 1961a, b), 50 hrs in *Anguilla anguilla* (KEYS, 1933) and 80 to 170 hrs in *Salmo gairdnerii* (HOUSTON, 1959). Of course, such response rates are a function of temperature and may be affected also by other environmental factors.

The rate of gill sodium flux adjustments is dependent on the direction of salinity change. Thus, when *Pleuronectes flesus* is transferred from sea water to fresh water, there is an 80 to 90% reduction in outflux within 20 to 30 mins, followed by a second reduction complete within 12 hrs. Adaptation after a change from fresh water to sea water is dependent on the period spent in fresh water, and 2 to 3 days may be necessary for complete adaptation (MOTAIS and MAETZ, 1964; MOTAIS, 1967). In *Fundulus heteroclitus*, a transfer from sea water to fresh water leads to instantaneous influx adjustment of the level of long-term adaptation to fresh water; however, in *Anguilla anguilla*, sodium influx is lower at transfer and several days are needed for adjustment (MAETZ and co-authors, 1967a, b).

### (b) Metabolism and Activity

#### *Metabolism*

The assessment of salinity effects on oxygen uptake is complicated by the fact that the oxygen content of the water depends (amongst other things) on its salinity; the higher the salinity the lower the oxygen content. As oxygen uptake of fishes is, to a large extent, governed by the concentration of oxygen in the water, it is often difficult to determine the responses due strictly to salinity; this problem has been fully discussed by KINNE (1964a; see also Chapter 9.3).

A further complicating factor is that asphyxiation may occur in fish placed in high salinities, for example in the tench *Tinca vulgaris* (CORDIER and MAURICE, 1957). This asphyxiation may have been the result of damage to the epithelial surfaces of the gills inhibiting oxygen transference, and again the effects of the salinity are not strictly metabolic (see also the pertinent discussion by KINNE, 1956a).

Finally, differences in salinity modify the specific gravity of the water and thus may result in differences in swimming effort and activity levels (see section on *Activity*, p. 1020) due to changes in buoyancy of the fish. Differences in buoyancy may again be reflected in changes in oxygen uptake (see also Chapter 4.31).

There are few data available on the effects of salinity on the oxygen uptake of fish eggs and larvae. The little information at hand suggests that, if eggs and larvae live in a salinity in which they can survive for long periods and to which they are fully adjusted, there are no measurable changes in oxygen uptake at different salinity levels. Using a sensitive reference diver technique, LASKER and THEILACKER (1962) found no differences in oxygen uptake in eggs and larvae of *Sardinops caerulea* in sea water, half sea water or double-strength sea water. HOLLIDAY and co-authors (1964), using the same and other techniques on the eggs and larvae of *Clupea harengus* in salinities of 5‰, 15‰, 35‰ and 50‰, observed differences in oxygen uptake only during the period after transfer when osmotic changes were taking place in the body fluids (Fig. 4-168). After body fluid regulation was complete, oxygen uptake returned to normal.

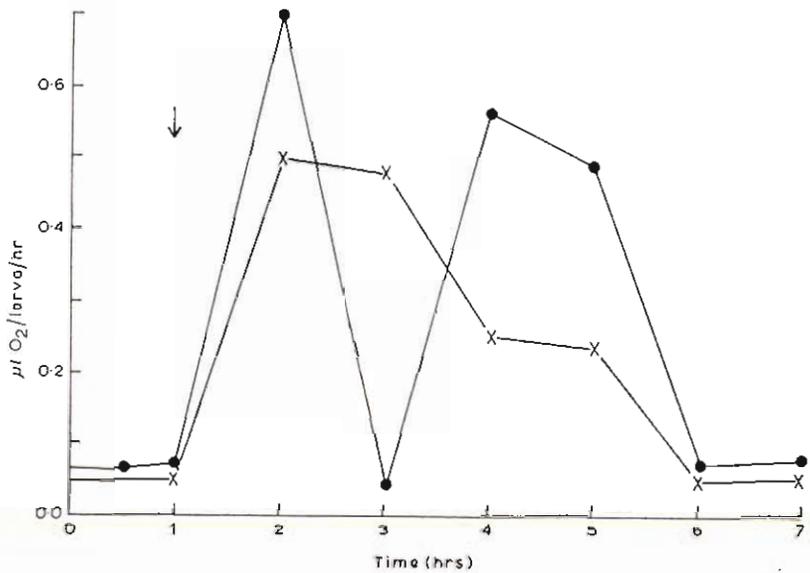


Fig. 4-168: Effect of abrupt salinity change on oxygen uptake at 8°C of anaesthetized embryos and larvae of the herring *Clupea harengus* X—X (just prehatched); ●—● (newly hatched). Arrow shows when transfer from 35‰ to 5‰ S took place. (After HOLLIDAY and co-authors, 1964; redrawn.)

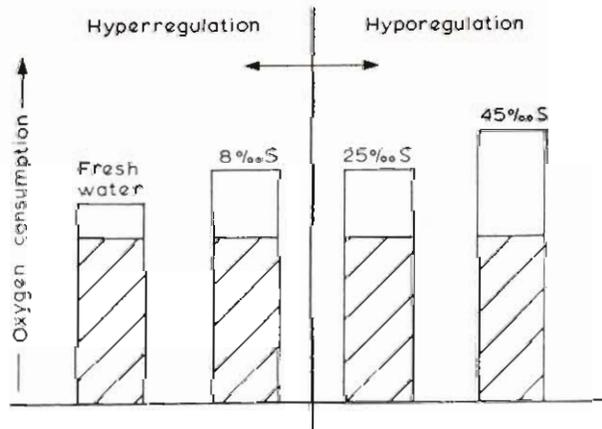


Fig. 4-169: Diagram of relative energy demands of the starry flounder *Platichthys stellatus*, in hypo-osmotic and hyperosmotic media. Oxygen consumption for basal cellular metabolism other than processes connected with osmoregulation are represented by the lower hatched areas of the columns. This portion is assumed to be unaffected by changes in salinity. The upper clear areas represent variable oxygen demands for osmoregulation. (After HICKMAN, 1959; redrawn.)

The study by HICKMAN (1959) on the oxygen uptake of *Platichthys stellatus*, *Parophrys vetulus* and *Citharichthys stigmaeus* reports some of the most interesting responses of postlarval and adult fish to salinity changes. Relatively small changes in salinity produce no measurable effects on the standard metabolism of *Platichthys stellatus*; however, if this fish is transferred from sea water to fresh water there is a significant drop in metabolic rate, which persists even after the fish has become adapted to the fresh water. The percentage decrease depends on the body size of the fish; it is greater in small than in large individuals. HICKMAN also found that metabolic rates of *Platichthys stellatus* in salinities above 35‰ are significantly greater (ca 15%) than in normal sea water. It is not clear in this case whether body size influences metabolic rate. Similar results were obtained with *Citharichthys stigmaeus*, in which increased salinity is accompanied by an increase in oxygen uptake, and the smaller individuals again show a greater percentage response than the larger ones. Both *Platichthys stellatus* and *Citharichthys stigmaeus* live normally in conditions where salinity might be expected to fluctuate; HICKMAN therefore compared the responses of these fishes to those of *Parophrys vetulus*, which can be regarded as a comparatively stenohaline marine fish. When *P. vetulus* was transferred from 35‰ to 58‰S (in which it would be expected to survive for less than 1 week) there was no change in oxygen uptake. HICKMAN's results and his interpretations are summarized in Fig. 4-169.

In regard to respiratory responses to changes in salinity, there are a number of conflicting accounts in the literature. Thus JOB (1959), working with the marine catfish *Plotosus anguillaris*, found a considerable increase in oxygen uptake in both young and adult individuals in sea water as compared to individuals living in water of low salinity. He interpreted this as being due to the increased metabolic cost of osmotic regulation. In contrast, RAFFY (1932, 1933, 1955), BULLIVANT (1961) and GORDON and co-authors (1965) found that salinity has no effect on the oxygen consumption of *Pleuronectes platessa*, *Oncorhynchus tshawytscha* and *Periopkthalmus sobrinus*.

It has so far proved difficult to obtain actual measurements of the energy used by the organs responsible for osmotic and ionic regulation in fish whilst under different conditions of stress. HOLMES and STOTT (1960) transferred *Salmo clarki clarki* acclimated to fresh water into 65‰ sea water, and then measured oxygen uptake of the kidney and gill tissues isolated from the transferred fish. The  $QO_2$  of the kidney tissue increased during the first 48 hrs following transfer, and remained significantly higher than in the controls staying in fresh water throughout the experiment, while the gill tissue responded with a decrease in oxygen uptake after transfer (Fig. 4-170a, b). HOLMES attributed the results, firstly to a rise in some antidiuretic processes of the kidney tubules, and secondly to the inhibition of the extrarenal sodium re-uptake mechanism, suggesting that this inhibition might be a factor in enhancing net sodium output.

Clearly, there is need for more experimental work on the metabolic costs of ion and osmoregulation. It is important in such studies to use homogeneous material and to pay attention to a number of other factors (WINBERG, 1956; FRY, 1957; BRETT, 1962). Genetic and environmentally induced variations can be minimized when the test fish are obtained from a given set of parents and raised under controlled environmental conditions (e.g. KINNE, 1962, 1964a, b).

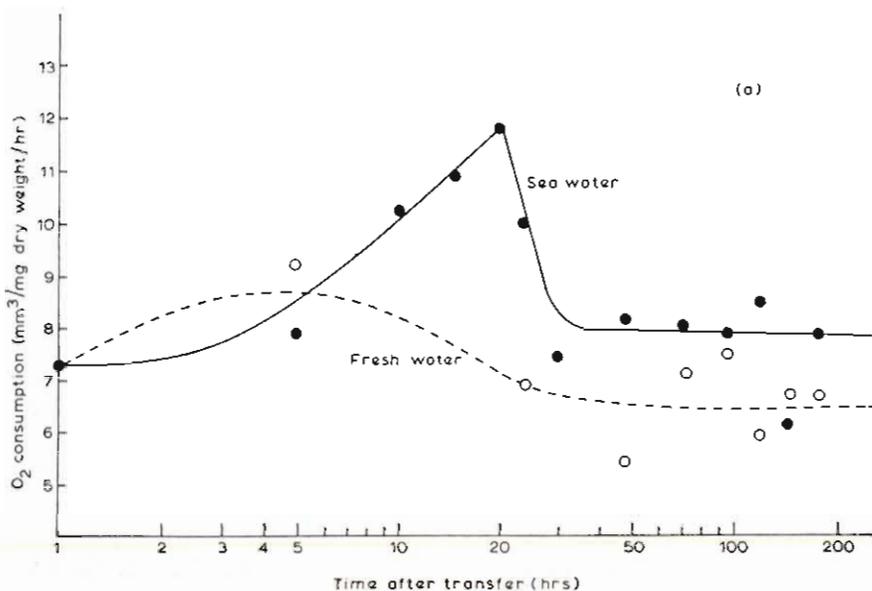


Fig. 4-170(a): Oxygen consumption of kidney tissue of cutthroat trout *Salmo clarki clarki* after transfer of the fish from fresh water into 65% sea water. (After HOLMES, W. N., and STOTT, G. H. 1960; modified.) Studies on the respiration rates of excretory tissues in the cutthroat trout (*Salmo clarki clarki*). II. Effect of transfer to sea-water. *Physiol. Zool.*, 33, 15-20. Copyright 1960 by the University of Chicago.

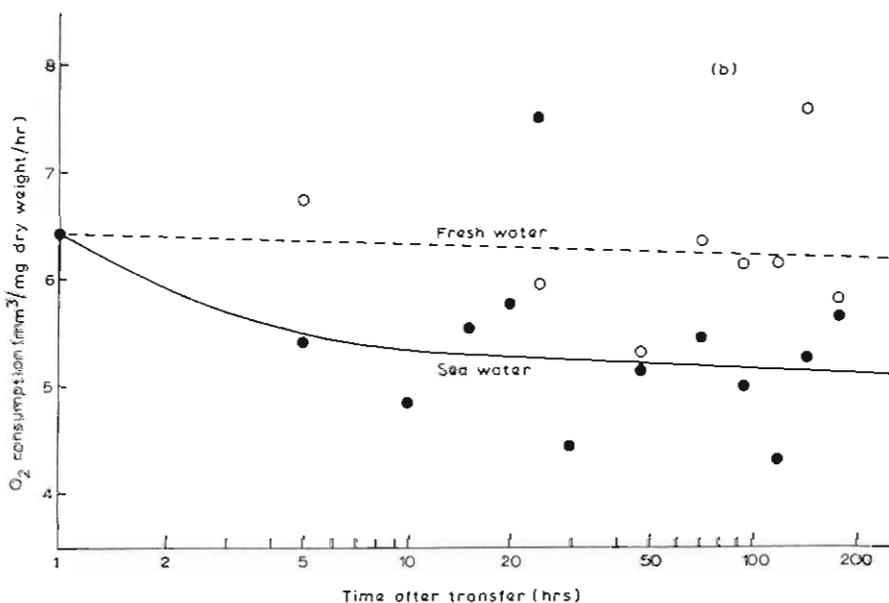


Fig. 4-170 (b): Oxygen consumption of gill tissue of cutthroat trout *Salmo clarki clarki* after transfer of the fish from fresh water into 65% sea water. See Fig. 170 (a). (After HOLMES and STOTT, 1960; modified.)

CANAGARATNAM (1959) reviewed the growth of fishes living in nature under different salinity conditions. He compared 11 species which occur in 2 or 3 habitats of different salinity and compared their sizes at maturity (Table 4-84). With the exception of *Osmerus mordax*, the larger members of the species were found in the most saline environment. A considerable amount of experimental evidence supports this conclusion. FOERSTER (1947) reared *Oncorhynchus nerka kenneerlyi* from eggs and released marked individuals at the yearling stage into an outlet stream to the sea. When 25 of these individuals were recaptured 4 years later they were found to be significantly larger than fish that had spent the corresponding period in fresh water. GIBSON and HIRST (1955), in experiments on juvenile *Lebistes*

Table 4-84

Sizes of adult fishes living in marine, brackish and freshwater environments. The precise stage of maturity is usually not given in the literature; sizes are mostly those of mature fish taken in a commercial or sport fishery. References quoted from CANAGARATNAM (1959)

Species	Marine	Brackish	Freshwater	Authors
<i>Coregonus clupeaformis</i> (whitefish)		403-466 mm 1359-1812 g		RAWSON (1946)
		479 mm, 2038 g (Redberry Lake, Saskatchewan)		RAWSON (1946)
			1132-1585 g (Lake Winnipeg, Manitoba)	HINKS (1943)
<i>Lates calceifer</i> (giant perch)	263 g (Bay of Bengal)	27-45 g (Australian estuaries)		ROUGHLEY (1953)
		1500 mm (Australian estuaries)		MUNRO (1955)
<i>Salmo gairdnerii</i> <i>gairdnerii</i> (steel- head trout)	1134 mm** (British Columbia)			CLEMENS and WILBY (1949)
<i>Salmo gairdnerii</i> <i>kamloops</i> ( <i>Kamloops</i> )			907 mm <sup>b</sup> (British Columbia)	CARL and CLEMENS (1953)
<i>Oncorhynchus</i> <i>nerka nerka</i> (sockeye)	830 mm (British Columbia)			CARL and CLEMENS (1953)
<i>O.n. kenneerlyi</i> (kokanee)			185-245 mm (Kootenay Lake, British Columbia)	VERNON (1957)

\*\*Maximum size on record

Table 4-84—Continued

Species	Marine	Brackish	Freshwater	Authors
<i>Chanos chanos</i> (milkfish)			600-1500 mm (Hawaiian fresh-water ponds)	JORDAN and EVERMANN (1903)
	1800 mm (Gulf of Mannar, Indian Ocean)			MUNRO (1955)
	Over 1500 mm (Indian Ocean)			WEBER and BEAUFORT (1913)
	1500 mm (Australian estuarine waters)			ROUGHLEY (1953)
	257 mm* (Krusadai, India)	403 mm* (Mandapam Camp, India)	604 mm* (Rameswaram, India)	CHIDAMBARAM and UNNY (1946)
<i>Clupea harengus</i> (Atlantic herring)	240-350 mm (Atlantic Ocean)	160-200 mm (Baltic Sea)		HODGSON (1934)
<i>Salmo salar</i> (Atlantic salmon)	480 mm (Nova Scotia)		350 mm (Grand Lake, Nova Scotia)	WILDER (1947)
<i>Pomolobus pseudoharengus</i> (alewife)	258 mm		145 mm (Lake Ontario)	PRITCHARD (1929)
<i>Osmerus mordax</i> (smelt)	150-250 mm (New Brunswick)		150-250 mm	McKENZIE (1946) DYMOND (1944)
<i>Salvelinus fontinalis</i> (eastern brook trout)	334 mm (New Brunswick)		274 mm (New Brunswick)	WILDER (1952)

\*These measurements were taken after only one year's growth of the milkfish in the various experimental ponds

*reticulatus*, showed that salinities of 25% sea water could produce faster growth than fresh water. *Oncorhynchus kisutch* and *Oncorhynchus nerka* grew more rapidly in saline water than in fresh water (CANAGARATNAM, 1959; Fig. 4-171). Seeking an explanation for his findings, CANAGARATNAM suggested that a fish living in fresh water must expend more energy than a marine fish to maintain osmotic gradients. This explanation is not easily reconciled with the results discussed previously, which indicate that oxygen uptake, at least in some fish, was less in fresh water.

KINNE (1960) made a detailed study of growth, food intake and food conversion in *Cyprinodon macularius* and his results may be used to illustrate the effects of salinity on fish-growth patterns. The experiments were performed using fresh

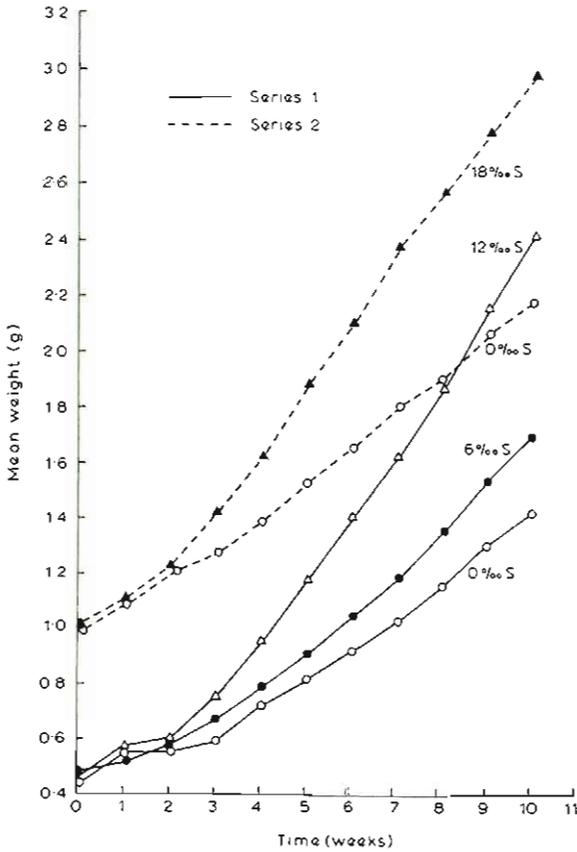


Fig. 4-171: Mean weekly wet weight of coho salmon *Oncorhynchus kisutch* in different salinities. (After CANAGARATNAM, 1959; modified.)

water, 15‰S (obtained by diluting sea water with fresh water), sea water (34‰ to 35‰S) and 55‰S (obtained by evaporation of sea water without heating). The salinities of 15‰ and 35‰ were nearest to the salinity optima of the population of *Cyprinodon macularius* used, and a temperature of 30° C was closest to the optimum temperature for the young of this fish. *C. macularius* were allowed to feed to satiation once per day. At 30° C, the fish grew at their greatest rate in 35‰S, and growth rates decreased in the order 35‰, 15‰, 55‰S and fresh water (Fig. 4-172). As KINNE points out, the effects of temperature and salinity acting together are of particular ecological and physiological interest; he was able to show that, in all 4 salinities tested, young *Cyprinodon macularius* grow best at 30° C; at low temperatures (15° and 20° C) the fish grow fastest in fresh water; at high temperatures of 30° and 35° C the fish grow fastest in 35‰ and 55‰S. Some of these relations are shown diagrammatically in Fig. 4-173. In seeking the explanation for these effects of salinity on growth, KINNE first noted that the actual food intake in the different salinities follows the same pattern as does the growth, i.e. most food is eaten in 35‰S, less in 15‰ and 55‰S, and least (less than half the amount eaten in sea

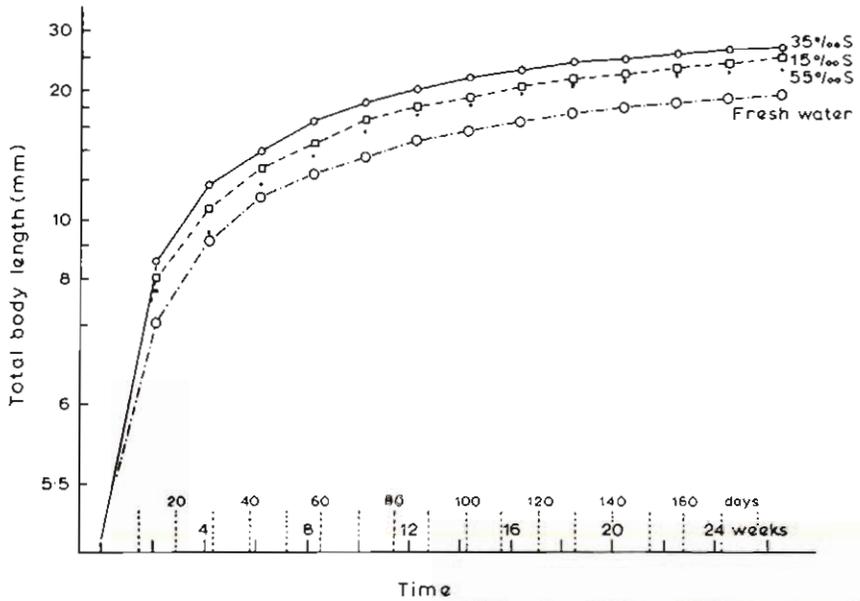


Fig. 4-172: Growth of *Cyprinodon macularius* in 4 different salinities at 30°C under restricted food supply. Each value represents the average total length of 12 individuals. All fish were raised under the given conditions. (After KINNE, O., 1960; redrawn.) Growth, food intake and food conversion in a euryplastic fish exposed to different temperatures and salinities. *Physiol. Zool.*, **33**, 288–317. Copyright 1960 by the University of Chicago.

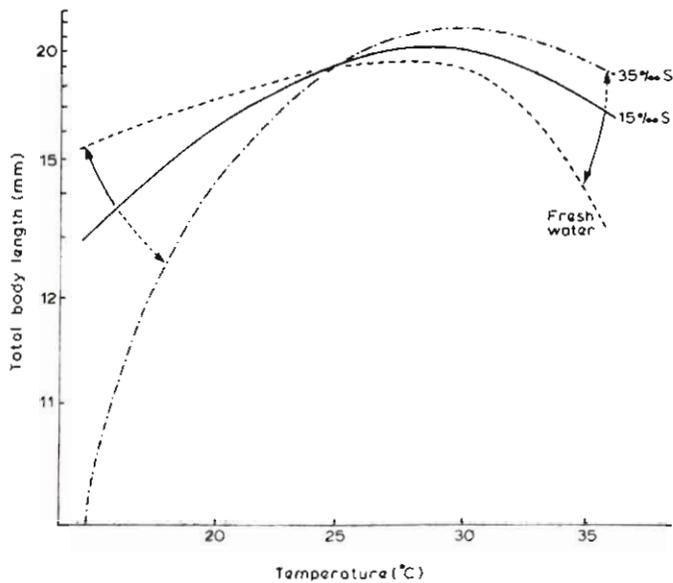


Fig. 4-173: Diagram of temperature-salinity relations in 12-week old *Cyprinodon macularius*. The curves are based on data obtained on fish raised under the given conditions. The temperature-growth curve, established for fish in a salinity of 15‰, rotates clockwise in lower salinities and counterclockwise in higher salinities. The curves intersect at approximately 25°C. See Fig. 4-172. (After KINNE, 1960; redrawn.)

water) in fresh water. These differences in food intake and growth are apparent no matter whether the food supply is restricted, as previously described, or unrestricted. It appears, therefore, that appetite drive is affected by salinity.

It is interesting to note in relation to KINNE's (1960) findings that BENNETT (personal communication), working on *Carassius auratus*, found a conditioned response to a light stimulus (using food as the unconditioned stimulus) to be performed more successfully when the salinity was raised from fresh water to 3‰; the conditioned response is still higher than the level of the control in fresh water when the salinity in the experimental tank was raised to 6‰.

KINNE (1960) went on to study the efficiency of food conversion (increase in dry weight of fish in relation to dry weight of food eaten). At a temperature of 30° C, and under conditions of restricted food supply, conversion efficiency attains a maximum level in a salinity of 15‰; it is less in 35‰ S and less still in fresh water (Fig. 4-174). There was evidence to show that the same trend is also true when fish are fed an unrestricted diet.

The effects of salinity on the oxygen uptake and on the growth of fish has been interpreted as being due, at least in part, to the different demands made on the metabolism of the fish by the regulatory mechanisms involved in adaptation to the environment.

The general pattern of regulation of blood and other body fluids to counteract osmotic and ionic changes resulting from a change in salinity is now well established, particularly for postlarval stages of fishes. Less is known in regard to developing eggs; but HOLLIDAY and JONES (1965, 1967) showed that the regulatory responses of the eggs of herring *Clupea harengus* and plaice *Pleuronectes platessa* are markedly different. The differences become apparent within 1 hr of fertilization. In *Clupea harengus*, the yolk is practically isosmotic with the medium 1 hr after

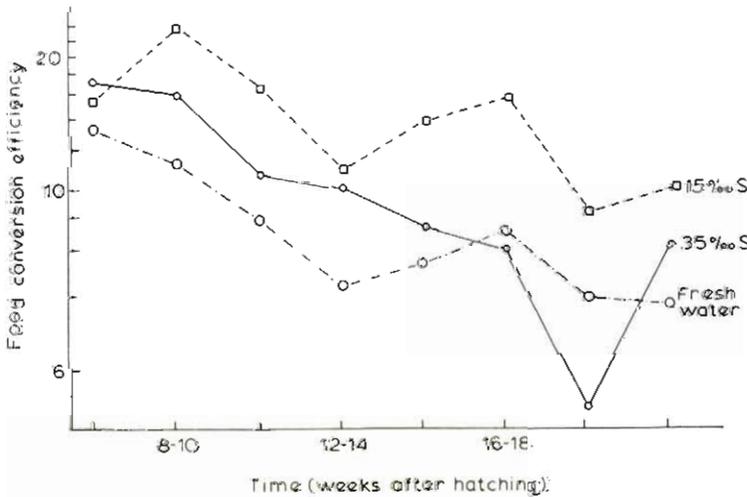


Fig. 4-174: Efficiency of food conversion in *Cyprinus macularius* exposed to 3 different salinity levels at 30° C under restricted food supply. Each value represents the average conversion efficiency per fish per 2 weeks; all average data are based on 12 individuals. See Fig. 4-172 and Fig. 4-173. (After KINNE, 1960; redrawn.)

fertilization; unfertilized eggs follow a similar trend. After 24 hrs, the unfertilized egg of *Pleuronectes platessa* is isosmotic with the medium, but the fertilized egg is still hypo-osmotic (Fig. 4-175). The differences between *C. harengus* and *P.*

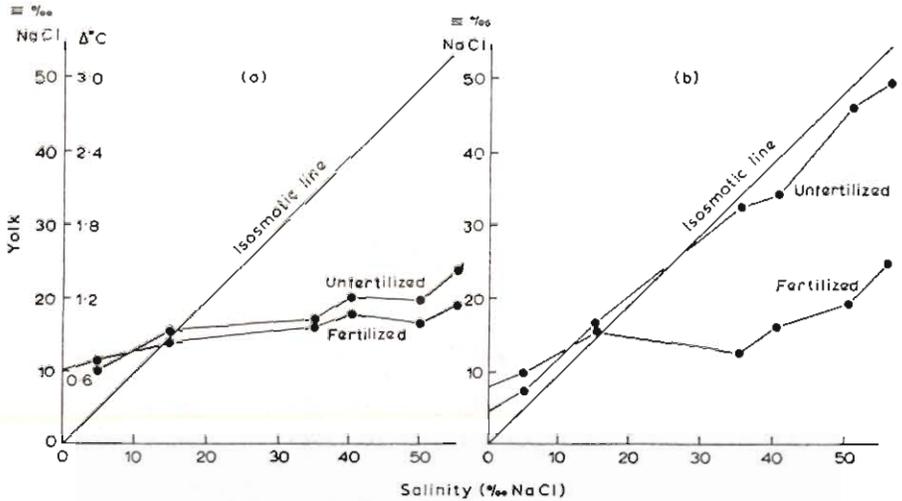


Fig. 4-175: The effects of salinity on the osmotic concentration of the yolk of unfertilized and fertilized eggs of *Pleuronectes platessa*, after 1 hr (a) and 24 hrs (b). (After HOLLIDAY and JONES, 1967; redrawn.)

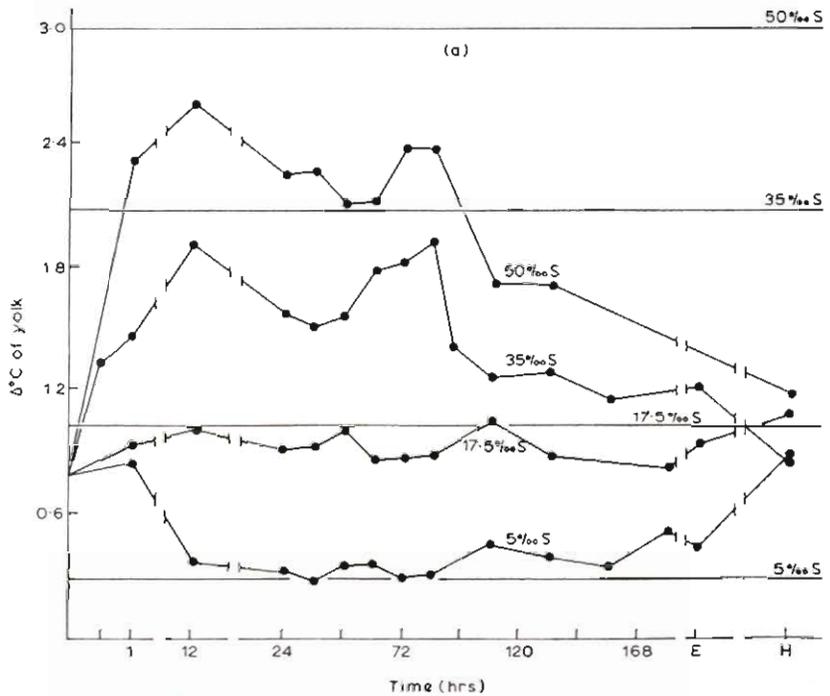


Fig. 4-176(a): Osmotic concentration of the yolk of the eggs of *Chupea harengus*, fertilized and incubated in the given salinities. E: eyed stage H: hatching. Salinities in ‰ NaCl. (After HOLLIDAY and JONES, 1965, 1967; modified.)

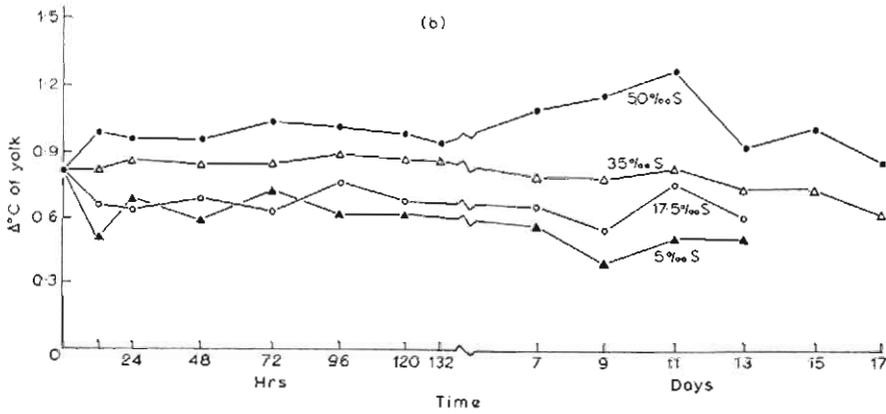


Fig. 4-176(b): Osmotic concentration of the yolk of the eggs of *Pleuronectes platessa*, fertilized and incubated in the given salinities. Salinities in ‰ NaCl. (After HOLLIDAY and JONES, 1965, 1967; modified.)

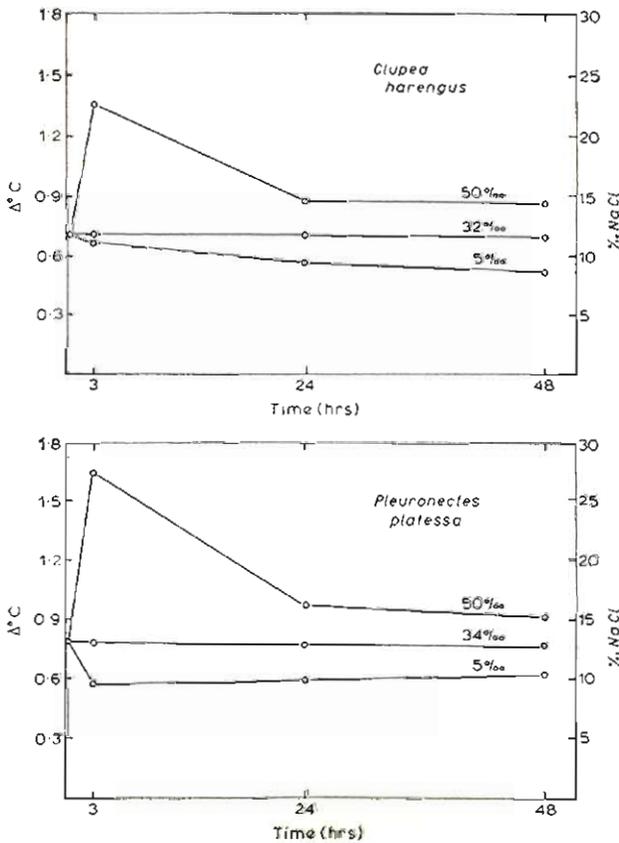


Fig. 4-177: Osmotic concentrations of larval body fluids in herring *Clupea harengus* and plaice *Pleuronectes platessa*. *P. platessa* larvae transferred from 34‰ S; *C. harengus* larvae transferred from 32‰ S. (After HOLLIDAY, 1965; redrawn.)

*platessa* persist until gastrulation is complete (Fig. 4-176a, b), at which time the yolk of the *C. harengus* egg returns to a level hypo-osmotic to the medium (Fig. 4-176a), a condition which the plaice egg maintains throughout the period from fertilization (Fig. 4-176b). It would appear that the fertilization membrane and periblast of the egg of *Pleuronectes platessa* possess regulatory properties not present in the egg of *Clupea harengus*. In the latter, regulatory ability is a property of the cells that overgrow the yolk during gastrulation.

After hatching, the larvae of both *Clupea harengus* and *Pleuronectes platessa* possess the ability to survive in a wide range of salinities (p. 998). This ability is based on short-term tissue tolerance to internal osmotic changes and regulation of body fluids to reverse the changes. Fig. 4-177 illustrates the changes in body fluids of larvae transferred from sea water to salinities of 5‰ or 50‰.

The changes in osmotic concentration of body fluids are reflected in changes in body weight of the larvae. These weight changes most probably indicate the movement of water (Fig. 4-178).

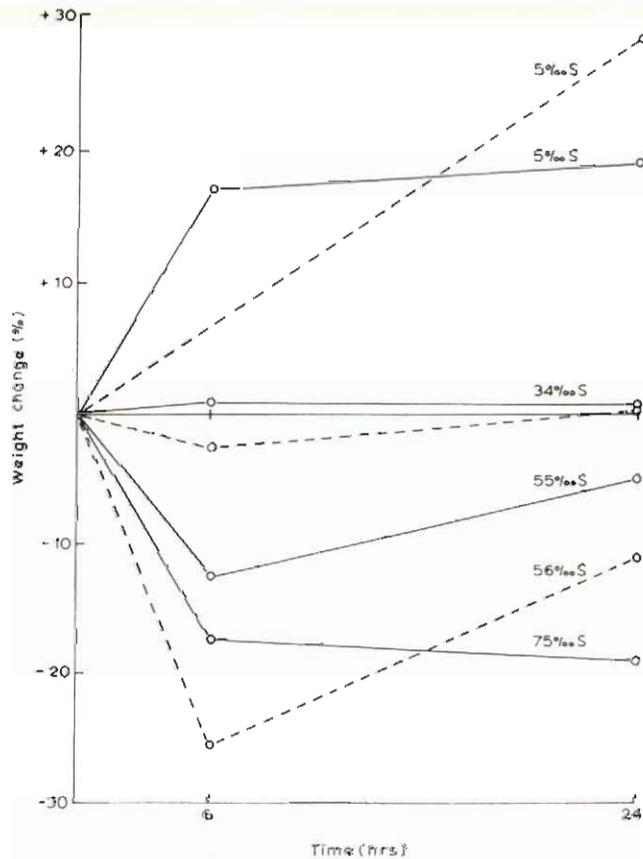


Fig. 4-178: Weight changes of fish larvae after transfer from sea water (34‰ S) to the various test salinities. — — — *Clupea harengus*. (Data from HOLLIDAY and BLAXTER, 1960). — — — *Pleuronectes platessa*. (After HOLLIDAY, 1965; redrawn.)

The change in regulatory pattern as a function of age has been discussed for *Pleuronectes platessa* by HOLLIDAY and JONES (1967). At metamorphosis there is an increased ability to survive in low salinities, while survival in high salinities is reduced. During the period between absorption of the yolk sac and completion of metamorphosis, the larva undergoes modifications in body form and behaviour. It becomes laterally flattened and changes from a pelagic to a demersal way of life. There are other structural changes that take place at this time. The yolk sac larvae become covered with a thin (2 to 3 $\mu$ ) two-layered epidermis; at metamorphosis the epidermis thickens as connective tissue is laid down and there is an increase in the number of pigment cells in the skin. In the yolk-sac larvae the gills are present only in a rudimentary form, the gill bars lacking branchial filaments; at the time of metamorphosis the gills are well-developed and the filaments abundant. It would seem that the ability of the yolk sac larvae to survive in high salinities is due to the regulatory ability of the undifferentiated epidermal tissues. The changes in structure of the skin which accompany metamorphosis render it unsuitable for either ionic or gaseous exchange, and these functions are confined to the gills. There is, therefore, a reduction of the surface area available for ionic transfer; in addition, this surface is localized in the head region, and hence body-fluid regulation is a function of both surface area availability and presence of a well-developed circulatory system. The change in ability to survive in low salinities, which takes place at metamorphosis, can again be attributed to the organ differentiation which occurs at this time. The yolk sac larvae have two pronephric glomeruli—each connected by a tubule to a urinary vesicle; by the time of metamorphosis the mesonephric glomeruli and tubules and a well-organized kidney have formed. This would almost certainly contribute to the greater survival in water of low salinity, both by increased rate of urine production and by the development of salt-retaining powers of the tubules. Such a hypothesis is supported by the fact that, in low salinities, the body fluids of the metamorphosed fish are maintained at a higher relative concentration than the body fluids of yolk-sac larvae.

The patterns of regulation and consequent distributions of water and electrolytes in adult sea-water fishes have been reviewed recently by BLACK (1957), ROBERTSON (1963), PROSSER and BROWN (1961), PARRY (1966), MAETZ (1968), CONTE (1969), HICKMAN and TRUMP (1969) and HOLMES and DONALDSON (1969). The reader is referred to these reviews for a detailed consideration of the problems of ion and osmoregulation in adult fishes, in salinities ranging from fresh water to sea water. General principles only will be considered here by reference to selected examples.

The cyclostome fishes, the Myxinoidea, have only a very limited ability to survive in water other than normal sea water; their body fluids are practically isosmotic with the medium in which they are found (SCHMIDT-NIELSON and SCHMIDT-NIELSON, 1923). This isosmoticity is based on the fact that the osmo-concentration of the blood is due almost entirely to inorganic ions. However, the ionic composition of the blood is different from that of sea water, especially in regard to the considerable reduction of the divalent calcium, magnesium and sulphate ions (ROBERTSON, 1963); clearly, this is affected by active, ion regulation. MORRIS (1965) studied the mechanisms regulating the ion composition of the plasma in *Myxine glutinosa* and emphasized the importance of the kidney in

this respect, its primary function being concerned with the excretion of the divalent ions. He found little evidence to indicate that the gills and gut exercised any regulatory role, either in terms of differential uptake or differential excretion of ions.

The members of the other cyclostome group, the Petromyzontidae, have blood which differs from sea water, not only in its ionic composition, but is also hypo-osmotic to it. These fishes are, therefore, faced with problems of ion and osmoregulation in salinities above and below about one-third sea water. The subject has been reviewed by MORRIS (1960) who has (1956, 1958) conducted an experimental study on osmoregulation in the river lamprey *Lampetra fluviatilis*; it spawns in fresh water and its eggs and larvae live in the rivers until, at metamorphosis, they migrate toward the sea. *L. fluviatilis* matures probably in estuarine waters and returns on its spawning migration into fresh waters. MORRIS (1958) studied the mechanism of osmoregulation in diluted sea water. The lampreys were adapted to 33% sea water (only slightly hypo-osmotic to their blood); they were then anaesthetized and weighed, their gut was blocked posteriorly and the urinary papilla ligatured. After recovery the lampreys were transferred to 50% sea water (considerably hyper-

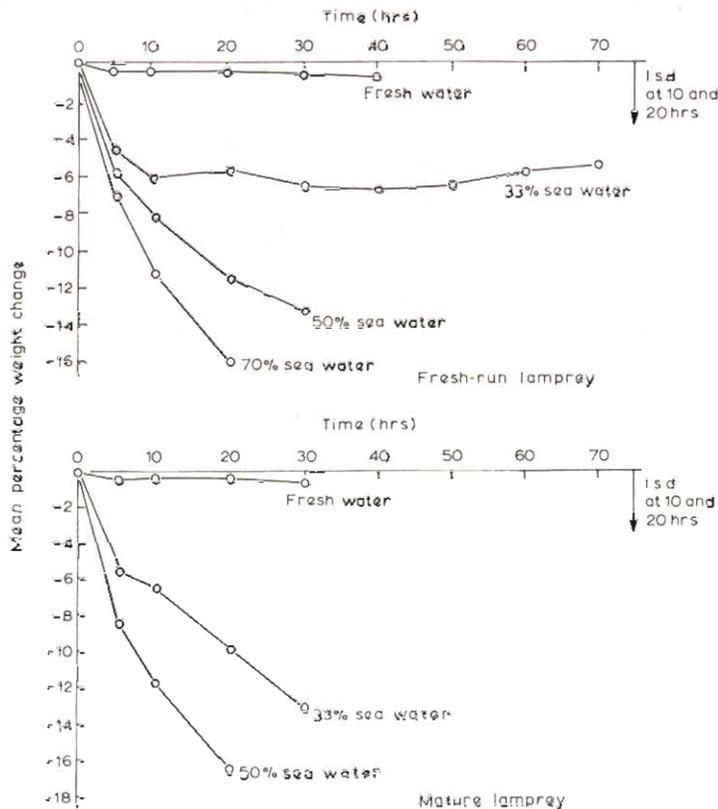


Fig. 4-179: Mean percentage weight changes in the lamprey *Lampetra fluviatilis* after exposure to various strengths of sea water. l.s.d.: least significant difference. (After MORRIS, 1956; redrawn.)

osmotic to their blood) containing the dye phenol red; 24 hrs later they were again anaesthetized, re-weighed and the volume of their gut fluid was measured. The rate of drinking was estimated from the concentration of phenol red present in the gut fluid. Samples of the serum, urine, gut fluid and medium were analyzed for freezing-point depression and chloride concentration. The results indicate that individuals which are successfully regulating (maintaining a constant body weight and a plasma osmotic pressure considerably hypo-osmotic to the environment) in sea water swallow ambient water and retain in their body more than 70% of this water to offset extrarenal osmotic body-water losses. This observation suggests a high rate of extrarenal water loss which, in turn, is indicative of a high degree of skin permeability. It was calculated that most of the chloride absorbed from the water swallowed had been actively excreted via an extrarenal route, namely, through the gills. Under sea-water conditions the volume of urine produced was very small.

As already described, the adult lamprey enters fresh water to spawn; at the same time it gradually loses its ability to regulate and survive in diluted sea water. This gradual loss occurs between the time that the fish first enters fresh water ('fresh-run' condition) and the time of sexual maturity. MORRIS (1956) compares the responses of lampreys in these two physiological conditions, exposing them to salinities up to 50% sea water. The mean percentage weight changes of the two test groups (reflecting the ability to maintain water balance) are shown in Fig. 4-179. 'Fresh-run' lampreys can maintain water balance in 33% sea water whilst mature fish lack this ability. Using two different methods to collect samples of urine (one by allowing the posterior end of the lamprey to project from the container of water in which it was kept through a membrane into a collecting tube, the other by canulating the urinary papilla), it was shown that the urine output in salinities corresponding to more than 33% sea water is negligible, but that it is high in lampreys in fresh water (Fig. 4-180). MORRIS was also able to correlate the loss of regulation ability in sea water and the corresponding rise in blood osmotic concentration with changes in the epithelial structure of the gills (p. 1030).

The mechanisms of ion and osmoregulation described for lampreys in fresh water and sea water are almost exactly the same as those in teleosts. The main difference between lampreys and teleosts is the considerably less water-permeable external body surface of the teleosts. Hence their rates of, for example, extrarenal water loss are much lower than in lampreys.

Regulation mechanisms in teleosts have received more attention than those of lampreys (see especially PARRY, 1966). Important recent work (discussed on p. 1001; MOTAIS, 1967), based on measurements of rates of ion flow across gills of euryhaline fishes, has shown that responses to salinity can be very rapid—a matter of minutes in fresh water. Clearly, such fast responses may be a critical factor in determining the survival capacity after abrupt salinity changes.

Elasmobranch fishes maintain in sea water a blood osmotic pressure slightly higher than that of the surrounding medium; this results in a net gain of water by osmosis. The inorganic contents of their blood are similar to those of teleosts, but supplemented by organic molecules, such as urea and trimethylamine oxide. In regard to ion regulation, the rectal gland is the primary site of excretion of the monovalent sodium and chloride ions (BURGER and HESS, 1960; BURGER, 1962;

WENDELL, 1965). Estuarine and freshwater-living elasmobranchs lower the concentration of organic molecules in their blood and thus reduce the osmotic gradient between internal and external media. Urine flow is high in freshwater, but low in sea-water living elasmobranchs.

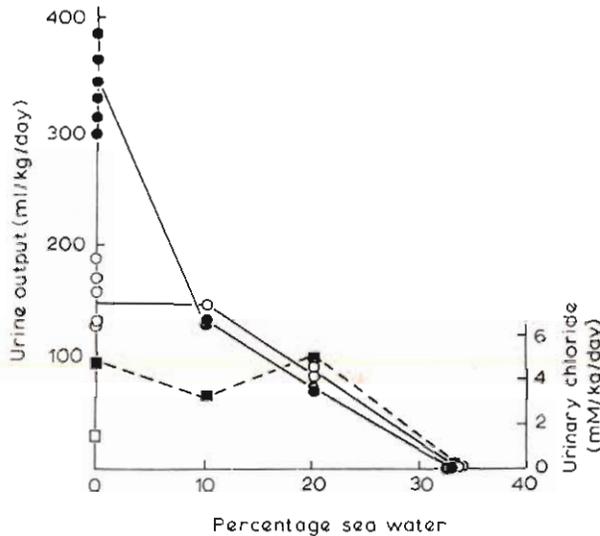


Fig. 4-180: Urine output and urinary chloride of *Lampetra fluviatilis* kept in various concentrations of sea water. (After MORRIS, 1956; redrawn.)

In addition to adjustments to salinity variations via regulation, fishes are also capable of non-genetic adaptation to salinity. KINNE (1962) demonstrated that rates of growth and food conversion efficiency are valuable indicators of functional adaptation to salinity; he extended his studies to investigate the effects of salinity at spawning on the offspring in *Cyprinodon macularius*. Batches of eggs spawned in one salinity were transferred after 3 to 6 hrs to other salinities, in which the eggs were incubated and hatched. The weights and lengths of the fish resulting from these hatchings were recorded; some of the findings are summarized in Table 4-85.

The results clearly demonstrate that conversion efficiencies are highest in fish hatching from eggs which had been allowed to remain in the salinity at spawning. The results were interpreted by KINNE (1962) as non-genetic adjustments which were initiated at or shortly after the eggs had been spawned and which took place during early ontogenetic development. There was no evidence to suggest that the changes brought about by salinity are transmitted to the next generation; the changes were, at least in part, irreversible somatic responses. A study of the underlying changes in cell chemistry would provide a fruitful field for research.

Genetic adaptations to salinity are not easy to list (KINNE, 1964a), but some structural differences in regulatory organs provide clear examples (p. 1032). There are also physiological differences, for example, in the presence or absence of particular hormones (see below) which may be considered genetic adaptations to salinity.

Table 4-85

The effect of the salinity at spawning and during incubation on the food conversion efficiency of the euryhaline fish *Cyprinodon macularius*. Average values, obtained on 9 to 22-week-old individuals fed on *Enchytraeus albidus* (After KINNE, 1962; modified)

Salinity at spawning (‰S)	Incubation and rearing conditions		Conversion efficiency
	Salinity (‰)	Temperature (°C)	
Fresh water	35	20	30.0
Fresh water	Fresh water	20	42.1
15	Fresh water	25	10.1
15	15	25	16.4
15	35	25	14.9
Fresh water	35	30	11.8
Fresh water	Fresh water	30	15.8
35	Fresh water	30	8.6
35	35	30	12.5

The relations between the activity of endocrine glands and salinity effects on fish metabolism may be expressed in at least two ways: (i) the influence of the state of gland activity on the response of the fish to a particular salinity; (ii) an alteration of gland activity due to a salinity change. While salinity is a potentially variable factor in the external environment, the level of circulating hormones is a potentially variable factor in the internal environment; the response of the fish is often governed by the interaction of the two systems. It will be more appropriate to consider some aspects of these problems in relation to migration (p. 1023); the discussion here will, in the main, be restricted to what may be termed 'metabolic' effects.

There has accumulated a considerable, if somewhat inconclusive, amount of information on the general way in which the endocrine system is involved in the processes of osmotic and ionic balance. Recent reviews include HOAR (1957), PICKFORD and ATZ (1957), PARRY (1966), BERN (1967), MAETZ (1968), HOAR and RANDALL (1969) and MAETZ and co-authors (1970).

It would appear that the pituitary gland exerts the primary control on water balance. Hypophysectomy of the estuarine fish *Fundulus heteroclitus* results in a loss of ability to survive in fresh water and salinities up to 13‰. The test fish die with very low concentrations of plasma chloride, less than half that of the unoperated controls. Injections of *Fundulus heteroclitus* pituitary extract enables the hypophysectomized fish to survive in fresh water, but extracts from the gland of *Pollachius virens*—a marine teleost—are ineffective (BURDEN, 1956).

Extending this work, PICKFORD and PHILLIPS (1959) found that when the hormone prolactin, known to be present in some teleost pituitaries, is injected into hypophysectomized *Fundulus heteroclitus* the ability to survive in fresh water becomes restored. BALL and PICKFORD (1964) described changes in pituitary-gland

cytology in *F. heteroclitus* kept in fresh water, indicating the site of prolactin secretion in this fish; they attributed the failure of the extracts of *Pollachius virens* pituitary gland to stimulate survival as being due to the low prolactin content of the material. The pituitary gland of other fishes has been shown to contain oxytocin-like substances, normally associated with an antidiuretic function (e.g. HELLER, 1956; ACHER and co-authors, 1962). A similar factor has been described by MOTAIS and MAETZ (1964) as influencing sodium regulation in the flounder *Pleuronectes flesus* in both fresh and sea water. Recent reviews on the effects of prolactin have been presented by BERN (1967), BERN and NICOLL (1968), BALL (1970) and MAETZ and co-authors (1970).

Ionic exchange appears to be controlled in marine fishes by adrenocorticosteroid hormones, both renal (CHESTER-JONES and co-authors, 1959, 1967) and extrarenal (HOLMES, 1959; BENTLEY and FOLLET, 1963) routes being affected. However,

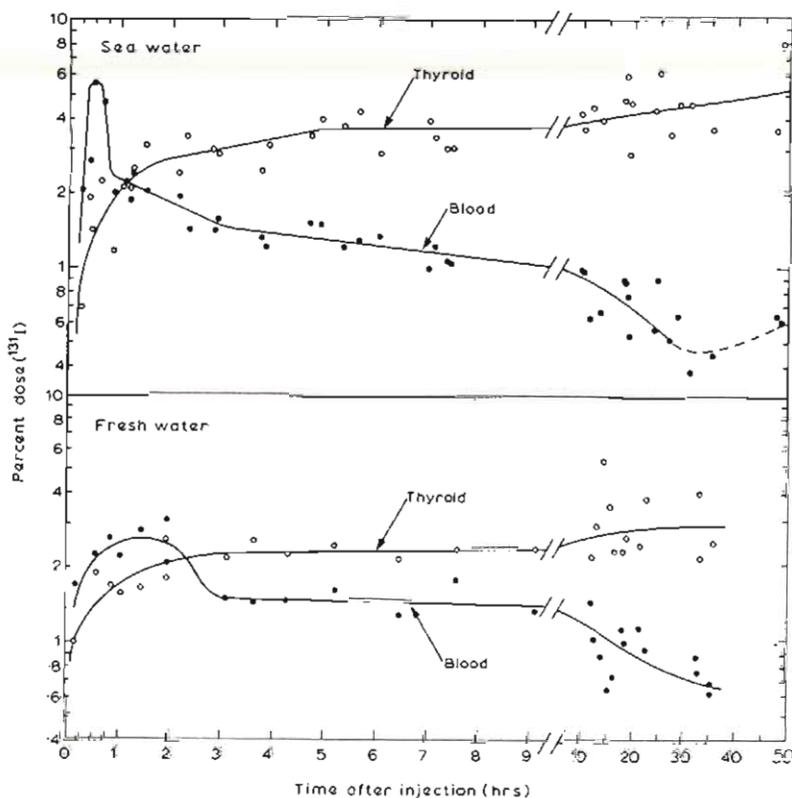


Fig. 4-181: Effect of salinity on thyroid radio-iodine uptake and blood radio-iodine disappearance rate in small *Platichthys stellatus*. Thyroid uptake (○) is expressed as percentage of dose accumulated by the whole gland; blood radio-iodine (●) is expressed as percentage of dose per gram of blood  $\times$  body weight/100. Radio-iodine is concentrated more rapidly in the thyroids of individuals exposed to sea water in spite of the more rapid disappearance of radio-iodine from their blood. Sea water: 29‰ S; fresh water reinforced with 40  $\mu$ g iodine per litre. (After HICKMAN, 1959; redrawn.)

some euryhaline fishes do not seem to react to these hormones, e.g. *Fundulus heteroclitus* (PICKFORD and PHILLIPS, 1959).

The activity of the thyroid gland has often been suggested to represent a primary factor in regard to metabolic responses of fishes to salinity changes. FONTAINE and associates (e.g. FONTAINE, 1943; FONTAINE and CALLAMAND, 1943) have made important contributions to this field, correlating the degree of activity of the thyroid gland with the migrations of the eel, at various stages in its life cycle from sea water to fresh water and vice versa. The subject has been reviewed by SMITH, D. C. W. (1955), HOAR (1957) and PICKFORD and ATZ (1957). The greater osmoregulatory demands made by fresh water on the metabolism of fishes result in an increase in thyroid activity (HOAR, 1952). However, adult *Salmo salar* had a high level of thyroid activity as they left the sea to enter fresh water, and the activity of their thyroid gland decreased as the fish moved upstream (FONTAINE and OLIVEREAU, 1947).

Many marine fishes, subjected to a decrease in salinity, respond with an increase in thyroid activity; but when freshwater fishes are subjected to a rise in salinity, thyroid activity decreases (LELOUP, 1948; OLIVEREAU, 1948, 1954). The latter fact was confirmed by SMITH, D. C. W. (1955), who also showed that injection of thyroxin raises, while injection of thiourea and thiourocil reduces, salinity tolerance of *Salmo trutta*. Injection of thyrotrophin (the pituitary hormone normally regarded as controlling thyroid activity) had no effect on salinity tolerance, but apparently increased thyroid activity. The results of injection of hormones derived from non-teleost forms should be interpreted with considerable caution; it seems unlikely that the thyroid gland is the main endocrine factor controlling osmoregulation (SMITH, D. C. W., 1955).

HICKMAN (1959) reviewed the subject and described experimental work on the starry flounder *Platichthys stellatus*, which set out to determine whether or not there is a difference in thyroid activity in fish adapted to fresh and sea water. He first ensured that both media had been equalized in terms of iodine content—an important factor not always considered by other workers. The activity of the gland was measured in terms of the clearance of radio-iodine from the blood (Fig. 4-181). From these results the thyroid clearance of radio-iodine from the blood was calculated (Table 4-86). Average clearance rates for flounders adapted to 29‰ S (0.197) were much higher than those for flounders adapted to fresh water (0.0135). HICKMAN points out that his results indicate an apparent caloriegenic action of the thyroid hormone in *Platichthys stellatus* subjected to a normal change in salinity, and suggests that the hormone may possibly stimulate the oxidative metabolism in the cells performing osmotic work. It is interesting in this context that LANGE and FUGELLI (1965) reported muscle cells of *Gasterosteus aculeatus* and *Platichthys flesus* to osmoregulate by adjusting the number of osmotically active particles (ninhydrin-positive substances and trimethylamine oxide) within the cell (see also Chapter 4.31).

There are still considerable gaps in our knowledge concerning the effects of salinity on metabolism of fishes. Unfortunately, the contributions published hitherto are often contradictory and confusing.

The economic implications are of great potential value, especially for fish hatchery and farming projects, where one of the objects is to provide environ-

Table 4-86

Thyroid clearance of radio-iodine from the blood of small *Platichthys stellatus* exposed to fresh water and water of 29‰ salinity, respectively. Clearance rates expressed as the volume of blood (as % body weight) cleared of radio-iodine by the thyroid per hour. Rates calculated from Fig. 4-181 (Data from HICKMAN, 1959)

Hrs after injection	Average blood <sup>131</sup> I concentration	Rates of thyroid uptake clearance	
		in freshwater	
3-4	1.500	.02	.0133
4-5	1.485	.02	.0135
5-6	1.470	.02	.0136
		Average value	.0135
		in 29‰S	
2-3	1.6	.27	.169
3-4	1.38	.28	.202
4-5	1.32	.29	.22
		Average value	.197

mental conditions most favourable for growth and least demanding in terms of other energy commitments. Increased interest in the development of hatcheries for marine fishes may stimulate more fundamental work on this subject at all stages of the life history (Volume III).

#### *Activity*

Salinity changes may affect the swimming activity of fishes in a number of ways. They may cause avoidance and escape responses, influence migratory behaviour, and alter the activity level due to alterations in buoyancy. They may limit activity via the availability of dissolved oxygen which decreases as salinity increases. Salinity may also have a direct effect on gaseous exchange; thus asphyxiation occurs in some fishes placed in water of high salinity (CORDIER and MAURICE, 1957); this effect may be due to a combination of damage to gill tissues and a decreased availability of ambient oxygen. Osmoregulatory work may raise the rate of standard metabolism and reduce the scope for activity (FRY, 1957). Changes in osmotic and ionic ratios in body fluids may inhibit or excite neuromuscular activity (see also Chapter 4.31, p. 945).

The pertinent literature is not extensive, but HOUSTON (1957, 1959) gives a detailed account of the effects of the locomotory activity of Pacific salmon fry (especially *Oncorhynchus keta*) upon transfer from fresh water to a salinity of 22‰ to 24‰. The fry were placed in an apparatus designed to measure their cruising speed, and their performances measured during the process of acclimatization to 22‰ to 24‰S. The degree of acclimatization was assessed by measuring the total body water and body chloride of the fry at the end of each experiment (Fig. 4-182). They indicate that the cruising speed of the fish becomes depressed immediately after

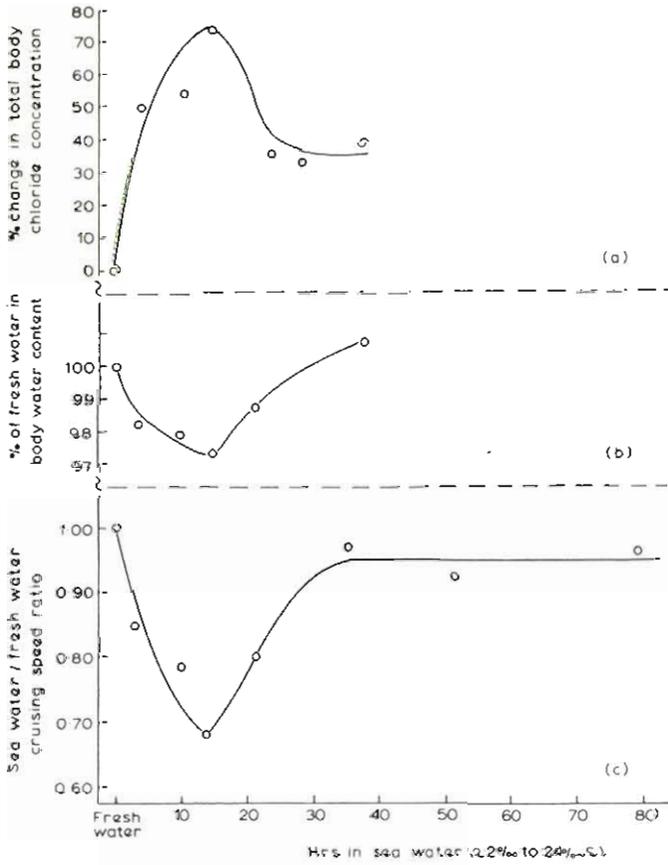


Fig. 4-182: The effects of abrupt transfer from fresh water to salt water (22‰ to 24‰ S) on salmon (*Oncorhynchus keta*) fry. (a) Percentage changes in total body-chloride concentration; (b) percentage of freshwater/body-water concentration; (c) Sea-water to fresh-water cruising speed ratio. (After HOUSTON, 1959; redrawn.)

transfer from fresh water to brackish water of 22‰ to 24‰ S. There is evidence that some recovery takes place, but throughout the course of the experimental period (80 hrs) the fish failed to regain the freshwater cruising speed. The response is therefore two-staged. The depression in cruising speed is most marked during the period when the fish experiences maximum osmotic change, as indicated by the percentage change in body chloride and water content; but it is particularly interesting that part of the depression persisted, even after the fish had apparently successfully made the change-over from a freshwater to a marine pattern of regulation. HOUSTON considered the results in relation to (i) the inhibition of the neuromusculature apparatus due to ionic changes in body fluids, (ii) the onerousness of an enhanced standard metabolic rate (due to the extra energy required for ion and osmoregulation in sea water) on the scope for activity and (iii) variation in the intensity of expression of a reotactic response due to decreased motivation. He suggested that points (i) and (ii) might account for the initial depression of

cruising speed, but that, after ionic and osmotic adjustment had taken place, the metabolic cost of regulation (point ii) could account for the failure to return completely to the original cruising speeds. Point (iii) was considered in the light of unpublished work by HOAR, who recorded spontaneous activity levels of *Oncorhynchus keta* acclimatized to fresh and sea water. Spontaneous activity was less in sea water, as was the intensity of schooling and the maintenance of directional swimming. Also relevant to this discussion is the work of BENNETT (personal communication), who showed that the performance of a conditioned response to light by *Carassius auratus* is enhanced by a slight increase in salinity (from fresh water to 6‰) but the response is made less efficiently in salinities over 6‰, which induces stress symptoms in the tested fish.

In regard to behavioural responses of fishes to a single stimulus or a combination of stimuli, it is important to distinguish between: (i) the absolute physiological sensitivity of the receptor as determined by, for example, electrophysiological techniques, (ii) the minimum stimulus to which the fish can be trained to respond as determined by conditioned-response experiments, and (iii) the minimum stimulus to which the fish can be observed to react under natural conditions (HARDEN-JONES, 1960). Considering these three aspects in relation to salinity responses, TATEDA (1964) demonstrated the presence of a salt receptor on the isolated barbel of *Parasilurus asotus*. The classic study by BULL (1938), who used a conditioned response technique on about 20 fish species, demonstrated that they were all able to be conditioned to respond to an abrupt change of salinity from 34‰ down to 30‰. The fishes could discriminate between salinities differing by about 0.5‰; *Gobius flavescens* was able to discriminate even between salinities differing by as little as 0.06‰.

Clearly, many fishes are capable of responding to environmental salinities; but the situation is complicated by the fact that the response to the external environment is often governed or modified by the internal physiological state. The work of BAGGERMAN (1960a, b), illustrates this point; her work also serves as a useful link between the parts of this subchapter dealing with salinity effects on metabolism, behaviour and endocrine system. BAGGERMAN used changes in salinity preference as an indicator of the change in the physiological state of the stickleback *Gasterosteus aculeatus*, as well as in the Pacific salmon species *Oncorhynchus keta*, *Oncorhynchus gorboscha*, *Oncorhynchus nerka* and *Oncorhynchus kisutch*. Briefly, it was found that at the beginning and the end of the migration period there are marked changes in salinity preferences (Fig. 4-183). Adult *Gasterosteus aculeatus* migrate from sea water to reproduce in fresh water in March to May, and in this period show a behavioural preference for fresh water under experimental conditions. After breeding they return to the sea for a period beginning in June, and at this time show a preference for salt water. The juvenile *G. aculeatus* (hatched in fresh water) migrate to the sea 4 to 6 weeks after hatching, and at this time show a preference for salt water. Pacific salmon exhibit a similar pattern of preferences: the fry of *O. keta*, *O. gorboscha* and *O. nerka*, immediately after hatching, reveal a preference for fresh water, but this quickly changes to a preference for salt water just before they migrate to the sea. The fry of *O. kisutch* do not migrate to the sea; there is only a short phase of salt-water preference, and this in fact is a preference for water of low salinity as distinct from full strength sea water. The

smolt stages of *O. nerka* and *O. kisutch* show a preference for salt water in spring, at which time they migrate to the sea. This preference for sea water is not found (and in some cases is reversed into a preference for fresh water) in smolts in late summer and autumn, i.e. after the migration season had ended. These fundamental response changes to salinity are brought about by changes in thyroid gland activity; an increased activity of this gland precedes migration and the activity decreases at the end of the migratory period (BAGGERMAN, 1960a, b, 1963).

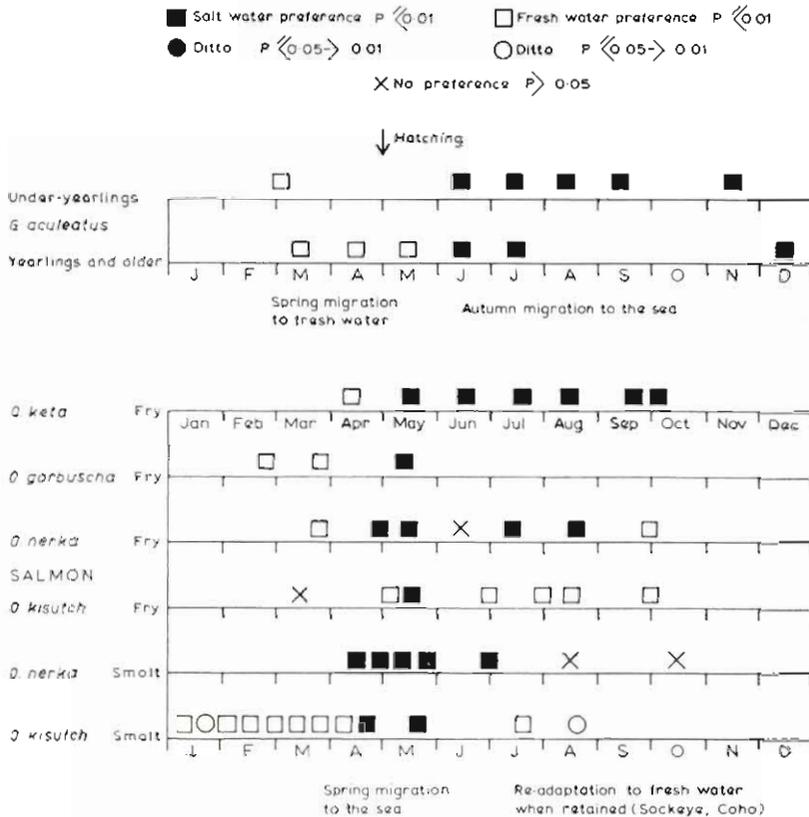


Fig. 4-183: Changes in salinity preference occurring at the beginning and end of the migration period in sticklebacks *Gasterosteus aculeatus* and juvenile *Oncorhynchus* sp. Each symbol represents the results of six tests or more. (After BAGGERMAN, 1960a; redrawn.)

Similarly, in the stickleback *Gasterosteus aculeatus*, thyroid-gland activity determines salinity preferences, but the effect of the thyroid hormone is the reverse of that in the salmon. High thyroid activity precedes seaward migration in the salmon, but freshwater migration in sticklebacks. However, the recent work of LEATHERLAND (1970a, b) indicates that the effects of thyroid may be indirect, and that prolactin may play a more important role.

BAGGERMAN (1960a, b) was also able to relate changes in salinity preference to day length (Fig. 4-184). In *Gasterosteus aculeatus* long days induce a preference for fresh water (a fact which correlates with spring migration). In juveniles of Pacific

salmon species, exposure to long days causes a change to salt-water preference and spring migration to the sea.

This work—demonstrating the connection between day length, pituitary activity, thyroid activity and salinity preference—illustrates the complexities which may underlie the response of a fish presented with a salinity choice situation. Generalizations are almost impossible, especially in view of the fact that salinity represents only one component of a whole spectrum of stimuli which may affect orientation patterns of migrating fish.

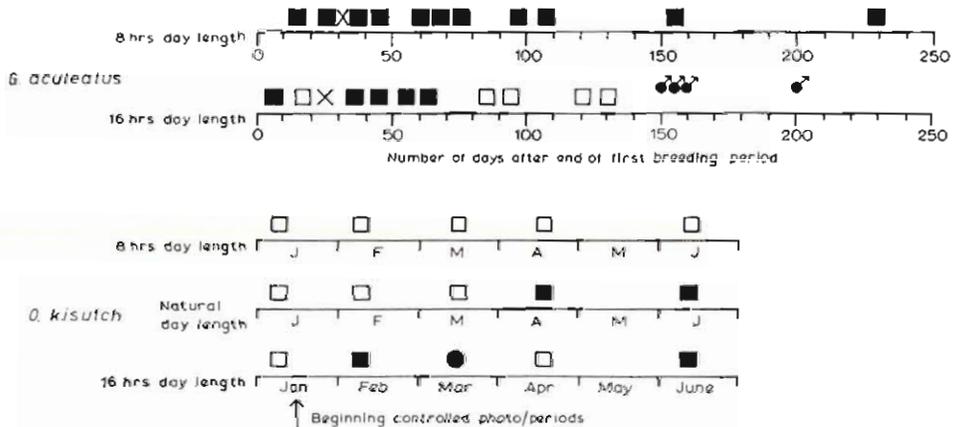


Fig. 4-184: Effect of the daily photoperiod length on the salinity preference in sticklebacks (*Gasterosteus aculeatus*) and coho salmon parr (*Oncorhynchus kisutch*) kept under constant artificial daily photoperiods and constant temperatures. For explanation of symbols consult Fig. 4-183. (After BAGGERMAN, 1960a; redrawn.)

CREUTZBERG (1961) gives an account on the orientation of migrating elvers of *Anguilla vulgaris* in a tidal area. The starting point of his investigation was the hypothesis that elvers move inshore on the flood tide in conditions of high salinity, and in the conditions of low salinity that accompany the ebbing tide, seek the bottom to prevent themselves being washed back seaward. Salinity preference, however, was not involved in the migration, but an attractive substance of natural fresh waters to which the elvers showed an innate response.

There is a tendency in some papers to correlate cause and effect in regard to salinity and behavioural responses, without adequate consideration of other, less easily detected or measured, variables of the environment.

### (c) Reproduction

This section deals with salinity effects on spawning and fertilization of eggs; it also considers development, percentage hatching and the hatching process itself.

A number of papers indicate that gametes of some teleost species are viable, at least for a short time, in a wide range of salinities. Upon their release into the water at spawning, gametes often experience great changes in osmoconcentration of their environment. Within the body of the parent fish they are in an environment with which they are practically isosmotic; upon entering the spawning

medium, pronounced osmotic gradients may occur; in view of their large surface areas relative to their volumes it might be expected that the gametes, especially the sperm, would be quite susceptible to such gradients. Only limited experimental information on this subject is available (see the review on clupeids by BLAXTER and HOLLIDAY, 1963). OUTRAM (1951) suggests that a sudden decrease in salinity initiates spawning in *Clupea pallasii*. According to YANAGIMACHI (1953), *Clupea pallasii* sperm remain fertile to some small extent after 12 hrs in sea water; but in 50‰ and 25‰ sea water, fertility is retained for at least 24 hrs. Sperm of the marine fish *Gillichthys mirabilis* do not survive in fresh water but remain viable in a wide range of salinities, with a period of longest mobility in 25‰ sea water (WEISEL, 1948).

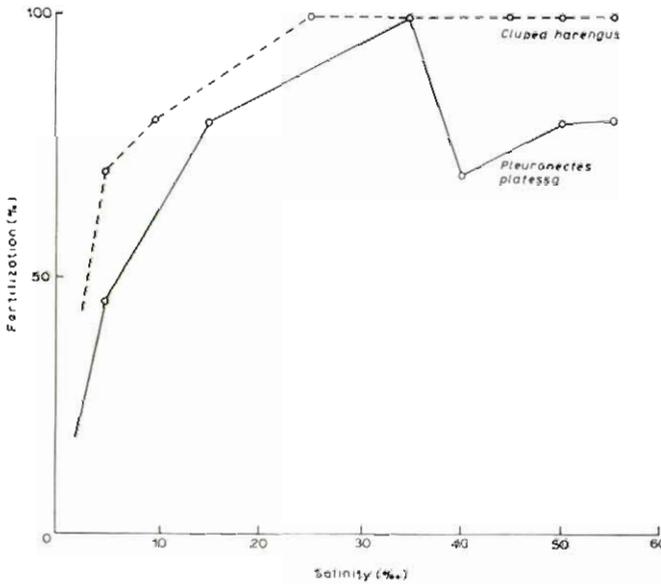


Fig. 4-185: Percentage fertilization of the eggs of *Clupea harengus* and *Pleuronectes platessa*. (After HOLLIDAY, 1965; redrawn.)

In general, gametes of fishes are expected to have only a short period of independent life; hence the period of tolerance in nature would not need to exceed that required for successful fertilization. HOLLIDAY and BLAXTER (1960) and HOLLIDAY (1965), taking percentage fertilization as a criterion of the survival of the gametes of *Clupea harengus* and *Pleuronectes platessa*, showed that a high percentage fertilization can be attained in salinities at least as high as 60‰, but percentage fertilization falls off in low salinities (Fig. 4-185).

The effects of salinity on the rate of embryonic development have been studied in a number of species. HEUTS (1947) found that the response of *Gasterosteus aculeatus* to salinity depends on the race of the species concerned, i.e. on the genotype. In some cases, salinity causes acceleration of development, in others retardation. Cross fertilizations between the races result in salinity responses characteristic of the race of the female parent. KINNE and KINNE (1962a, b) con-

ducted experimental work on *Cyprinodon macularius*, and KINNE (1964a) reviewed the effects of salinities on the rate of development of teleosts. In *C. macularius*, an increase in salinity produces progressive retardation of development (Fig. 4-186). However, it was found that this effect is not due directly to the ionic or osmotic strength of the medium but to the reduction in the amount of dissolved oxygen available to the eggs being incubated in the higher salinity. The effects could in fact be counteracted by artificially increasing the oxygen content of the ambient medium. In contrast to these results, there are reports of incubation periods being longer in low salinities, e.g. HOLLIDAY and BLAXTER (1960) found that eggs of *Clupea harengus* incubated in 5.9‰ and 11.5‰S took two days longer to hatch than eggs from the same parents incubated in salinities ranging from 22.7‰ to

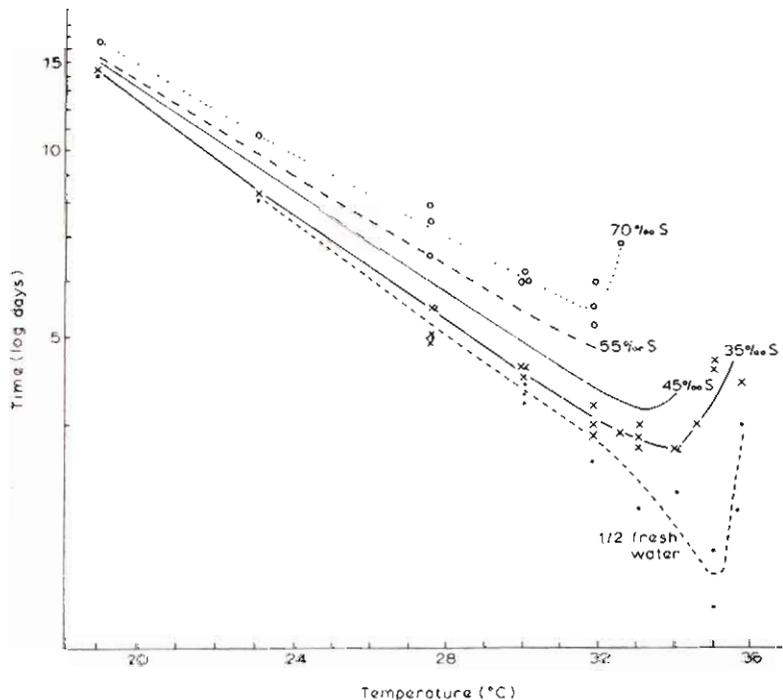


Fig. 4-186: Length of incubation periods in the euryhaline teleost *Cyprinodon macularius* at different constant temperatures as a function of salinity in  $100 \pm 5\%$  air saturated water. Individual data (those for 45‰ and 55‰S omitted);  $\frac{1}{2}$  fresh water = one part tap water, one part glass-distilled water. (After KINNE and KINNE, 1962b; redrawn.)

52.5‰, and VON WESTERHAGEN (1970) found that the eggs of *Gadus morhua*, *Pleuronectes platessa* and *Pleuronectes flesus* also developed more slowly in 15‰ to 20‰S than in higher salinities. Comparative studies on percentage of successful hatchings in herring *Clupea harengus*, plaice *Pleuronectes platessa* and cod *Gadus callarias* at different constant salinities (Fig. 4-187) indicate that *C. harengus* has a high tolerance throughout its development, especially in the lower salinities.

Eggs of the freshwater clupeid *Caspiotosa volgensis* do not develop normally in

salinities above 20‰ (OLIPHAN, 1940); hatching is most rapid between 5‰ and 15‰. OLIPHAN also reports that eggs of *Abramis brama* and *Lucioperca lucioperca* (also freshwater fishes) develop normally in salinities up to 10‰, but abnormal larvae hatched from the eggs if the salinities exceeded this level.

FORD (1929) and MCMYNN and HOAR (1953) reported an increase in mortality of the eggs of *Clupea harengus* and *Clupea pallasii* at the time of hatching in low salinities; the larvae were often found dead, partly emerged from the chorions. Increased mortality at hatching was also found in *Enchelyopus cimbrius* (BATTLE, 1930). It was interpreted as being due to the poorly developed tail musculature in larvae reared in the low salinities. Another possible explanation is that the low density of these salinities made it more difficult for the larvae to wriggle free of the chorion after it had ruptured.

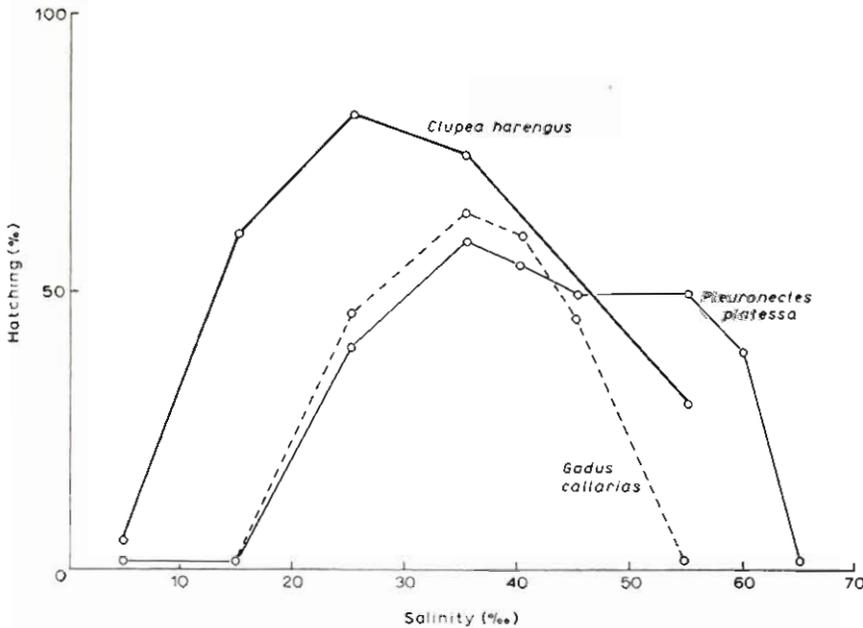


Fig. 4-187: Percentage hatching of the eggs of *Clupea harengus*, *Pleuronectes platessa* and *Gadus callarias*. (After HOLLIDAY, 1965; redrawn.)

Different ontogenetic stages may respond differently to a change in salinity; for example, the blastula stage of *Pleuronectes platessa* is little resistant (survival time) to low salinities, but after gastrulation, when the yolk surface is completely covered by a layer of cells, the tolerance is considerably greater (HOLLIDAY, 1965). A similar result has been presented by MCMYNN and HOAR (1953) for developing *Clupea pallasii* eggs. This phenomenon may be related to the fact that osmoregulation appears to be a property of the overgrowing cells (p. 1012).

Another aspect of reproduction, which has also been correlated with salinity, is the phenomenon of parthenogenesis. GALKINA (1957) reports parthenogenesis in *Clupea pallasii*; it occurred to its greatest extent in water of low salinities. VOLODIN (1956) induced parthenogenesis in *Clupea harengus* experimentally; he did not record the salinity in which the experiments were made; apparently salinity could have been as low as 4.9‰ (see also GALKINA, 1970).

(d) *Distribution*

Most of the data relating to the effects of salinity on the distribution of fishes come from field observations in which the distribution is related to local contemporary hydrographic conditions. It is often impossible to decide whether or not the link between the organism and this environmental factor is a direct one. For example, it was suggested by BUCHANAN-WOLLASTON (1915) that the distribution of the eggs of *Pleuronectes platessa* corresponds with water of a specific salinity, since egg density is related to particular isohalines, suggesting a causal correlation. However, the significance of this correlation is in considerable doubt; it is much more likely that the eggs were spawned in the path of a current of water of high salinity (GRAHAM, 1956). There are many other similar studies, but there has been little experimental work. Technical difficulties of establishing and maintaining stable salinity gradients other than vertical ones are considerable and obviously represent a major cause of this lack of work. The few reports available (e.g. BÜCKMANN and co-authors, 1953; KAMYSHLOV and GERASIMOV, 1960) suggest that sharp salinity gradients might act as barriers to the movement of fish—in this case *Clupea harengus*—in the sea and thus influence vertical distributions. Differences in specific gravity of waters of different salinity may also passively influence vertical distributions, especially of fish eggs and larvae.

MOHSON and EMERIT (1963) give a comprehensive account of the ability of the guppy *Lebistes reticulatus* to withstand high salinities. This fish normally inhabits the river systems of South America; it was suggested that the guppy has extended its distributional ranges by progressing from one river system to another, being able to survive the journey along the coast lines between neighbouring river systems.

In a sense, the distribution of fishes in relation to salinity represents the end result of what may be a long chain of responses. Some of the experiments described in previous sections of this subchapter indicate the various processes involved.

Knowledge of the resulting vertical and horizontal distributions is of great economic importance, but much more experimental work is required before an attempt can be made to explain or to predict particular situations.

### (3) Structural Responses

(a) *Size*

Salinity effects on growth rate and final body size at particular life-history stages of fishes have been referred to already (p. 1005). In experiments on *Clupea harengus* and *Pleuronectes platessa*, HOLLIDAY and BLAXTER (1960) and HOLLIDAY (1965) found clear differences in body size; larvae hatched from eggs incubated in low salinities (5‰ to 25‰) are longer and heavier than those hatched in high salinities (35‰ to 55‰). These size differences are almost certainly due to the greater water content of the larvae hatched in the low salinities. The yolk sacs of larvae hatched in salinities above 50‰ were shrunken, bright yellow and firm when touched. In salinities below 15‰, the yolk sacs were pale yellow and turgid. No differences could be found in the ultrastructure of the epidermal cells from the

newly hatched larvae of *Clupea harengus* reared in salinities from 5‰ to 50‰ (JONES and co-authors, 1966), although it has been postulated that these cells are the sites of regulation in the larvae. Cells in the epidermis of *Sardinops caerulea* larvae showed changes in volume immediately after transfer from 35‰ to 5‰ or 50‰S (LASKER and THREADGOLD, 1968). Most of the cells returned to normal within 6 hrs of the transfer. Structural changes were also found in other skin cells, designated 'chloride cells'.

The larvae used in these experiments were fully adapted to the water in which they were living, the eggs having been fertilized, incubated and hatched in them. There appears to be no account of cell size in larvae that have been transferred abruptly from one salinity to another. It might be expected that differences in cell size and possibly structure might be seen at the time of maximum regulation, i.e. during the few hours following such abrupt transfer. In eggs of *Gadus callarias* and *Pleuronectes platessa*, cells of the blastula cap react to a sudden salinity change by swelling in low salinities, and shrinking in high salinities (HOLLIDAY, 1965; HOLLIDAY and JONES, 1967). LANGE and FUGELLI (1965) concluded that, in adult *Gasterosteus aculeatus* and *Pleuronectes flesus*, the cell volumes were of equal size in sea-water and freshwater adapted fish (see *Internal Structures*, this chapter and Chapter 4.31).

#### (b) External Structures

Effects of salinity on body proportions and external characteristics is an area of study in which it is particularly difficult to separate the effects of a single environmental factor. Indeed, as will be seen, it is only in considering the combined effects of salinity with, for example, water temperature and oxygen content, that an attempt at a complete analysis can be made (see also Chapter 12).

There are a number of records of abnormalities of development associated with extremes of salinity. BATTLE (1930) reports deformities of the caudal and cardiac regions of *Enchelyopus cimbrius* in salinities up to 70‰. KRYZHANOVSKY (1956), working with *Clupea harengus membras* (the Baltic herring), found that, if the salinity of incubation was raised to 25‰ (eggs develop normally in 4‰ to 5‰S), there were abnormalities of the yolk sac (the yolk droplets were mis-shapen and the external surface crumpled). There were also internal abnormalities (p. 1032). HOLLIDAY (1965) reports caudal deformation in larvae of *Gadus callarias* hatched in supranormal salinities of 45‰. No deformities were found in the larvae of *Clupea harengus* and *Pleuronectes platessa* hatched in salinities up to 60‰.

SWEET and KINNE (1964) studied the effects of various salinity (fresh water, 35‰S, 70‰S)—temperature (26° to 36° C) combinations on the body proportions of freshly hatched *Cyprinodon macularius*. Length, depth and width of the whole body, and various parts of the body, were measured. The interactions between the effects of salinity and temperature are rather complex. In general, body lengths tend to decrease with increase in salinity. Body depths and widths tend to increase with decreasing salinity, resulting in an over-all reduction in the surface area to volume ratio. The measurements of body depths and widths indicate an increasing degree of growth disharmony in the order 35‰S < 70‰S < fresh water. However, as the authors point out, the individuals hatching in 35‰S were in-

cubated in the salinity at which the eggs were fertilized, while those in fresh water and 70‰S had been transferred from the salinity of fertilization (35‰) to the incubation salinities some short time after spawning. Previous work had indicated the deleterious effects on growth that follow such a transfer.

HEUTS (1947), working with two races of *Gasterosteus aculeatus*, found that the form living in brackish water has a higher number of lateral plates than that living in fresh water. Fin ray counts show that the two races also react differently to the same conditions; the freshwater form exhibits a negative correlation between ray count and the salinity in which it was reared, while the brackish-water form reveals a positive correlation. Results such as these are particularly important, since meristic characters often form the basis of taxonomic keys.

### (c) Internal Structures

Changes in cell structures of the gill tissues of fishes, caused by variations in salinity, have been reported in many papers. Well-documented accounts of such changes in *Lampetra fluviatilis* have been published by MORRIS (1957, 1958, 1960). If mature *L. fluviatilis* were captured immediately after re-entering fresh water during their spawning migration, some individuals could still regulate in salinities up to 50‰ sea water; others could not and died. On examination of the gill tissues, which have been shown to be the site of extrarenal chloride excretion, MORRIS

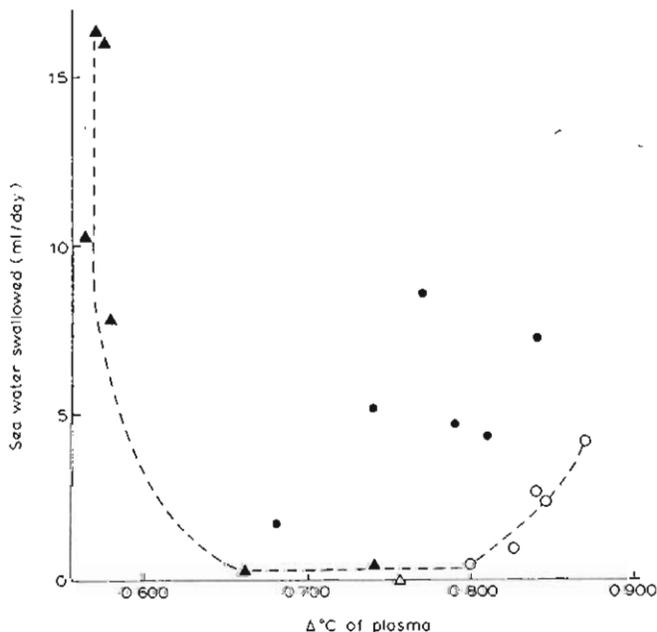


Fig. 4-188: Relation between swallowing capacity, chloride excretory cell assessment and plasma freezing-point depression ( $\Delta^{\circ}\text{C}$ ) in fresh-run *Lampetra fluviatilis* immersed in 50‰ sea water. Chloride excretory cell assessment ▲: many; ●: few; △: very few; ○: nil. (After MORRIS, 1958; redrawn.)

found large acidophil cells, similar to those discovered by KEYS and WILLMER (1932) in the gills of the eel. These cells were present only in some of the 'fresh-run' lampreys, while in individuals which could not regulate (survive) in sea water, the gill epithelium had changed: the acidophil cells had disintegrated and disappeared, and their place had been taken by new, much smaller, cells. Fig. 4-188 illustrates the relation between osmoregulatory capacity and the number of large acidophil cells present on the gills. MORRIS attributed chloride output to the large cells, and chloride uptake to the smaller cells which appeared in fresh water to be taking the place of the larger ones. Fig. 4-189 illustrates the change-over in cell-type distribution after entering fresh water.

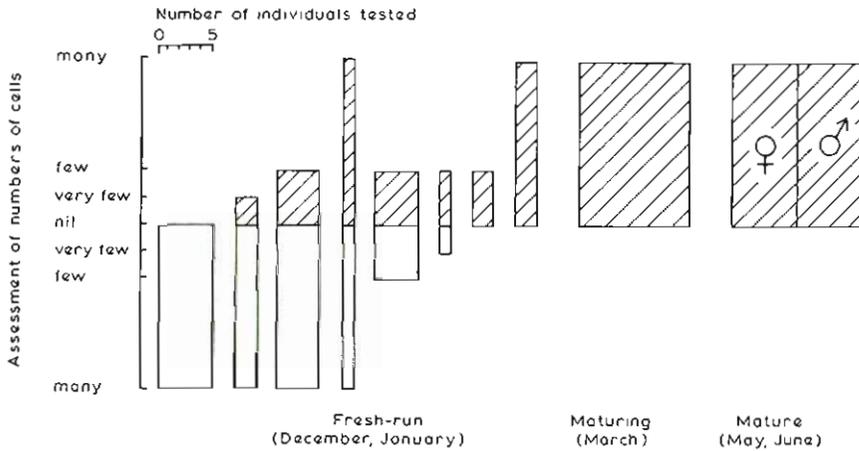


Fig. 4-189: Distribution of some of the different types of secretory cells in the gills of *Lampetra fluviatilis* taken at various stages of their spawning migration in fresh water. Unshaded areas: 'chloride-output cells'; shaded areas: 'chloride-uptake cells'. Mature males have male glandular cells in addition to 'chloride-uptake cells'. (After MORRIS, 1958; redrawn.)

There are many other records of differences in acidophil cells of the gill epithelium in different salinities. KEYS and WILLMER (1932) first suggested that the cells are the specific sites of extrarenal chloride excretion. COPELAND (1950), GETMAN (1950), COLOMBO (1961a, b), VICKERS (1961), and others have described cytological changes in the cells of fish transferred from fresh water to sea water and vice versa. WOODHEAD and WOODHEAD (1959) report an increase in gill cell numbers in *Gadus callarias* undergoing a breakdown in osmoregulatory ability in sea water. Electron microscope studies appear to confirm the characteristic structure of these cells no matter where they occur, either between species or in different organs of the same individual (COPELAND and DALTON, 1959; KESSEL and BEAMS, 1960; DOYLE and GORECKI, 1961; HOLLIDAY and PARRY, 1962).

THREADGOLD and HOUSTON (1961) described the ultrastructure of the cells in certain salmonids subjected to freshwater and sea-water conditions; these authors correlated the ultrastructure of the cells with the ability of the fishes to regulate. There were differences between the parr form of *Salmo salar* in fresh water and the smolt form of the same species kept for 72 hrs in sea water. The mitochondria in the cells of the latter were often vacuolated, in some instances

they were ruptured and the cristae were being shed into the cytoplasm. The cells of a smolt kept for 10 days in sea water presented the appearance of far less physiological activity, resembling much more those of the parr in fresh water.

It is difficult to obtain direct evidence of the precise function of these cells. They appear to change in their ultrastructure and activity in different salinities and their presence appears necessary for the survival of fish in some salinities; see for example CONTE (1965, 1969). Whether or not their primary function is ion regulation, or whether their changes reflect a response to one or more of the other variables associated with the change in salinity—e.g., the amount of dissolved oxygen or changes in metabolic rate—still awaits final elucidation.

There are records of structural changes in other sites of regulation. Thus *Oncorhynchus gorbuscha* reared in sea-water conditions have fewer kidney glomeruli than members of the same species raised in fresh water (FORD, 1958). When *Etroplus maculatus* was subjected to a salinity change, structural differences occurred both in kidneys and gut (VIRABHADRACHARI, 1961). In high salinities, there was an increase in the thickness of the gut wall and in the number of goblet cells of the epithelial gut lining. In low salinities, structural changes in glomeruli and tubules of the kidney occurred.

Generally, marine fishes have less well-developed kidneys (smaller size and number of glomeruli) than freshwater fishes (MARSHALL and SMITH, 1930; MARSHALL, 1934). The rectal gland of the elasmobranch *Carcharinus leucas* living in fresh water is smaller and appears at least partially reduced when compared with marine representatives of the same species (OGURI, 1964).

HEMPEL and BLAXTER (1961) made a study of the influence of various environmental factors on the meristic characters of *Clupea harengus*. They showed that the mean myotome counts of larvae hatched from eggs incubated in salinities ranging from 5‰ to 50‰ are highest in the higher salinities. HESS (1936) reported a correlation between low salinities and high vertebral counts in *Gobius microps*.

When eggs of *Clupea harengus membras* develop in water of abnormally high salinity (25‰), the larvae hatch with structural defects that include the inflation of the alimentary canal behind the liver and its filling with dense substance, periods of cessation of cardiac activity, and distortion of the otic capsule as well as underdevelopment of the semicircular canals (KRYZHANOVSKY, 1956).

The visual pigment in the rods of freshwater fishes is porphyropsin; in marine fishes it is rhodopsin. There is a change-over in pigment as migratory fishes change their environment (WALD, 1958, 1960, 1963). If *Etroplus maculatus* (a euryhaline fish inhabiting freshwater) is acclimated to 100% sea water in the laboratory, then the predominant visual pigment changes from porphyropsin to rhodopsin. In 50% sea water, *E. maculatus* reveals a transitory phase (VIRABHADRACHARI and co-authors, 1967).

#### (4) Conclusions

The responses of fishes to salinity are often the net result of a number of factors; these include not only the salt content of the water, but also associated variables such as oxygen content, specific gravity (density) of the water, and its ionic composition.

There is no simple definition of the response to salinity that can be applied to a fish throughout its life history. Salinity may affect organismic functions and structures differently at different ontogenetic or physiological stages. In addition, the events at any one time in the life of a fish may be determined, at least to some extent, by the conditions experienced at some earlier stage of growth and development (non-genetic adaptation).

Future studies should be concerned as much with fluctuations of the internal as of the external environment of the fish under consideration; simultaneous studies of both are desirable if cause-effect relations are to be assessed properly. Much experimental work is designed to measure what a fish is capable of doing; what it actually does under natural conditions may often be quite different.

Economic considerations have provided the stimulus for much of the work described; they are also a springboard for future work, this is perhaps especially true of marine fish hatchery and farming projects (HEMPEL, 1970; KINNE and BULNHEIM, 1970; Volume III).

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## 5. WATER MOVEMENT

### 5.0 GENERAL INTRODUCTION

R. RIEDL

#### (1) General Aspects of Water Movement

The term water movement is taken here to embrace all motions which may occur in the water of oceans and coastal areas, e.g. currents, tides, circulations, horizontal and vertical water exchanges. The primary driving forces of the different kinds of water movement are: moon phases, climate, wind, rotation of the earth, gravitation and sun radiation.

Until recently, the study of marine water movement has been exclusively or primarily a domain of the physical oceanographers. The biologist will find information pertinent to his interests in SVERDRUP and co-authors (1954) and DIETRICH and KALLE (1957). Biological consequences of water movement have only recently begun to attract more interest among marine ecologists. In view of the biological results obtained thus far, it seems quite clear that terminology and approaches employed by physical oceanographers will have to be modified, at least in some instances, to meet the needs required in ecological studies. On the other hand, research concerning the biological effects of water movement is only just beginning to develop a sound basis which may provide a platform for useful definitions and terms (e.g. RIEDL, 1964b, 1969).

The importance of water movement as an ecological factor is frequently badly underestimated. Water movement is an extremely potent ecological factor, which may exert effects comparable to those of light and temperature. Without water movement all life would cease to exist after a short while (GESSNER, 1955, p. 201).

The speed of diffusion is 10,000 times slower in water than in air. This diffusion rate is insufficient to produce the minimum water exchange required for the maintenance of marine life; diffusion as exchange mechanism would carry the effects of an increase in  $O_2$  content from 7 to 9  $cm^3/l$  at the sea surface into a depth of 10 m in some 2,000 years. Nutrition, metabolic activities, life cycles, food chains—in short, the whole cycle of production, transformation and degradation of organic matter in the seas—become significantly affected by any changes in water-movement patterns.

The biological effects of water movement are difficult to analyze, particularly for the following reasons: (i) Water movement is not an environmental factor in the strict sense of that term, but serves as transportation medium for other factors such as temperature, salinity, food—in fact practically all other environmental factors except ionizing radiation (Chapter 11). At the same time, some of these factors, i.e. temperature or salinity, may, in turn, affect speed and direction of the water movement. (ii) Direction, speed and frequency pattern of water movements may be very differentiated according to the great variety of entities which cause or modify them; this is especially so in littoral areas. (iii) A single process of water

motion comprises simultaneously various different physical parameters. (iv) Only in open areas and over considerable stretches of space and time does it become possible to predict direction, speed and fluctuation patterns of water movements with some degree of exactness. (v) The same physical process may cause different biological effects.

The biological effects of water movement have recently been discussed in detail by RIEDL (1969). For further details and for problems related to an attempt to categorize water-movement processes and pertinent biological effects, the reader is referred to that review.

## (2) Measuring Water Movement: Methods

The parameters of water movement are: speed and drift (measured in m/sec, miles/hr, or knots), exchange of water volume ( $\text{m}^3/\text{m}^2/\text{hr}$ ), hydrodynamic pressure or ram pressure ( $\text{g}/\text{dm}^2$ ), surf phenomena ( $\text{tons}/\text{m}^2$ ) and modifications in hydrostatic pressure (atm,  $\text{kg}/\text{cm}^2$ , decibars or cm-distance from water level). Mixing processes based on turbulence (exchange) become effective after overcoming molecular cohesion. This dynamic viscosity  $\eta$  is, at  $20^\circ\text{C}$  and 37‰ S,  $0.0109 \text{ g}\cdot\text{cm}^{-1}\cdot\text{sec}^{-1}$  (the power required to move, within the medium, a quadrant of  $1 \text{ cm}^3$  fluid over a distance of 1 cm within 1 sec). The kinematic viscosity (quotient of dynamic viscosity  $\eta$  and density  $\rho$ ) tends to reduce the initial movement.

The methods employed are characterized by a vast heterogeneity of technical devices, difficulties in obtaining suitable values both in regard to minimum and maximum intensities, and by the fact that indirect methods play an unusually important role. For more detailed information consult THORADE (1933), JOSEPH (1948), ISAACS and ISELIN (1954), BÖHNECKE (1955), PRANDTL (1957), BARNES (1959), LACHMANN (1961), LUMLEY (1962), EAGLESON and VAN DE WATERING (1964), KATYS (1964), HAHN (1965), FORSTNER and RUETZLER (1969), and others.

### (a) Direct Methods

In the past, most direct measurements of water movement have been conducted with mechanical devices; these are now being replaced by a number of electronic apparatuses capable of automatic, long-term registrations. Mechanical devices, such as propeller-driven current meters with stabilization fins and compasses, have been modified for optic registration (RAUSCHELBACH, 1924; EKMAN, 1953), and electrical transmission (ARX, 1950) has led to the construction of modern current meters. A detailed description of the various devices is not possible here.

In the littoral area, thermistor measurements (heat loss principle) have been introduced (RIEDL and FORSTNER, 1968; FORSTNER and RUETZLER, 1970; RIEDL and MACHAN, 1971). Heat loss of a small, heated thermistor, relative to the ambient habitat temperature, reveals the speed of water particles. Directions of water movement are added—a reasonable way to assess the circulating water movements in the surf area. The dominating directions can be determined by a pair of thermistors mounted in a tube-cross

Surf phenomena ( $\text{tons}/\text{m}^2$ ) are often recorded mechanically (in deep water by displacement of a pendulum; at the surface with a Pitot tube). In the future, the

use of electromagnetic, 'piezoelectric' and magnetodynamic systems, as well as the principle of deformation of solid bodies, appears more convenient.

Hydrostatic pressure differences can be measured with the help of marographs, manometers or membrane boxes with electric recording systems (MILLER and ZEIGLER, 1964; SCHIFFMAN, 1965; Chapter 8.0).

The metric assessment of water exchange phenomena (GESSNER, 1955) has been attempted by determining the disintegration speed of gypsum balls, employing the principle of dilution of the periphery of satiated solutions (MUUS, 1968).

### (b) *Indirect Methods*

The indirect methods for assessing parameters of water movement still play an unusually important role, due to the difficulties involved in conducting exact direct measurements.

Indirect methods for determining water movements are of great importance for practical as well as theoretical reasons. The limits of the practical aspects are related to the scarcity of fixed points in high sea areas, disturbances at the microscopical level by the measuring procedure itself, as well as to the difficulty of recording long-term means and short-term extreme values simultaneously. Calculation is—for theoretical reasons—frequently superior to measurement, because the individual measurement series of a factor can only be interpreted as one of the symbols of a complex process. Two procedures must be distinguished: the calculation procedure and the analogy procedure.

Employing the calculation procedure, the marine ecologist extrapolates from available, or already determined phenomena, to less readily available, or still undetermined ones. Thus one can extrapolate from the local current and tide the current values above the bottom profile (RIEDL, 1964b) and relate them to the body orientation of sedentary organisms with large surface areas. One can calculate from the average behaviour of surface waves the pendulum movement of water particles above the benthos (RIEDL, 1964a), or assess the depths of different water bodies and compare these with the arrangement of sedentarians. Or one can estimate from two coastal angles and the surf intensity the degree of the reduction of the primary forces (RIEDL, 1966), and establish the correlation between zonations, based on the degree of exposition and the actual secondary forces acting upon the benthonic animal populations in question. In model experiments, one can finally deduce from the behaviour of the boundary layer the phenomena to be expected to occur on the lattice-work of filter-feeders with large surface areas (RIEDL and FORSTNER, 1968).

In the analogy procedure, on the other hand, the marine ecologist draws conclusions—as soon as the cause-effect relationship is revealed—from a known effect via its cause on a hitherto unknown effect. Changes in temperature, for example, can reveal information—via the movement of bordering parameters—on water exchange processes in a given benthonic animal population; the height of the halophytic zone gives information on the degree of exposition of sedentarians to local hydrodynamic forces; the amount of fine sediment in a surf area allows assessment of the duration of the minima of the agitation intensity (RIEDL, 1964b, 1966). Finally, the marine ecologist can deduce from the arrangement of

benthonic organisms the pattern of water movement (RIEDL, 1959), and from that the amount of water current stress to which other groups of co-existing organisms are exposed.

### (3) Water Movement in Oceans and Coastal Waters

The differences between minimum and maximum values of water movement intensities are unusually large; the fluctuation patterns seem, in fact, more complex than in any other abiotic environmental factor. The orders of magnitude on which biological considerations may be based vary from vast areas of 1,000 to 10,000 km<sup>2</sup> (permanent surface currents) to 10 to 100 μm<sup>2</sup> (interstitial water between sand grains).

Some maximum values may illustrate the extent and power of changes in water movements: wave lengths have been measured up to 1000 m, wave heights to 45 m, tide-level differences to 15 m, depth ranges of waves to 500 m, surf pressures to 100 t/m<sup>2</sup>, spray heights to 50 m, current speeds in shallow or narrow coastal areas to 5 m/sec, particle speeds in the orbital movement to 3 m/sec and particle speeds in rocky surf regions to 15 m/sec.

## 5. WATER MOVEMENT

### 5.1 BACTERIA, FUNGI AND BLUE-GREEN ALGAE

*Editor's Note:* The amount of information available on responses of bacteria, fungi and blue-green algae to water movement does not yet provide a suitable basis for a review. This insufficiency of pertinent knowledge has been established in discussions with numerous marine microbiologists.



## 5. WATER MOVEMENT

### 5.2 PLANTS

H. SCHWENKE

#### (1) Introduction

##### (a) *General Aspects*

Water movement is, without doubt, of great importance for marine plant life. A general account of the effects of this ecological factor has been presented, for example, by GESSNER (1955) in one of the few reviews available to date on this subject. According to GESSNER'S view, water movement affects life processes of hydrophytes in a variety of ways, ranging from influences on cytomorphological aspects to structural effects on whole vegetations.

If we consider the fact that diffusion processes in absolutely motionless water bodies, e.g. the diffusion of oxygen, are so slow that marine life cannot exist without turbulence and exchange of water masses, it becomes quite clear that the factor 'water movement' and its numerous aspects represent a basic prerequisite for the origin and evolution of life in oceans and coastal waters.

Such a comprehensive perspective—as important and basically correct as it may be—also creates special difficulties. We still know little about the cytomorphological consequences of water movements (GESSNER, 1955, p. 196). The multiplicity of correlations between cellular properties of submerged plants and water movements would force us to view almost the whole field of hydrophyte physiology under the aspect of hydrodynamic influences. At the same time, a consequent treatment of water movement effects on structural properties of plant communities (vegetations) would require inclusion of most of our present knowledge on the ecological dynamics of marine benthos vegetations in this chapter, because of its close dependence upon the motions of the surrounding water.

Today, marine ecologists focus their attention on a more restricted view of our problem. The present view can be characterized by the search for a better quantitative expression of the factor water movement itself, with the intention of proceeding, in this way, towards a sounder understanding of the biological consequences. This trend has considerably shifted the focal point from primarily biological and physiological aspects to methodological problems of adequate measurements. Most marine ecologists concerned with water movement studies appear to concentrate on attempts to assess the multitude of relations between water movements and biological phenomena by reducing them to certain 'type relations'. In view of this drive for typification and formalization, the marine biologist is confronted with the difficult task of working out a suitable conceptual hydrodynamic fundament before he can turn back to studying primarily ecological or physiological aspects.

Even though the direction in which water movement studies are likely to proceed has thus been mapped out, our pertinent knowledge is still very small. Most

marine zoologists and botanists agree on this point. In a number of papers, RIEDL (Chapters 5.0, 5.3) has pointed out the avenues we must follow to approach our goal, but he has also listed the considerable difficulties which still have to be overcome (see also RIEDL, 1969).

To the present author, the difficulties involved appear to be related primarily to:

(i) The still insufficient competence of marine ecologists in regard to hydrodynamic problems, and the lack of knowledge of physical oceanographers or hydro-construction engineers about ecological problems. Co-operation between both groups is highly desirable.

(ii) The technical problems of accurate measurements. Oceanographers still pay little attention to quantitative measurements of water movement in coastal shallow waters and in surf areas (a critical review on applicable methods has been published, for example, by KRAUSE and STRUCK, 1969). Progress may be stimulated by the recent impetus which a related field has received: the hydrodynamics of submarine sand movements off the European and North African coasts.

(iii) The problems involved in applying suitable criteria for the assessment of the responses of marine plants. Marine animals respond more actively and often more obviously than plants. The marine botanist has particular difficulties with respect to direct effects on phytoplankton. Various responses of benthonic marine plants are adequately observable: (a) all dislocations due to the mobility of the substrate adhered to, drifting of plants which survive if detached from their substratum, and changes in species composition of plant communities; (b) structural changes in vegetations such as observed in littoral belt formations; (c) macro- and microscopic habitus modifications induced by water movement. Cellular responses are more difficult to assess; they are known from laboratory experiments, the results of which cannot, however, be extended to field conditions without further qualifications.

#### *(b) Typology of Water Movements with respect to Responses of Aquatic Plants*

The marine botanist views the multiplicity of motility phenomena of water bodies in regard to their effects on marine plant life. He distinguishes the categories outlined below.

The marine phytoplankton is affected by:

- (i) Large-scale and small-scale (local) water currents within the photic layers. They serve as transportation medium.
- (ii) Macro-turbulences and large-scale vertical circulations. They influence the availability of nutrients for the primary productivity in surface layers and can act as limiting factors by transporting phytoplankton forms to dark, lethal depths.
- (iii) Horizontal dislocations. They may transport marine phytoplankton to areas with unsuitable conditions, for example, of temperature or salinity (estuaries, bays, etc.).
- (iv) Direct mechanical stress. It may lead to damages or structural adjustments.

The marine phytobenthos is affected by:

- (i) Fast bottom currents **with high hydrodynamic effectiveness**. Examples are:
  - (a) Canal currents: rapid jet-inforced (narrow passages) water movements with a high hydrodynamic potential (tidal rapids).
  - (b) Heavy tidal currents: these may, especially under poor substrate conditions for attachment (moving stones, gravel, sand), prohibit plant settlement (e.g. along the German North Sea coasts).
  - (c) Current systems of estuaries on tide-affected coasts; ebb currents are especially effective.
  - (d) Longitudinal surf currents, notably along shallow coastal areas with gravel or sand substrates moved about by hydrodynamic forces (Kiel Bay, Baltic Sea).
- (ii) Low intensity surface currents. These are of special interest to the marine botanists. Two forms can be distinguished:
  - (a) Drift currents transporting pelagic (Sargasso Sea) or detached benthonic plants.
  - (b) Currents transporting solid bodies, especially drifting ice, exerting mechanical effects on benthonic plants.
- (iii) Surf and wave action. These are of great ecological importance. For practical purposes the following differentiation is suggested:
  - (a) Surf and wave action as a temporary factor; in quiet sea areas with only brief periods of heavy winds.
  - (b) Surf and wave action as a fairly constant factor; on exposed oceanic coasts with frequent storms and almost permanent swell. The intensity of surf and wave action on exposed coasts affects the extension of supralittoral and splash zones. In extreme cases, constant ship traffic may create a noticeable supralittoral wave action zone—even on otherwise protected, tideless coasts (Baltic Sea).
- (iv) Niveau fluctuations. This purposely rather abstract term comprises variations in sea level which exert the most powerful effects on benthonic vegetations. We can distinguish:
  - (a) Niveau fluctuations on coasts with pronounced tidal water level variations which may be modified secondarily by local geomorphological conditions. In the intertidal region, benthonic vegetations form, to a larger extent, zonation belts according to their species-specific tolerance to air exposure during low tides (Chapter 4.2). The decisive characteristic of the niveau fluctuations in question is its strict periodicity (its 'biological reliability').
  - (b) Niveau fluctuations on coasts with weak or practically no tides are aperiodic and caused by meteorological circumstances. Aperiodic water level variations are of considerable importance for the littoral benthonic vegetation. Coasts with weak tides are frequently found in European seas more or less separated from the oceans (Baltic Sea, Mediterranean Sea, Black Sea). It would be wrong to adopt for these seas typologies of water movement effects designed to meet the situation found on tide-intensive coasts, e.g. those in Brittany, or the Bay of St. Malo (France).

For practical reasons, further distinction is necessary:

- ( $\alpha$ ) Brief aperiodic niveau fluctuations, e.g. in the Kiel Bay (western Baltic Sea) with accumulated annual amplitudes and emersion periods comparable (according to calculations by SCHRAMM, 1968) to tidal variations near Den Helder (Holland).
- ( $\beta$ ) Long-term meteorologic-climatic niveau fluctuations with seasonal-orientated rhythms. An example is the regular spring water-level variation found in the eastern Baltic Sea. Due to their long duration, they cause, within a certain littoral zone, a vegetation-free period.

Small and micro-turbulences have been neglected here because they represent—according to our previously expressed views—general prerequisites for marine plant life, providing nutrients and dissolved gases. The same applies basically also for large-scale horizontal and vertical circulations in regard to phytoplankton organisms.

A 'negative' aspect of water movement must be mentioned here, namely, water stagnation in extremely quiet and protected areas. Water stagnation has, no doubt, functional and structural consequences for individuals and communities of benthonic plants.

In regard to niveau fluctuations, a special property must be pointed out. While the types of water movement referred to above affect drifting or attached organisms almost exclusively in the form of hydrodynamic forces, this pertains to niveau fluctuations only in part. Even though niveau fluctuations possess a hydrodynamic component (tidal currents or comparable processes in the case of aperiodical water level variations), their dominating ecological effect manifests itself in the periodical or aperiodical emersion (air exposure) of the littoral benthos vegetation. During emersion the littoral plant is exposed to a specific complex of local environmental factors (extreme solar radiation, thermal stress, hypo- and hyperosmotic stress, wind effects), the sum of which is referred to as desiccation (Chapters 4.2, 4.31). While tolerance to desiccation is of great importance to the intertidal benthos vegetation, it is only peripherally related to the factor water movement, in regard to the connotation of that term applied in the present chapter.

## (2) Functional Responses

A clear distinction between functional and structural responses of plants to variations in water movement is frequently difficult. While proper differentiation can be made, in most cases, at the individual level, this becomes increasingly difficult as one proceeds to the supra-individual level (population, vegetation, ecosystem).

### (a) *Tolerance*

Water movement can act as a life-limiting entity in a variety of ways. The complexity of this environmental factor, as well as the differences in living conditions in the free water and on the sea bottom of shallow waters, makes it especially difficult to evaluate water movement effects on plankton and benthos under a unifying aspect. If maximum forces of water movement lead to the destruction of

benthonic plant communities, such vegetation destroying effects will be dealt with under *Structural Responses*; they are to be distinguished from effects which determine the composition of benthonic vegetations.

#### *Primary limiting forces*

**This term refers to forces which act directly through the kinetics of a water body** (Chapter 5.3). While the term may be useful for benthonic plants, it creates certain problems in regard to planktonic forms.

(i) Planktonic plants are not, under normal conditions, directly affected by the kinetics of the water body maintaining them. They are 'embedded' in the moving water and drift along at identical speeds and in the same directions. Under extreme conditions, however, detrimental effects of water movement appear possible, e.g. in the surf zone, when fast-moving water hits on solid bodies, or if waves break during heavy seas. Experimental investigations into such phenomena are extremely difficult, so that we still know very little about them. To a certain extent, one could also visualize the kinetics of a transporting water body as a life-limiting quantity, if phytoplankton communities are dislocated horizontally and thus exposed to detrimental temperatures or salinities, or if they are dislocated vertically into unfavourable light conditions.

(ii) Benthonic plants of exposed habitats are adapted to tolerate high hydrodynamic pressure and its secondary consequences. GESSNER (1955) compares their body forms to that of the 'Langen Krummen' in IBSEN's 'Peer Gynt'; their bodies are built in such a way that they offer little resistance to flowing water and permit high elasticity. On the other hand, heavy storms can lead to detachment of large numbers of attached benthonic plants. In such cases one can speak of vegetation destroying forces (see *Structural Responses*).

#### *Secondary limiting forces*

These are due to water motions (normally of near-minimum intensities) transporting other ecofactors (such as heat, salinity or nutrients) and thus affecting plant life (Chapter 5.3). According to definition, the effects of secondary limiting forces are restricted to benthonic organisms. The lower limiting intensities are represented by stagnation, i.e. a case in which unfavourable ambient water conditions (critical temperatures, gas or nutrient concentrations) are no longer removed from the plant concerned. In such situations, plants adapted to life in exposed habitats (e.g. species of *Alaria*, *Blidingia*, *Bangia*, *Plocamium*, *Porphyra*) respond more sensitively to stagnating water than those of quiet deep habitats (e.g. the red algae *Delesseria sanguinea* and *Phycodrys sinuosa*).

In general, it can be said that stagnation exerts less detrimental effects on benthonic plants than on sessile animals (Chapter 5.3). A similar situation appears to exist in regard to maximum intensities of a secondary limiting factor: the sediment and sand transport by water movement. Covering by sediment or sand may occur in low-growing algae beds, but hardly ever in large benthonic algae. Littoral seaweeds such as *Fucus vesiculosus* or *F. serratus* growing on rubble substrates of sandy shallow offshore areas (e.g. of the Baltic Sea) may even profit from moderate sand covering, since that process leads to over-all stabilization of the substrate (SCHWENKE, 1965a; see also Chapter 7).

Sea-grasses, such as *Zostera marina*, can grow higher with increasing sand covering. This may, however, cause a secondary danger by gradually lifting the plants to high above average water level.

### *Tertiary limiting forces*

These become effective via the distribution of stable and mobile substrates relative to water movements (Chapter 5.3). Tertiary forces also apply, according to the concept involved, to benthonic organisms only. They may, under certain circumstances, attain considerable importance for littoral algal communities, particularly on coastal stretches with rubble substrate, and—most important—on alluvial and diluvial sediment coasts, e.g. of the North Sea and Baltic Sea. In regard to the North Sea coast, REYNKE (1889) pointed out that the powerful tidal currents keep the sparse rubble substrates in motion and thus prevent settlement and development of benthonic algae.

### *(b) Metabolism and Activity*

The question as to the relationship between metabolic processes and water movement is closely connected with the connotation given to the term 'water movement'. If we restrict that term to hydrodynamic macro-effects with clearly recordable consequences for functional and structural components of hydrophytes—and such restriction is preferred by the present author—microstructural and very slow movements (important as they may be in regard to the physiology of water plants) remain outside our consideration (see also *Introduction* to this chapter).

In regard to hydrodynamic macro-effects it seems reasonable to assume that the habitat dependence of many littoral algae on certain degrees of surf exposure is correlated to specific physiological adjustments. However, hardly any unequivocal evidence of such adjustments is available.

First attempts towards tackling this complex situation have been undertaken by CONOVER (1968). He tried to combine model experiments conducted under laboratory conditions with observations *in situ*. His major point is that the growth of benthonic plants in exposed habitats with vigorous water movement is more luxurious than that in quiet bays—a fact which can hardly be denied, even though it refers primarily to density and species diversity of the benthonic vegetation as a whole, but not necessarily to a single species. This latter statement is documented by the fact that the area investigated by CONOVER (estuaries and lagoons along the coast of Texas, USA) contains (as do, for example, the quiet bays of the Baltic Sea) plant species which exhibit luxurious growth (in the Baltic Sea, *Enteromorpha linza*, *Petalonia fascia* or *Dumontia incrassata*). We must, therefore, also take into consideration that water movement may have induced increases in metabolic rates as a function of habitat conditions, a response possibly dominated by genetic adaptation. In fact, CONOVER comes to the conclusion (Fig. 5-1) that differences in standing crop as a function of water movement speed make it possible to distinguish between communities of quiet lagoons and surf-exposed littoral habitats.

Laboratory model experiments in a running sea-water system—in which Indian ink particles simulate important nutrient substances (such as phosphate

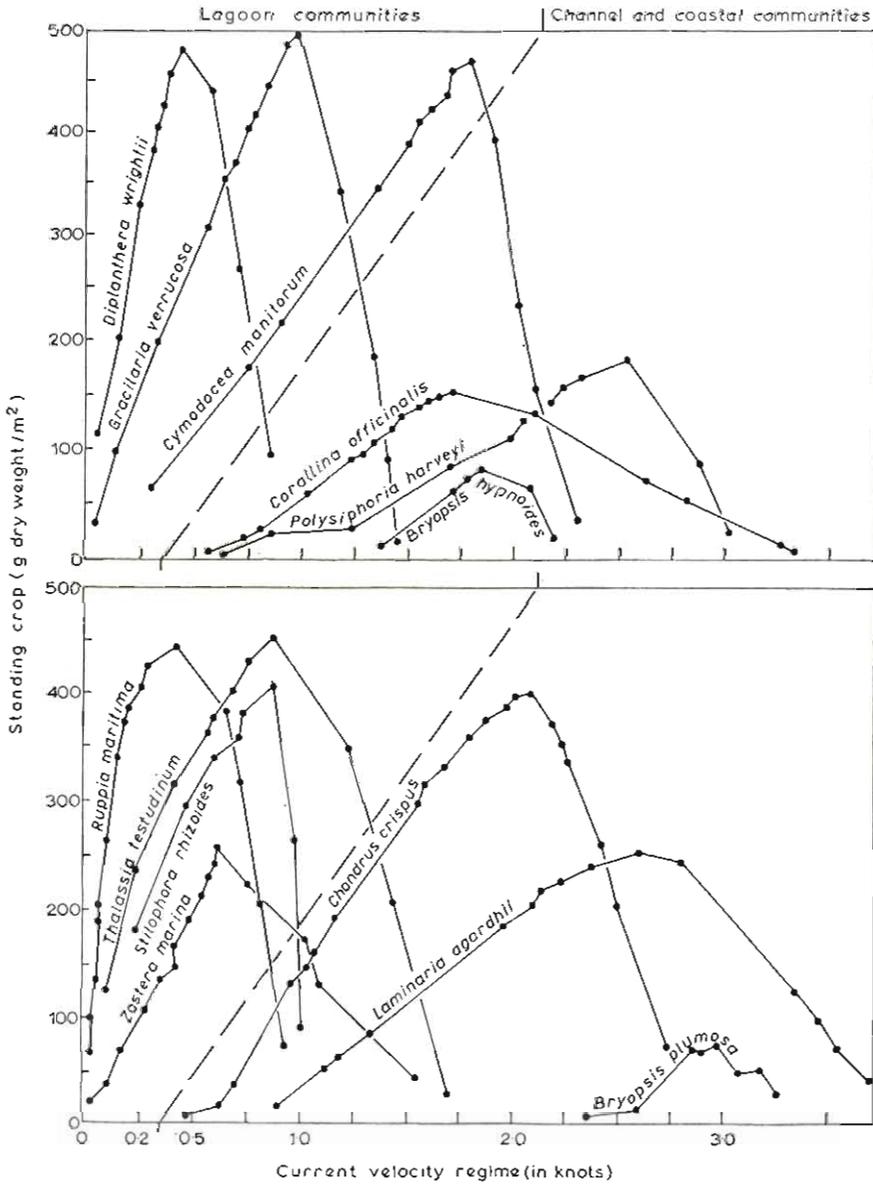


Fig. 5-1: Standing crop data for a number of important benthonic plant taxa as a function of water movement. It is possible to separate lagoon from channel and coastal communities on the basis of water current regimes. Temperature: Charlestown Pond, Rhode Island and Great Pond, Falmouth, Mass., USA: 23° to 25° C; Redish Bay and Port Aransas, Texas, USA: 25° to 28° C. Salinity: 29‰ to 31‰. (After CONOVER, 1968; modified.)

ions) and millipore-filters the plant organism—demonstrate the dependence of particle uptake on water movement intensity. As a next step, determinations of the standing crop of algae and sea-grass communities in habitats with different intensities of water movement are compared to the results obtained in the model experiments (Fig. 5-2).

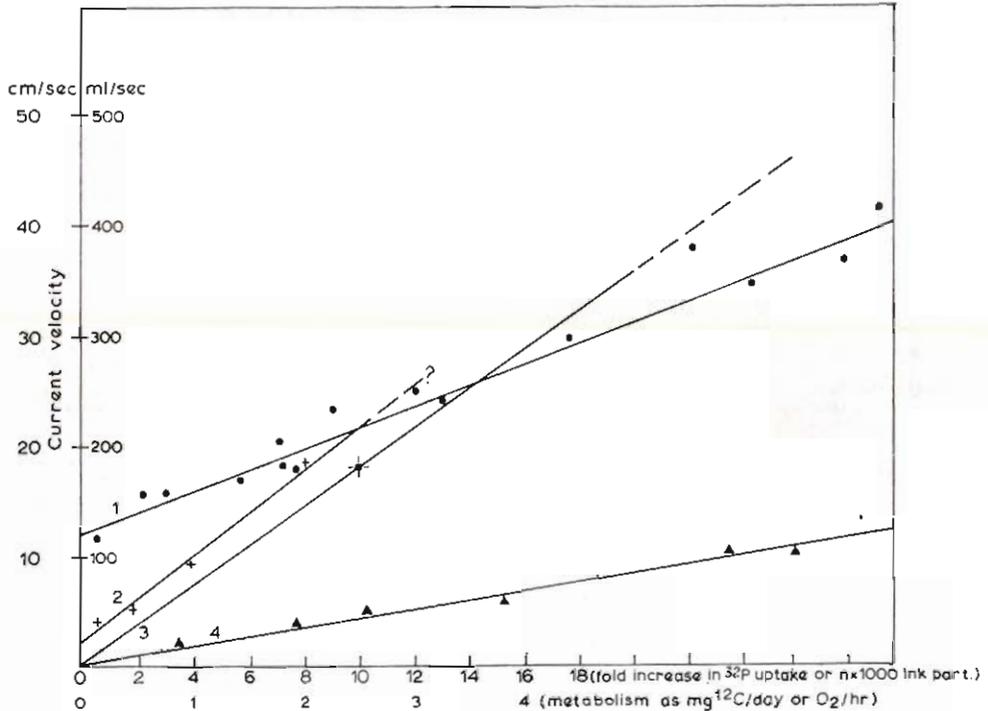


Fig. 5-2: Comparative metabolic rates of plants as a function of water movement (current velocity). 1: *Zostera marina*; metabolism expressed in mg  $^{12}\text{C}/\text{day}$  versus current velocity (ml/sec). 2: Aufwuchs; metabolism in mg  $\text{O}_2/\text{hr}$  vs current velocity (cm/sec; data from ODUM and HOSKIN, 1957). 3: *Oedogonium* sp.;  $^{32}\text{P}$  uptake vs current velocity (cm/sec; data from WHITFORD, 1961). 4: Number of ink particles caught by a Millipore membrane filter per 5-sec interval. (After CONOVER, 1968; modified.)

MATSUMOTO (1959) has shown that water movement is essential for the normal growth of *Porphyra tenera*: 20 cm/sec in normal sea water, 10 cm/sec in nutrient-rich, and 30 cm/sec in nutrient-deficient water.

As is well known, gas exchange represents the most intensive cell physiological exchange parameter. We may expect, therefore, relations to the factor water movement also in regard to the intensity of gas exchange between plant and environment. Some basic relations are known from experiments devoted to measurements of rates of respiration and photosynthesis.

Thus, GESSNER (1938, in: GESSNER, 1955) observed, during photosynthesis studies on submersed aquatic plants, that frequent water exchange in the culture vessels resulted, even at high light intensities (40,000 to 60,000 lux), in a constant photosynthetic rate throughout the day ( $\text{O}_2$  determination according to Winkler),

whereas the bubble-count method yields, at high light intensities, after only a few hours, a decreasing photosynthesis rate in *Elodea canadensis* (ARNOLD, 1931). The application of the bubble-count method requires completely stagnant water and the presence of an O<sub>2</sub>-saturated water mantle around the test object. Obviously, the water stagnation is responsible for the resulting difference in metabolic performance.

Following these experiments on limnic forms, gas exchange has been studied frequently also in marine algae exposed to non-moving and moving waters (e.g. PRINTZ, 1942; STEEMANN NIELSEN, 1942). NATH (1955) and NELLEN (1966) have conducted studies on optimum rotation speeds, employing rotation-light-thermostats (e.g. 9 rotations/min with a disc diameter of 50 cm). Rotation-light-thermostats are used for gas-exchange determinations (O<sub>2</sub> determination according to the Winkler method) making use of so-called 'incubators' for productivity studies in planktology. GESSNER (1955) employed culture vessels rotating in a horizontal 'Klinostat' illuminated from an—also rotating—artificial light source.

NATH (1967), in his experiments devoted primarily to methodological analyses of the effects of different O<sub>2</sub> tensions (manometric O<sub>2</sub> determination in the Warburg apparatus), demonstrated that the shaking movements of the manometers *per se*, as well as the shaking frequency and amplitude, affect the respiratory performance of *Fucus vesiculosus* and *F. serratus* (Fig. 5-3).

The importance of such experiments should not be over-estimated, since the very complex phenomenon is still in its initial phase of investigation. This has been duly stressed by GESSNER (1955). In essence, only the importance of the stagnation effect has been clearly demonstrated, while the quantitative relationships are still insufficiently documented. Some pertinent data are listed in Table 5-1.

Table 5-1

Influence of water movement on rates of photosynthesis and respiration in marine algae (Data from PRINTZ, 1942; after GESSNER, 1955; modified)

Increase of photosynthesis in moving water (%)		Inhibition of respiration in stagnating water (%)
<i>Halidrys siliquosa</i>	135.0	
<i>Chorda filum</i>	102.9	53.1
<i>Ascophyllum nodosum</i>	100.6	
<i>Fucus serratus</i>	88.9	32.6
<i>Fucus vesiculosus</i>	65.8	30.1
<i>Ceramium rubrum</i>	5.2	8.5

While the stagnation effect can easily be demonstrated under experimental conditions in the laboratory, it is uncertain whether stagnation is of importance under ecological conditions in the sea. The marine benthos offers a broad spectrum of habitats with permanently or temporarily pronounced differences in the intensity of water movements: exposed and protected biotopes, quiet bays, areas

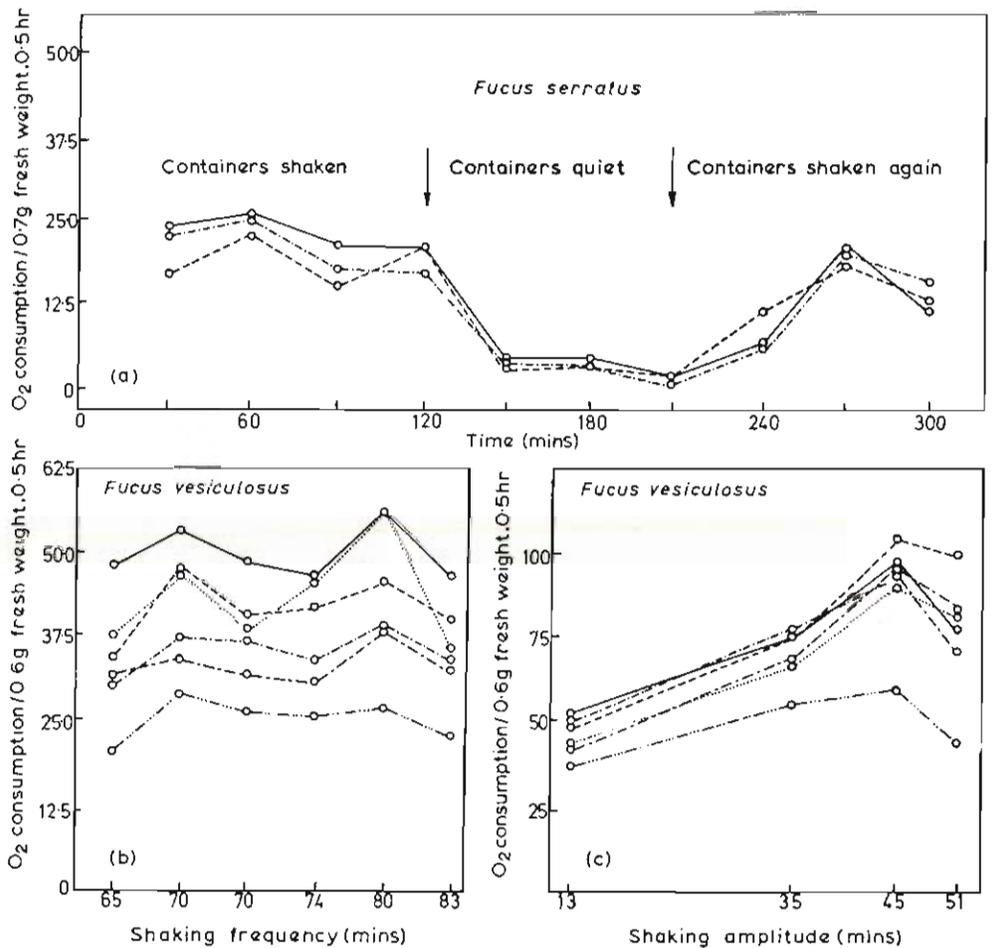


Fig. 5-3: Water movement effects on metabolic rate (O<sub>2</sub> consumption in Warburg apparatus) in *Fucus serratus* and *F. vesiculosus*. (a) Effect of alternating shaking and non-shaking periods; (b) effect of shaking frequency; (c) effect of shaking amplitude. (After NATH, 1967; modified.)

with continuous surf action, coasts with extensive tidal currents, etc. In general, sublittoral habitats may be expected to be characterized by less water movement than littoral ones, and it can be assumed that, within sublittoral vegetations, zones of practically stagnating water may occur, at least temporarily. Presumably, sublittoral plants are adjusted also ecologically to such low turbulences. Thus GESSNER (1955) pointed out that deeper growing forms of the benthos near Helgoland (southern North Sea), e.g. species such as *Furcellaria fastigiata*, *Membranoptera alata*, *Ceramium* sp., and particularly *Phycodrys rubens*, reveal a significantly smaller stagnation-caused respiratory inhibition (about 10% and less) than typical surface forms, such as species of *Cladophora*, *Chondrus crispus*, *Fucus vesiculosus* and *F. serratus* (about 50%).

According to SCHWENKE (1960), deep-growing red algae of the Kiel Bay (western Baltic Sea), such as *Delesseria sanguinea* and *Phycodrys rubens*, survive for months,

at temperatures between 0° and 5° C, in stagnating water (without water exchange). This observation indicates that these forms are able to adjust their gas-exchange intensity to extremely adverse supply conditions. There was no measurable growth under such conditions.

The question whether the water in the incubation apparatus should be quiet or agitated has also played a role in developing techniques for measuring quantitative aspects of primary production in the sea. Based on investigations by STEEMANN NIELSEN (1952), DOTY and OGURI (1958) have examined the effect of water movement on the results of experiments on metabolic performance. They come to the conclusion that—rather independent of the degree and the method of water movement—there is, in any case, augmentation of productivity of 30 to 50% (Table 5-2). DOTY and OGURI interpret the physiological effects of water movement in the cancellation of the stagnation effect with its unfavourable diffusion gradients. This interpretation is in accordance with the point of view expressed above. However, DOTY and OGURI leave open the question, whether natural conditions in the sea are more equivalent to laboratory measurements in agitated or stagnating water.

Table 5-2

Comparative rates of primary production as a function of water movement.

L: Light bottles; D: dark bottles (After DOTY and OGURI, 1958; modified)

Experimental condition	Number of tests	Light intensity	Productivity (% of control)	Productivity (mean value)
A Water shaken uniformly for 50 oscillations in a half-filled 5 gallon carboy before drawing each sample of the series. Control drawn before shaking began.	1	L	135	L 158 D 104
	2	D	105	
		L	158	
	3	D	116	
		L	171	
	4	D	96	
		L	168	
	D	100		
B Water stirred with tygon-covered stirrer at about 1000 r.p.m. for successive 3-min periods between the serially numbered samplings. Control drawn before stirring began.	1	L	96*	L 138
	2	L	90*	
	3	L	140	
	4	L	127	
	5	L	123	
	6	L	144	
	7	L	146	
	8	L	148	
C Water in bottle rocked about 30 cycles per min through an arc of ca 60° during incubation. No rocking during incubation of control.	Rocked	L	118	L 118

\* Not used in computing mean percentage values

(c) *Reproduction*

Water movement is an important factor in regard to the transportation of reproductive stages (gametes, spores) of marine plants. This general statement requires no specific documentation. Upon settlement of spores or germlings, however, the transportation effect changes into a problem of resistance of newly attached stages to the dynamic forces of water movement. Some pertinent observations have been summarized by BONEY (1966). Spores of *Gelidium amansii* fix to the substrate surface within a 10-min contact period. Tetraspores of *Polysiphonia lanosa* attach fast to a glass surface so that they can no longer be removed with a suction pipette. In general, attachment is achieved via slime excretion, depending on kind and structure of the substrate surface area.

NORTH and co-authors (1969) reported experiments on spore settling of *Macrocystis pyrifera*. A rotating disk was placed in a spore suspension and then examined for settled spores. Their results indicate that relative movement between water and substrate inhibits settling. In order to determine quantitative effects, microscope slides were exposed for 4 mins to a dense spore suspension flowing at varying rates across the slide surface. Rate of flow was controlled by moving the slide back and forth at a given speed through the suspension. After exposure, the slide was placed in nutrient sea water for 5 days to allow germination and development of gametophytes. Thus, only living spores that had attached to these slides were taken into account; concentrations of gametophytes were determined on each slide. Almost any water movement reduces the ability of the spores to settle on the slide. Even gentle wave surge substantially diminishes the rate of settling; this conclusion is supported by field experiments.

Relationships between gamete release of intertidal algae and variations in habitat water levels are influenced largely by desiccation, and, therefore, have been dealt with in Chapter 4.2.

Water movement may exert certain negative effects on reproduction. Thus originally holobenthic algae, which have adjusted to a floating way of life (e.g. the floating *Sargassum* forms of the western Atlantic Ocean or *Furcellaria fastigiata* forma *aegugropila* of the Kattegat) are characterized by sterility and reproduce only asexually.

(d) *Distribution*

*Planktonic plants*

'Plankton' is defined as that great portion of life in oceans and coastal waters which drifts under the influence of water currents. Hence, the very definition of this term points to its dependence on water movement. However, it is not this basic relationship which is to be considered here, but the, probably, most important secondary effects. Large-scale and small-scale current systems of the seas and the complex water movements in the estuaries act on the marine phytoplankton as transportation media. Transportation causes more or less pronounced changes of other environmental factors—such as light (Chapter 2), temperature (Chapter 3), salinity (Chapter 4) and nutrition (Volumes III and IV)—to which most phytoplankters respond with great sensitivity. Insofar as current systems, in addition to other factors, sustain the continuity of phytoplankton communities (BRAARUD

and co-authors, 1953), this stabilization effect can, without difficulty, be considered as a special case of the transportation effect.

Large-scale oceanic current systems are primarily responsible for the geographic distribution of plankton communities. As in all biogeographic large-scale differentiations, the temperature factor is likely to act also in this case as ecological master factor (Chapter 3). Certain plankton organisms can, as is well known, be used to identify water bodies transported by the current systems; they are called 'Leitformen' or indicators, in the sense of KÜNNE (1937). In large-scale systems, such forms are mainly zooplankters, e.g. chaetognaths, copepods and medusae (consult, for example, RUSSELL, 1935, in regard to the areas around England; also FRASER, 1952, 1968). This observation may be related to the fact that being an indicator species requires—also in regard to time—sufficient resistance against the gradual changes in environmental factor intensities correlated to the transportation process. Zooplankters may, with certain limitations, act also as indicators of vertical water movements (Chapter 5.3).

In the current systems of smaller sea areas, phytoplankters may also function as indicators of the water bodies. Terminologically, two overlapping phenomena must be distinguished here: plankton succession and plankton sequence. Plankton succession refers to the successive appearance and disappearance of relatively short-lived plankton communities, caused by seasonal changes in intensities of environmental factors (particularly light and temperature) in an individual unmixed water body. Plankton sequence (GRAN and BRAARUD, 1935) refers to changes in phytoplankton populations as a consequence of the mixing of different water bodies (at a defined geographical point of a given sea area), characterized by different environmental parameters and, hence, by specific plankton communities.

In the North Sea, BRAARUD and co-authors (1953; summarized in GESSNER, 1957, 1959) have, in an excellent account, characterized 16 different water body qualities on the basis of parallel differences in phytoplankton communities. In this relatively small sea area, which nevertheless receives a great number of different water types, salinity differences become more important as characterizing attributes of the various water bodies than do temperature differences.

The 16 water bodies differentiated are listed below:

- (1) Inflowing Atlantic water; 35.42‰ S; indicators: *Coccolithus* (= *Pontosphaera*) *huxleyi* and *Exuviaella baltica*.
- (2) Local Atlantic water; 35.26‰ S; indicator: *Skeletonema costatum*.
- (3) Water near the Faeröe Islands; 35.26‰ S; rich in diatoms: *Thalassiosira gravida*, *Chaetoceros debilis*, *Nitzschia delicatissima*.
- (4) Water near the Shetland Islands, salinity similar to (3); rich in diatoms: *Asterionella japonica*, *Chaetoceros debilis*, and others.
- (5) Water south of (4); indicator: *Thalassiosira nordenskiöldi*.
- (6) Water near the coast, south of (5); indicator: *Rhizosolenia fragilissima*.
- (7) Coastal water between Firth of Tay and the Humber estuary; rich in diatoms: *Chaetoceros*, *Nitzschia*, *Asterionella*.
- (8) Coastal water south of (7); indicators: *Chaetoceros danicus*.
- (9) Water from the mouth of the English Channel; rich in bottom diatoms such as *Melosira sulcata*, *Bellerophon malleus*, *Biddulphia* sp. and others.

- (10) and (11) Coastal water in the German Bight and off North Jutland, respectively; rich in diatoms: *Cerataulina bergoni*, *Eucampia zoodiacus*; also in *Phaeocystis* sp.
- (12) Kattegat water; indicator: *Chaetoceros tortissimus*.
- (13) Skagerrak, Norwegian coastal water; poor in diatoms; peridineans: *Ceratium* sp., *Exuviaella baltica*, *Peridinium trochoideum*.
- (14) Central high sea water, Dogger Bank; indicator: *Rhizosolenia imbicata* var. *shrubsolei*; furthermore, peridineans similar to those listed in (13).
- (15) Southward streaming Atlantic water; poor in plankton; indicators: *Coccolithus huxleyi* and *Exuviaella baltica*; small admixtures of coastal diatoms.
- (16) Mixed water of the northern North Sea, without specific characteristics.

The areas occupied by these plankton communities show, in addition, an impressive congruence with the streamline pattern of the surface drift currents in the northern North Sea, according to the chart by TAIT (1937; Fig. in: GESSNER, 1957, 1959).

Extreme salinity differences are also characteristic of the complex water movement processes in the estuaries of large rivers and their hydrographic zones of influence.

A classic study on this subject is the paper by THIEMANN (1934). He investigated, during the first 'Meteor' Expedition, the estuaries of some South American (Amazonas-Pará, La Plata) and African (Niger-Bonny, Bimbia, Cameroun, Congo) rivers and, for comparison and deepening of the insights gained, also the estuary of the River Elbe (Germany). In wide-mouthed rivers, THIEMANN has, on the basis of population density and composition of plankton communities, differentiated between coastal and river brackish water. In narrow-mouthed rivers (Bonny, Bimbia, Cameroun) such differentiation is not possible, since the plankton of the lowest river parts is predominantly marine.

The water movement processes are controlled by the freshwater discharge of the rivers, which depends on climatic factors and on tidal mechanisms in the estuary, which, in turn, are influenced by wind conditions. The biological effect is, basically, a simple one: freshwater plankters as well as stenohaline marine organisms die in the brackish transition zone. This mass mortality causes an increase in nutrient substances which allows an increase of population density of euryhaline marine diatoms, for example, species of *Coscinodiscus* and *Biddulphia*.

On the basis of his observations, THIEMANN (1934) has constructed the diagram of the mouth area of an ideal river, illustrated in Fig. 5-4.

### *Benthonic plants*

In regard to distribution patterns of benthonic marine plants, which are influenced by water movement, two different types must be distinguished: drifting benthonic plants and holobenthonic plants.

*Drifting benthonic plants.* The mechanism of distribution due to water movements is, in drifting benthonic plants, quite similar to that in planktonic plants. Permanently drifting plants or (originally fixed) plants detached in the surf zone can be transported by water currents over considerable distances, or may be concentrated in a certain sea area by circulating current systems.

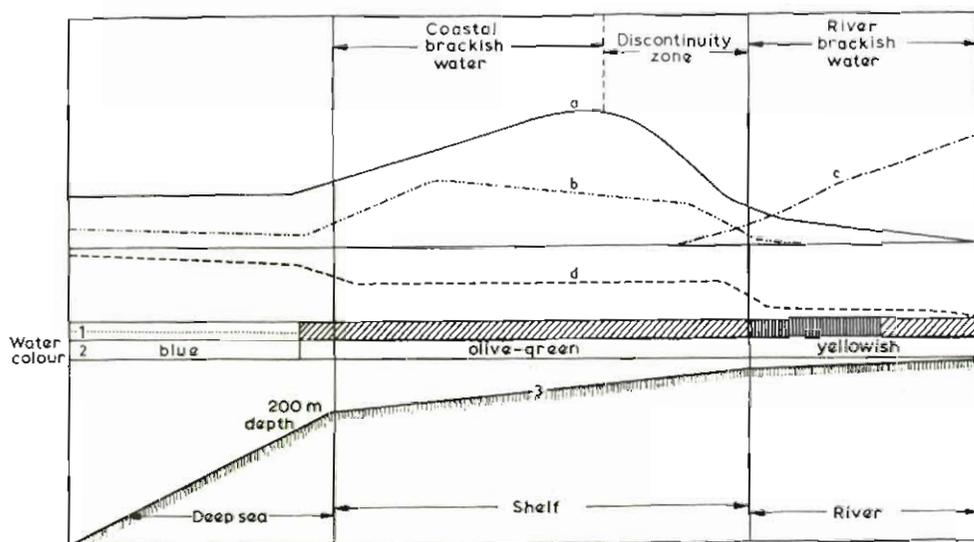


Fig. 5-4: Plankton, detritus content, water colour and water depth in the mouth region of an ideal river. a: marine diatoms, b: appendicularians c: freshwater algae, d: salinity (relative values). 1: detritus content (dots: poor; oblique hatching: medium; vertical hatching: heavy); 2: water colour; 3: water depth. (After THIEMANN, 1934; modified.)

The best known examples of current-dependent plant concentrations are the drifting *Sargassum* forms of the western Atlantic Ocean (detailed documentation in: GESSNER, 1955).

Today, it is assumed that the two major *Sargassum* species (*S. natans* and *S. fluitans*) are true eupelagic forms which never carry attachment organs and reproduce only vegetatively (asexually); they harbour a specific epizoic fauna, which is indicative of a high phylogenetic age of these drifting forms. The old view that drifting *Sargassum* species represent detached epilithic counterparts of plants from neighbouring coastal areas can, according to detailed studies (especially by PARR, 1939, who also made quantitative assessments), no longer be maintained. Certainly, detached *Sargassum* forms also are present in the drifting communities; however, these holobenthonic (e.g. *S. polyceratium*) or quasi-pelagic (e.g. *S. hystrix*) forms can be clearly differentiated from the main mass of eupelagic representatives. It must be mentioned though that the taxonomic identification of *Sargassum* species is a difficult—if in the present context secondary—problem. Thus, the species names referred to above must be viewed with some reservation; for this reason some authors, e.g. WINGE (1923), have employed neutral names for the various types.

In view of their proved autonomy, the eupelagic *Sargassum* communities of the western Atlantic Ocean are considered, and rightly so, to be the greatest homogeneous vegetation system on earth; the existence of this system in the central quiet waters of the Sargasso Sea is primarily due to the stabilizing effects of gigantic circulating water currents composed of the North Equatorial Current, Gulf Stream and the Canaries Current.

The total mass of the drifting *Sargassum* species has been estimated by GESSNER (1955), on the basis of quantitative investigations by PARR (1939). In the central area of the Sargasso Sea, each square nautical mile contains several tons of algae; the total area of about 2 million square miles contains between 4 and 11 million tons (fresh weight) of algae.

The characteristic stripe-formed patterns of the drifting seaweeds are assumed to be due to water movements; it appears that the stripes become stabilized by borderlines between adjacent turbulence units of the water body.

*Sargassum* species also represent the major forms in drifting seaweed communities of Japanese waters. Their seasonal appearance and special distribution have been investigated by YOSHIDA (1963), because of the obvious correlations to fisheries research. The Japanese drifting seaweeds are, however, exclusively derivatives of holobenthonic species, which have become detached and dislocated by water currents. Of the 50 *Sargassum* species of the Japanese coasts, YOSHIDA was able to record 23 representatives in drifting state; further, 13 other algae species and 4 marine phanerogams. Another difference to the situation in the Sargasso Sea is that the *Sargassum* species of Japanese waters are transported predominantly by near-coastal currents and hardly ever leave the coastal area. In the regions of the large-scale warm ocean currents (Kuroshio, Tsushima) only a few drifting *Sargassum* species are found.

Marking experiments revealed that drifting seaweeds travel about 20 km per day. They are found especially during the months May to July. Of course, the time of appearance and composition of the drifting seaweed masses depend largely on the biology of the parent benthos vegetation.

The degree to which holobenthonic marine algae may, in general, be displaced from their primary benthonic habitat can be demonstrated particularly well on coasts which, owing to their geological properties, have very little benthonic vegetation of their own. Examples are the sandy coasts of the North Sea near Jutland and the North Frisian Islands. ROSENVIINGE (1906) found 48 drifting algae along the Danish west coast, most of them epiphytic on species of the large brown algae genera *Himantothalia* and *Ascophyllum*. KORNMAN (1952) reports that 30 of these algae are also known from the North Sea island Sylt and that an additional 28 species were found drifting in that area. The primary habitats of these algae are presumably the rocky coasts of England and, especially, of Scotland. However, for some algae (*Laminaria saccharina*, *L. hyperborea*, *Desmarestia aculeata*, *Dalssonia sanguinea*) closer located solid substrates areas must be assumed to represent the original habitats.

In isolated marine areas also, drifting, or at least loose-lying algae play a considerable role in the whole local system, e.g. under the specific substrate ecological conditions in the Baltic Sea. Littoral rocky areas are found in the Baltic Sea in a few places only (Swedish coast, reef archipelagos off the Swedish and Finnish coasts), while plain sandy beaches with diluvial boulders of different sizes are widespread; as is well known, the reason for this is the geological youth and the history of this isolated sea area. In the western part, the transition between Baltic and North Sea, intensive current systems are of importance; the geomorphological structure of the whole basin is responsible for the fact that more or less extended quiet-water zones could establish themselves.

Benthos algae, which are attached only during their subadult stages and normally float as adults in quiet bays, will be mentioned only briefly; examples are *Ulva lactuca*, species of *Monostroma*, *Chaetomorpha linum*, but also species of *Cladophora* and *Enteromorpha*. Following the *Sargassum* terminology, these forms may be called quasi-pelagical.

However, there are also plants which, in this sense, may be called eupelagic, with the restriction that they do not drift at the water surface. In the Baltic Sea, particularly in the western part, the most important representative of this group is the red alga *Furcellaria fastigiata* (L.) LAM. forma *aegagropila* REINKE; according to investigations by AUSTIN (1960), this form is clearly an ecotype of *F. fastigiata*. The forma *aegagropila* must have developed from the originally holobenthonic form (just as the *Sargassum* seaweeds of the Sargasso Sea). It appears in large quantities especially in Aalborg Bight of the western Kattegat, and for many years has increasingly been harvested (recently at the rate of 18,000 t per year) for the production of agar (DANAGAR).

In the last few years, there have been indications of over-harvesting of the *Furcellaria fastigiata* population; obviously, repopulation is not significantly supported by detached specimens but depends on autochthonous specimens of the forma *aegagropila*, due to the special hydrographic conditions in the Aalborg Bight. In addition to specific morphological characteristics (p. 1111), sterility and exclusively asexual reproduction are indicative of the autonomy of this ecotype, similar to the situation in the western Atlantic *Sargassum* seaweeds and other drifting forms. The ecotype is therefore closely related to the 'migration forms' of *Fucus vesiculosus*, as described by BAUCH (1954) and OVERBECK (1956), from the 'Boddengewässer' of the Baltic Sea island Rügen.

A migration type of plants which is related to water-movement dependent partial mobility of small particulate gravel substrates exists in the Baltic Sea. In contrast to the drifting forms dealt with above (detached epilithic algae, autochthonous ecotypes of originally holobenthonic species, quasi-pelagic adult forms with attached subadult stages), we refer here to truly epilithic growth forms from usually quiet sea areas, which are, during aperiodic increases in water-movement intensity, transported together with their immediate attachment substrate (e.g. species of *Fucus* on fist-size stones, or sublittoral red algal species of the genera *Furcellaria*, *Ceramium* and *Polysiphonia* on gravel). In the Kiel Bay of the western Baltic Sea, such transportation, due to unusually intense water movement, was directly observed by employing underwater television (SCHWENKE, 1965a) or via marking experiments (SCHWENKE, 1968).

In general, it may be concluded that the errant (drifting) component in the marine benthos vegetation is considerably more important, when compared to the adnate (substrate-attached) algae and the radicate (rooted) phanerogams, than hitherto assumed.

*Holobenthonic plants.* As indicated earlier in this chapter, the effect of water movement on the distribution of holobenthonic plants is—where the concept of distribution is regarded as a functional aspect—difficult to document when viewed from the present-day scientific standpoint. The modern concept of distribution is extremely comprehensive; it requires closer specification and subdivision into partial aspects, such as geographical distribution or local distribution. In regard to

intertidal rocky coasts, LEWIS (1964) has provided an excellent account; he uses the term 'patterns of distribution' for describing space-related assemblages of benthonic organisms.

Functional aspects in the distribution of intertidal holobenthonic plants can be considered in the light of autecological relations to desiccation and of adjustments to wave exposure. However, the distribution of many holobenthonic algae in the periodically emersed littoral does not depend exclusively on their species-specific emersion tolerance; it is, frequently to a large extent, related also to the degree of mutual protection against critical desiccation stress (Chapter 4.2). Mutual protection of single plants within a given vegetation applies also to wave exposure. Consequently, water movement effects on patterns of benthonic plant distribution involve the specific structure of supra-individual assemblages of organisms.

### (3) Structural Responses

In marine plants, water movement can affect structural aspects in various ways. However, a reliable and detailed analysis of structural responses has been possible as yet only in a few instances. In most cases, only the mere presence of a relation between water movement and plant structure as such is known, or assumed, to exist, without knowledge of causative intercorrelations. Frequently, ecological interpretations have been made, without a sufficiently sound fundament, which later proved to be wrong. Progress in this complicated problem proceeds very slowly.

#### (a) Size

The thallus size of benthonic algae may be affected by water movement. However, the interrelations are very complex and can be considered, at most, as secondary water movement effects. Usually, the primary causal effects have not yet been investigated.

It is known that many algae of the surf zone tend toward dwarf growth with increasing wave exposure. However, dwarf growth is by no means a general result of increasing wave action. BAUCH (1954) and OVERBECK (1956) demonstrated that *Fucus vesiculosus* forms delicate dwarf forms of only a few centimetres in height especially in the quiet and shallow 'Boddengewässer' of the island Rügen and near Hiddensee (inner Baltic Sea). In these cases, it could be ascertained that this reduction in final size is not due to the sub-oceanic local salinity. Such dwarf forms have been reported also from salt marshes of the British and French coasts.

Among the dwarf forms of the inner Baltic Sea, two types can be distinguished. Type 1 lives (with the help of attachment discs) epilithic on boulders; type 2 lies around loose and has been interpreted as a migration form by SCHILLER (1909) and BAUCH (1954), derived from adventive differentiations or regenerates of normal *Fucus* thalli, and then displaced into still-water areas.

On the other hand, luxuriant forms often develop in extremely protected localities with quiet water. In the western Baltic Sea, such forms are, for example, *Enteromorpha linza*, *Ilea fascia* and *Dumontia incrassata*.

*(b) External Structures*

Water movement effects on external plant structures involve different phenomena in planktonic and benthonic forms. For this reason, the information available will be considered under the two subheadings: planktonic plants and benthonic plants.

*Planktonic plants*

Well-known external structures in plankton-living plants are the so-called 'Schwebefortsätze' (suspension or floating processes). The history of investigating these structures provides examples of premature interpretations of cause and effect. For a comprehensive discussion of this problem the reader is referred to GESSNER (1955).

Floating of plankters has originally been viewed as a special case of sinking, in which the sinking velocity becomes zero. Such a view involves a number of parameters, particularly the densities of medium and organism, water viscosity and structural sinking resistance of the plankton organism. Density and viscosity of sea water are a function of temperature and salinity (Chapters 1, 3.0 and 4.0). Consequently, complex correlations result, which make a satisfying analysis difficult.

The simple concept of increasing structural sinking resistance provided by the formation of suspension processes—for which, at the beginning, apparently convincing proof had been obtained by experiments testing the events during sinking—can no longer be accepted without qualification. WESENBERG-LUND (*in*: GESSNER, 1955) has pointed out, in a much-discussed theory, that there exist relations between variations in the shape of *Ceratium* species ('Temporalvariationen') and the annual variations in water temperature (see also Chapter 3). According to this theory, warm waters are inhabited by forms with maximum relative surface areas because of the diminished suspension capacity of the ambient medium. Such an assumption claims that water temperature influences indirectly—via changes in density and viscosity—growth and differentiation processes of the organism concerned. However, HUBER-PESTALOZZI and NIPKOW (1922/23), have provided proof that temperature acts directly on the ontogenetic differentiation processes. KARSTEN (1907) claimed that species of *Ceratium* of the warm Indian Ocean have larger and more diverse horns than their counterparts of the cooler Atlantic Ocean; but PETERS (1932) demonstrated that, in this case also, the assumed relation between external structures in the *Ceratium* species and the density or viscosity of the ambient water does not exist. UTERMÖHL (1925) contributed significantly to clarifying the pertinent relationships. He placed, in a simple but revealing experiment, bottles containing plankton organisms into the habitat water and demonstrated that the removal of convection currents causes fast sinking. In agreement with UTERMÖHL, we visualize the so-called suspension processes of plankters primarily as a mechanism receiving uplift from turbulences. In fact, small-scale turbulent water movements are of great importance for phytoplankters in regard to the duration of their remaining in the upper productive water layers.

Specific experiments for testing structural responses of marine plants to water

movement require at least two prerequisites: successful cultivation and suitable experimental designs for simulating various kinds of water movement (Chapter 5.0). These prerequisites cannot yet be met in most cases and, therefore, experimental evidence of structural responses to water movement is scarce. Modest attempts towards experimental analyses have, however, been undertaken. NAUMANN (1925), who speaks of 'experimental morphology' of plankters, has conducted experiments on the structure of *Microcystis aeruginosa* colonies cultivated in tanks with quiet or moving water. *M. aeruginosa* forms large, frequently perforated, colonies within a remarkably loose jelly mass when exposed to non-moving water; it forms small, more densely arranged colonies within a firm jelly mass when cultivated in moving water.

According to SCHÖNE (1969), sea motions of force 4 diminish chain lengths of the diatom *Skeletonema costatum* on average by about 25%; sea motions of force 7 reduce chain lengths by 40 to 50%. SCHÖNE assumes air bubbles of the wind-moved water to represent the mechanically effective factor. In cells of *Chaetoceros curvisetus*, he demonstrated also microscopic modifications in plasmatic structure due to mechanical stress; the number of cells revealing protoplasmatic damages depends on the intensity of sea motions. It was possible, furthermore, to break diatom chains during cultivation experiments by applying different intensities of water aeration (air bubbles), resulting in different degrees of water movement. Increased water movement results, at the same time, in augmented growth rates; in *Skeletonema costatum* cultures, a water-movement induced increase in total cell volume of 90% was observed.

Observations *in situ* reveal fast re-establishment of normal diatom chain lengths following a reduction of the degree of sea motions. The causative relationships are not clear. It is possible, for example, that broken chains sink to far greater water depths. Experiments with artificially broken diatom chains indicate higher rates of cell division than in comparable cultures with unbroken chains. In summary, our knowledge on structural responses of phytoplankters to water movement is still extremely poor.

#### *Benthonic plants*

Variations in external structures of benthonic marine plants can be categorized relatively easily in terms of different growth types. The fact that relations exist between these growth types and habitat-specific water-movement patterns almost forces itself upon the investigator. OLTMANN (1923) differentiated growth types of benthonic algae which resemble cushions, discs and crusts, whips, flowing bushes and small trees, as well as leaf-algae and net algae. Cushions, discs and crusts and the whip type were interpreted by OLTMANN as adaptations to life in the surf region, while he assumed net algae to be adjusted to quiet waters; the large leaf areas of algae such as *Laminaria saccharina* appeared to him 'unpractical', while in the latticed, perforated leaf areas, e.g. in species of *Agardhim* or in the morphology of *Alaria* species, with their compact whip-shaped middle rib and the elastic wings on both sides, he saw progress in overcoming an inappropriate construction principle.

However, OLTMANN (1923) realized that it is not water movement alone which affects external plant structures. Cushions, discs and crusts are not restricted to

the surf zone, and *Fucus* species, which tolerate at least moderate wave exposure, do not seem optimally adjusted to such habitat water movement patterns; the same applies to the delicate-skinned *Porphyra* species. Ideal whip forms, such as *Himanthalia elongata*, do not occur exclusively—others, such as *Chorda filum*, not at all—in exposed habitats. Furthermore, it appears problematic to visualize the beautiful lattice-form of *Claudea elegans* purely under the aspect of adjustments to water movement.

The truth appears to lie, in this case also, in the middle. Certainly, the soft floating algae thalli represent, in principle, a useful hydrodynamic construction, as do cushion, disc and crust forms. Unelastic forms with an easily destructible habitus, e.g. stiff, upright body surfaces or stiff ramifications, are absent in algae; and the few marine kormophytes, the sea-grasses, generally follow the flowing construction principle.

Certainly, several algae employ rather 'inappropriate' structural designs in terms of hydrodynamic stability. Young specimens of *Laminaria saccharina*, for example, offer, during their very dense primary growth phase (up to a thallus size of about 1 m), a significant structural resistance to moving water. Near Helgoland (southern North Sea), during heavy storms, they frequently become detached together with parts of their soft rocky substratum (red sand stone). On the other hand, the primary growth phase results in a too dense population, which requires a certain abatement (reduction in individual numbers per unit substrate surface) in order to warrant sufficient light for attaining adulthood.

On extreme surf beaten coasts, a pronounced selection takes place, according to the degree of structural plant body resistance to water movement. But it would be wrong to attempt to relate each structural characteristic of an algal thallus to possible effects of water movement.

Clearly affected by water movement is the formation of the 'aegagropila type' in originally benthonic algae. The resulting ball-shaped, rounded growth form represents a water-movement conditioned adaptation to a loose lying way of life on the sea floor. Examples are *Cladophora aegagropila* of the inner Baltic Sea, which forms balls of 1 to 6 cm diameter (WAERN, 1952) and *Furcellaria fastigiata* forma *aegagropila* of the western and inner Baltic Sea (REINKE, 1889; LAKOWITZ, 1929). Material from the Aalborg Bight (western Kattegat) has been examined by AUSTIN (1960). A characteristic structural modification is the increase in numbers of short ramifications near the thallus periphery which results, due to the radial structure of the *aegagropila* type, in a closed surface area simulating that of a ball.

Prerequisites for the formation of the *aegagropila* type are mechanical resistance, independence of light or gravity-orientation of growth, and the capacity for asexual (vegetative) reproduction in the loose-lying condition (AUSTIN, 1960). Related to the *aegagropila* type are the so-called sea balls or 'Seeknödel' (OLTMANN, 1923), which consist of dead organic material, e.g. the *Posidonia* balls of the European Mediterranean Sea.

The intensity of fixation of a 'sessile' plant to its substrate depends, to a large extent, on methods and organs of attachment. These are not directly dependent on the growth type of the thallus, although its structural resistance to water movement modifies, of course, secondarily the total resulting hydrodynamical

stress endured by the attachment organ. We may distinguish mainly three types of attachment organs:

- (i) Rhizoids which can enter soft substrates; root-like connections of certain green algae thalli (e.g. species of *Caulerpa*, *Halimeda*, *Penicillus*) to soft bottom substrates via penetrating rhizoids.
- (ii) Inconspicuous rhizoids (most so-called 'fine algae') or voluminous root-like attachment organs ('hold fasts') of seaweeds; attachment to, or embracing of, parts of hard bottom substrates.
- (iii) Fusion of rhizoids to an attachment disc (e.g. species of *Chorda*, *Fucus*, *Halidrys*); planar attachment to hard bottom substrates. Crust and disc algae may be considered extreme cases of this type; the same applies to the well-known red alga *Corallopsis opuntia* of the Indian coral reefs, which has rhizoid-shaped photosynthetic organs (SVEDELIUS, 1906).

For the sake of completeness, also the roots of the marine kormophytes inhabiting soft bottom substrates should be mentioned here. Examples are species of *Zostera* and *Posidonia*.

There are intermediate stages between attachment mechanisms to hard and soft bottom substrates. MOSS (1950) showed that the attachment hyphae of *Fucus vesiculosus* are capable of penetrating into wooden substrates and—in the case of epiphytic growth—into intercellular structures of the base plant (e.g. species of *Fucus* and *Ascophyllum*). In seaweeds with hold fasts, subadult stages have attachment discs; the claw-like rhizoids of adult specimens are secondary adventive structures (e.g. GESSNER, 1955).

The relationship between this attachment organ structure and hydrodynamic stress is obvious. In salt marshes, *Fucus vesiculosus* (BAKER, 1912; BAKER and BLANDFORD, 1916), *Pelvetia canaliculata* and *Ascophyllum nodosum* (COTTON, 1912) do not form attachment organs. Similarly, in the mud flat areas of the German North Sea coasts, *Fucus mytili* (originally described by NIENBURG, 1925; nowadays considered to be an ecotype of *F. vesiculosus*) does not differentiate attachment organs, but is maintained in position by byssus threads of the mussel *Mytilus edulis*. On the Scottish coasts, MOSS (1948) has demonstrated that the intensity of water movement influences the formation of attachment hyphae in *Fucus vesiculosus*. In the quiet water of the inner Baltic Sea near Rügen and Hiddensee, dwarf forms of *Fucus vesiculosus* differentiate secondary support hyphae in small numbers only or not at all (OVERBECK, 1956).

On the tidal coasts of the British Isles, the occurrence of *Fucus* species depends clearly on the degree of wave exposure (COISWAY, 1954). Protected coasts harbour the species *F. spiralis*, *F. vesiculosus* and *F. serratus*; moderately exposed coasts are inhabited by *F. spiralis* (reduced in size) and *F. vesiculosus* (without air bladders); heavily exposed coasts are occupied only by *F. spiralis* forma *limitatus*. None of the *Fucus* species inhabits areas with maximum wave exposure.

Hold fasts of *Macrocystis* species often break loose large blocks of rock and, floating with the help of their swim bladders, carry them out to sea (e.g. GESSNER, 1955). Surprisingly, little work has been done so far on the forces required to break loose the attachment organs from their substrate. In *Ascophyllum nodosum*, rupture resistance of stipites amounts to 37.6 kg/cm<sup>2</sup>, in *Fucus serratus* to 40.8

kg/cm<sup>2</sup>, in *Laminaria digitata* to 41.9 kg/cm<sup>2</sup>, and in *F. vesiculosus* to 45.5 kg/cm<sup>2</sup> (DELF, 1932).

Recent investigations by CHARTERS and co-authors (1969) deal with measurable hydrodynamic stress endured by the whole thallus of a brown seaweed. During field studies on *Eisenia arborea*, conducted on a sublittoral cliff of the island Santa Cruz (California, USA), water current speeds were measured employing a ball tensiometer; at the same time, the authors studied the structural resistance of the stipes to bending and hydrodynamic drag of the frond.

During field studies, bending movements of the stipes of *Eisenia arborea*—due to the to and fro motions of the surf currents—were recorded. In laboratory experiments, bending tests were conducted by attaching weights to the algae and by determination of the hydrodynamic drag of branches and fronds; during the latter tests, the algae were placed in a circular cement aquarium (a whirlpool water tunnel).

Plants from different habitats revealed different bending properties. The stipe of *Eisenia arborea* from surf habitats is more elastic than that of comparable material from quiet water areas. The importance of the work by CHARTERS and co-authors (1969) lies not so much in this result *per se*, but in their experimental design and their attempts towards a mathematical-physical assessment of the hydrodynamic drag effect.

#### (c) Internal Structures

Little is known about water movement effects on internal anatomical structures of marine plants. MÜLLER-STOLL and KÜNZENBACH (1956) reported anatomical modifications in dwarf forms of *Fucus vesiculosus*, and KRISTENSEN (1968) claimed that Fucaceae of the English and French coasts have thicker cell walls in exposed than in sheltered habitats (Table 5-3).

Table 5-3

Thickness (in microns) of the walls of parenchyma cells of Fucaceae from exposed and sheltered habitats in North Wales. Average values and maximum deviations (After KRISTENSEN, 1968; modified)

Species	Bull Bay (exposed)	Amlwch, Anglesey (sheltered)	Church Island (sheltered)
<i>Pelvetia canaliculata</i>	1.6 ± 0.1	1.4 ± 0.1	1.3 ± 0.1
<i>Fucus spiralis</i>	1.3 ± 0.3	1.3 ± 0.3	1.3 ± 0.4
<i>Ascophyllum nodosum</i>	1.4 ± 0.2	1.0 ± 0.2	0.9 ± 0.2
<i>Fucus serratus</i>	1.6 ± 0.4	0.9 ± 0.3	0.8 ± 0.1

#### (d) Supra-individual Structures

Supra-individual structures of marine plants, i.e. structural components of vegetations, are influenced to a considerable degree by water movement. The pertinent literature on responses of benthonic plants is impressive.

However, not all structural aspects of benthos vegetations are related to water movement. The structure of benthos algae assemblages is the result of the extremely complicated interrelationship of a number of environmental factors, among which water movement plays an important role—especially on tidal rocky coasts. Another ecological master factor in such habitats is desiccation (Chapters 4.2, 4.31). In the following sections, we shall consider general structural characteristics of benthonic marine vegetations which appear to be primarily influenced by water movement.

*Water movement as prerequisite and inhibitor of the benthonic vegetation*

A given minimum intensity of water movement can be an important prerequisite for certain benthonic plants ('expositiophiles'). The vertical range of water level fluctuations determines—together with other environmental factors—the size of the local surface area which may be inhabited.

Critical minimum intensities of water movement appear to be of importance for littoral vegetations, particularly on tropical coasts. An example has been provided by GESSNER and HAMMER (1967) for the Caribbean coast of eastern Venezuela. While exposed rocky littoral areas entertain a well-developed vegetation, sheltered areas and quiet bays are characterized by a poor vegetation; some sheltered areas may carry a vegetation during the first, rather windy part of the year (predominantly east and northeast winds), but not during the second, rather calm part. The authors cited consider this phenomenon to be correlated also to temperature effects. On the basis of his investigations on the coasts of the neighbouring island of Curaçao, VAN DEN HOEK (1969) calls attention to other possibilities of interpretation. He assumes that the interrelation between the degree of water movement and the development of vegetation is indirect: Heavy wave action hinders the development of corals, and, in the absence of corals, the great swarms of herbivorous fishes and the plant-eating sea-urchin *Diadema antillarum* also do not occur. Consequently, the vegetation can develop much better. In quiet water, the presence of herbivorous fishes and *D. antillarum* suppresses the development of an algal vegetation.

Littoral vegetations are clearly affected by water movement. Extreme intensities of water movement may completely inhibit the establishment of littoral vegetation belts. Such inhibition is especially pronounced if the presence of fast currents is combined with unsuitable substrate conditions. To a certain extent, such a negative combination is effective along the Danish and German North Sea coasts. In addition, some components of the benthonic vegetation 'do not like' wave and surf exposure ('expositiophobes').

*Structure-formative effects of water movement on the benthonic vegetation*

In the marine phytobenthos, water movements may cause horizontal and vertical zonations and, in this way, cause horizontal and vertical gradients in vegetation structures. Horizontal distribution gradients are primarily due to currents, vertical ones to fluctuations in water level; however, a strict differentiation between these two structural aspects is not possible. The impression that the two aspects can be separated, is based on the one-sided orientation hitherto employed in studies on vertical zonations found on rocky intertidal coasts; both

horizontal and vertical aspects are present side by side in the phytobenthos of plain-sloped coasts with weak tides, and here are difficult to differentiate.

Horizontal distribution patterns based on water movement, can be demonstrated, particularly in places where tidal currents flow through narrow passages (tidal rapids). An example is provided by the Lough Ine Rapids in southwest Ireland (BASSINDALE and co-authors, 1948; see also LEWIS, 1964, 1968), with current speeds of 2 to 3 m/sec (about 6 knots); in other cases, even higher speeds have been recorded. Tidal rapids occur especially on coasts with pronounced topographical differentiation. Consequently, most habitats on such coasts represent the sheltered type, inhabited by an expositiophobe benthos vegetation. In the rapids themselves, the quiet-water vegetation (e.g. *Laminaria saccharina*, *Halidrys siliquosa*, *Codium tomentosum*) is replaced by assemblages typical of more exposed coasts (e.g. *Laminaria digitata*, *L. hyperborea*, *Saccorhiza polyschides*; Fig. 5-5). Another case of water-movement dependent horizontal distribution patterns has been reported for shallow sea areas with partially mobile boulder

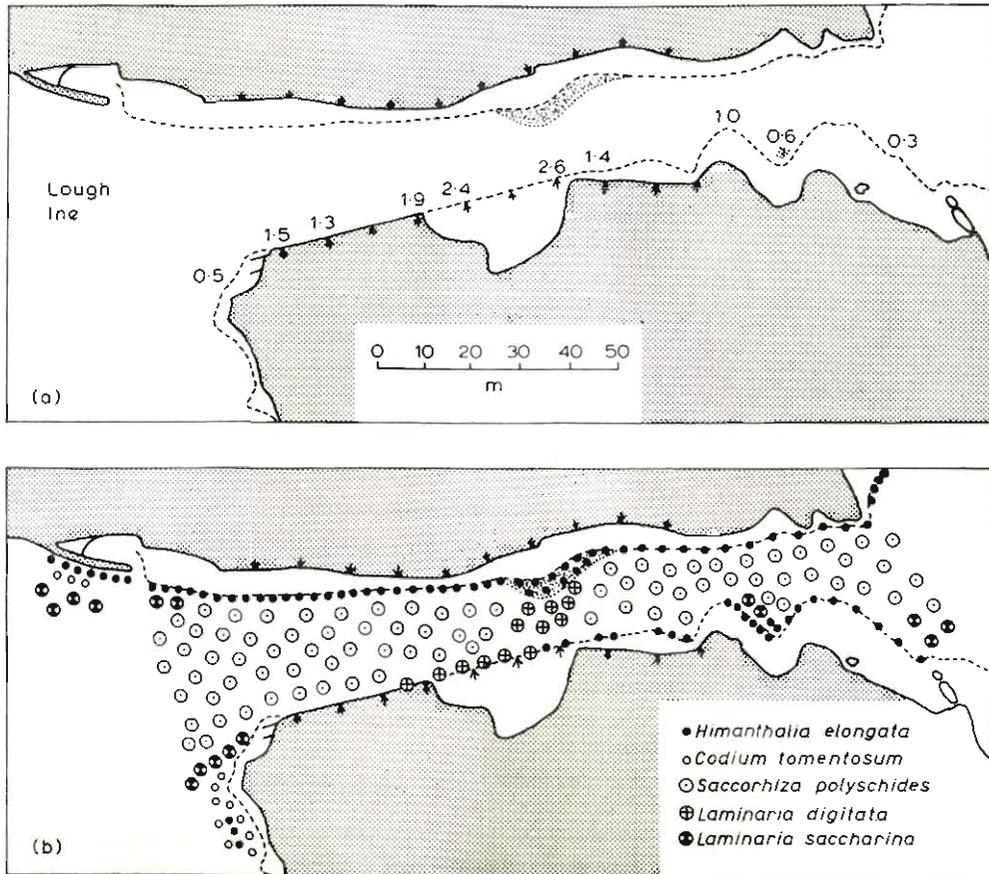


Fig. 5-5: Relation between water movement and algal distribution. Lough Ine Rapids, Ireland. (a) Maximum water current speed in m/sec. (After EBLING and co-authors, 1948; modified.) (b) Distribution of dominant sublittoral algae. (After BASSINDALE and co-authors, 1948; modified.)

substrates (e.g. in the western Baltic Sea). The term 'partially mobile' infers here that some of the vegetation-carrying boulders are of such a small size that they can be transported by sea bottom currents. The result of partial substrate mobility is an instable mosaic structure of the local vegetation (SCHWENKE, 1964, 1968).

Vertical distribution patterns are based predominantly on the degree of tidal fluctuations, surf intensity and frequency, geomorphology of the coast (coastal

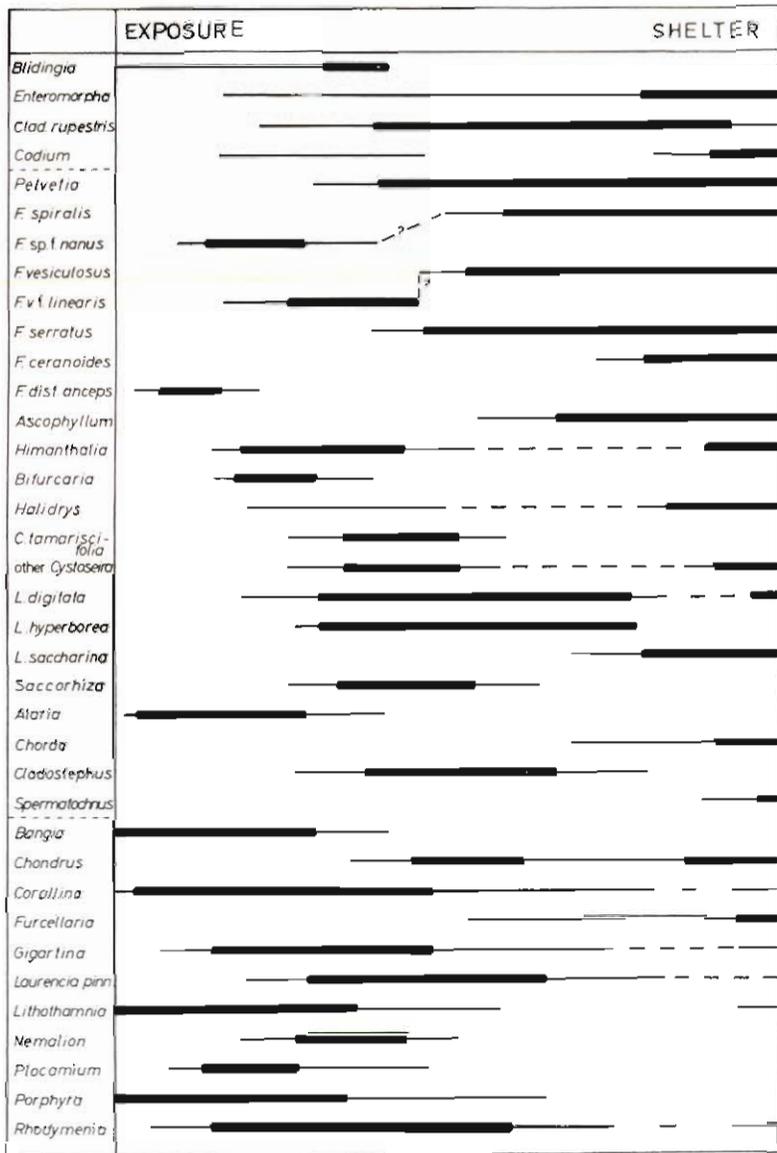


Fig. 5-6: Relative distribution of some important littoral and sub-littoral algae between exposed and sheltered habitats. *Clad.*: *Cladostephus*, *F.*: *Fucus*, *C.*: *Cystoseira*, *L.*: *Laminaria*. (After LEWIS, 1964; modified.)

slope), and size of vegetation components (large seaweeds or small forms). Tidal-dependent emersion periods and their effects on the intertidal forms have been dealt with in Chapters 4.2 and 4.31. We shall concentrate here on wave and surf effects. The most recent account on this frequently treated topic is—as far as the situation along the northwest European tidal coasts is concerned—the paper by LEWIS (1964).

On surf-exposed rocky shores, the so-called supralittoral region can attain considerable size. Along the coasts of the Faröes, for example, the supralittoral may extend up to 30 m above average water level (BÖRGESSEN, 1908). As a result, the supralittoral stretches over a total area comparable to that occupied by the eulittoral and sublittoral together. LEWIS (1964) has argued that, in such cases, a clear boundary between eulittoral and supralittoral no longer exists and that the term 'supralittoral' is, consequently, superfluous. Fig. 1-26 illustrates LEWIS' view of the relations between littoral zonation and water level heights (allowing for the exposition factor). Similar views were presented by older authors at the beginning of this century.

While such views might be valid for tidal rocky coasts, the situation in arid climates is somewhat different on rocky coasts with weak surf action (e.g. European Mediterranean Sea) or plain-sloped coasts with weak tides (e.g. Baltic Sea). For the Adriatic Sea, ERCEGOVIĆ (1934, 1959) has demonstrated the formation of microzonations in relatively small areas, based on the characteristic small-form vegetation, including benthonic blue-green algae. In the Baltic Sea, the relations between wave exposition and littoral zonation have attracted considerable attention; earlier papers have been reviewed by DU RIETZ (1947). In contrast to the extreme example provided by BÖRGESSEN (1908), vegetation structures must be assessed here in dimensions of decimetres. For the Baltic Sea, the discussion on the problem of littoral zonation has lasted for decades; there is no doubt, it will continue for some time to come.

The surf intensity determines not only the extent of the littoral settling area but also the floristic structure of the benthonic vegetation, because different species of marine benthos algae are adjusted in different ways to life in moving water. Fig. 5-6 lists the most important littoral algae of the European coasts, according to their relations to surf exposure. JONES (1959) has demonstrated the dependence of the littoral vegetation structure on the degree of exposure to water movement on the basis of the situation observed near Bardsey, Irish Sea (Fig. 5-7). BURROWS and co-authors (1954) compared exposed and sheltered habitats on the Fair Isle (between the Orkneys and Shetlands). Unfortunately, very extreme surf habitats with permanent wave action are practically inaccessible; hence, only less extreme habitats on the east coast of the island could be compared. Nevertheless, the upper limit of the *Blidingia minima* and *Porphyra umbilicalis* vegetation was in the exposed habitat some 5 m (about 16 feet), in the sheltered one some 1.5 m (about 5 feet), higher than an arbitrarily chosen reference line.

SOUTHWARD and ORTON (1954) investigated a wave breaker in the bight of Plymouth (England). The surface areas studied were oriented exactly in a north-south direction. Consequently, in addition to water-movement effects, light effects may be expected to modify the resulting picture. KINGSBURY (1962) attempted to relate the vegetation structures found in an exposed habitat and those

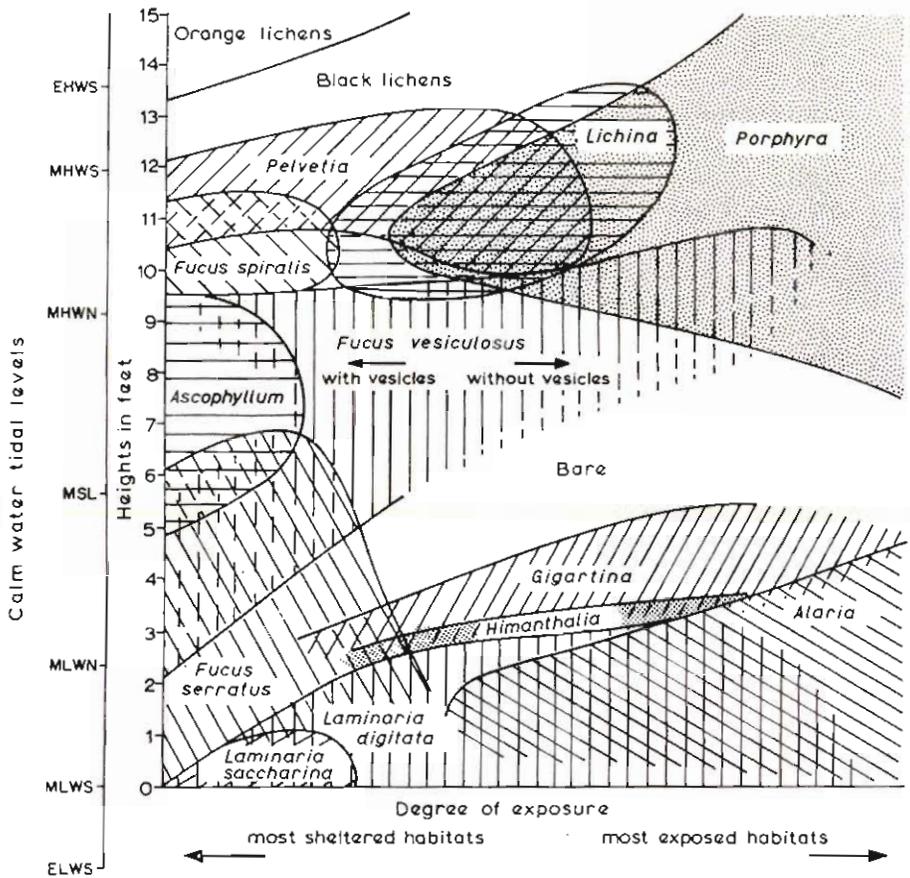


Fig. 5-7: Vertical zonation of the more prominent intertidal algae on Bardsey Island, Wales. The diagram illustrates the effect of increasing exposure to wave action on the establishment of the intertidal flora. EHWS: extreme high water—spring tide; MHWS: mean high water—spring tide; MHWN: mean high water—neap tide; MSL: mean sea level; MLWN: mean low water—neap tide; MLWS: mean low water—spring tide; ELWS: extreme low water—spring tide. (After JONES, 1959; modified.)

observed in a sheltered habitat to differences in wind exposure; he tried to exclude differences in other environmental factors, as well as seasonal differences in regard to the test periods selected. KINGSBURY reports modifications in number and composition of the species present, in height of the zonation belts, and, in *Fucus vesiculosus*, in number of swim bladders and in germling numbers per surface area. Average amounts of biomass are equal in both habitats.

GURJANOVA (1968) attempted to assess, in addition to the degree of exposure, the effects of variations in strength of tidal currents. She conducted her studies on the coasts of the northern seas of the USSR (Barents Sea, White Sea, North Pacific Ocean). Higher current speeds (5-6 knots = 2.5-3 m/sec, or higher) lead to reductions in species number; at the same time, sublittoral species occupy a higher, littoral ones a lower level, than usual (Fig. 5-8).

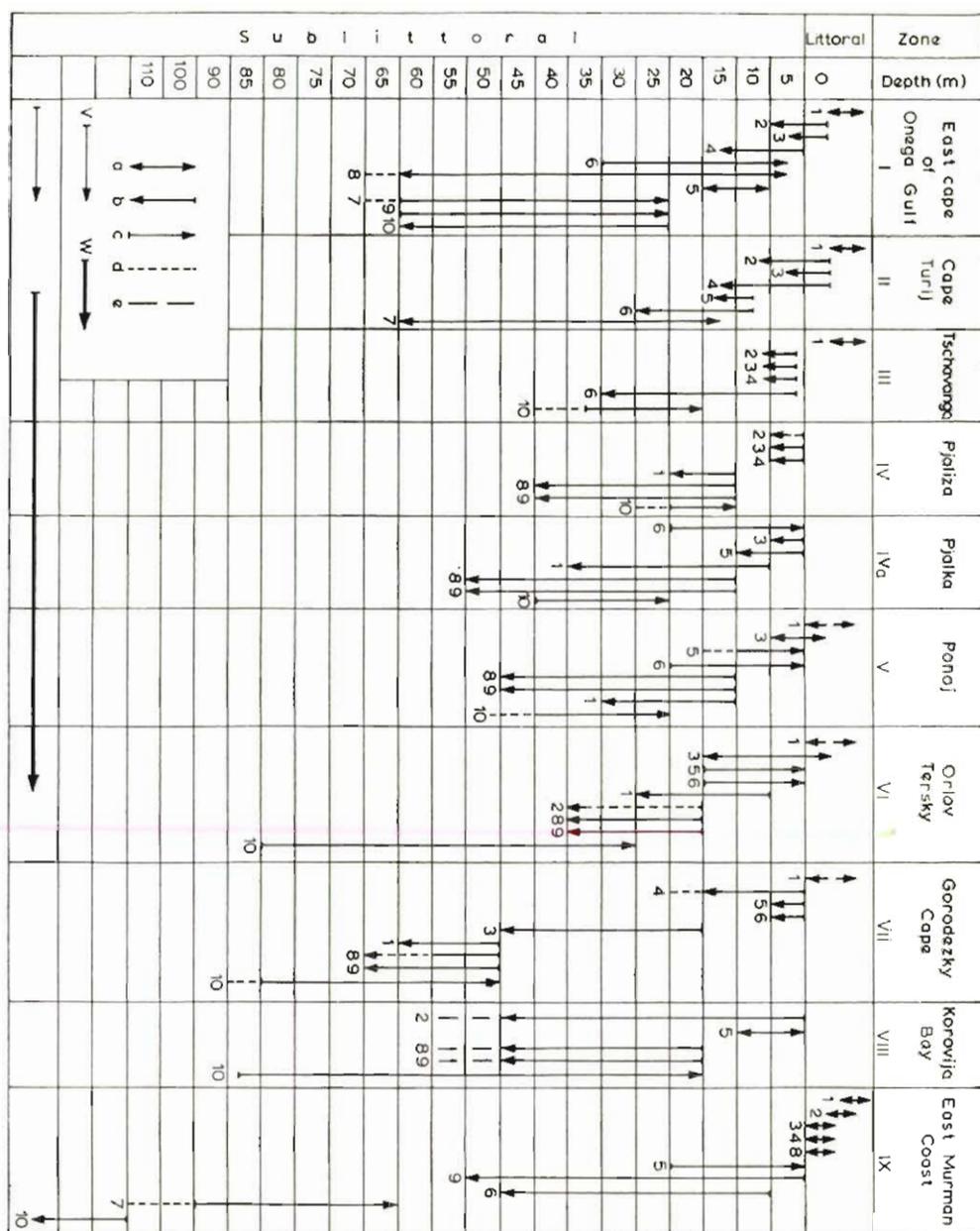


Fig. 5-8: Influence of strength of tidal currents on the vertical distribution of littoral organisms along the coasts of the White Sea and Barents Sea. a: Normal distributional range; b: organisms found at lower levels than normal; c: organisms found at higher levels than normal; d: scattered occurrence; e: organisms from deeper water found higher up. V: speed of tidal currents 2-3 knots; W: speed of tidal currents from 2-3 up to 5-6 knots. 1: *Balanus balanoides*; 2: *Mytilus edulis*; 3: red algae *Rhodymenia palmata*, *Halosaccion ramentaceum* and *Polydora rotundus*; 4: *Fucus serratus*; 5: *Laminaria saccharina*; 6: red algae *Ptilota pectinata*, *Delesseria* sp. and *Odonthalia dentata*; 7: community of *Rhynchonella psittacea*; 8: community of *Balanus crenatus*; 9: populations of *Verruca stroemi*; 10: community of sponges, hydroids and bryozoans. (After GURJANOVA, 1968; modified.)

The relations established between degree of exposure to water movement and structure of benthonic vegetation have economical consequences also. It may be difficult to assess the amount of commercially useful algae in archipelagos with many small rocky islands. Therefore, GREINER and BAARDSETH (1966) have developed a two-stage sampling method of estimating seaweed quantities along the Norwegian coast. This method allows estimation from a chart of the amounts of algae present. An important step of this method is the determination of the exposure index. A circle, divided into 40 sectors, is made around the chart point in question; a sector which extends over 7.5 km open sea is considered 'open'; the number of open sectors determines the exposure index. The method is based on the ecological experience, that the population density of *Ascophyllum nodosum* decreases with increasing exposure index, while the density of *Laminaria digitata* increases; *Fucus vesiculosus* responds indifferently, and *F. serratus* appears to decrease from a maximum towards both ends of the exposure index scale.

#### *Destructional effects of water movement on the benthonic vegetation*

Heavy storms cause severe damage to the benthonic vegetation. CHARTERS and co-authors (1969) have pointed out that benthonic marine plants face similar structural problems as terrestrial plants exposed to windy climates. According to their calculations, surf current velocities of 0.5 to 2 m/sec are comparable to wind velocities of 14 to 16 m/sec. Based on measurements by JONES and DEMETROPOULOS (1968), CHARTERS and co-authors have calculated that a surf current speed of 14 m/sec is equivalent to a wind velocity of 400 m/sec.

In spite of structural adjustments, benthonic plants suffer heavy losses on windy coasts. Quantitative assessments of such losses are known from coasts on which marine algae are used commercially. On the Scottish coasts, for example, a 'May cast' (mainly due to natural 'fall of leaves') and a 'winter cast' (due to storms) are differentiated. According to WALKER and RICHARDSON (1955), the average biomass of laminarians dropped in 1952 from 18.1 tons/acre following a May cast and an early winter cast to 12.0 tons/acre; even in water depths down to 10 m, losses of up to about 50% occurred. This figure represents a certain contrast to the commonly held claim that wind-caused waves and surf lose their energy fast with increasing depth.

In the southern North Sea near the island Helgoland, heavy storms are followed by considerable damages to the *Laminaria* vegetation. The destructive, wind-induced effects of water movement are accentuated here by the rather soft, red sandstone substrate. In subtropical and tropical areas, cyclones (hurricanes) cause even more extensive destruction among the phytobenthos. THOMAS and co-authors (1961) described the effects of hurricane 'Donna' on turtle-grass beds and algae vegetation of coral reefs in Biscayne Bay (Florida, USA). Sea-grasses were either uprooted or covered by sand and crumbled reef material. On coral reefs, the heaviest losses were caused by tearing of reef parts.

Negative effects of water movement on the benthonic vegetation are particularly pronounced in sea areas with mobile, diluvial boulder substrates (e.g. some parts of the Baltic Sea). In such areas, structural instability of the phytobenthos represents a normal condition. In corresponding Baltic Sea areas, *Fucus vesiculosus* of 40 to 80 cm thallus length grow on fist-size stones; on a stone with a surface area

of  $4 \times 8$  cm, up to 75 *Chorda filum* of about 140 cm length were counted (SCHWENKE, 1970). Such epilithic growth results in considerable plant surface areas for hydrodynamic drag. Consequently, during winter storms—but also during occasional summer storms—gigantic masses of algae can be washed ashore. In the summer of 1968, for example, the beaches of tourist places along the Bight of Lübeck (Federal Republic of Germany) had to be cleaned of considerable masses of detached algae.

In the Bay of Gdansk (Baltic Sea) negative effects of water movement on vegetation structures have been reported by KORNAS and co-authors (1960).

On coasts with regular, or occasional, ice formation, water movement can exert pronounced destructional effects on the local vegetation. The destruction of an existing vegetation belt, or the inhibition of the formation of such a belt, occurs in two ways: (i) drift-ice damages the vegetation by cutting or rubbing motions (parallel to sea-level fluctuations); (ii) ground-ice, when it floats up from the sea bottom, injures the vegetation of shallow coastal waters. Along arctic and sub-arctic coasts the eulittoral is typically devoid of any vegetation, or entertains only a scarce vegetation (annual benthos algae) during the summer (KJELLMAN, 1877; LUND, 1959; SVENDSEN, 1959; WILCE, 1959, and others). Ice formation can occur also in coastal areas of temperate zones, e.g. in the northern Baltic Sea, where moving ice, together with the seasonal water level depression in spring, exerts destructive effects on the vegetation; each year, the local eulittoral vegetation belt (about 0.5 m wide) must be re-established by annual summer algae (e.g. WAERN, 1952). Occasional cold ice winters may also lead to destruction of the *Fucus* vegetation in the western Baltic Sea (Chapter 3.2).

The benthonic vegetation often exerts a protective function in regard to land loss or land reclamation (e.g. LUND, 1941; HOFFMANN, 1952; SCHWENKE, 1965b). Hence, in the last few years, English, Danish and German marine ecologists have conducted experiments with artificial seaweeds (made of polypropylene or a similar material); in one experiment, about 14,000 'plants' were used on an area of  $1000 \times 125$  feet =  $309.8 \times 38.1$  m. Such artificial vegetation can reduce critical intensities of water movements and help to protect coastal areas endangered by land loss due to extensive water movement.



## 5. WATER MOVEMENT

### 5.3 ANIMALS

R. RIEDL

#### (1) Introduction

Most information available on responses of marine animals to variations in water movement has been produced very recently. In view of the considerable importance of the factor water movement for life in oceans and coastal waters, the present status of our knowledge can only be considered a first step into a vast new field of research.

The importance of large-scale ocean currents to the dispersal of marine animals has been realized for at least one and a half centuries (HUMBOLDT and BONPLANDT, 1818). DARWIN (1837, 1842) observed that there is more intensive coral growth on the turbulent outer sides of reefs. The postulation of JONES (1912) and KÜKENTHAL (1925)—the existence of a correlation between growth forms of corals and degree of exposure to water movement—is now generally accepted. More subtle correlations, however, remained undetected by older authors because of inadequate methods and technologies.

Direct observation by SCUBA divers revealed, for the first time, that the positioning of sedentary, and the orientation of passive, planar filter-feeders are both related to directive components of water movement. In recent years, underwater research has greatly advanced our capacity for conducting observations and experiments in the sea (c.g. RIEDL, 1947, 1956a, 1967; KINNE, 1970a, b) and has introduced new means for investigating detailed aspects of organismic responses to water movement.

The information obtained so far on animal responses to water movement has not yet attained the degree of completeness and soundness as in other environmental factors studied for a longer period of time. However, a surprising complex of factor intercorrelations has been discovered, which points to the central position of water movement among other environmental factors in oceans and coastal waters (see also RIEDL, 1969 and Chapter 5.0). There exists, in fact, a formidable diversity of interrelationships between water movement and biological processes.

#### (2) Functional Responses

Few experiments have been conducted in order to examine functional responses of living systems to water movement. Almost all our knowledge is derived from descriptive ecological information obtained in coastal waters. This situation results from the relatively recent development of scientific diving and model techniques. While other environmental factors such as light, temperature and salinity have been controlled and manipulated in laboratory experiments for a long time, the factor water movement has so far been largely neglected. In labor-

atory experiments, water particle movement is usually of the order of millimetres per second, whereas littoral organisms are adapted to water movement speeds of decimetres or even metres per second, but rarely to values below centimetres per second.

Marine ecologists have only just begun to measure the magnitude of water movements in the benthos. Assessments of organismic performance are largely based on the determination of qualitative correlations between environmental factor intensities and the biological characteristics of the organisms considered.

#### (a) Tolerance

Water movement constitutes, in several ways, a limiting factor for animal survival. While in other environmental factors maximum and minimum values usually determine sufficiently the range tolerated, additional aspects must be considered in regard to water movement: (i) In aquatic habitats, water movement is the principal means of transport for many other environmental factors (Chapter 5.0). (ii) Water movement acts at widely different levels and magnitudes (from particle velocity to tidal pressure). (iii) Water movement attains varied ecological significance, depending on the combined effects of its various aspects and on their fluctuation patterns.

Primary limiting forces act directly through water motion; they occur naturally only in the region of maximum intensity values (see also Chapter 5.2). Water stagnation in itself is not necessarily harmful. Depending upon the rate of water replacement, at most distribution and reproduction of species with non-motile resting stages could be impeded.

Near maximum values exert various limiting effects. At 'particle velocity', the degree of mechanical resistance may definitely be limiting. Usually, however, animals attached to rock surfaces withstand velocities of 10 times local average values; however, these are seldom attained. Similarly, particle velocity only moderately limits the distribution of the microfauna (RIEDL, 1966).

The magnitudes of 'wave pressure' may reach 100 tons per m<sup>2</sup> in a torrential channel, but clearly play only a minor biological role in the habitat. Hydrodynamic forces which move a rock weighing 15 tons cannot detach a healthy barnacle *Balanus perforatus* from its substratum (RIEDL, 1964b).

Secondary limiting forces are ecologically more effective than the primary ones (see also Chapter 5.2). They act via the transport function of the moving medium, and are effective primarily in the range of near minimum values.

In the minimum range we are dealing with stagnation processes. The limiting effects are due primarily to unsuitable gas and nutrient levels, but also to abolition or removal of suitable temperatures, etc., or to exhausted (nutritionally poor) water envelopes around the organisms. In regard to critical gas and nitrate levels, the intensities of water movement which cause limiting conditions must be determined. The clearest case occurs when the water movement is almost completely stopped; a few seconds of water stagnation (e.g. by covering benthonic algae with a bell glass) suffice to narcotize by asphyxiation small tubeless polychaetes of the family Sabellidae; stagnation periods of 2 to 3 hrs (algal substrate *in vitro*; method of deterioration of climate 'Klimaverschlechterung'; RIEDL, 1953, 1966) allow the

oxygen concentration to fall from 9 to 5 or 3 mg O<sub>2</sub>/l and thus to become intolerable to most of the animal inhabitants. Also, the lack of movement of fine sediment may rapidly lead to catastrophic consequences for many sedentary animals (hydroids, sponges; RIEDL, 1966).

At maximum intensities of secondary limiting forces, sediment fractions are transported by the water. Dense suspensions of mud in the water layers nearest to the sea bottom are detrimental to local filter-feeders. Jostling of shell and coarse sand, or violent water turbulence over a shallow, rocky shore, drives away sedentary organisms.

Tertiary limiting forces are associated, for example, with the movement-dependent distribution of stable and mobile components of sea bottoms (see also Chapter 5.2). A small decrease in the degree of exposure in that critical region, in which the predominance of erosion of a rocky bottom gives way to a predominance of sediment deposition, may upset the entire ecological balance and destroy the local ecosystem within a short time. Stones and gravel moved about by breakers in the surf region prevent the epifauna from settling.

#### *(b) Metabolism and Activity*

Water movement clearly affects quantitative aspects of metabolism and activity, including aspects of behaviour. However, even a definite correlation between rate of growth and current velocity does not shed sufficient light on the underlying biological causes. Metabolic responses of non-sedentary planar filter-feeders can most probably be explained by relating water movement intensity and food intake. But in sedentary species, such as the sea-fans, more complex situations have been reported (WAINWRIGHT and DILLON, 1969). Their activity phases cannot be completely understood in terms of changes in water-movement intensities, and in regard to the changes in metabolic rate observed, we are forced to rely mainly on hypotheses.

#### *Metabolism*

Coral reefs grow faster when exposed to water movement. Previous assumptions that a better supply of plankton organisms was the cause of differences in growth are now considered unlikely; the plankton density inside the reef is greater than on the outside (MOTODA, 1940; JOHNSON, 1949, 1954); moreover, the ecological significance of the symbiotic algae of corals (Zooxanthellae in the tissues, and filamentous green algae in the skeleton) is now realized (e.g. DOTY, 1954; ODUM and ODUM, 1955). It is much more likely that slower growth rates are associated with slower removal of CO<sub>2</sub>. In enclosed and protected lagoons, the oxygen level can fall, due to the respiratory activities of the local fauna and flora, to 18% of the saturation value during the night (ORR and MOORHOUSE, 1933); such decline is not possible in the water surrounding the reef because of high rates of water mixing. The range of temperature fluctuations also could be of importance; in the stagnant inside waters, temperatures fluctuate about 7 to 12 C°, in the moving outside waters only about 1 to 3 C° (MAYER, 1918; WELLS, 1952, 1957).

In submarine caves, a correlation exists between population development of filter-feeders and the amount of plankton brought in by the moving water. Active

filter-feeders living on  $1 \text{ m}^2$  may move 2 to  $8 \text{ m}^3$  of water per hour by their filtering activities. On the average,  $1.5 \text{ m}^3/\text{hr}$  of water is required for each  $\text{m}^2$  of substratum occupied by filter-feeders; in most caves, particularly in their less accessible parts, the amount of water movement is not adequate to such demands. The result is a decrease in population density of filter-feeders to between  $1/100$  and  $1/10,000$  of the density found in central or entrance regions of the caves (filtering rates: JØRGENSEN 1955; review: RIEDL, 1966). In submarine rock reefs, population densities of filter-feeding colonizers decrease with increasing water depth (PEQUEGNAT, 1961); this phenomenon is similarly explicable on the basis of reduced rates of water movement.

### Activity

Many marine animals reduce their activities if the intensity of water movement is too great. Motile animals hide away and external filter-feeders withdraw their filtering apparatus. With too little water movement, on the other hand, the activity of filtering organs (gills) often increases.

Changes in mode of filtration are especially illuminating in species of the barnacle family Balanidae. The Balanidae occupy an intermediate position between the actively and passively filtering sedentary animals. Balanid species occupying deeper waters can only feed by beating their cirri, whereas chthamalids of the outer surf zone feed passively, holding out their appendages rigidly into the moving water. *Balanus perforatus* even changes its mode of filtration from active to passive as water movement increases (Fig. 5-9). During this process, the type of food also changes. Mesh size of the passively extended appendages amounts to  $33 \mu\text{m}$ ; active beating, however, drives a water current through the only  $1 \mu\text{m}$  wide feather-like setae of the first two legs, which are not spread out (SOUTHWARD, 1955; CRISP and SOUTHWARD, 1961; RIEDL, 1966). Consequently, under conditions of fast water movement, primarily zooplankton is caught, whilst under conditions

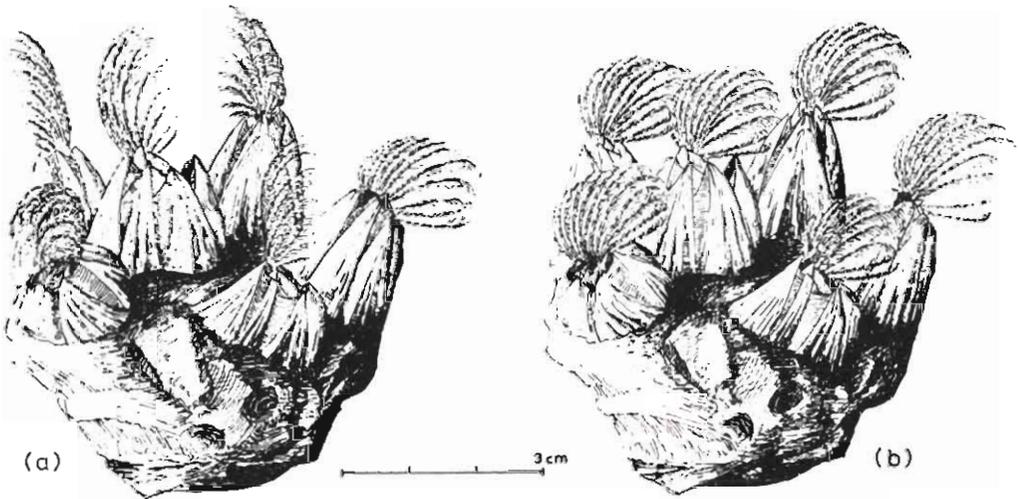


Fig. 5-9: Change from active to passive filtration in the cirripede *Balanus perforatus*. (a) Active beating of cirri in the frontal plane; (b) passive filtration by turning all appendages into the water current (all cirri are drawn fully extended). (After RIEDL, 1966.)

of slower water movement the onset of autonomous activity results in greater catch efficiency by including the usually abundant smaller phytoplankton forms. More detailed studies on such responses to water movement are likely to reveal interesting quantitative correlations between energy expenditure, food obtained, and economy of animal activity. A number of adjustments lead to extension of the active phase over a wide amplitude of water movement conditions; this can be deduced from several structural responses (p. 1141).

Behavioural responses related to water movement-dependent orientation, position or posture have been reported for individuals and colonies of various animals. Non-sedentary forms respond by changing direction, speed or attitude of locomotion relative to water movement conditions: the responses of sedentary forms can best be assessed in terms of their settlement patterns, since the behaviour of their larvae is still largely unknown.

Amongst non-sedentary species, the behaviour of external filter-feeders is influenced particularly by water movement. An example is the echinoderm *Heterometra savignyi* of the Red Sea (MAGNUS, 1962-64, 1963a, 1964), which in the twilight, and especially at night, turns all its arms into a single plane against the direction of the prevailing water current (Figs 5-10, 5-11). Its fine-meshed filter-fan—consisting of 20 arms, pinnules and innumerable, stiffly extended tentacles—is held with the aboral surface against the water current and, with a tidal stream of

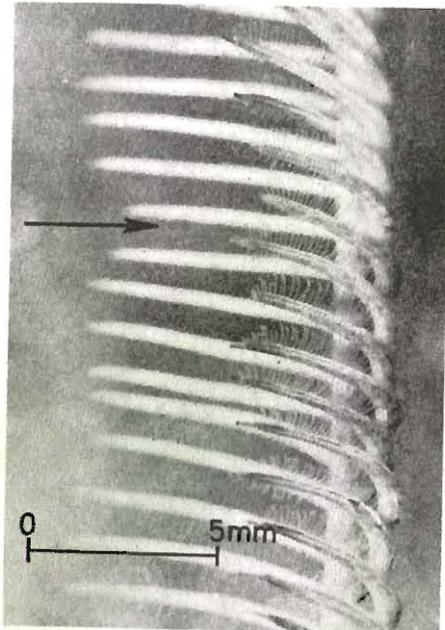


Fig. 5-10 (a): Filter traps of the echinoderm *Heterometra savignyi*. Lateral view; note the partly opened food grooves on the pinnules, fringed by tentacles bent likewise against the direction of the current (arrow). (After MAGNUS, 1963a, 1964.)

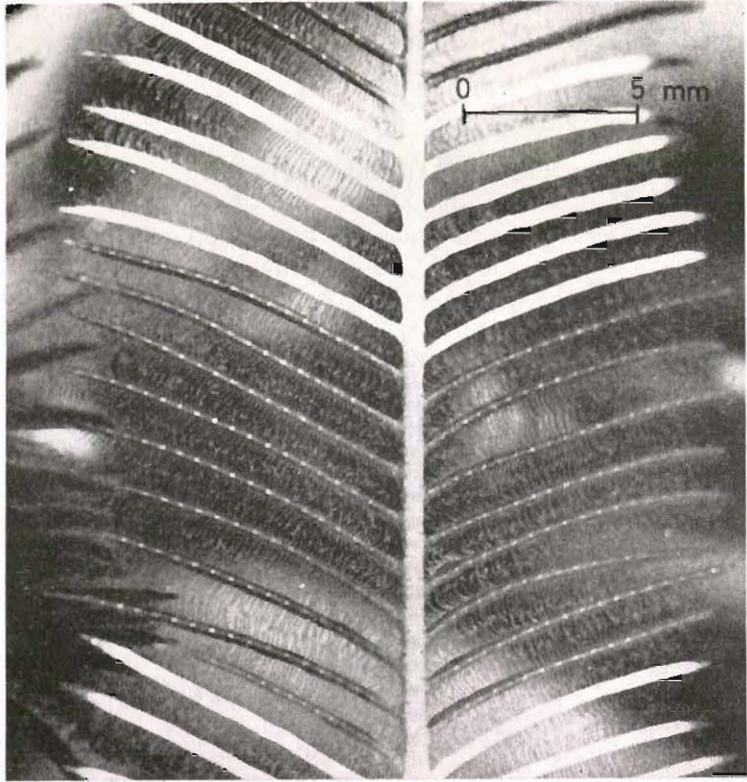


Fig. 5-10 (b): Filter traps of the echinoderm *Heterometra savignyi*. Aboral side of a white spotted arm. (After MAGNUS, 1963a, 1964.)

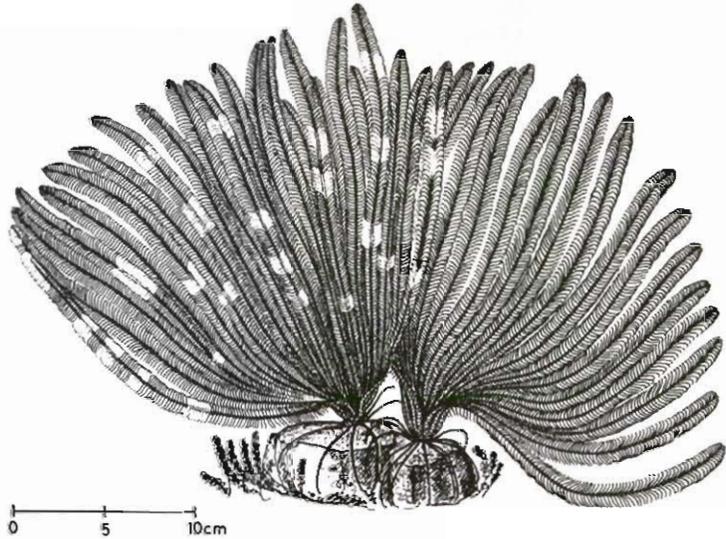


Fig. 5-11: Formation of a common filter trap by two individuals of the echinoderm *Heterometra savignyi* (the left individual carries white spots). (After MAGNUS, 1964.)



Fig. 5-12: Positioning of filters of a dense population of the echinoderm *Ophiothrix fragilis* in 75 m water depth at a surface current speed of 0.3 knots. (After CABIOCH, 1967.)

2 cm/sec, allows about 60 l/min to pass through it. Automatic submarine photography (EMERY, 1952; MENZIES, 1963) shows this type of behaviour to be widespread. Lacking the fan formation, but no less dependent on water currents, are the brittle stars. At moderate water-current speeds, members of the population of *Ophiothrix fragilis*, which often occupies large areas, all extend their arms (VEVERS, 1952; CZIHAK, 1956; RIEDL, 1956b; CABIOCH, 1967; see also Fig. 5-12); *Ophiocoma scolopendrinu* filters the surface film of the tidal current (MAGNUS, 1963b, 1964). The rare semi-sedentary species, in which the body areas exposed to the water current are anatomically fixed, e.g. the sea-pens, also turn (passively) into the water current (MAGNUS, 1966). Under conditions of changing water-current directions, *Scytaliopsis djiboutiensis* of shallow coastal waters twists its body up to 180°, continuously maintaining its positioning relative to the water current (Fig. 5-13); if further twisting is required, it also turns its stalk. The large species occupying deeper, two-dimensional flowing water bodies will probably exhibit such behaviour even more clearly. Up to the present, however, they have not been accessible for investigation.

In internal filter-feeders, one would expect a lesser degree of orientation to water current direction; they are less dependent on water movement. Nevertheless, diving investigations have shown (HARTNOLL, 1967) that the scallop *Pecten maximus* tends to turn into the water current in such a manner that the deep tidal current assists its own filtering activity.

Inhabitants of the eulittoral change their activity with the tides. Limpets and shore gastropods are inactive during air exposure caused by low tides, and resume activity at high tide. The gastropod *Planaxis sulcatus* of the Red Sea

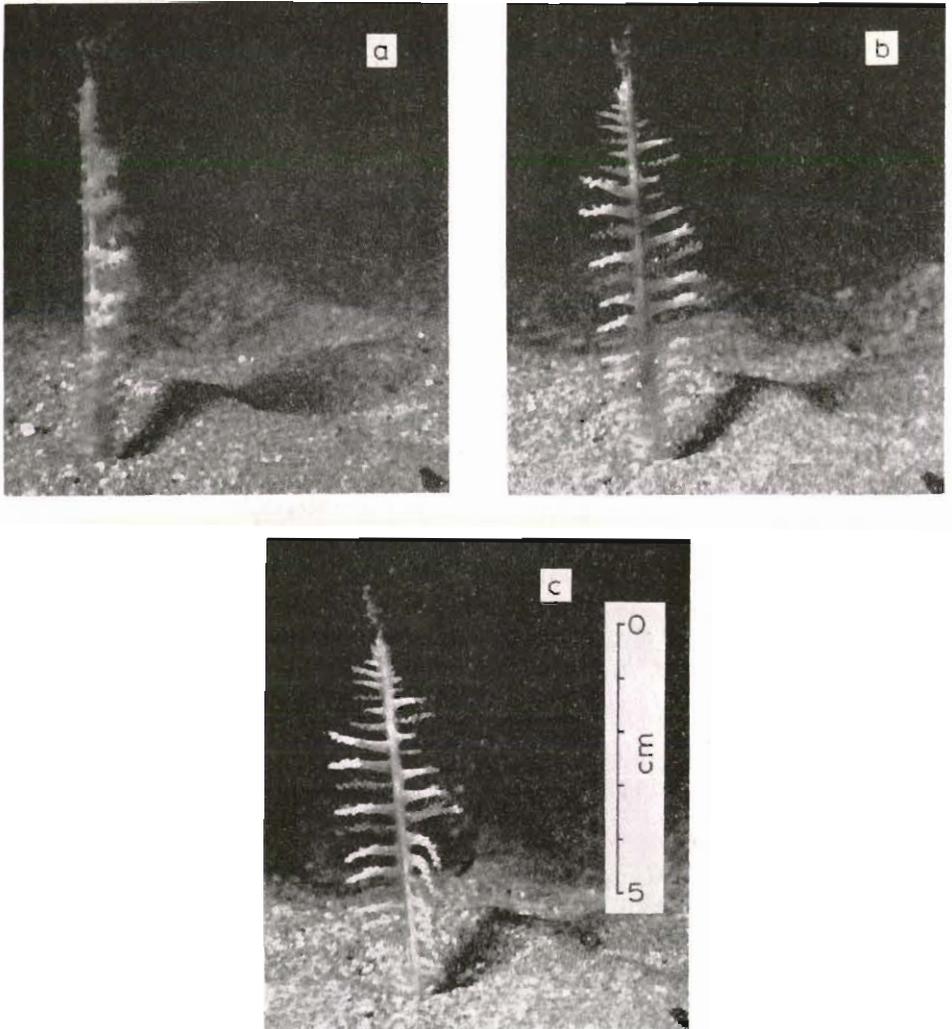


Fig. 5-13: Body positioning of the shallow-water sea-pen *Scytaliopsis djiboutiensis* relative to the direction of the water movement through  $90^\circ$ . (a) Water movement from left to right and back; (b) water movement from left background to right foreground; (c) water movement from foreground to background of picture. (After MAGNUS, 1966.)

follows the water's edge; if the latter shifts faster than the snails can move, they remain on the spot and form dense clusters (MAGNUS and HAACKER, 1968).

Amongst sedentary species, the passive filter-feeders with large surface areas have revealed relationships between the positioning of their body surfaces and the principal direction of the water movement. Among hydroids, particular attention has been paid to species of the genus *Plumularia* as well as to *Halocordyle disticha* and *Eudendrium rameum*; among the anthozoans, to *Eunicella cavolinii* (ABEL, 1959; BROMHALL, 1959; RIEDL, 1959, 1964a, 1966; SVOBODA, 1970). It has become apparent that the major surface areas of the hydroid colonies are positioned so

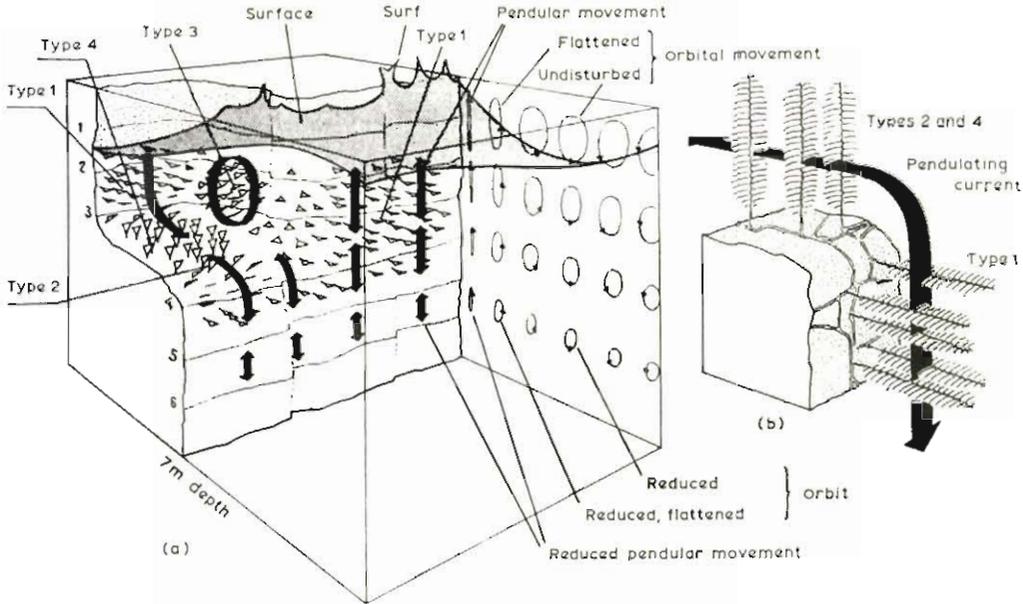


Fig. 5-14: Positioning of planar hydroids in an oscillating water body. Four forms of water movement (surface movement, surf, pendular movement, orbital movement) and four positions of the hydroids (Types 1 to 4) have been deduced from the local conditions. (a) General view; (b) detailed view. (After RIEDL, 1964b; modified.)

accurately and consistently at right angles to the principal direction of water movement (Fig. 5-14) that detailed local hydrodynamic relationships can be deduced. Thus current charts in submarine caves as well as the boundaries between oscillating water bodies and unidimensionally flowing water bodies (second critical depth) can be assessed on the basis of the orientation of the sedentary forms mentioned (Fig. 5-15). On shallow reefs in Florida (USA), sea-fans of the genus *Gorgonia* orientate parallel to each other, normally as a function of wave movement. However, fans less than 10 cm in height show no preferred orientation. Cross sections of fan stems, indicating re-orientation of many large fans, and mechanical properties of the fan 'blade' suggest that the preferred orientation of the sea-fans may be explained by purely passive adjustments (WAINWRIGHT and DILLON, 1969).

In the active internal filter-feeders inhabiting areas below the second critical depth, behaviour depends on the water current. The mollusc *Microcosmus vulgaris* customarily turns the opening of its inhalent siphon directly against the current unless thick mud suspension clouds pass by near the bottom (MONNIOT, 1967); if the mud suspension becomes too dense, the siphon is turned sideways to the current.

Regional stenosis (selection of sheltered localities in strongly agitated waters, but of exposed localities in still waters) is related to the behaviour of the larvae (HASS, 1949; ABEL, 1959; RIEDL, 1959, 1966). The growth forms of anatomically non-rigid planar species, e.g. of the genera *Eudendrium* and *Eunicella*, are again attributable to the interaction between water movement and structure (pp. 1142, 1143).

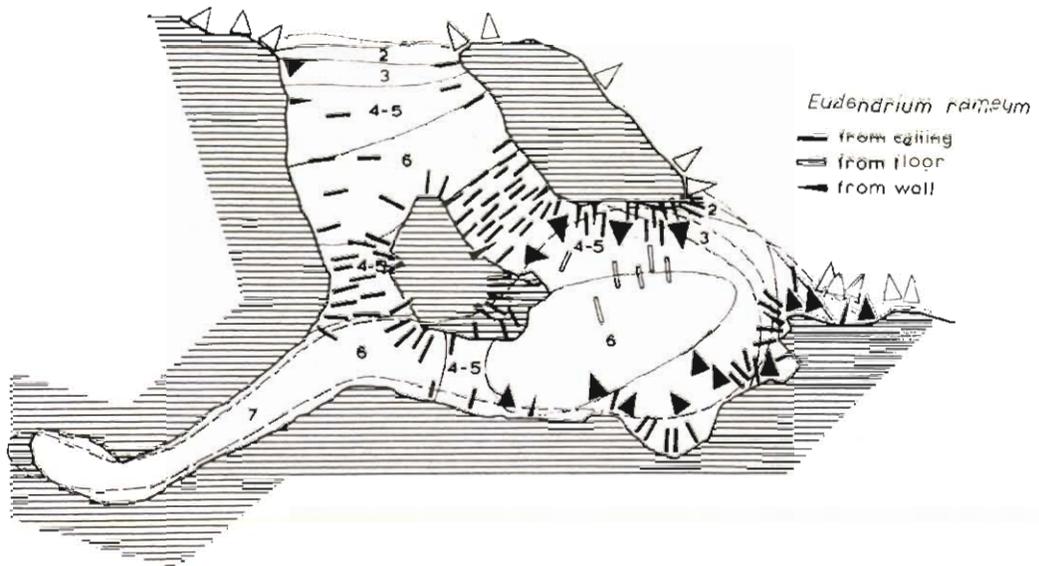


Fig. 5-15: Position of planar hydroids *Eudendrium rameum* (filled symbols) and *Halocoryte disticha* (open symbols) in a submarine cave (section; rock parts hatched). Lines: borders of hydroid zones 2 to 7. Water currents, reconstructed from the consistent positioning of hydroids, are illustrated in Fig. 5-14. (After RIEDL, 1966; modified.)

### (c) Reproduction

Two basic correlations between water movement and reproduction of marine animals are apparent; they refer to (i) production of gametes, and (ii) critical times of population replenishment. For both, however, exact quantitative data are not yet available.

Indirect evidence suggests that hydroid populations, which occur over wide gradients of water-movement intensities, show poor growth at limiting intensities near the peripheries of their respective habitats, but maximum growth in the centre of their distributional areas (RIEDL, 1959, 1966). These differences in growth are paralleled by differences in the percentage of fertile colonies. Consequently, a quantitative relation may be expected between water movement patterns and sexual or asexual reproduction of the hydroid colonies.

Critical times of population replenishment often depend on certain conditions of water movement. This is true, for example, for the liberation of spermatozoa and eggs, copulation, larval hatching and larval settlement. The holothurians provide an example concerning the liberation of spermatozoa. The males raise 2/3 of their body off the sea bottom and discharge their sperm with the onset of increased currents. Dependence of egg development, copulation and critical larval phases on water movement is known, for example, from eulittoral cirripedes, particularly in species of the genera *Balanus* and *Chthamalus*. While sufficient periods of submersion are always required (Chapter 4.31), liberation and settlement of larvae may be stimulated by appropriate water movements.

*(d) Distribution*

Water movement exerts influences on many phenomena affecting distributional patterns of marine animals. In addition to light (Chapter 2), temperature (Chapter 3), salinity (Chapter 4), substratum (Chapter 7) and pressure (Chapter 8), the distribution of animals in oceans and coastal waters is affected primarily by water movement. The extent to which water movements may influence animal distributions varies considerably according to spatial dimensions, the specific requirements of the animal concerned and the intensity variations of local water-movement patterns.

Large-scale geographic distributions of marine animals involve ocean-wide dimensions. Small-scale local distributions depend on restricted boundary layers involving dimensions down to metres or even centimetres. In terms of ocean-wide dimensions, water movement acts in essence via primary aspects and to some extent via secondary aspects (transportation of water body characteristics); within the smaller dimensions, tertiary aspects play so prominent a role that these will be treated first.

*Tertiary aspects influencing animal distributions*

Tertiary aspects are not connected with the water body itself but with its boundaries, air and substratum. Fluctuations in water level due to tide, seiches, wind pressure and wave action are the decisive factors in the eulittoral and in the outer surf zones. The zonation of benthonic animals in these border biotopes of the sea can be attributed almost exclusively to the height and rhythm of water-level amplitudes. Reviews of this wide field of marine ecology have been published by

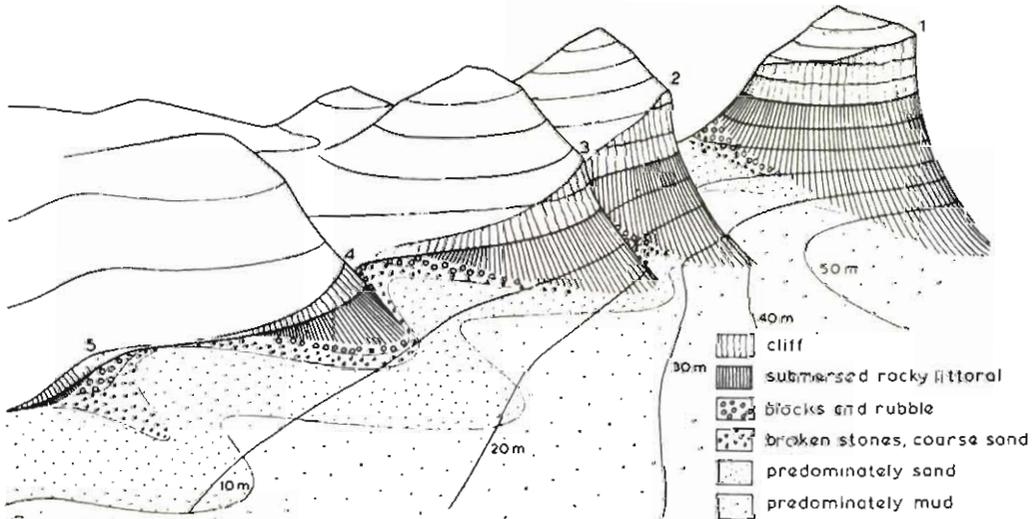


Fig. 5-16: Typical arrangement of substrates as a function of water movement patterns and the degree of coast inclination. Coastal region of Sorrento, Italy. 1: Punta Carena, 2: Capo di Sorrento, 3: Punta Gradelle, 4: Capo d'Orlando, 5: Scoglio Revigliano. (After RIEOL, 1966; modified.)

STEPHENSON and STEPHENSON (1949) and DOTY (1957) on rocky shores, HEDGPETH (1957) on sandy shores, GERLACH (1958) on mangroves, and KORRINGA (1957) on lunar periodicity.

The distribution of substrates (Chapter 7) is the next factor which affects fundamentally the distribution of benthonic animals, and substrate distribution is, in turn, determined principally by water movement. The degree of water movement and the abundance of sediment collectors account primarily for the balance of sediment removal versus sediment deposition, as well as for processes of sorting and the spatial arrangement of sediments. Consequently, one finds not only sharp

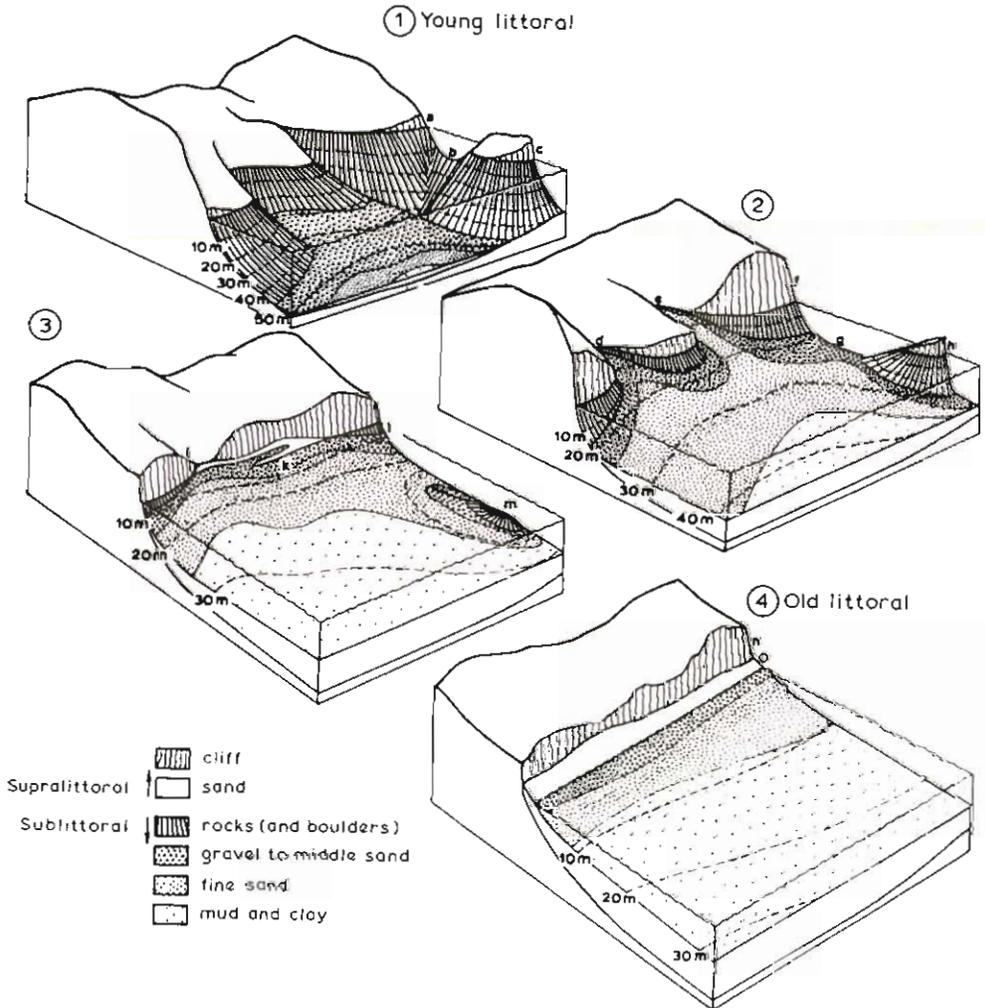


Fig. 5-17: Typical changes in littoral habitats, primarily due to the degree of exposure to water movement and the increasing age of the coast line. (1) to (4): Phases of increasing age. a: Beginning cliff formation, b: submerged rocky ridge, c: island, d: gravel bay, e: sand bay, f: high cliff, g: sand saddle, h: erag, i: beginning formation of a sandy beach, k: sandbank, l: disappearing rocky littoral, m: rocky shoal, n: continuous row of cliffs, o: closed continuous sand beach. (After RIEDL, 1966; modified.)

dividing lines between different faunistic assemblages, but also extremely regular patterns of benthonic animal distributions (Fig. 5-16). A detailed, pertinent review has been published by RIEDL (1966). The close relations of animal distributions to substrate properties (Chapter 7) can be explained by specific adaptations of the species in question to solid substrates, to interstitial systems of different grain sizes, or to soft or semiliquid sediments; such edaphic relations result, in turn, in specific climatic and, ultimately, trophic conditions. On the other hand, the arrangement of substrates can be explained on the basis of geological, geomorphological and climatical properties of the coastline under consideration (Fig. 5-17), which depends largely on its age and other historical aspects (JOHNSON, 1919; VALENTIN, 1952; RIEDL, 1966).

The exposure-dependent substrate stability is especially revealing. The size of the substrate units ranges from mobile fine rubble to almost completely stable huge boulders (Fig. 5-18). Organismic settlements depend clearly on the degree of motility of the substrate. The total amount of settlement decreases with increased average substrate motility. Exposure-dependent substrate stability offers unique possibilities for studying requirements for solid foundations by sedentary forms and aspects of competition for space (RIEDL, 1964b, 1966; RÜETZLER, 1965a).

#### *Primary and secondary aspects influencing animal distributions*

Primary and secondary aspects refer both to the intensity of water movement and to the properties of the water body in regard to other transporting hydrographic parameters.

The importance of water movement intensity becomes especially clear if we consider the bathymetric zones of the littoral dimension. The four sublittoral water body types (lacerating, oscillating, unidimensionally and two-dimensionally flowing) with their faunistic elements depend predominantly on water movement. LORENZ (1863) had already predicted such a correlation; his observations were fully confirmed some 100 years later (RIEDL, 1964a, 1966).

The lacerating water body of the inner surf zone is characterized by animals which are adapted to high wave pressures (ram pressures), i.e. species of *Patella*, *Balanus*, *Haliotis* and calcified corals. The oscillating water body is characterized by the arrangement of planar passive filter-feeders parallel to the coast. The second critical depth (Fig. 5-19) typically contains organisms with irregular body plane orientations, e.g. *Eunicella cavolinii*. The unidimensionally flowing water body in the rocky declivity below the area of wave action is characterized by animals orientated at right angles to the coast. In the two-dimensionally flowing water body of the littoral plains, radial forms of passive filter-feeders predominate (Fig. 5-20).

Passive types, such as hydroids and anthozoans, are particularly dependent on adequate degrees of water movement. Animals on the rocky littoral slope show as many as 7 distinct faunistic zones replacing each other (RIEDL, 1959). The gradients between these faunistic zones decrease from active external filter-feeders (bryozoans, sedentary polychaetes) to internal filter-feeders (lamellibranchs, poriferans, ascidians), that is, with decreasing dependence on water movement. The active internal filter feeders of the endolithion (boring sponges and bivalves) reveal, finally, distributional patterns without definite zonation.

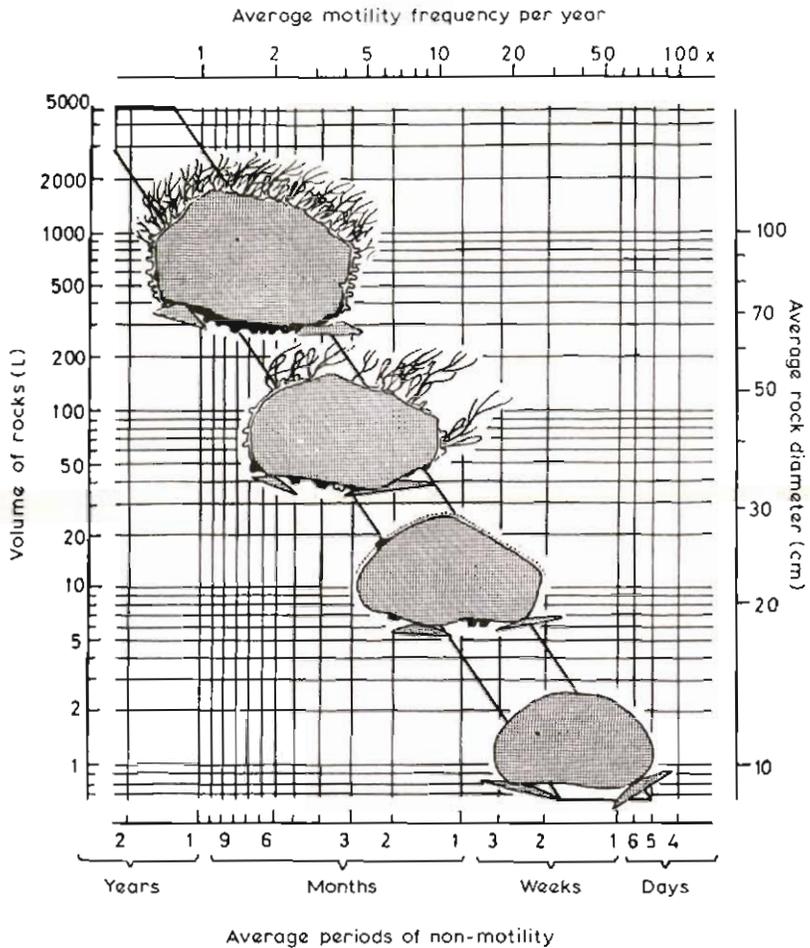


Fig. 5-18: Degree of motility and of organismic settlement as a function of substrate size. Large boulders (300 l volume or more, which remain non-motile for 1 year or more) support growth similar to non-motile rocks; the top of the boulder carries typical phytal assemblages, the sides phytal-shadow assemblages, the bottom (if free of the ground) cave assemblages. Boulders of 40 to 150 l (which are moved at least for brief periods during the year) harbour similar organismic assemblage zonation; however, these are less pronounced and the side zone begins to disappear. Boulders of 5 to 30 l (which remain in place for months only) typically support fast-growing algae mats on their top region, as well as a few young sedentary animals distributed over the surface area. Stones of less than 2.5 l (which do not remain in place for more than weeks) reveal no zonation and carry endolithic forms only. (After RIEDL, 1964b; modified.)

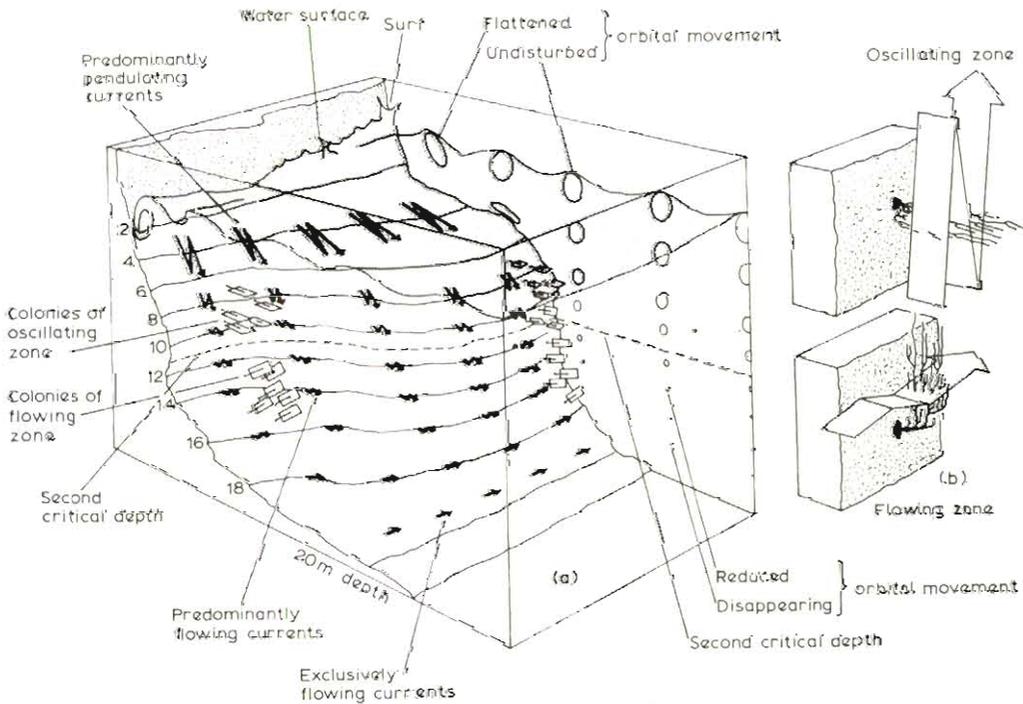


Fig. 5-19: Position of the second critical depth (broken line) and body orientation of the colonial planar gorgonid *Eumicella carolinii*. Bottom water currents, composed of pendulating and longitudinal flowing coast currents, are indicated as heavy black arrows in the general view (a), as white arrows in the detailed view (b). Note the orientation of the gorgonian colonies. (After RIEDL, 1964b; modified.)

Non-sedentary animals also show marked distributional gradients in regard to water movement. Among the suprademersal and demersal (bottom-living) fishes, the different swimming types should be mentioned (HIATT and STRASBURG, 1960; ABEL, 1961; EIBL-EIBESFELDT, 1964).

The changing degree of exposure of the coastline is paralleled by corresponding changes in animal populations. With decreasing exposure—which depends on coast inclination, angle of wave attack, prevailing winds, and fetch—the critical depths ascend, and the inner surf and unidimensional flow zones disappear. Again, the same 7 zones of hydroid populations (RIEDL, 1959, 1964b) can be traced; they provide an indication of mean exposure values (Fig. 5-21).

The degree of substrate exposure reveals further aspects which affect benthonic animal distributions. These aspects are connected with water-movement gradients near the substrate, with detours of the water-flow direction, and with the establishment of new, weak currents. Strong gradients of water movement and their effects upon the distribution of marine animals have recently been studied in submarine caves (RIEDL, 1959, 1966) and in the interior space of seaweed beds (ORT, 1967). The steep water-current gradients, particularly in pocket caves, again reveal the sequence of the 7 hydroid zones and, in general, comparable groupings of other sedentary organisms. The slowing down of the water current in algal beds by about

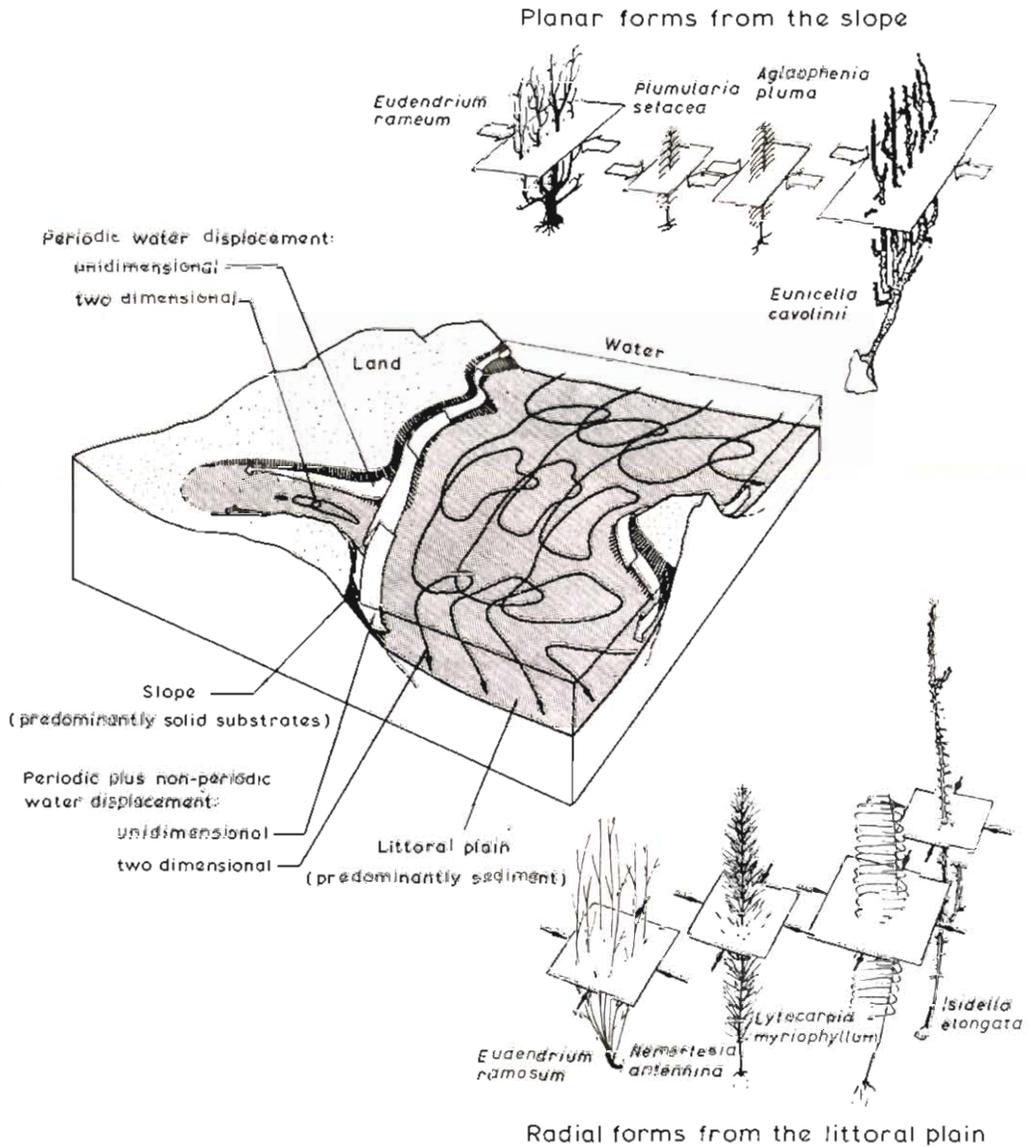


Fig. 5-20: The third critical depth lies between slope and littoral plain, and between unidimensional (white arrows) and two-dimensional (curved black arrows) flowing water bodies. Of the representatives of passive filter-feeders (selected from related taxonomic groups), the planar forms occur on the slope, the radial ones in the plain. (After RIEDL, 1966; modified.)

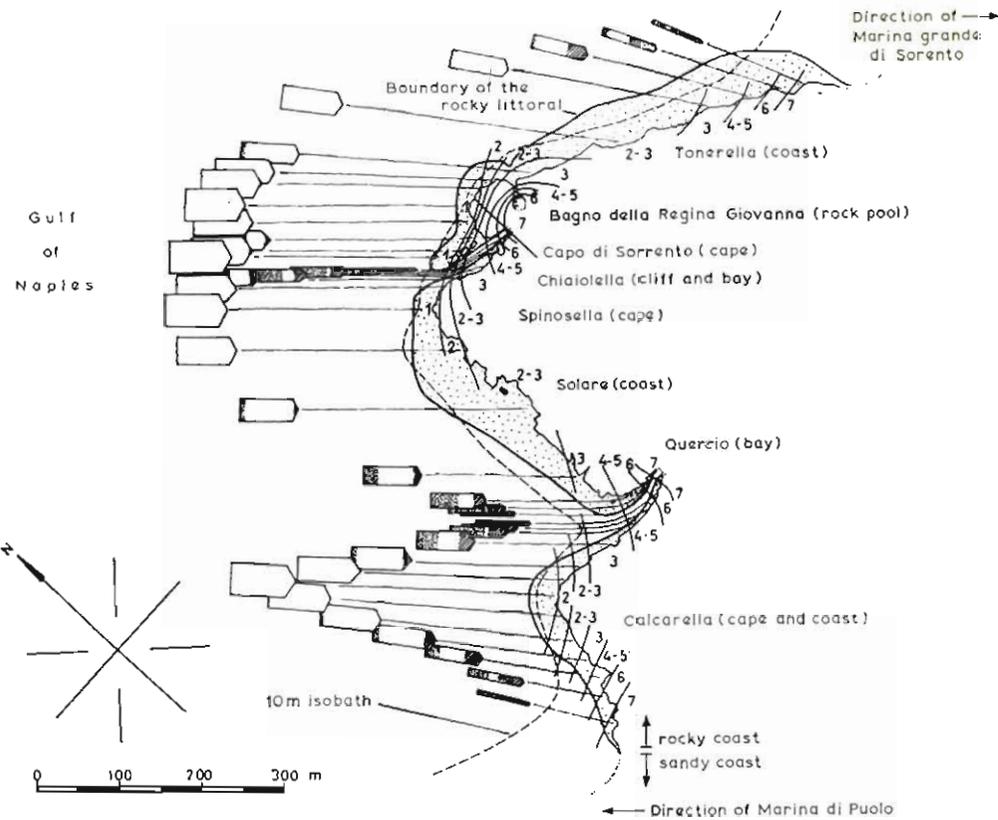


Fig. 5-21: Relationship between coast exposure and hydroid zones (1 to 7). Cape Sorrento, Gulf of Naples, Italy. The sequence of the hydroid zones (indicated by different widths of arrows), indicative of the coast inclination (dotted arrow sections) and the angle of attack of the prevailing wave direction (hatched arrow sections), which can be estimated from the boundary between the rocky shore level and the 10 m isobath. (After RIEDL, 1964b; modified.)

2 decimals explains the occurrence of benthonic microfauna elements with little power to hold on to the substrate. The microhabitat selection of passive filter-feeders on both distributional boundaries is most illuminating. *Parerythropodium* sp., for example, occurs in the calm deep waters in habitats with maximum exposure on tall-growing gorgonians; but they form, at the upper exposed regions, crusts pressed flat into sheltered crevices.

In submarine caves, water-movement directions may undergo frequent changes. The distribution of the planar filter-feeders is so consistently perpendicular to the prevailing direction of the water movement (Fig. 5-15), that water current charts can be drawn on the basis of their positions (RIEDL, 1959, 1966, p. 359).

Regarding water currents produced by marine animals themselves, the phenomena of xenorheophily should be mentioned (RIEDL, 1966); it refers to a situation in which animals prefer microhabitats which are under the influence of water currents produced by other animals. The preference of the foraminiferan *Miniacina miniacea* for mouth rims of balanids, of the calcified sponge *Antho involvens*

and the calcified anemone *Parazoanthus axinellae* for large poriferans (RIEDL, 1966), and of the hydroid genera *Lar* and *Podocoryna* for the mouth rims of polychaete tubes and snail shells are examples of xenorheophily. It often represents the primary cause of symbiotic relationships.

The exposure conditions in the boundary layer are barely accessible for study yet. Nevertheless, they appear even more important than the ones mentioned above because they directly affect the organisms (RIEDL and FORSTNER, 1968). The thickness of the boundary layer depends a good deal on the size of the surface area exposed to the current. It is of interest that hydroids which live on abiotic substrates have a minimum body height of 3 to 5 mm (among the smallest Mediterranean forms are representatives of the genera *Cladonema*, *Eleutheria*, *Podocoryna*, *Campanopsis* and *Orthopyxis*). For passive filter-feeders it would be detrimental to sink completely into the almost motionless water within such a boundary layer. On the other hand, epizoic hydroids with body heights of as little as 0.5 mm, e.g. representatives of the genera *Hebellopis* and *Cuspidella*, can exist perfectly well on their living substrates; on the delicate lattice-work of their substrates, the boundary layer develops a maximum thickness of only fractions of a millimetre.

#### *Ocean-wide geographic distributions*

Ocean-wide geographic distributions of marine animals are affected—as has already been mentioned—by primary and secondary aspects of water movements, as well as by the transportation capacities and hydrological characteristics of large water bodies. The distribution of the hydrological characteristics of a theoretically ideal ocean (ZENKEVITCH, 1948) is not in complete agreement with the real situation (Fig. 5-22a). If permanent winds are superimposed on this hypothetical ocean (FLEMING, 1957) as a symbol of the surface currents (Fig. 5-22b), if the deep currents are added, and if the influence of the corrected coasts, depths and areas of density changes are included, a picture quite similar to reality would be

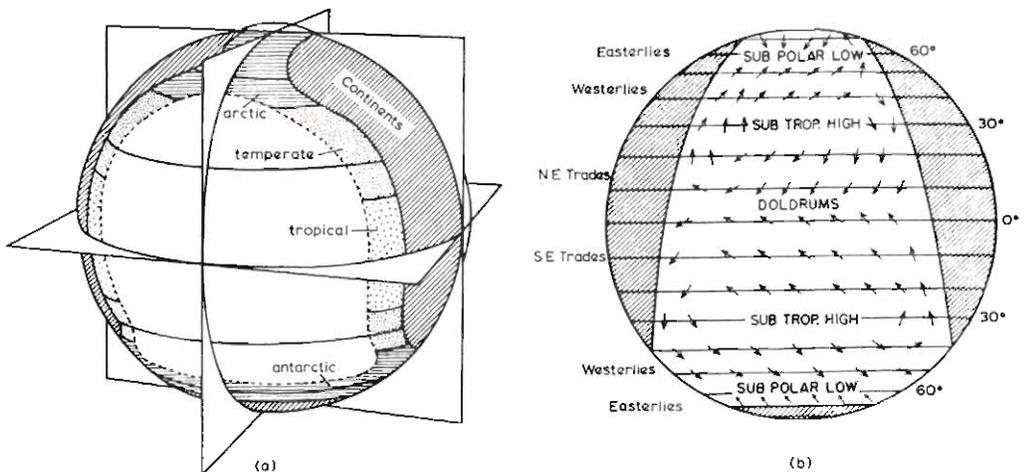


Fig. 5-22: Diagrams of climatic zones and their displacement according to the prevailing winds and circulations in an ideal ocean. (a) Geographical classification of the littoral zones without references to currents. (After ZENKEVITCH, 1948, from FRIEDRICH, 1965; modified.) (b) Surface wind circulation. (After FLEMING, 1957; modified.)

obtained. If it were further possible to blend together phylogeny on the one hand and the palaeogeography and climatology on the other, the general patterns of zoogeography in the marine environment should emerge. Indeed, much of the abundantly available material of marine zoogeography (EKMAN, 1953) corresponds with this concept.

Information on the primary actions of ocean-wide water movements, especially in regard to quantitative aspects of water dislocation, can be obtained from surface current charts (velocities, constancies and boundaries of currents). Information on secondary actions, particularly with respect to transport of heat and salinity, is contained in charts presenting abnormalities of oceanic temperatures and salinities (e.g. DIETRICH and KALLE, 1957).

Classic examples of ocean-wide displacements of individuals (expatriation) are the occurrence of the warm-water Lepadidae off the Scandinavian coasts due to the Gulf Stream Drift, and the dislocation of larvae of littoral animals up to 500 miles into the open sea (MILEIKOVSKY, 1968; SCHELTEMA, 1970).

### (3) Structural Responses

In marine animals, numerous correlations are known to exist between body size, external or internal body structures on the one hand, and the conditions of water movement in their respective habitats on the other. Water movement dynamics of small dimensions (littoral areas), which are particularly important for benthonic animals, must be studied *in situ* employing diving techniques and automatic photography (e.g. BOADEN, 1968; RIEDL, 1969). Underwater exploration and experimentation has added a new dimension to marine ecological *in situ* studies in coastal waters. In 1969, marine ecologists conducted successful experiments even under adverse conditions of water movement, temperature and visibility in the rough waters of the North Sea (3-week mission of the Underwater Laboratory 'Helgoland' at 23 m depth; KINNE, 1970a, b). Even though the development of adequate technologies for *in situ* studies has a long way to go (RIEDL, 1967, 1969), such breakthroughs open up new perspectives.

#### (a) Size

Many marine animals reveal a relationship between their body size and the water depth at which they live. In particular, colonies of passive filter-feeders often form ecotypes with different body sizes. Colony height of cnidarians usually increases with depth, i.e. decreasing intensity of water movement. This may be illustrated by three representatives belonging to the Hydroidea, Madreporaria and Gorgonaria, respectively. *Aglaophenia pluma* attains maximum heights of 1 to 1.5 cm in the inner surf zone and the upper oscillatory zone of the littoral water body. In the two-dimensionally flowing water body of the deeper littoral plains, it becomes branched and attains a height of more than 10 cm (Fig. 5-23). *Cladocora cespitosa* is calcified and often barely 1 cm high in the surf zone, but in the deeper water grows to a colony height of 50 cm. *Eunicella cavolinii* attains, at its upper boundary of distribution, a height of often only 5 to 6 cm (dwarf form), but in greater depths and in the innermost areas of submarine caves with quiet water it

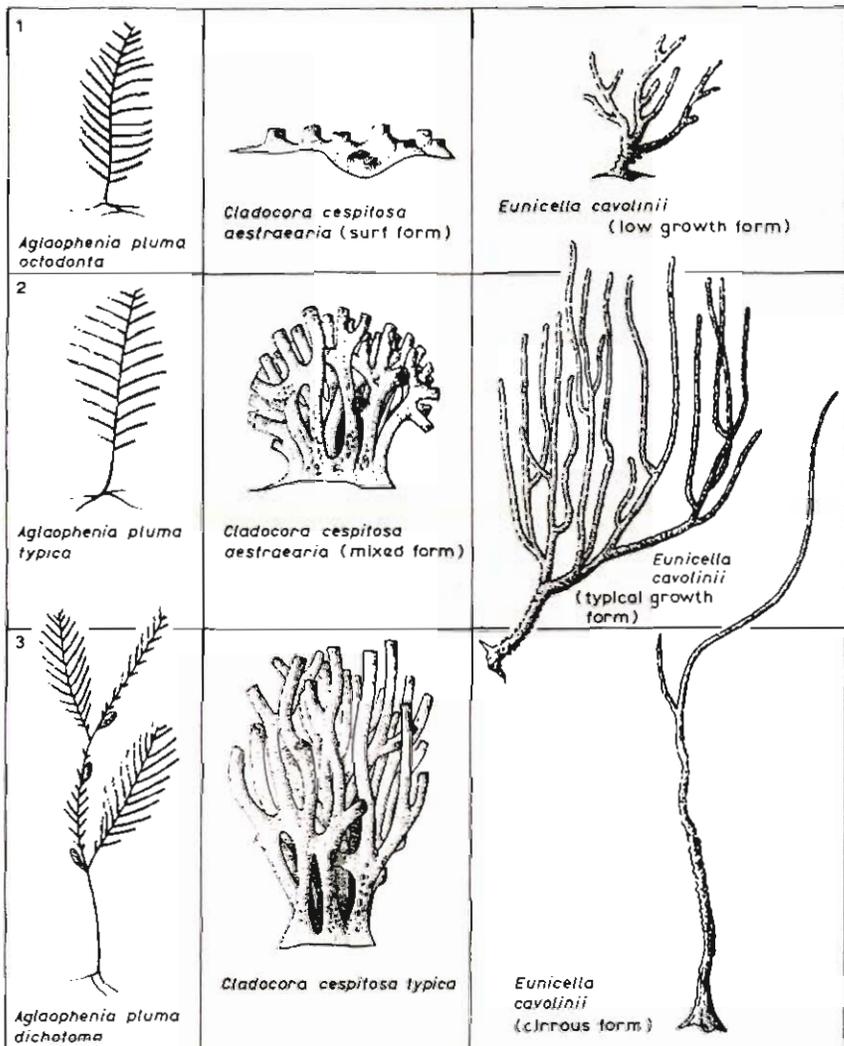


Fig. 5-23: Structural responses of some sedentary organisms. (1) surf and upper oscillatory zones, (2) lower oscillatory zone, (3) current zone. *Aglaophenia pluma*, *Cladocora cespitosa* and *Eunicella cavolinii* increase in size with increasing water depth, i.e. with decreasing water movement. (After RIEDL, 1966; modified.)

branches out and reaches heights of 1 m or more (ABEL, 1959; RIEDL, 1959, 1964b, 1966).

Even more notable differences are found if we do not restrict our examples to the variability within a given species (intraspecific variation), but compare different species within a genus or higher systematic categories (interspecific variation). Next to the hydroids, the poriferans respond most strikingly in this respect (RIEDL, 1966). Thus the genus *Axinella* (Fig. 5-24) is represented in fast-moving water by the flat encrusted *A. damicornis* but in deeper water by the tall-growing *A. poly-*

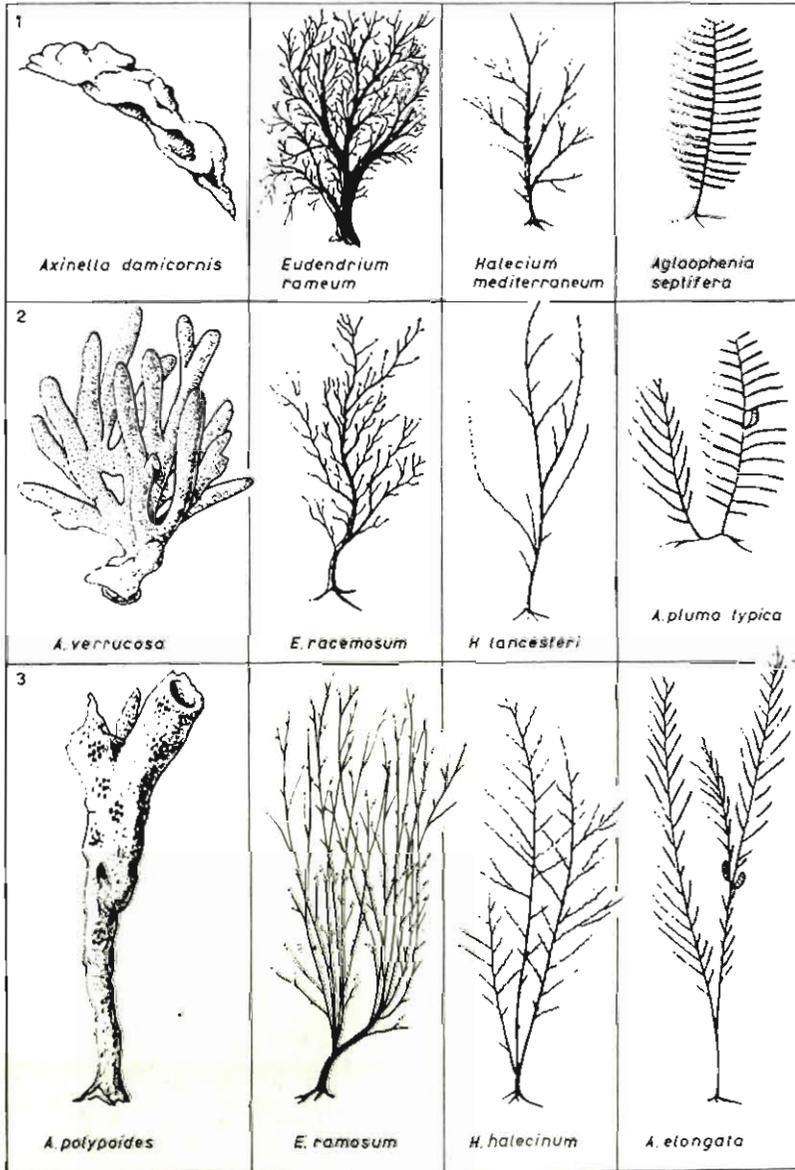


Fig. 5-24: Modifications of growth form of sedentary animals of the genera *Axinella* (poriferans), *Eudendrium*, *Halecium*, and *Aglaophenia* (hydroids). Sites (1) to (3) correspond with those given in legend to Fig. 5-23. (After RIEDL, 1966; modified.)

*poides*. The differences become still more pronounced if representatives of different families are compared. Among the echinoderms, the compact, low Pennatulidae occupy the shallows, the more than 2 m long Funiculinidae the greater depths. In many instances, the present diversity of species, genera and families may have evolved from different ecotypes of originally one single species via progressive habitat adaptation.

A further relation between water movement and body size can be reported from the regions of minimum water velocity. On flat substrates, the smallest of the passive filter-feeders do not exceed heights of 3 to 5 mm (RIEDL and FORSTNER, 1968); they still protrude somewhat from the average thickness of the boundary layer. Active filter-feeders, on the other hand, such as calcified bryozoans with a total height of scarcely 1 mm, are completely embedded in the boundary layer. Low forms of passive filter-feeders are encountered as epizoa on tall hydroids, where the thickness of the boundary layer attains the smallest values.

#### (b) *External Structures*

The more closely marine animals depend on water movement, the easier it is to determine the correlation between their external body structures and water-movement dynamics. The degree of such a correlation appears to increase from endo- to epibiotic non-sedentarians to sedentary animals, and among these from active internal and external filter-feeders to passive filter-feeders.

Possible relationships between water movement and external structures have hardly been substantiated as yet in non-sedentary animals, at least not with regard to cases in which water movement represents the primary controlling factor. A dependence of the shell thickness of molluses, for example, on the degree of water movement has by no means been generally ascertained (thin-shelled *Rissoa* in algal beds of the surf, thick-shelled *Aporrhais* in quiet mud bottoms). It is fairly obvious that the disc forms of the Porcellidiidae (harpacticoids), Patellaceae (limpets) and Gobiesocidae (sucker fishes) constitute an adaptive feature, for all these marine animals occur together in shallow, exposed waters, but do not possess any discoid ancestors. Only within more closely related groups is it possible to substantiate a segregation of species with tough and delicate body covers on the basis of the degree of exposure to water movement (DOMMASNES, 1968).

Structural relationships among sedentary animals have been studied from five different aspects; these will be discussed in the following five paragraphs.

Height and degree of body branching depend greatly on the intensity of water movement. Differences in height have been mentioned above. Under conditions of maximum water movement, small forms may be pressed into the layer of minimum water movement, thus providing even less surface for friction. Tall growth in deep water has the advantage of avoiding stagnating bottom layers with excessive turbidity (RIEDL, 1966). The degree of branching is usually correlated with differences in body height. The spectrum ranges from completely unbranched encrusting forms, to forms with a progressively increasing surface to volume ratio, to columnar or threadlike forms (*Axinella*; Fig. 5-24).

Relationships of functional symmetry may be influenced by the mode of water

movement in the habitat. It has already been stated that the oscillatory and unidimensionally flowing currents exert a selective influence on flattened planar forms among the passive filter-feeders. However, in two-dimensionally flowing currents on littoral plains, beyond the wave region, functionally radial forms are favoured (Fig. 5-20). This is possibly connected with the fact that water currents flow in all directions in this region. However, taxonomically quite closely related groups may be represented by forms with flattened as well as radially symmetrical bodies in these two water-body types: the genus *Eudendrium* by *E. rameum* and *E. ramosum*; the subfamilies Plumulariinae and Aglaopheniinae by the flattened *Plumularia setacea* and *Aglaophenia pluma* as well as by radial species of *Nemertesia* and *Lytocarpia*; the order Gorgonacea by several genera of flattened Plexauridae and Gorgoniidae of the littoral zone as against radial representatives of Primnoidae and Isididae occupying greater depths. Forms of transition between the different types of body shape are most revealing. In colonies of the Eudendriidae, for example, the choice of flattened versus radial growth is

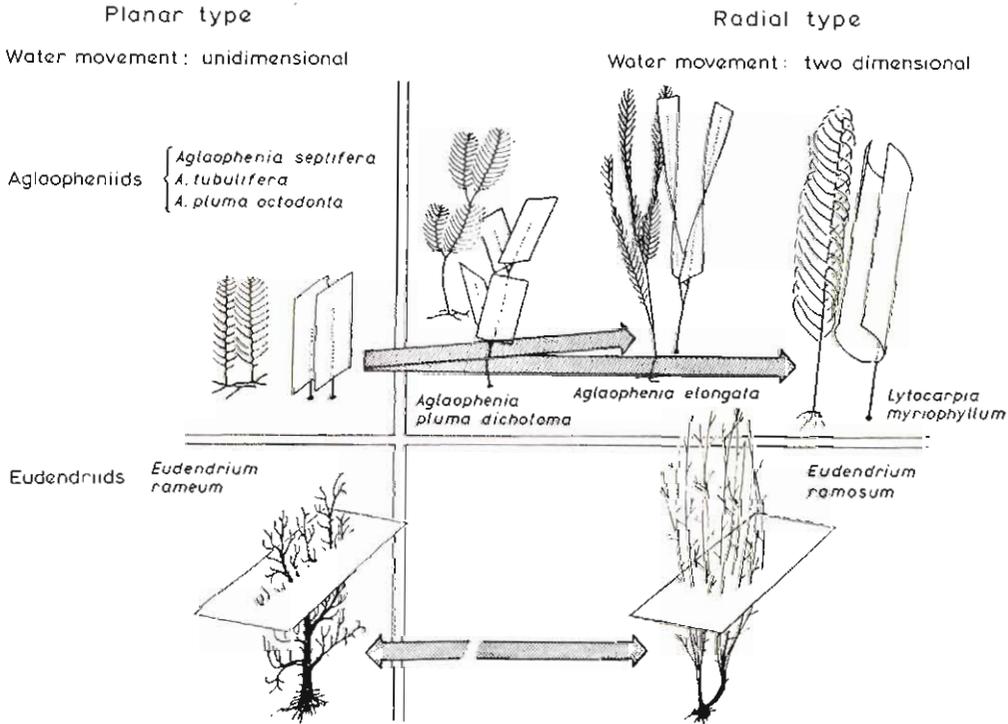


Fig. 5-25: Water movement-induced structural modifications in closely related hydroids. (After RIEDL, 1966; modified.)

not predetermined. However, *Eudendrium rameum* colonies are nearly always flattened and *Eudendrium ramosum* colonies in most cases radial (Fig. 5-25). Among the aglaopheniids with their originally planar colony form, secondary modifications towards functionally radial symmetry are exemplified by *Aglaophenia*

*phenia pluma* f. *dichotoma*, *A. elongata* and *Lytocarpia myriophyllum*. This modification is effected by turning or bending of body surfaces, with the result of better utilization of multidirectional water currents (RIEDL, 1966).

Population density and number of hydranths per colony increase with increasing exposure to water movement. This relation has been observed in submarine caves even over short distances. Hydroid species with low population density and small numbers of hydranths per colony are progressively replaced by those of greater density and larger number of hydranths as the intensity of water movement increases; the number of hydranths per cm<sup>2</sup> rises from 10 to 5000. It is interesting to note that the 12 main species are arranged—irrespective of their taxonomic position—in a closely corresponding order of increasing hydranth density. In this order, the Campanulariidae take the lowest places, the Aglaopheniidae the highest. Growth forms with greater hydranth density require a higher influx of nutrient particles; consequently they tend to occupy more exposed habitats. It is not yet understood why growth forms with few polyps are not in a similarly advantageous position in locations with plentiful food supplies (RIEDL, 1959, 1964b, 1966). Comparable responses are revealed by horny corals; in shallow reefs, for example, they are represented by *Gorgonia* species with 0.5 million hydranths per colony and a maximum of 2.5 million per m<sup>2</sup>; while in quiet deep waters they are represented by such forms as *Isidella elongata* with 300 hydranths per colony and presumably less than 100 hydranths per m<sup>2</sup>. In species of *Pennatularia* also, the number of hydranths per colony decreases 10 to 100 times from the shallow littoral (*Pennatulina penniformia*) to the extralittoral (*Pennatulina verticillata*). Detailed ecological data are not yet available.

Animals of the boundary layer reveal a number of structural adjustments. In gorgonaceans with flattened colony growth, a special arrangement of polyps can frequently be observed. Usually, the polyps are evenly arranged around the axes of the branches; but in flattened growth forms they are positioned closer to the principal plane of the colony, forming four-line arrangements. An indication of a row arrangement can be observed in *Eunicella cavolinii*; with slender and bushy growth forms of this species, the polyps are evenly distributed around the axes; with flattened forms, the four-line arrangement gradually becomes apparent. The four-line arrangement seems to be quite fixed within primary planar growth forms, such as species of the sea-fan genus *Gorgonia*. An advantage of this polyp arrangement is evident; the colony attains optimum utilization of the plankton passing it. Near the cylindrical rods of the lattice, represented by this type of colonial growth, particle velocity increases, but behind them parallel to the axis (Fig. 5-26), occurs a pair of vortices with greatly diminished water flow. Therefore, with moderate water movement, the stretched-out polyps extend into the strongest current; with greater water movement, however, they (at least those on the lee side) are forced into the vortices and hence exposed to diminished current speeds. This response pattern has the advantage of permitting the colony to utilize a much greater total range of water velocities and thus to remain active for a longer period of time (RIEDL and FORSTNER, 1968). However, the feeding procedure in some gorgonians is still a problem (KANWISHER and WAINWRIGHT, 1967; WAINWRIGHT, 1967).

The influence on the boundary layer of microstructures may be illustrated by referring to three different aspects: The effect of the structure on the minimum

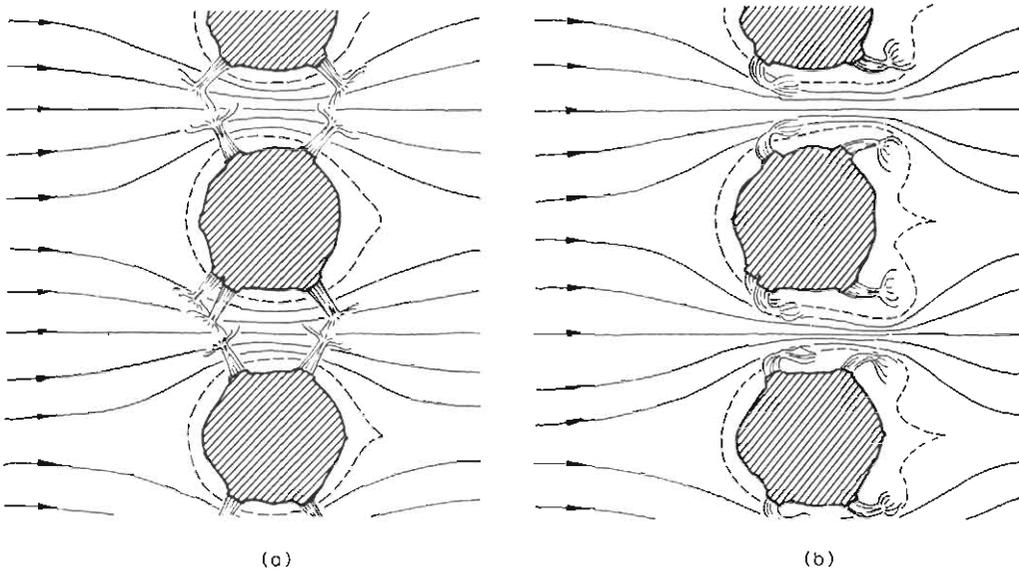


Fig. 5-26: Significance of boundary layer dimensions for the positioning of polyps on planar gorgonian colonies. Diagrammatic stem sections. (a) Under conditions of low water movement intensities, polyps extend into maximum current velocities. (b) Rapid water movement displaces the lee-side polyps into minimum current velocities of the vortices. (After RIEDL and FORSTNER, 1968; modified.)

velocity layer current, the effect of the current produced by the animal itself and the effect of structures on the self-produced current.

The bryozoans, whose structure and activity are related to the boundary layer, often carry pores on their frontal areas, as well as oöcia and spines around their orifices. Pores lead to a marked increase in frictional resistance (WIEGHARDT, 1953), whereby the absolute pore dimensions matter less than the ratio of breadth to depth. Spines (as they occur with great regularity in free-standing, exposed Ancestrulae) and spherical oöcia form barriers which produce eddies (Fig. 5-27; SCHLICHTING, 1937; SCHULTZ-GRÜNOW, 1956) similar to currents around the tentacular apparatus of bryozoans. It must be advantageous to such delicate, active external filter-feeders if they succeed in slowing down the water movement and, still more important, channelling it into the desired directions.

The poriferans of shallow waters often exhibit bulbous, smooth forms which are easily overrun by fast-moving water. The hydrodynamic pressure distribution over the sponge body must be very uneven, a fact which can hardly be advantageous for maintaining a uniform rate of flow in the communicating canal system. Interestingly, experiments on an analogous case of a rapidly expanding canal reveal that the turbulence and disturbance of the boundary layer, occurring at the point where the canal cross-section alters, do not occur if the boundary water is continuously sucked away (PRANDTL and TIETJENS, 1929-31); boundary layer and uniform pressure distribution are then maintained. The advantages of a uniform distribution of pores over the entire sponge surface may thus be connected with the stabilization of the boundary layer and the hydrodynamic pressure.

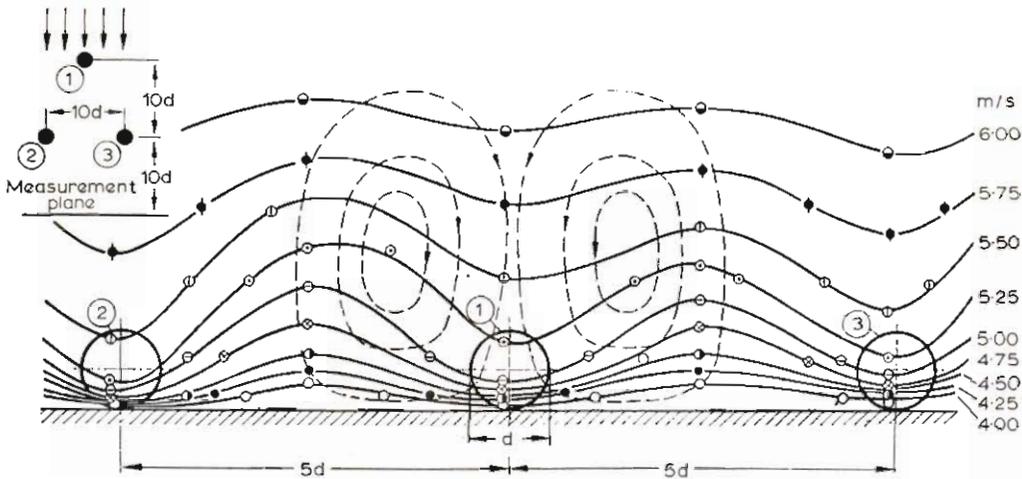


Fig. 5-27: Water movement behind a row of spheres on a flat surface in the boundary layer region: Solid lines: isotachs (points of equal velocity); broken lines: secondary currents (the initial movement runs perpendicular to the plane of the graph; measurement order entered top left;  $d$ : diameter of spheres = 4 mm). (After SCHULTZ-GRÜNOW; from SCHLICHTING, 1956; modified.)

Active internal filter-feeders dispose of their waste water in a single stream. The undesired waste water is thus ejected more forcibly. Some forms possess, at the end of this ejection jet, fine ridges of skin, barriers of spicules (*Sycon*, *Leucosolenia*) or of spines (*Halocynthia*). These structures have the hydrodynamic effect of keeping the region where water mixing begins further away from the body.

#### (c) Internal Structures

From the multiplicity of relationships between water movement and external structures, one must expect changes of internal structures to be no less numerous. However, water movement effects on internal body structures have hardly been investigated.

The only pertinent study that has come to the reviewer's attention was conducted on poriferans. Simultaneous *in situ* studies by skin divers and anatomical analyses revealed that, in exposed habitats, sponge species examined may contain inside their body larger spicules (SARÀ, 1964) or a denser arrangement of spicules (RUETZLER, 1965b); both modifications lead to increased stability of internal body structures.

#### (4) Conclusions

HUMBOLDT and BONPLANDT (1818) and DARWIN (1842) referred to the significance of water movement for marine animals. The great complexity and diversity of correlations, however, is only now beginning to manifest itself. The application of modern underwater technologies makes it possible to study the correlations between habitat characteristics and behaviour in the natural environment.

All marine animals depend to some degree on water movement for many of their functions and structures. In terms of ocean-wide dynamics, water movement acts essentially via primary aspects, while in terms of littoral dynamics tertiary aspects increase in importance. Small-scale relationships near the substrate and the boundary layer are dominated by primary and secondary aspects, involving direction of water movement and transport of gases and nutrients.

Biologically, the degree of dependence of marine animals on water movement is a function of their belonging to different ecotypes in the sense of 'Lebensformtypen'. The dependence generally increases from non-sedentary to sedentary animals, from internal filter-feeders to external filter-feeders, and from active to passive filter-feeders.

Similarly, the effect of water movement shifts according to the habitat. It increases with the number and variability of exposure values. These reveal gradients from coastal to deeper waters and stratifications according to their distance from solid, current-exposed substrate surfaces. The degree of dependence on water movement increases in these layers in the order endofauna, mesofauna, crusted fauna, epifauna; as well as from pelagic, via suprademersal, to demersal free-swimming forms.

Methodologically, up to the present time, descriptive information still predominates. However, the foundations of exact quantitative measurements are rapidly being laid. Simulation of natural conditions and experimental studies have just begun. The universal importance of the factorial hierarchy presented in this review is recognized.

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## 6. TURBIDITY

### 6.0 GENERAL INTRODUCTION

C. G. WILBER

#### (1) General Aspects of Turbidity

A definition of turbidity which has been presented by the United States Geological Survey is as follows:

'Turbidity is the optical property of a suspension with reference to the extent to which the penetration of light is inhibited by the presence of insoluble material. Turbidity is a function on both the concentration and particle size of the suspended material. Although it is reported in terms of parts per million of silica, it is only partly synonymous with the weight of sediment per unit volume of water' (UNITED STATES GEOLOGICAL SURVEY, 1964.)

According to WELCH (1948), the standard unit of measuring turbidity is that condition produced by one part per million (ppm) of silica (Fuller's earth) in distilled water. WELCH has described various quantitative methods for measuring turbidity.

Turbidity, which is ordinarily seen as cloudiness in water, is an optical property of water. If a beam of light passes through muddy water, its intensity is reduced due to suspended material. This reduction is a measure of the water's turbidity. The suspended material may be fine insoluble particles, either inorganic such as clay, silt, and sand, or organic such as industrial or domestic wastes (SWENSON and BALDWIN, 1965). Turbidity modifies the transmission of light through a column of the sea water; the total extinction varies proportionally to the concentration of suspended solid material which causes the turbidity. The amount of light scattering varies directly with the degree of turbidity. Particle size determines the nature of the light scattering; for example, the shorter wavelengths of light are more readily scattered by small suspended particles than are the longer wavelengths; large particles scatter light of all frequencies with about the same effectiveness (WILLIAMS, 1962; Chapter 2.0).

There is substantial literature dealing with turbidity and its effects in relation to freshwater streams, rivers, and lakes. The subject is of great interest to engineers and geologists as well as to biologists. Recently, two important reports have been published covering the problem in fresh waters (COLBY, 1963; SCHUMM, 1963). No similar treatises are yet available for the oceans and their estuaries. Many of the principles and suggestions included in these two references may have applications, within reasonable limits, to aspects of the marine environment.

This introduction to turbidity is limited to the phenomena associated with reduced transparency of water brought about by suspended solid material. It does not cover the phenomenon known as 'turbidity currents'. These latter have little in common with turbidity as defined in this section. JOHNSON (1964) has recently reviewed our present knowledge on turbidity currents.

## (2) Measuring Turbidity: Methods

One of the fundamentally difficult aspects of dealing with turbidity data is the fact that various methods have been used to estimate the degree of turbidity. For example, in a survey on the chemical and physical characteristics of Chincoteague Bay, made by the Chesapeake Bay Institute of the Johns Hopkins University (USA), a measure of turbidity was obtained by measuring the transmission through a 5 cm cell containing the sample at wavelengths of 425, 525, and 650 m $\mu$ , respectively, with a Fisher Filter Photometer. The turbidity values were then converted to extinction for a 10 cm cell in order to conform with units used by the Chesapeake Bay Institute for reporting turbidity data (MCGARY and SEILING, 1953).

Extensive use has been made of photo-electric cells to measure the transparency of ocean water. A variety of colour filters are used to estimate the extinction coefficient for narrow wavelengths of light. The data generally indicate that in the ocean the extinction coefficient varies widely for any given wavelength of light. Even the clearest ocean water shows a wide variation in extinction coefficient, much greater than is found for pure water in the laboratory. In coastal waters which are turbid the extinction coefficient varies even more. With increasing turbidity of the water, the region of the minimum extinction coefficient (maximum transparency) is shifted toward the red end of the spectrum (SVERDRUP, 1954).

Particulate carbon contributes to the turbidity of sea water; it can be measured by concentrating the material on a glass wool filter, after which it is subjected to combustion at high temperature. The method is said to have a precision of plus or

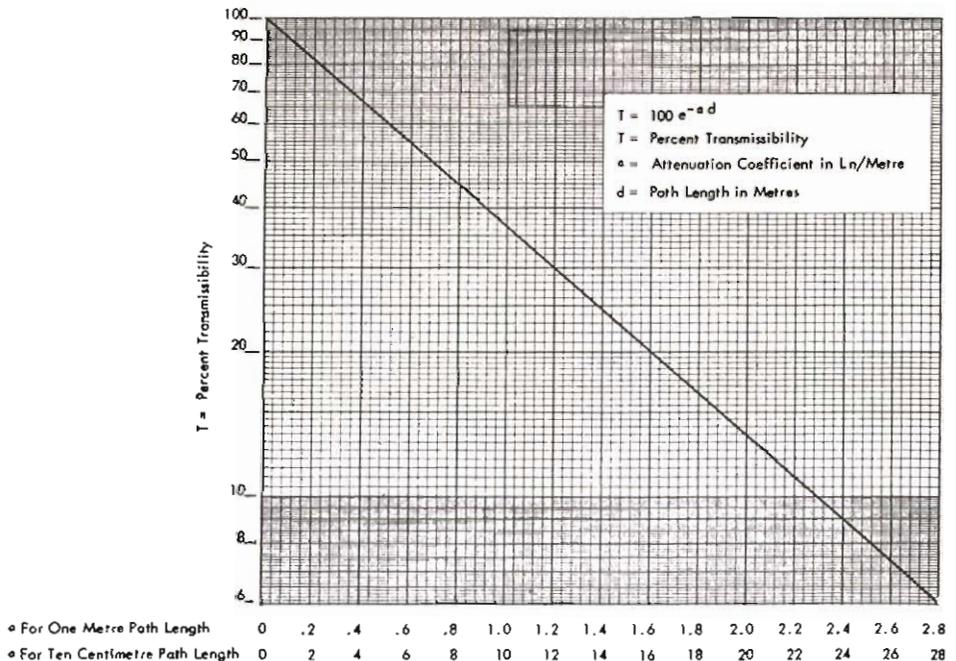


Fig. 6-1: Percent transmission of light in sea water plotted against attenuation coefficient as determined by a 1 m and a 10 cm 'transmissometer'. (Courtesy of Hydro Products, San Diego, California, USA.)

minus 10  $\mu\text{g}$  of carbon in the range of 0 to 500  $\mu\text{g}$  carbon/l (MENZEL and VACCARO, 1964).

With experience and practice, observations made with the Secchi-Disc lead to better than 10% accuracy. The Secchi-Disc gives an estimate of the average absorption coefficient ( $k$ ) between the surface and the Secchi-Disc depth reading ( $D$ ); where depth  $D$  is greater than a few metres,  $k$  equals  $1.7/D$  (PACKARD, 1964).

Suspended material in ocean water can be estimated by filtration or absorption methods (BARNES, 1959). The standard methods of turbidity estimation depend on visual identification of some object immersed at varying depths in turbid water (SCOTT, 1944).

A widely accepted standard method for turbidity estimation is the 'Jackson Candle Method' (AMERICAN PUBLIC HEALTH ASSOCIATION, 1965). The principle of the method is simple: Turbidity measurements are based on the light path through a suspension which just causes the image of the flame of a standard candle to disappear, that is, to become indistinguishable against the general background illumination, when the flame is viewed through the suspension. Waters of low turbidity have a longer light path than those of higher turbidity. Cross comparisons of the results from the candle method with those from various other instruments do not check uniformly.

NISHIZAWA and his colleagues have developed a useful turbidity meter (FUKUDA and co-authors, 1954; NISHIZAWA and co-authors, 1954; INOUE and co-authors, 1955) and have used it to (i) evaluate the effect of turbidity on the visibility of net twines (INOUE and co-authors, 1958); (ii) to describe turbidity distribution in the China Sea (NISHIZAWA and INOUE, 1958); and (iii) to study the variation of turbidity in a short column of ocean water (NISHIZAWA and INOUE, 1964).

MAXIMUM PROBABLE UNDERWATER VISIBILITY RANGE VS. TRANSMISSIBILITY

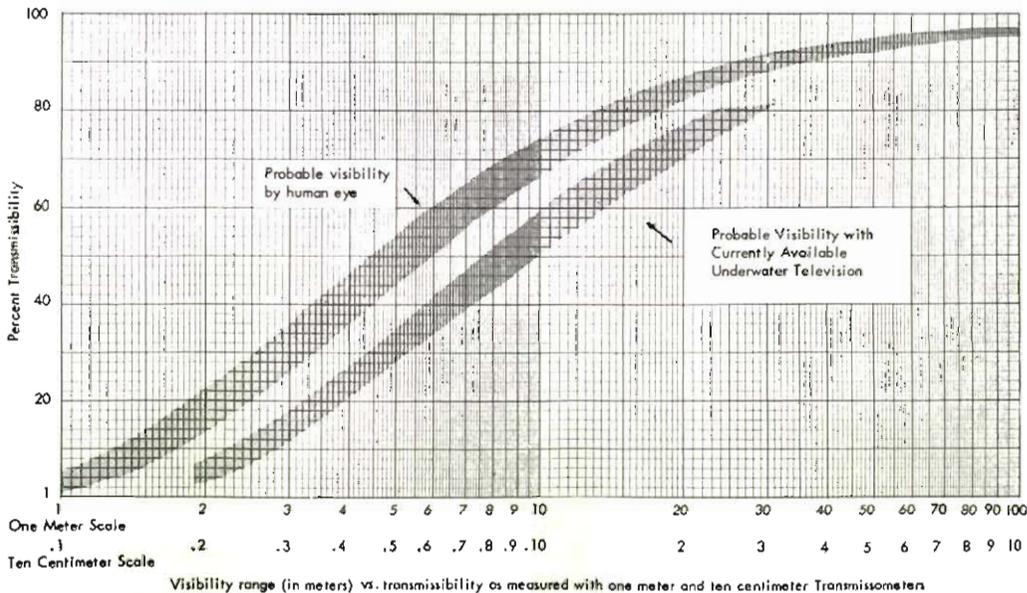


Fig. 6-2: Range of visibility (in m) plotted against percent transmission as measured with 1 m and 10 cm 'transmissometers'. (Courtesy of Hydro Products.)

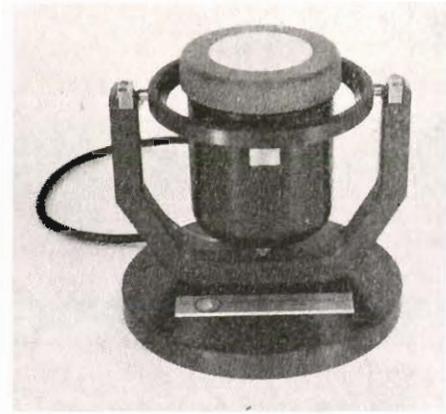


Fig. 6-3(a): Relative irradiance meter. Deck sensor for measuring illumination at surface of ocean.

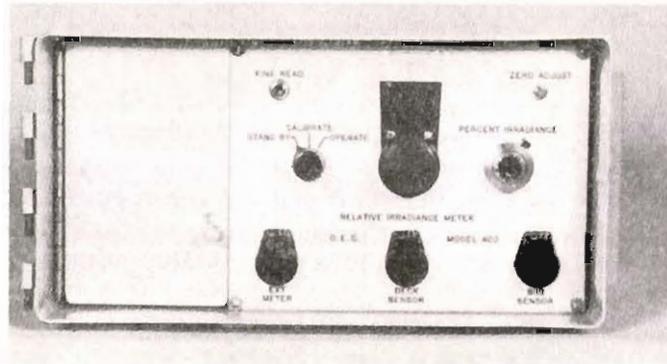


Fig. 6-3(b): Relative irradiance meter. Deck module.

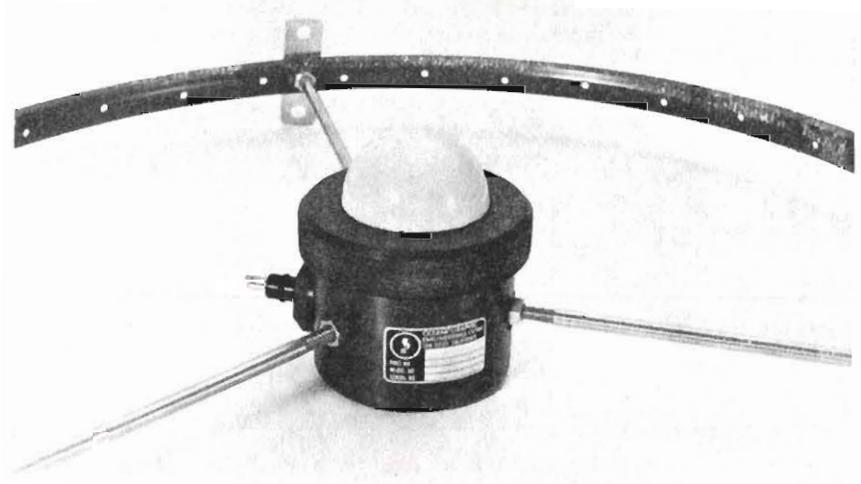


Fig. 6-3(c): Relative irradiance meter. Underwater sensor for measuring illumination at a given depth below the surface. (Courtesy of Hydro Products.)

Commercial instruments are now available for measuring turbidity and relating it to underwater visibility (Figs 6-1, 6-2). Another device is the relative irradiance meter which measures illumination levels below the surface relative to surface illumination (Fig. 6-3). It is now possible to predict, with a useful degree of accuracy, underwater visibility for the human eye and for television cameras from measured water turbidity (BRIGGS and HATCHETT, 1965; see also Chapter 2.0).

A classical discussion of the penetration of light into the oceans was published by LE GRAND (1939) who included a detailed discussion of turbidity from theoretical as well as observational points of view. Turbidity, which in general decreases as one moves away from coastal waters, considerably modifies light which penetrates into the sea. The general extinction coefficient may be defined as

$$F = F_0 e^{-cx}$$

where  $F_0$  and  $F$  are respectively light intensity before and after passing through an 'epaisseur' of water ( $x$ ), and  $e$  is the base of Napierian logarithms (2.718);  $c$  is the extinction coefficient. The relation holds only for monochromatic light.

Suspended particles modify the penetration of light into the sea in a number of ways. If the suspended particles are relatively large and dark coloured, they will absorb significant amounts of light of all wavelengths; suspended carbon acts in this manner. If the particles have a bright surface, a combination of absorption and diffusion of light results, which depends on the colour of the particles. Small, transparent particles present a complex situation which permits no clear-cut summary. The oceans contain an enormous number of particles of all sizes. Thus, the relative importance of absorption and diffusion in determining the final extinction coefficient is not easy to assess. The extinction coefficient ( $c$ ) of sea water is the summation of the true coefficient of absorption and the apparent coefficient of absorption resulting from diffusion of light. The product of the vertical extinction coefficient and the depth of visibility of the Secchi-Disc is said to vary from 1.5 in turbid water to 4 in very clear water. LE GRAND's (1939) monograph should be consulted for details.

### (3) Turbidity in Oceans and Coastal Waters

JERLOV (1951) made a detailed study of the transparency of sea water as part of the Swedish Deep Sea Expedition (1947 to 1948). As a rule, the transparency of ocean water is rather constant. Water from the Sargasso Sea shows the highest degree of clarity found in natural water. In deep sea water, which contains little particulate matter, transparency values approaching 97% transmission are common—a condition found in doubly distilled water.

In turbid water, transparency decreases as a result of yellow substance in the water. According to JERLOV (1951), yellow substance is practically absent in the clearest ocean water, but in water of normal particle content there is a noticeable production of it. Upwelling water contains abnormally large amounts of yellow substance. Even in the oceanic divergences, there are indications of higher contents than particles would account for. JERLOV further suggests a supply of yellow substance from deep water layers, where disintegration of carbohydrates takes place.

JERLOV's (1951) results are particularly applicable to tropical and subtropical

Table 6-1

Percent transmission of normal sunlight per m of ocean water  
(After JERLOV, 1951)

Kind of ocean water	Wavelength (m $\mu$ ) of normal sunlight				
	310	425	550	600	650
Very clear ocean water	86	97.8	97.2	85	70
Ocean water relatively high turbidity	69	93.5	93.5	80	67

waters. In northern or arctic waters, greater turbidity is expected. Table 6-1, compiled from data presented by JERLOV, illustrates the percent transmission of normal sunlight per metre of ocean water for very clear water and for ocean water of relatively high turbidity (see also Chapter 2.0).

It seems clear that in estuaries, an important source of sediment for making the water turbid (other than stream load) is the tidal channels. The water above a tidal flat is likely to be most turbid just before high tide, whereas that in the deep water is most turbid at or before low tide and least turbid at high tide (EMERY and STEVENSON, 1957).

The turbidity of an estuary is determined, to a large extent, by the turbidity of the water from rivers and streams entering it. Streams entering a given estuary do not have the same degree of turbidity. For example, of the three main rivers discharging into the Sacramento-San Joaquin Estuary (U.S.A), the Sacramento River at Rio Vista has a turbidity of 1 to 600 ppm, the Mokelumne River at Woodbridge, 0 to 70 ppm, and the San Joaquin River at Mossdale, 0 to 125 ppm. Tidal action, of course, mixes these three kinds of water. It is important to emphasize, however, that the turbidity of a given estuary is never constant; it varies seasonally and locally (KELLEY, 1966).

Observations indicate that turbidity of offshore waters can be changed as a result of pollution from sewer outfalls. For example, in the Bay of Saronicos, which is near Athens (Greece), the suspended solid matter varies from 45 to 485 mg/l (EDIPIDIS and HATZIKAKIDIS, 1964). In the same locations, the dissolved organic matter varies from 15 to 112 mg/l. The results suggest that turbidity measurements in the sea may be of some value in alerting scientists to possible contamination of inshore waters from sewage and other polluting effluents.

#### (4) Selected Turbidity Data

##### (a) *Indian Ocean*

Turbidity and transparency measurements have been used to classify and isolate various water masses in the ocean. For example, PAVLOV (1961) measured water transparency as the main optical characteristic of water masses in the Indian Ocean. He came to the general conclusion that water masses of the northern Indian Ocean are characterized by high absolute values of transparency (75 to 85% on the average). The characterization of water masses, in spite of small

differences in absolute values of transparency, is facilitated by the presence of silt charge zones, displaying themselves to some degree on the borders of adjacent water masses. They are evidently caused by accumulation of organic and inorganic suspensions in the zones of water transformation, due to increased hydrological gradients. Other optical parameters, such as spectral transparency and light diffusion characteristics of sea water, are also different in different water bodies. In fact, hydro-optical characteristics are good indices for different individual water masses (Chapter 2).

During the International Indian Ocean Expedition, Japanese investigators made occasional measurements of water transparencies. They report average water transparencies of about 39 to 40 m using the Secchi-Disc (DATA OF OCEANOGRAPHIC OBSERVATIONS AND EXPLORATORY FISHING, 1965).

Table 6-2 lists turbidity values for water from various parts of the Bay of Bengal (India).

Table 6-2

Turbidity measurements in the Bay of Bengal (India) at different locations obtained by use of the Secchi-Disc. k: extinction coefficient, calculated (After SATYANARAYANA RAO, 1957)

Location		Secchi value	
Latitude N	Longitude E	m	k
		(approx.)	
14° 50' 0"	82° 04' 0"	23	0.075
13° 11' 5"	80° 21' 4"	15	0.119
13° 29' 0"	80° 40' 5"	20	0.088
15° 33' 5"	80° 47' 5"	4	0.485
15° 57' 0"	82° 03' 0"	14	0.129
16° 21' 0"	82° 09' 0"	16	0.111
17° 35' 7"	82° 22' 5"	10	0.181
17° 22' 3"	83° 27' 4"	24	0.072
18° 52' 0"	85° 05' 0"	25	0.071
20° 22' 0"	87° 23' 5"	13	0.138
20° 52' 0"	89° 00' 0"	21	0.085
21° 13' 0"	89° 13' 0"	11	0.166
17° 25' 5"	83° 22' 0"	37	0.048
16° 45' 2"	82° 30' 5"	2	1.116

(b) *Gulf of Mexico*

As with most studies on turbidity in the oceans, there are only meagre data from the Gulf of Mexico. Special scientific reports, from the Bureau of Fisheries of the U.S. Department of the Interior, include turbidity indices for selected points in the Mississippi Sound and Lake Pontchartrain. Turbidity is expressed as the percentage transmission of light through the sample. No correlations were made with values for extinction coefficient or direct Secchi-Disc measurements. The transparency data are quite inadequate to meet the increasing demands of researchers (SHOEMAKER, 1954).

*(c) North Sea*

In the North Sea, water of low salinity usually has high turbidity values; water from the Atlantic Ocean, which comes into the region around the British Isles, has a higher salinity and a lower turbidity (NEUMANN and PIERSON, 1966). Clear, open ocean water is most transparent for blue light of about 0.47 to 0.48  $\mu$ , whereas in turbid coastal waters maximum transparency shifts to about 0.55  $\mu$ , the yellow-green.

*(d) Atlantic Ocean*

Some examples of suspended solid material in the North Atlantic were recorded by Soviet Russian investigators in 1960: Sargasso Sea: 0.2 mg/l; off Brittany: 1.0 to 0.5 mg/l; North Atlantic Current: 1.0 to 0.5 mg/l; Newfoundland Slope: 1.0 mg/l; Azores: 1.0 mg/l; over-all variation: 0.2 to 3.5 mg/l.

The composition of the suspended material was: coccolith mineral of North Atlantic water mass, detritus mineral in Sargasso Sea, and diatom mineral off Newfoundland (VIKHRENKO, 1964).

Studies on optical characteristics in the Atlantic Ocean using a photometer indicate that the attenuation of illumination with depths follows an approximate exponential law. In relatively transparent waters, the slope of the attenuation curves decreases sometimes with greater depths; in turbid waters there is sometimes an increase of slope (NAUMIN and co-authors, 1964). As water transparency decreases, there occurs a shift of the transmission maximum in the direction of longer wavelengths. Data obtained for turbid waters show a considerable variation from the theoretical curve. It is proposed that this variation results from the absorption and scattering of light which occurs on large planktonic particles (Table 6-3).

Table 6-3

Water transparency along the South Atlantic coast of the United States expressed as m to which a Secchi Disc is visible (After ANDERSON and co-authors, 1956)

Latitude N	Longitude W	m
27° 40'	79° 41'	33
28° 20'	79° 48'	37
28° 18'	80° 10'	14
28° 20'	80° 32'	4
29° 00'	79° 26'	22
26° 19'	76° 44'	26

*(e) Other Areas*

Turbid waters have been found in strange and isolated locations in the oceans. For example, in the Aleutian Trench turbid water, occurs from about 5666 m to the bottom which is about 6947 m. This so-called nepheloid layer contains 10

times the amount of suspended material ordinarily found in the bottom waters of the Pacific Ocean. EWING and THORNDIKE (1966) have suggested that this turbidity results from the action of a turbidity current, probably one which accompanied an earthquake.

These so-called nepheloid layers may be anywhere from 230 to 1950 m in thickness. Particulate matter in various oceanic surface waters is reported to vary between 800 and 2500  $\mu\text{g/l}$  (JØRGENSEN, 1966). Inshore waters show much higher values. The average particulate matter in the ocean water off Plymouth (England) is 3820  $\mu\text{g/l}$  with an annual variation of 2700 to nearly 6000  $\mu\text{g/l}$ . In the Long Island Sound, values up to 7500  $\mu\text{g/l}$  are recorded. Certain areas of the oceans have relatively enormous loads of suspended particulate matter; thus the Danish Wadden Sea may contain as much as 300,000  $\mu\text{g/l}$  of suspended material. In deep offshore waters there is ordinarily less suspended material.

In Chesapeake Bay (USA), measurements of light intensities 3 m below the surface in the middle of the Bay gave virtually the same values as measurements made 0.3 m below the surface near the mouth of the Patapsco River. Other estuaries in which measurements have been made give similar results: San Diego Bay, San Pedro Bay in USA, and Jade Bay in Germany (OLSON and co-authors, 1941).

NISHIZAWA and INOUE (1958) have reported extensive new observations on turbidity and its distribution, especially in the East China Sea and in the neighbourhood of Japan and the northern Pacific Ocean generally. They have also reviewed and discussed the literature on turbidity in general with special reference to phytoplankton (see also NISHIZAWA and co-authors, 1954; INOUE and co-authors, 1955, 1958; and NISHIZAWA and INOUE, 1964).



## 6. TURBIDITY

### 6.1 BACTERIA, FUNGI AND BLUE-GREEN ALGAE

G. RHEINHEIMER

#### (1) Introduction

The influence of turbidity on bacteria, fungi and blue-green algae is mainly an indirect one but nevertheless much more important than usually assumed. However, we have only a very limited knowledge on this factor as yet. Early authors have already stressed the importance of seston (filterable particulate matter) as a substrate for micro-organisms of surface waters (ZOBELL, 1946). Seston consists of tripton (minerogenous particulate material and organogenous detritus) and plankton (DIETRICH and KALLE, 1957). Later investigations confirmed that most of the marine bacteria and fungi, as well as some of the blue-green algae, live on or in the seston—bacteria especially on organogenous detritus or on minerogenous particles—while lower fungi prefer living phyto- and zooplankton. This fact can be explained by the assumption that micro-organisms find much better nutrient conditions on the suspended material than in the surrounding sea water. Heterotrophic bacteria and fungi can feed directly on organic material, or, in an indirect way, on inorganic or organic nutrients adsorbed to inorganic particles. Therefore the concentration of nutrients is much higher on particulate matter than in the surrounding water. In the open oceans, the low concentration of organic nutrients is mostly the limiting factor for bacterial growth. It is only on the tripton particles that bacteria have a chance to find enough nutrients for multiplication. Therefore, bacterial counts are often directly proportional to the tripton content of the water.

Furthermore, relations between turbidity and the factors light and radiation can be of some importance for microbial life in the sea. The depth of the euphotic zone, and therefore the distribution of the blue-green algae as well as of higher green plants, depends on turbidity. But turbidity may also prevent or reduce detrimental effects of light on non-pigmented bacteria (see also Chapters 2 and 11).

The effects of turbidity on micro-organisms are much more complex in coastal waters—especially in estuaries with high turbidity maxima—than in the open oceans. Periodically changing water movements may cause sedimentation and resuspension of detritus as well as of micro-organisms. In calm waters sedimentation prevails; this may cause a sudden decrease of bacterial counts obtained in sewage or river water flowing into the sea.

#### (2) Functional Responses

##### (a) *Tolerance*

Turbidity extremes do not seem to limit the existence of bacteria and fungi directly. Our present knowledge indicates that practically all known species of

these groups may exist indefinitely in waters with either high or low turbidity. Only a few of them will grow well in waters with extremely low turbidity, because they require a certain minimum concentration of floating particles. Below this minimum, substrate density for potential attachment and nutrient conditions is insufficient. Some blue-green algae may suffer from lack of light under conditions of maximum turbidity. Exact, detailed data on tolerance are still lacking.

(b) *Metabolism and Activity*

The relations between turbidity and availability of nutrients are of great importance for the life and activity of bacteria in oceans and coastal waters. The concentrations of dissolved organic nutrients, such as proteins, amino acids, carbohydrates, etc., seem to be too low for bacterial growth in wide parts of the open oceans. The same holds true for inorganic nutrients, such as ammonia, nitrate and phosphate. Under these conditions higher bacterial activity is only possible on detritus particles. According to ZOBELL (1946), solid surfaces promote activities of bacteria in dilute nutrient solutions primarily by absorbing organic matter. Glass and other inert solids may absorb quantities from 2 to 27% of the organic matter contained in sea water. By such adsorptive concentration of nutrients, solid surfaces enable bacteria to develop in media otherwise too dilute for growth. Solid surfaces retard the diffusion away from bacteria of exoenzymes and partially digested food. Large molecules of organic matter must be converted into soluble substances by bacterial exoenzymes before the food can be assimilated. Consequently, in a dilute solution such as sea water, free floating bacteria may not be able to digest and adsorb enough nutrient to provide for their organic requirements. However, when the bacterial cells and organic nutrients are juxtaposed on solid surfaces, the bacteria may absorb more effectively food which has been rendered soluble by the exoenzymes. Anchored bacteria are less influenced by molecular bombardment (with the resultant Brownian movement and diffusion) tending to separate them from their exoenzymes and hydrolyzates. Furthermore, solid surfaces probably facilitate the orientation of exoenzymes in the most advantageous position, thereby increasing their stability and activity.

'The beneficial effects of solid surfaces in dilute nutrient solutions help to explain why marine bacteria generally occur intimately associated with solid particles' (ZOBELL, 1946).

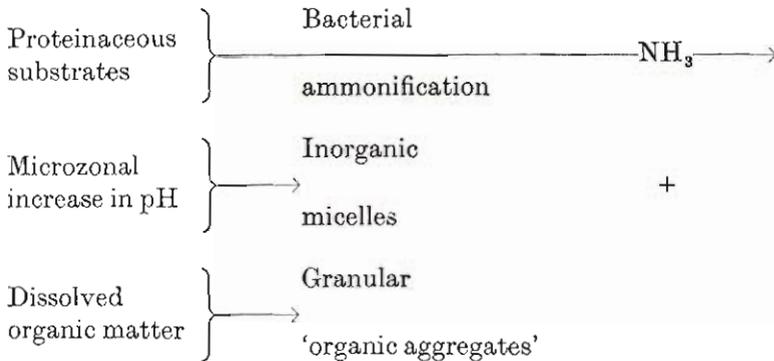
According to KROGH (1934), sea water contains from 4 to 5 mg of total organic matter per litre. Generally, 10% of this may be found in particles. RILEY (1963) observed that

'much of the non-living particulate organic matter in sea water consists of delicate, plate-like aggregates ranging in size from 5  $\mu$  to several mm in diameter. The aggregates are amorphous matrices containing both organic and inorganic materials with inclusion of bacteria and phytoplankton'.

They appear to be formed by adsorption of dissolved organic matter, for example on bubbles and other naturally occurring surfaces, in the sea. RILEY and co-authors (1964) concluded from their observations and supporting experimental data that

dissolved organic matter secreted by phytoplankton is readily converted into solids via adsorption by near surface bubbles. They found that in tropical and subtropical waters of the North Atlantic Ocean such organic aggregates have a carbon content greatly exceeding that of living phytoplankton. These aggregates provide a substrate for bacterial growth; they will be altered by bacterial activity. Therefore, they have at least the same importance for bacterial life in the ocean as have dead plankton and parts of other organisms.

In Narragansett Bay, Rhode Island, USA, SIEBURTH (1968) found (besides these flake or sheet-folded aggregates presumably formed by bubble action) another, more granular type. When adding sodium hydroxide or ammonium hydroxide solutions to sea water, loose amorphous micelles of calcium carbonate and magnesium hydroxide are formed. Such inorganic micelles are similar in size, structure and acid solubility to the granular-type micelles; these micelles adsorb dissolved organic matter and apparently concentrate them, within relatively short periods of time,  $100 \times$  more than in the suspending water. The loose flocculent layer of amorphous material at the water sediment interface may also be similar. At least part of the organic aggregate fraction seems to be composed of inorganic micelles brought out of solution by bacterial activities. DREW (1914) demonstrated that marine bacteria can precipitate calcium carbonate. The precipitation and concentration of calcium and magnesium by a marine bacterium (GREENFIELD, 1963) is believed to be due to precipitation by ammonia and selective adsorption by the cell surface (CARROLL and co-authors, 1965). SIEBURTH's studies have shown that 'organic aggregates'—like precipitates—can be formed by mixed cultures in sea water enriched with peptone or casein, but not with glucose and ammonium chloride (SIEBURTH, 1965). The following hypothetical mechanism for the formation of granular type 'organic aggregates' by bacteria has been suggested by SIEBURTH (1968):



The formation of organic aggregates and their enlargement by further adsorption of organic compounds may be one of the reasons why, in large parts of the open oceans, the concentration of dissolved nutrients is too low for bacterial growth. As a consequence, nearly all bacteria can be found attached to particulate matter.

Turbidity influences microbial metabolism and activities not only in waters with extremely low nutrient concentrations. In some coastal waters, nutrient conditions for bacteria are, according to ZOBELL (1946), better on particles than in the surrounding water. Therefore, the solid surface effect (p. 1168) can be observed in all

parts of the seas, with the possible exception of badly polluted harbours and bays. In the harbour of Naples (Italy), JANNASCH (1955) found free-living bacteria but no micro-organisms attached to particles, while in the Gulf of Naples 0.002% and in the open Mediterranean 34% of total bacteria were attached to particulate matter. However, RHEINHEIMER (1965) observed considerable numbers of attached bacteria even in the most polluted parts of the Elbe estuary (Germany). Many bacteria are living here on organic particles from excrements, paper, plant and animal fibres, etc. ZOBELL (1946) and WOOD (1965) stress that organic contents of water are among the most important factors influencing the distribution and activity of bacteria in the sea. Increases in the availability of organic nutrients are almost always accompanied by increasing bacterial growth. The low concentration of organic matter in the water of the open sea and the lack of enough particles to concentrate the bacterial nutrients are believed to be the principal factors which account for the extremely low bacterial activities in the open sea. However, an increase of turbidity generally will cause an increase in the availability of nutrients and in consequence increasing bacterial populations. Future attention should be focused, more than in the past, on the relations between turbidity and bacterial activity in the sea. The particulate matter not only improves the nutritional conditions for microbes but, possibly, tends also to inactivate bactericidal substances.

Under conditions of high nutrient concentrations—especially in polluted coastal waters—turbidity may also influence the availability of oxygen. JANNASCH (1960) concluded from experiments with *Pseudomonas stutzeri* that anaerobic microzones with possible denitrification may be formed around particles with dense bacterial populations, even in waters with relatively high oxygen saturation.

#### (c) *Reproduction*

ZOBELL and ANDERSON (1936) have pointed out that, in dilute nutrient solution containing less than 10 mg organic matter per litre, solid surfaces promote the reproduction of bacteria.

In the open oceans, normal reproduction of most bacteria and fungi seems to be possible only if attached to particulate matter, because—as has already been explained—nutrient concentrations in the surrounding free water are extremely low. Bacteria reproduce mainly on detritus particles—some Phycomycetes prefer living on phyto- and zooplankton species. The reproduction of photosynthetic blue-green algae is less dependent on the concentration of particulate matter.

#### (d) *Distribution*

Turbidity is one of the most important factors controlling horizontal and vertical distributions of bacteria and fungi in the oceans. There exist close relations, too, between turbidity and the distribution of blue-green algae; these are particularly evident in estuaries and polluted coastal waters. A significant increase of turbidity in the open oceans and in most coastal waters is very often accompanied by increasing bacteria counts, while a decrease of turbidity generally causes decreasing numbers of bacteria (GILLBRICHT, 1961). This interrelation is sometimes striking

in waters with a halo- or thermocline, where turbidity and bacteria counts may attain maximum values (Fig. 6-4). OPPENHEIMER and JANNASCH (1962) found about 10 times higher values in turbid areas than in clear water in the shallow Redfish Bay near Port Aransas, Texas; they employed direct microscopic methods for enumerating bacterial counts.

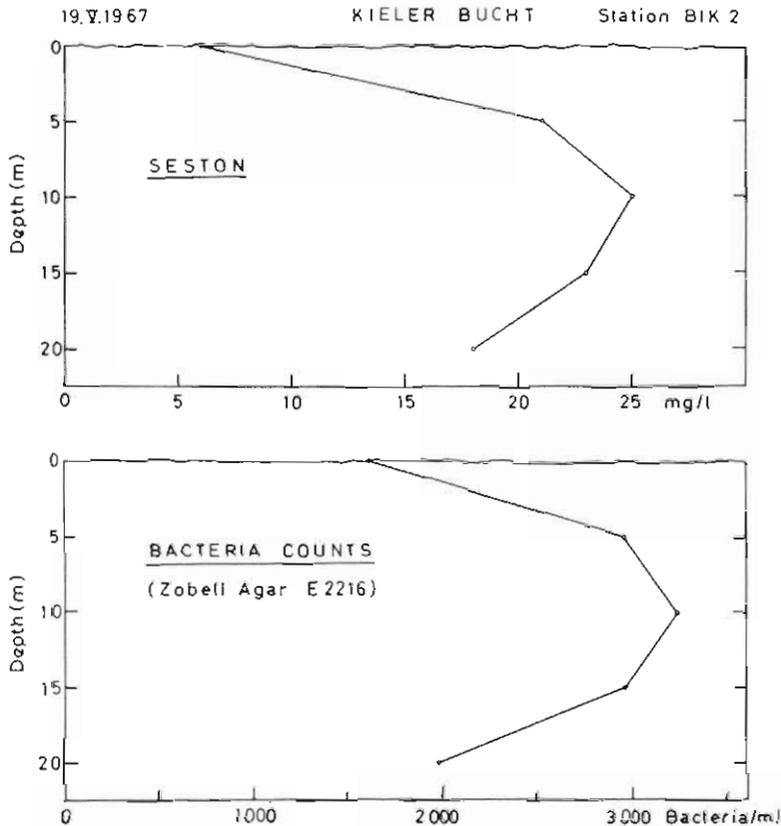


Fig. 6-4: Correlation between seston concentration and bacteria counts in the Kiel Bay (Western Baltic Sea). Above the halo- and thermocline (between 10 and 15 m), both seston concentration and bacterial numbers attain maximum values. (Original.)

Not only the quantity, but also the quality of turbidity influences the distribution of bacteria. The most obvious relations are those between detritus concentration and bacteria counts; changes in the former will mostly be accompanied by parallel changes in the latter. In contrast, increase in living phyto- or zooplankton may cause a reduction in bacterial numbers because of antibiotic production or increased activity of bacteria-feeding organisms. Breakdown of plankton blooms causes a sudden increase in numbers of bacteria and fungi.

Little is known about the influence of colloidal and soluble turbidity fractions on the distribution of micro-organisms (also measured by transparency measurements). In coastal waters, yellow substances may exert considerable influences on

water transparency and distribution of photosynthetic micro-organisms. Very complicated relations between turbidity and distribution of bacteria may be found in estuaries with extensive periodic or aperiodic water movements. According to KOSKE and co-authors (1966), there is a zone of high turbidity maxima in the Elbe estuary (Germany) which is mainly affected by high detritus concentrations—in this zone, the distribution of bacteria is largely a function of tidal variations in sedimentation. Tidal stagnancy causes sedimentation of detritus and bacteria.

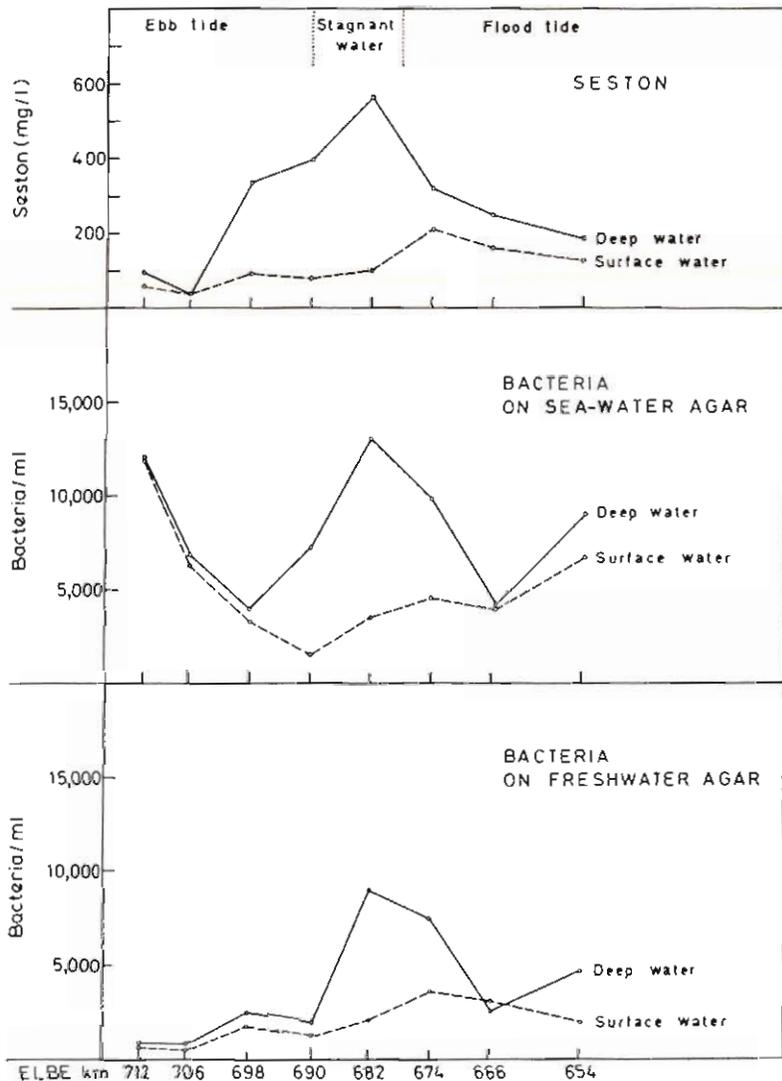


Fig. 6-5: Relations between seston (consisting mainly of detritus) concentration and bacteria counts in the Elbe estuary (Germany) along a profile between Altenbruch (km 712) and Stadersand (km 654). During tidal stagnancy, seston concentration and bacteria counts (obtained both on sea-water and on freshwater agar) increase in the bottom water (1 m above ground). (Original.)

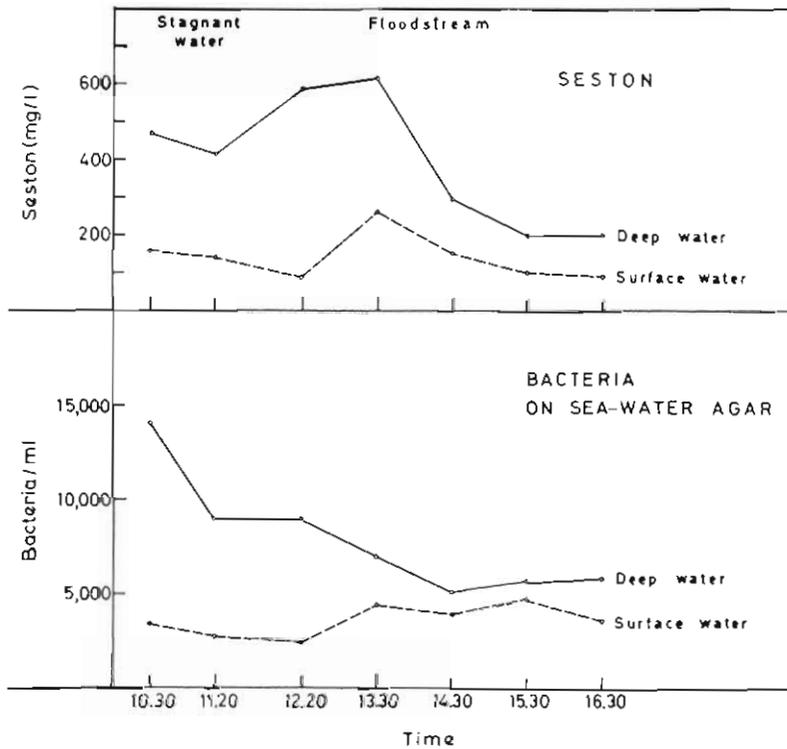


Fig. 6-6: Seston (consisting mainly of detritus) concentration and bacteria counts (obtained on ZOBELL-Agar 2216 E) in surface and bottom water of the Elbe estuary (Scheelenkuhlen, Germany, October 7, 1964, 10.30 to 16.30). With increasing flood stream, differences in seston concentration and bacteria counts in surface and bottom water decrease. (Original.)

Consequently, bacteria counts obtained near the ground of the estuary are much higher than at the surface. With the beginning flood, detritus and bacteria are resuspended again and distributed throughout the whole water column, resulting in little difference between detritus concentration and bacteria counts at the ground and the surface during the time of the strongest water flow (Figs 6-5, 6-6). Microscopical investigations of water samples showed that not only the bacteria move up and down with the detritus particles, but fungi and blue-green algae also (and, of course, other phyto- as well as zooplankton organisms). These periodic, pronounced vertical movements of bacteria, fungi and blue-green algae are restricted to the zone of highest turbidity; they could not be observed in estuary zones with low turbidity (RHEINHEIMER, 1967). In calm waters—for example in wind-protected bays—the turbidity of inflowing rivers quickly decreases due to sedimentation, and there is no periodical resuspension of particulate matter. This is a reason for the sudden decrease of bacteria counts in polluted river water entering the sea. According to ZOBELL (1946), sedimentation is a very important factor, removing bacteria from coastal sea-water areas particularly in places with significant land drainage. In such localities, precipitation and sedimentation of sus-

pended matter are accelerated by flocculation, which occurs when fresh water is mixed with sea water. Presumably, sedimentation is primarily responsible for the localization of sea-water pollution by land drainage, as manifested by the rapidity with which bacterial populations decrease with increasing distance from sewage outfalls and from river mouths. In such places, the bacterial populations decrease much more rapidly than can be accounted for by dilution alone (ZOBELL, 1946).

Of course, the influence of salinity should not be neglected. However, changes in salinity can hardly cause such a sudden disappearance of bacteria as has sometimes been observed in river mouths (Chapter 4.1).

In the open oceans, sedimentation is not the prime cause of the paucity of bacteria. Sedimentation occurs much more slowly here due to a dearth of suspended particles (ZOBELL, 1946). However, sedimentation processes help to explain the vertical distribution of bacteria in the sea. For example, the increase in tur-

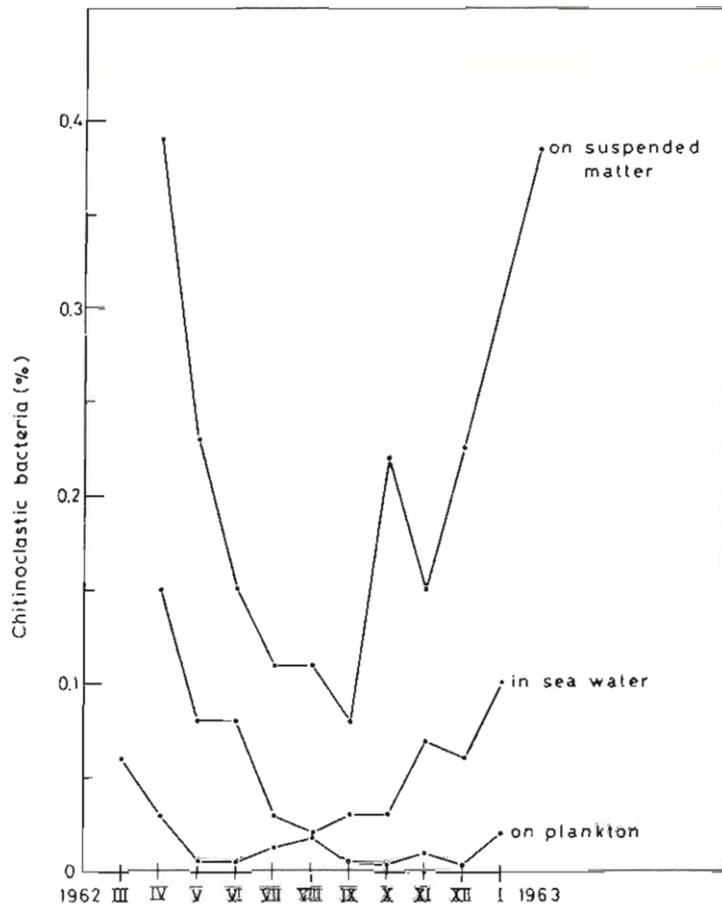


Fig. 6-7: Distribution of chitinoclastic bacteria on suspended matter, in sea water, and on plankton in the Aburatsubo Inlet (Japan). Most chitinoclastic bacteria were found on suspended matter, less in sea water and still less on plankton. (After SEKI and TAGA, 1963; modified).

bidity and bacteria at a halo- or thermocline (p. 1171) seems to be caused by an accumulation of sedimenting seston particles, which are unable to penetrate below the zone of higher water density.

Turbidity not only influences the distribution but also the species composition of the bacterial flora. In the Aburatsubo Inlet (Japan), SEKI and TAGA (1963) found more chitinoclastic bacteria (5 species of the genus *Beneckeia*) on suspended matter than on plankton and in the open sea water (Fig. 6-7). Quality and composition of turbidity, especially of its detritus fraction, may be expected to exert great influence on the composition of bacterial populations; however, there is hardly any pertinent information available as yet.

### (3) Structural Responses

Turbidity may affect size and shape of bacteria indirectly via changes in the relations between turbidity and nutrient conditions. In the open Mediterranean Sea, 52% of the total bacteria counts (direct microscopical enumeration on membrane filters) are cocci below  $1\ \mu$  in diameter, in the Gulf of Naples (Italy) 14% and in the highly polluted harbour of Naples only 0.09% (JANNASCH, 1955). On the other hand, in the open Mediterranean there are no rods larger than  $2\ \mu$ , while in the Gulf there are 35% and in the harbour 96% of the total bacteria counts. OPPENHEIMER and JANNASCH (1962) found, in shallow bays near Port Aransas, Texas, 90.9% to 99.5% cocci while in the sediments of the bays, rod-shaped bacteria were predominating. JANNASCH (1955) and RHEINHEIMER (1965) report that several bacteria species (*Bacillus subtilis*, *Proteus vulgaris*, *Pseudomonas fluorescens* and *Sarcina lutea*) are smaller in waters containing low nutrient concentrations than in those with high nutrient concentrations. In media with an extremely poor nutrient supply, *Bacillus subtilis* and *Proteus vulgaris* (*Bacterium vulgare*) grow smaller and smaller until they represent tiny coccoid cells ('Kümmerformen'); these are able to grow to normal shaped rods again if supplied with sufficient nutrients.

In great parts of the open oceans, many of the free-living bacteria are probably too small to be recognized, even if the best light microscope equipment is used. They are generally coccoid cells with diameters considerably below  $1\ \mu$ . Bacterial cells of normal size and shape—for example rod- and vibrio-forms of  $1\ \mu$  length or more—may be found only if attached to particulate matter, due to the more favourable nutrient conditions. Not only in the open oceans but also in many coastal waters is it difficult to find normal-sized bacteria unless they are attached to particles. In the Baltic Sea, for example, the greater part of the free-living bacteria seems to consist of tiny coccoid cells, most of which grow to straight or curved rods of normal size under laboratory conditions. Normal-sized and shaped free-living bacteria can be found in large numbers only in more or less polluted waters near the shore, especially in bays or harbours.

No information is available at present on turbidity effects on the size and shape of fungi and blue-green algae.



## 6. TURBIDITY

### 6.2 PLANTS

E. HAGMEIER

#### (1) Introduction

Turbidity influences marine plants primarily by its effect on the degree of light penetration. Direct contacts between floating particles and plants, or absorptive properties of suspended matter changing the content of soluted chemicals, are of secondary importance.

The responses of marine plants to light have been dealt with in Chapter 2.2. Transformation and reduction in intensity of underwater light are largely determined by three factors. Of these, turbidity is the most effective one; the other two factors are absorption by water molecules, and by dissolved substances. Measurements of light extinction or of visibility summarize the effect of these three factors and, therefore, give no detailed picture of turbidity distribution in the seas. However, several authors have provided rather good correlations among the three factors for special conditions and limited sea areas (e.g., POSTMA, 1961; OTTO, 1966).

A more specific criterion for the amount of suspended particles present in the sea is the Tyndall effect, which has been measured on a larger scale during the Swedish Deep-Sea Expedition, and later by GONS (1967). The graphs presented by JERLOV (1953) give an idea about turbidity conditions in different oceans and coastal waters. Numbers and sizes of the suspended particles can be estimated via microscopical analysis after sedimentation (KREY, 1961); however, such a procedure takes a great deal of time and is rather tedious for the operator. A quicker assessment can be obtained by using a Coulter counter (HOBSON, 1967; SHELDON and PARSONS, 1967).

Frequently, only the dry weight of the particulate matter is given as a measure of turbidity in the sea (for methodical details consult BANSE and co-authors, 1963). The data obtained range from some micrograms per litre in the open ocean (HAGMEIER, 1964) to several grams per litre in the Wadden Sea (LÜNEBURG, 1953).

Of special interest for plant life in the seas are details of turbidity distributions: Accumulations in convergence zones and in the proximity of discontinuity layers (LENZ, 1965), annual variations in particle content (BUCHAN and co-authors, 1967), dependence of turbidity in shallow waters on the sea's state of agitation (POSTMA, 1954), and relations between particle content in the water and the amount of sedimentation per unit time (ZERTZSCHEL, 1965). The deepest sediment layers are found near coastal areas with high turbidity, whereas sediment layers on the floor of the open oceans are mostly quite thin (EWING and EWING, 1964).

High turbidity in coastal areas is caused by particles, introduced from the land via rivers and winds, and by increased plankton productivity, due to nutrient

advection from rivers or upwellings. Thus, turbidity in the seas consists of inorganic and organic components; plants may cause turbidity and reduction in the intensity of underwater light by their own productivity.

## (2) Functional Responses

### (a) *Tolerance*

Conclusive observations on tolerance of phytoplankton to varying intensities of turbidity do not seem to exist. However, certain variations in abundance of plant populations in coastal waters may reflect differences in resistance to particle contacts. The responses of benthic marine plants to moving bottom particles such as gravel, sand or silt, and to sedimentation are important for their well-being and have practical consequences for the reclamation of land.

Centric bottom diatoms are able to withstand sediment movements; the valve structure of the cells is strong, but not heavy, and a considerable resistance against unfavourable chemicals has been observed (VON STOSCH, 1956). The diatoms survive in sediments developing  $H_2S$ , and even in the digestive tract of predators.

Another remarkable example of a high degree of tolerance to sedimentation and moving turbidity particles are the eel-grasses (of the genus *Zostera*). They are capable of producing new leaves, if the old ones are damaged or buried, and their roots and rhizomes can even survive in sapropel environments (NIENBURG, 1927).

The glasswort *Salicornia herbacea*, which is important for land reclamation, chokes when the sediment layer burying it becomes too high; it cannot form adventive roots or sprouts (LINKE, 1937). In contrast, the grass *Atropis maritima* compensates for turbidity very effectively (NIENBURG, 1927).

### (b) *Metabolism and Activity*

It is very difficult to assess the effects of turbidity on metabolism and activity of marine plants. There is hardly any pertinent information available. Some shade forms, both planktonic and benthonic, are able to achieve a positive assimilation balance under unfavourable conditions of turbidity. The major effect of turbidity on metabolism and activity acts, no doubt, through changes in light intensity and quality. However, intensive sedimentation could conceivably also affect the exchange process between plant and environment.

High-latitude algae can survive and even grow during long periods of darkness: during winter, when solar radiation is minimal and the sea may be covered with ice (KANWISHER, 1966; LÜNING, 1968). Under such circumstances, the plants reduce their respiration and live on reserve products accumulated during the summer. Reduction of metabolic rates in resting spores is also an adaptation for passing unfavourable conditions, frequently caused by high turbidity.

In temperate regions, the bloom of dinoflagellate and diatom populations during the summer months—especially in species with high light-saturation values—appears to be a response both to rising amounts of incoming radiation and to a reduction of turbidity. For further information on responses of plants to light consult Chapter 2.2.

Locomotory responses to turbidity have been reported for bottom-living diatoms. These unicellular plants are able to maintain their position between shifting sediment particles, and to penetrate through the sediment.

Many centric diatoms can excrete gelatinous substances which enable them to stick to other cells or to sand particles (VON STOSCH, 1956). Through this activity, small mats are formed which are not turned over during times of normal water movement and hence may modify the substrate characteristics. Under optimal conditions, the diatoms can develop dense populations, which cover large bottom areas.

A well-defined community of pennate diatoms exists in tidal zones. The members of this community are able to move about quite swiftly; observations and experiments about this phenomenon have been published by ALEEM (1950), FAURÉ-FREMIET (1951), CALLOME and DEBYSER (1954), WOHLBERG (1954), NULTSCH (1962) and others. Velocities of locomotion range between 15 and 25  $\mu$ /sec. Because of their ability to penetrate freshly fallen silt and to form protective layers on sediment surfaces, bottom diatoms are of importance as 'pioneers' in reducing substrate movements and in land reclamation (see also Chapters 5 and 7).

#### (c) *Reproduction*

Definite, detailed relations between turbidity and rate or mode of reproduction of marine plants have not yet been established. As to benthonic plants, CONOVER (1964) mentions the widespread reproductive sterility of sea-grasses and algae in Texas lagoons and ascribes this to heavy turbidity: clay particles tend to filter out light wavelengths which have been shown to be essential for the development of normal reproductive organs in terrestrial plants.

According to VON STOSCH (1956), certain centric diatoms reproduce only vegetatively during their life at the sea bottom; sexual reproduction occurs when the cells are stirred up and become planktonic. Whether increased light intensities or a direct influence of turbidity particles is involved, has not yet been explored.

#### (d) *Distribution*

Turbidity may also modify distributional patterns relative to space and time both in phytoplankton and phytobenthos. However, no detailed evidence is available from literature.

Maximum depths for algal growth, recorded for different coasts (GESSNER, 1955, p. 43), reflect parallel differences in water turbidity. LEWIS (1964) mentions that *Himantidium loveni* is absent from the more turbid eastern part of the English Channel (see also Chapter 6.3).

When assessing observations on horizontal and vertical distributions of algae, one should take into consideration the kind of substratum (Chapter 7.2); in addition, competition between co-existing species can also be a decisive factor. Finally, in littoral areas, the duration of exposure to air strongly influences the distribution of benthonic algae (Chapter 4.2). In most cases, it is impossible to decide on the grounds of purely observational evidence which of the environmental factors involved is of primary ecological importance.

### (3) Structural Responses

No conclusive papers reporting direct effects of different intensities of turbidity on structural aspects in marine plants have come to the reviewer's attention.

Among the centric diatoms, *Aulacodiscus* sp. wears on its cell surface large ribs of a foamy texture (VON STOSCH, 1956). Such structural peculiarities may explain the astonishing fact observed by STEELE and BAIRD (1968) that a considerable amount of primary productivity can be maintained in the shallow waters of a beach where wave action effectively stirs up the upper sand layer.

Most pennate diatoms possess a raphe, a slit in their valve, through which the plasma can achieve contact with the surrounding medium and thereby initiate locomotion of the whole cell. This locomotory mechanism seems not yet fully explored (NULTSCH, 1962); it represents a structural adjustment to life in motile substrates and is, no doubt, of great ecological importance.

The arrangement and stability of the fibres in leaves of eel-grass species provide the necessary strength and elasticity to endure particle contacts and wave action (SCULTHORPE, 1967).

There is great need for detailed experiments under controlled conditions in order to assess more clearly the possible responses of marine plants to different intensities of turbidity.

## 6. TURBIDITY

### 6.3 ANIMALS

C. G. WILBER

#### (1) Introduction

Information concerning the effects of turbidity and of suspended solid material on fish, shellfish, or fish food in marine waters is highly controversial. The amount of reliable material is limited. Some results suggest that concentrations of suspended matter in the region of 200 ppm damage the gills of fish; higher concentrations are said to inhibit feeding activity of fish. Whether these data have any realistic application to estuarine or migratory fish is not clear. Under many conditions in unpolluted estuaries, turbidity may run from 200 to 5000 ppm, while thriving salmon fisheries are supported in addition to significant populations of marine fish and shellfish. These contradictory pieces of evidence suggest that much more investigation is essential before hard and final conclusions can be made concerning the biological effects of turbidity on marine animals.

#### (2) Functional Responses

##### (a) *Tolerance*

SLANINA (1962) studied the effect of mineral suspended solids on fish. He exposed rainbow trout *Salmo gairdnerii* to concentrations of mineral solids varying from 1 to 100 g/l for up to 8 days. The results indicated that this species can survive in concentrations of suspended solids up to 100 g/l without any visible effects. These fish also survived apparently when kept in concentrations as high as 300 g/l; a histological examination of the tissues indicated that there was an increase in 'mucilagization' in the gill lamellae with increased concentration of suspended mineral solids. Proliferation of epithelial cells of the gills was apparent in concentrations as low as 20 g/l. What these threshold changes mean in the overall biology in the species is not known. However, the data do suggest that relatively low concentrations of suspended solids may bring about changes in structure, and possibly function, of important tissues of fish.

In a review of the effects of inorganic sediment on aquatic life of streams, CORDONE and KELLEY (1961) write:

'There is abundant evidence that sediment is detrimental to aquatic life in salmon and trout streams. The adult fishes themselves can apparently stand normal high concentrations without harm, but deposition of sediments on the bottom of the stream will reduce the survival of eggs and alevins, reduce aquatic insect fauna, and destroy needed shelter. There can scarcely be any doubt that prolonged turbidity of any great degree is also harmful.'

The UNITED STATES GEOLOGICAL SURVEY (1964) has supported studies dealing with the biological effects of suspended sediment on rainbow trout *Salmo gairdnerii* and cutthroat trout *Salmo clarkii* eggs: Sediment settling into a redd or spawning ground caused decreases in the permeability of the gravel and the velocity of the interstitial water movement. When the suspended sediment passing over a redd reached an accumulated total of 60 or more tons, the seepage velocity showed a perceptible decrease. As the accumulated total suspended-sediment load increased progressively beyond this level, there was a corresponding decrease in the seepage velocity. Redds exposed to an accumulated load of 290 tons of suspended sediment had the highest egg mortality; redds with the lowest suspended-sediment load, highest seepage velocity, and the highest dissolved oxygen concentration had the greatest egg survival.

A review of the literature clearly demonstrates that much of the experimental and observational work dealing with the effects of turbidity and of suspended solid materials on aquatic animals has been devoted to fresh waters; broader insight into turbidity effects on marine animals may be obtained by reference to a number of these investigations. HERBERT and MERKENS (1961) made an experimental study of the effect of suspended mineral solids on the survival of trout. They devised a special aquarium which would maintain solids in suspension. For the solid material they used commercial grades of kaolin and diatomaceous earth. The concentrations studied varied from 0 to 810 ppm of suspended solids. The test species used was the rainbow trout *Salmo gairdnerii* RICHARDSON. The results of these studies indicate that there is no difference in harmful effects between kaolin and diatomaceous earth. A concentration of 30 ppm suspended solids shows no difference in survival time as compared with controls. However, concentrations of 90 ppm cause some mortality, suggesting that—under conditions of these experiments—90 ppm suspended solids seem to have an adverse effect. There is no question that suspended solids are harmful to the rainbow trout in concentrations of 270 ppm or higher. Trout kept for some weeks in the higher concentrations of solids are almost white in colour.

Despite the fact that high concentrations of suspended solids have a lethal effect on rainbow trout, there is no evidence that suspended solids modify growth rates of trout which survive in a given critical concentration. The observational data do not permit the construction of a dose response curve. It seems evident that survival chances for an individual trout are less in an environment containing 90 to 810 ppm suspended solids than for trout in cleaner waters. The action of the solids appears in most part to potentiate the effects of other adverse environmental factor intensities. Reviewing turbidity effects on freshwater fishes, OOSTEN (1949) concludes that average turbidities up to at least 200 ppm of silica are virtually harmless. On the other hand, KEMP (1949) maintains that pollution of the Potomac River Basin (USA) by soil is dangerous to fish when turbidities of 3000 ppm are maintained for a period of 10 days. It is interesting to note that in the Potomac River Basin turbidities have risen as high as 6000 ppm. It has also been suggested that turbidities as high as 245 ppm may not be harmful to fish—quite to the contrary, they have been postulated as being helpful in protecting fish from predators (WARD, 1938a, b).

A comprehensive study was made on the effects of artificially induced turbidity,

using 16 species of freshwater fish (WALLEN, 1951). The average fatal turbidity, expressed in mg montmorillonite clay per litre (units), varied from about 40,000 for the rock bass *Ambloplites rupestris* exposed for  $3\frac{1}{2}$  days, to over 200,000 for the black bullhead *Ictalurus melas* exposed for an average of 17 days. At turbidities causing death, opercular cavities were found to be matted with soil, and gills had a layer of soil on them. Symptoms of distress generally appeared at turbidities much lower than those producing death. Harmful effects were observed as the turbidity approached 20,000 units (McKEE and WOLF, 1963).

Reports on the effects of turbidity on shellfish cultures are confusing and sometimes contradictory. It has been maintained that excessive turbidity inhibits the feeding mechanisms of oysters and freshwater mussels, and that this, in turn, restricts the growth of the affected organisms (COKER and co-authors, 1919). According to other information, an increase in turbidity of the water surrounding dredging operations does not increase the mortality of oysters (LUNZ, 1938). It has also been said that some oysters live and reproduce successfully in waters which carry rather large amounts of silt and clay (LOOSANOFF and TOMMERS, 1948). KORRINGA (1952), on the other hand, found that silt and other substances which produce turbidity, e.g. kaolin or chalk, at concentrations as low as 0.1 mg/l bring about a reduction in the rate of water pumping by oysters.

GUNTER (1953) surveyed the effect of the Bonnet Carre Spillway on oyster beds in the Mississippi Sound (USA). In 1950, for example, the spillway was operated for 38 days with a total discharge of over 14,000,000,000 m<sup>3</sup>. The average depth of fill in the spillway was 13.7 cm; the total fill was 3,828,000 m<sup>3</sup>. The sediment is reported to settle out in a fan-like area at the mouth of the floodway, covering an area of about 77.66 km<sup>2</sup>; this area is about 5% of the total bottom of Lake Pontchartrain into which the spillway opens. In the spillway the concentration of suspended material is slightly over 1000 ppm; on the lake side the turbidity drops to 400 ppm or less. As the flood of water moves into Lake Pontchartrain, the velocity drops to zero within a few miles. All but the very finest particles fall out of suspension; these remain suspended for an indefinite period of time. There has been much concern that these periodic deluges of silt may have harmful effects on the lake as an environment for economically important aquatic organisms; but GUNTER says: 'There is no proof that this environment is hurt.' He further maintains that oysters living in areas where they will not bury themselves in their own faeces are not bothered by ordinary sediment. This may be true in general.

GUNTER (1953) does, however, admit that in Lake Pontchartrain (USA) motile marine organisms are chased out into Lake Borgne and beyond and that certain non-motile forms are killed. A small area of the bottom of Lake Pontchartrain is covered with a mud deposit. No deposit of mud or silt affects any beds or bottoms of Mississippi Sound and adjacent waters following spillway openings. Most mud and silt is deposited in the floodway proper and in Lake Pontchartrain.

In years of heavy spillway discharge, about 100% of the oysters in Mississippi Sound west of Bay St. Louis are killed. Except for one major seed bed (Grand Bank, in the western Sound) the oysters in this region are of little economic importance. East of that line to Pass Christian, mortality is about 50%; in the northern Louisiana Marsh, it ranges up to 100% but is considerably less southward (GUNTER, 1953).

*(b) Metabolism and Activity*

In most filter-feeders, rates of feeding are not dependent upon the degree of turbidity below certain levels. However, if turbidity becomes too great, clogging of filters with particles will reduce feeding rates. On the other hand, certain filter feeders apparently transport water through their bodies at a rate which depends on the concentration of suspended particles. The problem has recently been reviewed by JØRGENSEN (1966).

The silt, which is always found in connection with turbid waters, may harm animals not usually exposed to it, by hindering their settlement or by clogging feeding mechanisms. Absence of silt from coastal rapids accounts—as do effective settlement and favourable feeding conditions—for the rich marine faunas usually found in such areas (LEWIS, 1964).

LOOSANOFF and TOMMERS (1948) studied the effect of suspended solid material on feeding rates of oysters. They measured the rate of water pumping and the pattern of shell movement using a kymograph. Oysters were exposed to concentrations of turbidity-causing substances ranging from 0.1 to 4.0 g/l. The substances used included Fuller's earth, silt, kaolin and calcium carbonate. Even relatively small quantities of suspended material resulted in a decrease of pumping rate. In turbid water equal to 0.1 g silt/l there was an average reduction in pumping rate of 57%; at 1 g/l reduction increased to 80% and at 3 or 4 g/l to about 94%. Kymograph records indicated that there was a change in amplitude and pattern of shell movements in oysters kept in turbid water. Oysters previously exposed even to the highest concentrations of suspended material recovered very quickly when returned to clear sea water; in most instances there was an overshoot in pumping rate for a period of time during recovery. On the basis of these experiments, LOOSANOFF and TOMMERS concluded that oysters are very sensitive to suspended silt and other substances and that a correlation exists between increase in concentration of such substances and decrease in pumping rate. Very high concentrations may inhibit pumping completely. The relations between concentration of food organisms and filtering rates have recently been studied and reviewed by WINTER (1969) in *Arctica islandica* and *Modiolus modiolus*.

Dead and dying adult oysters found in turbid waters invariably contain large amounts of silt in their gills (LOOSANOFF, 1961). Although oysters will continue to feed in relatively turbid waters, feeding efficiency is greater in less turbid environments. KORRINGA (1952) concluded that killing of oysters during winter was greatest in rough weather and in turbid waters; apparently oysters exposed to cold are unable to clear their gills of silt and hence die (see also Chapter 3.31).

A number of animals have developed specialized structures which protect them against excessive amounts of silt. Some of these species even seem to thrive in waters which are very turbid. NEEDHAM and LLOYD (1930) have described some of these protective structures.

Water turbidity may also affect activity patterns and behaviour of marine animals. Changes in behaviour due to turbidity have been reported for several species of fishes; they may be of considerable economic importance. Thus certain kinds of trap nets seem to catch best during stormy weather (salmon and eel trap

nets in the Baltic Sea). Catches by gill net are said to be higher in turbid waters after storms. However, fishing grounds and catches of smaller pelagic fish, such as herring, can be drastically changed during and after storms (HELA and LAEVASTU, 1961). Gill nets and some types of trap nets are more effective in turbid water; long-lining for fish such as tuna is much more effective in clear water. The catch of albacore *Germa alalunga*, taken by gill net on the surface, for example, may be significantly affected by water transparency. There is every possibility that water clarity may be an important ecological and behavioural factor in the oceans in that the efficiency of sight feeders will be reduced as turbidity increases (see also Chapter 2.3).

Knowledge of sea-water turbidity has a practical value for commercial fishermen. The number of *Germa alalunga* taken by gill-netting or by surface trolling varies as a function of turbidity. In clear water trolling is more efficient than in turbid water. This relation may be expressed as  $Y = 17.25 - 114.64x$ ;  $r = -0.738$ ,  $P < 0.01$ ; where  $Y$  is the troll catch and  $x$  the extinction coefficient, which increases with increasing turbidity. Gill nets are more efficient in turbid water. This situation may be expressed as  $Y = 335.9x - 0.66$ ;  $r = 0.37$ ,  $P > 0.05$ ; where  $Y$  is gill net catch and  $x$  the extinction coefficient. The relation between troll catch and gill net catch has been expressed as follows:

$$\frac{\text{Troll} \times 100}{\text{Gill Net}} = 0.0000394 \left( \frac{1.7}{\text{extinction coefficient}} \right) 4.55$$

The increased troll efficiency is a power function of the change in water clarity (Chapter 2.32). Since the theoretical maximum power function of troll catches alone is about 3, the residual of 1.55 may be associated with the reverse effect that water clarity has on the catching efficiency of the gill net (MURPHY, 1959).

### (c) Reproduction

There are some 9000 species of marine invertebrates with free swimming larvae, which spend a significant portion of their life influenced by light (Chapter 2.31). Studies indicate that 82% of the pelagic larvae of these species are photopositive in their reaction; they tend to migrate toward the water surface in response to light; 12% of these species have larvae which do not react to light; 6% of the larvae are photonegative. Most pelagic larvae in their sensitive stages, i.e., when they are most pronouncedly photopositive, show a preference for a diffuse light which is not of too high an intensity. Larvae in a pronouncedly photonegative stage may become strongly photopositive after being in darkness for a long period of time. Whether total darkness is essential for this change is not clear. It might be that long exposure to reduced light intensity, caused by increased turbidity, may also trigger such a response.

To a certain extent, some turbidity in the water in which larvae are living during metamorphosis may be desirable. It is well known that ultra-violet light is lethal to gametes and larvae (Chapter 2). Some turbidity would serve as a shield to protect these organisms from the injurious effects of ultra-violet radiation. It is known further that adult populations of intertidal animals seem to prefer shaded areas. It seems clear, therefore, that a certain amount of turbidity in marine environments

is favourable for the development of eggs and larvae and for the thriving of intertidal organisms (THORSON, 1964).

The settling of turbid material to the bottom of a body of water may prevent effective attachment of molluscan spat, a situation which would result in decreased reproductive rates of the species. Apparently a layer of settled material, only 1 or 2 mm thick, is sufficient to prevent satisfactory oyster 'sets' (GALTSOFF, 1964). The settlement of turbid materials on oyster grounds in Delaware Bay (USA) may in part account for the rapid disappearance of the oyster from that area.

A study was made by HARRISON and FARINA (1965) in which three species of pulmonate snails (*Bulinus globosus*, *Biomphalaria pfefferi* and *Lymnaea natalensis*) were used to evaluate the effect of naturally turbid water on reproduction and breeding in fresh water. The turbidity was caused by kaolin mixed with illite or sericite or both. In one series of experiments snails were exposed to turbid water while they were laying eggs. The water contained 360 mg of suspended solids per litre; the egg capsules swelled up and the embryos died. In one of the species, no eggs were laid once the snails were exposed to turbid water. After the water was centrifuged clear of suspended material, capsules and embryos remained normal. A second series of experiments used water which contained 190 mg of suspended solids per litre. In this water, capsules tended to be slightly distorted, and some embryos died in 3 to 7 days. In one of the species, the capsules showed only a slight distortion with normal development of the embryos. In all cases, if the water was first centrifuged clear, embryos were normal as were the egg capsules.

The snail *Lymnaea natalensis* showed no adverse reaction to the most turbid water used; obviously adults of this species have an unusual resistance to the effects of turbidity; however, reproduction was severely reduced. It is easily seen, therefore, that environmental turbidity, which may not directly kill adult individuals, could quickly eradicate a species by preventing satisfactory reproduction.

Eggs and larvae of oysters are sensitive to suspended material in the water. A concentration of 0.25 g silt/l results in a reduction of egg survival to 73% of that of controls held in clear water. If the oyster eggs are kept in a silt concentration of 0.5 g/l, about 30% of the eggs survive and undergo development; in 1 or 2 g/l virtually 100% of the eggs perish (LOOSANOFF, 1965). Adverse effects on growth are observed at a concentration of 0.75 g/l; if the concentration is 1.5 g/l or greater, virtually no growth occurs in the larvae; none of the larvae reach metamorphosis in concentrations of 3 or 4 g silt/l. Recent experiments by LOOSANOFF (1965) have suggested that the sizes and shapes of turbidity-creating particles are important in regard to the degree of damage they cause to eggs and larvae.

LOOSANOFF (1961) and DAVIS (1960) have studied the effects of experimentally produced turbidity on the developing eggs of the oyster *Crassostrea virginica* and the clam *Mercenaria (Venus) mercenaria*. Small amounts of suspended material stimulated motion of the larvae. As a rule, oyster eggs are more readily harmed by excessive silt than clam eggs. In 0.25 g silt/l, about 73% of the oyster eggs survived whereas well over 95% of the clam eggs developed to the 'straight hinge stage'; in water containing 0.5 g silt/l all clam eggs developed while only 31% of the oyster eggs survived (DAVIS, 1960).

In turbidity caused by kaolin or Fuller's earth, eggs of *Crassostrea virginica* survived better than eggs of *Mercenaria mercenaria*. In water containing about 1.0 g

of kaolin or Fuller's earth per litre, virtually all *C. virginica* eggs developed to the 'straight hinge stage' whereas only 37% of *M. mercenaria* eggs in kaolin and 57% in Fuller's earth survived. Despite the fact that some *M. mercenaria* eggs may develop normally in turbidities of 4.0 g/l of clay, chalk, or Fuller's earth, the percentage of eggs showing normal development varies inversely with the degree of turbidity.

Many marine fish species spawn in freshwater streams. A most critical period in the life history of a fish is during the egg and larval stages. Critical intensities of turbidity in the waters surrounding these developmental stages could have profound effects on the future of the population. Some developing fish eggs accumulate a heavy coating of sediment if held in turbid water (STUART, 1953; KINNE and ROSENTHAL, 1967). Many of these eggs do not hatch. Fish larvae also show greater than normal mortality in heavily turbid waters.

#### (d) Distribution

It was pointed out many years ago that one of the major effects of excessive turbidity in estuarine areas is to eliminate economically important shellfish. It is known, for example, that oyster beds of the upper Chesapeake Bay (USA) are disappearing wherever excessive quantities of sediment from tributary streams accumulate on the floor of the Bay. Oysters require hard rock, shell, or sand bottoms; muddy bottoms and oysters seem to be incompatible. Where oozy silt, washed in from the eroding farmlands which drain into the Bay, covers the bottom, oysters suffer or die (BENNETT, 1946).

Sheltered bays often have a varied population of marine organisms as a result of reduced wave action. Along open coasts, fresh water and sediment, brought to the ocean from streams, are dispersed readily. However, in enclosed arms of the sea such as bays and the like, even a small stream can exert a relatively great influence on salinity and turbidity of the enclosed body of water. This situation results from the fact that water movement (Chapter 5) is relatively weak (LEWIS, 1964). Most sheltered shores suffer from an accumulation of silt. A high percentage of animals that inhabit rocks as their usual habitat are filter feeders. Therefore, waters of high turbidity, and the deposition of mud over the individual, tend to eliminate these animals from their habitat.

Bays which are covered with silt usually have turbid waters. Waters of high turbidity are also found along eroding coast lines with a calcareous composition. These characteristics often modify the distribution of animals by inhibiting the penetration of light (Chapter 2) into the water. Variation in penetration of sunlight is especially pronounced in areas with large tidal ranges.

A variety of physico-chemical factors may be acting in concert to limit species distributions; it is suggested, however, that species of the plant genera *Himantalia*, *Bifurcaria* (and perhaps *Alaria*, *Gigartina* and *Rhodymenia*; Chapter 6.2) are affected by light penetration (Chapter 2.0). *Himantalia*, which normally occurs on open coasts, is absent from the more turbid eastern half of the English Channel, but can be luxuriant in extreme shelter elsewhere, provided tidal scours ensure clear water (LEWIS, 1964). Such changes in plant growth may significantly affect the distribution of marine animals. It is important to realize that, in the open ocean

with adequate diffusion currents, many local physical factors are not important in determining the distribution of species. Where wave action is virtually absent, turbidity and silt take on utmost significance.

DOTY (1957) has summarized briefly the relation between turbidity and zonation of marine organisms. He says it has been thought that lower light intensities correlated with increased turbidities were responsible for the upward shift of the subtidal biota toward the heads of fjords and in shallow water. At Durham, New Hampshire, near the head of Great Bay (USA), a heavy load of waste and silt was borne at salinities of about 7‰ as a more or less homogeneous suspension. This suspension became differentiated farther down the bay where the salinity was 14‰, resulting in surface scum and large discrete flocculae beneath the water surface. Below, at salinities of about 22‰, the water was clear with no surface scum, and what appeared to be the flocculae from upstream aggregated into strands in otherwise clear water. At somewhat higher salinities (ca. 28‰), the bay water became clear and devoid of visible suspended matter. Light penetration and bottom characteristics are closely correlated with these phenomena, interpreted as sedimentation and 'salting-out' of colloids (which may be expected in such a strong electrolyte solution as sea water). Only a few photosynthetic organisms exist on the bottoms along the upper reaches of the bay, even where the upper shore areas, exposed by low tide, are heavily populated by marine forms. Turbidity and decrease in salinity may not uniformly be the primary causes of the upward shifts inshore of subtidal forms. In deeper waters, the pH tends to be lower, e.g. 7.5, than at the surface, where it may rise toward 8.2 and higher with intensive photosynthesis rates, or drop below 7 as one passes into an extreme brackish or low-oxygen area (DOTY, 1957).

In a part of the North Sea, a so-called 'turbidity screen' develops each year. This screen forms in conjunction with the pycnocline in summer and covers nearly the entire study area (DIETRICH, 1963). The turbidity screen is located at a depth of 30 to 40 m. It consists of phytoplankton and chlorophyll resulting from the spring-time phytoplankton bloom. The layer provides a rich storehouse of food during the summer season for zooplankton and fish.

Storms cause high turbidity in shallow waters, a condition which restricts the shoreward distribution of certain fish that cannot tolerate turbid conditions (ROBINS, 1957).

### (3) Structural Responses

No structural responses to turbidity are unique to marine animals. Structures developed by a variety of aquatic animals in response to turbidity and sedimentation have been described by NEEDHAM and LLOYD (1930).

#### (a) Size

There are no studies on final body size reached by marine animals in relation to turbidity. Studies on brown trout, *Salmo trutta*, exposed naturally to turbid waters resulting from china-clay wastes, indicate no measurable effects on the length of fish (HERBERT and co-authors, 1961). Estimations of 'condition' or 'plumpness'

(derived from the relation of length to weight) indicate that trout from turbid waters grew normally and apparently found adequate food of the right quality in the environment. Suspended solids from china-clay workings in concentrations of 1000 ppm markedly reduced the abundance of brown trout; suspensions of about 60 ppm had no adverse effect (HERBERT and co-authors, 1961).

(b) *External Structures*

Among fin fish there are no data suggesting that turbidity of the water can bring about a change in external body shape or in structures of the body surface.

Chambering, blisters, and other anomalies of shell structure are known in molluscs; they are probably the result of invasion of the mantle cavity by foreign bodies (GALTSOFF, 1964). Possibly the settlement of suspended particles could be a source of such foreign particles.

(c) *Internal Structures*

Histopathological examination of the gills from trout *Salmo gairdnerii* that died in various concentrations of suspended solids indicates that certain damage to the gills results from exposure to high turbidities. In concentrations as low as 270 ppm of suspended solids, the cells of the epithelial layer of the gills were much thicker than in the controls; in some places there was a fusion of adjacent lamellae; this fusion took place most often at the tips of the gill lamellae. No abnormal gills were observed in fish kept in concentrations of suspended solids lower than 270 ppm. It is important to realize that although some individuals showed damage to the gills when exposed to 270 ppm of diatomaceous earth, not all *S. gairdnerii* were adversely affected in that concentration, even after exposures of 8 months. It was further observed that trout in suspensions of diatomaceous earth of 270 ppm or more suffered a greater incidence and intensity of fin rot than did controls (HERBERT and MERKENS, 1961).

Results of this sort suggest that the turbidities found in the open ocean, or even in most coastal waters, should not be expected to cause anatomical or histological damage to fish. Relatively long exposures to fairly high concentrations of turbidity are needed to cause lesions of the gills.

Too little is known on turbidity effects on internal structures of invertebrate tissues to lend support to histopathological comments at this time.

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# AUTHOR INDEX

*Numbers in italics refer to those pages on which the Author's work is stated in full.*

- ABE, K., 778-780, *1081*  
ABEL, E. F., 1130, 1131, 1137, 1147, *1149*  
ABONYI, A., 983, *1033*  
ACHER, R., 1018, *1033*  
ACKEFORS, H., 822, 954, 974, *1033*  
ADOLPH, E. F., 900, *1033*  
D'AGOSTINO, A. S., 832, 950, 951, *1033, 1071*  
AISENBERG, E. I., 884, *1066*  
ALABASTER, J. S., 1188, *1191*  
ALEEM, A. A., 812, 816, *1033, 1179, 1190*  
ALEXANDER, W. B., 830, *1033*  
ALEXANDROW, W. J., 884, *1066*  
ALLANSON, B. R., 847, *1033*  
ALLEE, W. C., 954, 974, *1033, 1052*  
ALLEN, M. B., 693, 695, 698, *1033*  
ALMAZOV, A. M., 825, 828, *1033, 1034*  
ALTMAN, P. L., 1000, *1034*  
ALTNER, H., 920, *1038*  
AMBERSON, W. R., 876, *1034*  
D'ANCONA, U., 822, *1034*  
ANDERSEN, B., 885, *1034*  
ANDERSON, D. Q., 1170, *1194*  
ANDERSON, J. D., 893, 932, *1034*  
ANDERSON, W. W., 1164, *1190*  
ANDREWARTHA, H. G., 974, *1034*  
ANDREWS, E. A., 975, 977, *1034*  
ANDREWS, W. R. H., 890, 891, 895, *1062*  
ANGINO, E. E., 687, *1034*  
APLEY, M. L., 943, *1073*  
ARBER, A., 707, *1034*  
AREY, L. B., 926, *1034*  
ARMSTRONG, F. A. J., 834, *1082*  
ARNOLD, A., 760, *1034, 1099, 1149*  
ARNOLD, D. C., 941, *1034*  
ARNON, D. I., 698, 747, *1033, 1038*  
ARTOM, C., 983, 994, *1034*  
ARX, W., 1086, *1149*  
ATZ, J., 1015, 1019, *1070*  
AUGENFELD, J. M., 851, *1034*  
AUSTIN, A. P., 1107, 1111, *1149*  
AUSTIN, M., 694, *1070*  
AVENS, A. C., 941, *1034*  
AX, P., 832, 949, *1034*  
AX, R., 832, 949, *1034*  
AYERS, J. C., 988, *1034*  
AYERS, J. L., JR., 835, 939, *1072*  
  
BAALEN, C. VAN, 693, 699, *1034*  
BAARDSETH, E., 1120, *1151*  
BAAS BECKING, L. G. M., 832, *1038*  
  
BACESCU, M., 832, *1070*  
BAGGERMAN, B., 1022-1024, *1034*  
BAILEY, J. E., 998, *1052*  
BAIRD, I. E., 1180, *1193*  
BAKER, S. M., 782, 785, 786, 810, 815, *1034, 1112, 1149*  
BALDWIN, E., 825, *1034*  
BALDWIN, H. L., 1157, *1193*  
BALL, J. N., 1017, 1018, *1034*  
BANSE, K., 969, 977, *1034, 1035, 1178, 1190*  
BARGHOORN, E. S., 691, *1035*  
BARHAM, E. G., 969, *1035*  
BARKMANN, J. J., 810, *1035*  
BARLIOTTI, C., 1113, 1120, *1150*  
BARLOW, G. W., 997, *1035*  
BARNES, H., 686, 825, 851, 852, 859, 862, 875, 895, 920, 973, *1035, 1073, 1086, 1149, 1159, 1190*  
BARNES, M., 851, 852, 862, 920, 973, *1035*  
BARNES, R. S. K., 912, 932, 974, *1035*  
BARR, L., 868, 869, 894, 895, *1049*  
BARY, B. M., 954, *1035*  
BASKINA, V. P., 829, *1036*  
BASSINDALE, R., 830, *1033, 1115, 1149, 1150*  
BATESON, W., 982, *1035*  
BATTAGLIA, B., 833, 841, 842, 890, 893, 912, 974, 975, 977, *1035*  
BATTLE, H. I., 997, 1027, 1029, *1035*  
BAUCH, R., 1108, *1149*  
BAUMBERGER, J. P., 913, *1035*  
BAYER, E., 687, *1036*  
BEADLE, L. C., 868, 871, 872, 885, 895, 899, 904, 913, 921-923, *1036*  
BEAMS, H. W., 1031, *1056*  
BEAUMONT, A. R., 953, *1050*  
BEKLEMISCHEW, V. N., 829, *1036*  
BELDING, H. S., 876, *1082*  
BELIAEV, G. M., 834, 842, 875, 877, 926, *1036, 1037*  
BELLINI, E., 820, *1079*  
BELSKY, M. M., 698, *1049, 1076*  
BENNETT, H. H., 1187, *1190*  
BENTLEY, P. J., 1018, *1036*  
BERGER, E., 864, 870, 886, 895, 917, *1036*  
BERGQUIST, P. L., 730, *1036*  
BERKELEY, C., 699, *1036*  
BERN, H. A., 1017, 1018, *1036*  
BERTHOLD, G., 717, 724, 810, *1036*  
BETHIE, A., 885, 886, 895, 899, 900, 913, 945, *1036*

- BEYER, A., 921, 922, 1037  
 BHAT, J. V., 691, 1037  
 BIALASCEWICZ, K., 886, 889, 913, 1037  
 BIDWELL, R. G. S., 772, 1037  
 BIEBL, R., 707, 708, 710, 711, 714-719, 730, 761, 779, 820, 1037  
 BIELLING, M. C., 695, 701, 1030  
 BILLINGS, G. K., 687, 689, 690, 695, 701, 1034  
 BINYON, J., 894, 1037  
 BIRCH, L. C., 974, 1034  
 BIRSSTEIN, J. A., 834, 1037  
 BLACK, V. S., 885, 1000, 1013, 1037  
 BLACKBURN, M., 969, 1037  
 BLACKER, R. W., 954, 1037  
 BLANDFORD, M. H., 1112, 1149  
 BLAXTER, J. H. S., 997, 1001, 1002, 1012, 1025, 1026, 1028, 1032, 1037, 1052, 1053  
 BLEI, M., 759, 1037  
 BLISS, D. E., 873, 921, 988, 1037  
 BOADEN, P. J., 1141, 1149  
 BOARDMAN, D. L., 945, 1037  
 BOCK, K. J., 875, 1037  
 BÖHNECKE, G., 1086, 1149  
 BÖRGESEN, F., 810, 813, 814, 1037, 1117, 1149  
 BOËTIUS, I., 1003, 1049  
 BOETTGER, C. R., 976, 1037  
 BOGUCKI, M., 899, 913, 1038  
 BOKENHAM, N. A. H., 847, 848, 1038  
 BOND, R. M., 983, 1038  
 BONEY, A. D., 1102, 1150  
 BONPLANDT, A., 1123, 1148, 1151  
 BOOKHOUT, C. G., 842, 843, 845, 879, 880-882, 909, 1042  
 BOONE, E., 832, 1038  
 BORG, F., 977, 1038  
 BOROFFKA, I., 899, 917, 919, 920, 929, 1038  
 BORSUK, V., 926, 1038  
 BOUGIS, P., 834, 1038  
 BOURRELLY, P., 804, 806, 1038  
 BOUXIN, H., 875, 877, 1038  
 BOVAIRD, J., 864, 1062  
 BOVE, C., 747, 1038  
 BOVE, J. M., 747, 1038  
 BOWDEN, K. F., 960, 1038  
 BOX, G. E. P., 843, 880, 1038  
 BOYLE, P. R., 905, 926, 1038  
 BRAARUD, T., 756, 802, 1038, 1102, 1103, 1150, 1151  
 BRATTSTRÖM, H., 946, 1038  
 BREDER, C. M., 839, 1038  
 BRENKO, M. Hrs., 883, 1038  
 BRETT, J. R., 1003, 1039  
 BREWER, P. G., 821, 1039  
 BRICTEUX-GREGOIRE, S., 913, 1055  
 BRIGGS, R. O., 1161, 1190  
 BROCKMANN, C., 797, 1039  
 BROEKEMA, M. M. M., 868, 925, 941, 1039  
 BROEKHUYSEN, G. J., 825, 834, 835, 847, 934, 950, 1039  
 BROMHALL, J. D., 1130, 1150  
 BROOM, J. G., 969, 1074  
 BROWN, A. C., 847, 1039  
 BROWN, A. D., 701, 1039  
 BROWN, F. A., JR., 825, 885, 1000, 1013, 1039, 1070  
 BROWN, R., 885, 1039  
 BRUST, H. F., 1165, 1192  
 BRYAN, G. W., 833, 870, 890, 893, 913, 974, 1035, 1039  
 BRZYSKI, B., 1121, 1152  
 BUCHAN, S., 1177, 1190  
 BUCHANAN-WOLLASTON, H. J., 1028, 1039  
 BUCKMIRE, F. L. A., 701, 702, 1039  
 BUDDE, H., 809, 810, 1039  
 BUDDENBROCK, W. VON, 885, 1039  
 BÜCKMANN, A., 1028, 1039  
 BÜNNING, E., 727, 732, 1039  
 BUGLIO, B., 687, 1073  
 BUKATSCH, F., 694, 695, 1039  
 BULL, H. O., 1022, 1039  
 BULLIVANT, J. S., 1003, 1039  
 BULNHEIM, H.-P., 687, 953, 1033, 1040, 1059  
 BURBANCK, W. D., 875, 907, 912, 924, 1040, 1047, 1075  
 BURDEN, C. E., 1017, 1040  
 BURGER, J. W., 894, 1015, 1040  
 BURROWS, E. M., 816, 1040, 1117, 1150  
 BURTON, R. F., 885, 1040  
 CABIOCH, L., 1129, 1150  
 CALABRESE, A., 883, 953, 1038, 1040  
 CALLAMAND, O., 1019, 1047  
 CALLOME, B., 1179, 1190  
 CANAGARATNAM, P., 1005-1007, 1040  
 CAPEN, R. L., 868, 873, 894, 913, 1050  
 CAPSTICK, C. K., 830, 1040  
 CARAUSU, S., 832, 1070  
 CAREFOOT, T. H., 892, 894, 913, 925, 1043  
 CARGO, D. G., 833, 948, 1040  
 CARPELAN, L. H., 825, 1040  
 CARRIKER, M. R., 822, 969, 1040  
 CARROLL, J. J., 1169, 1190  
 CASPERS, H., 800, 822, 827, 922, 974, 1040  
 CASSIDY, J. D., 995, 1061  
 CASTENHOLZ, R. W., 815, 1040  
 CAUDRI, L. W. D., 974, 1041  
 CHAN, D. K. O., 1018, 1041  
 CHAPMAN, V. J., 726, 730, 772, 795, 815, 817, 1041

- CHAPMAN-ANDRESEN, C., 885, *1041*  
 CHARTERS, A. C., 1113, 1120, *1150*  
 CHARTIER-BARADUC, M. M., 1001, *1063*  
 CHAUVET, J., 1018, *1033*  
 CHAUVET, M. T., 1018, *1033*  
 CHEN, T. Y., 876, *1041*  
 CHESTER-JONES, I., 1018, *1041*  
 CHIA, F. S., 911, *1046*  
 CHOW, T. J., 687, 868, 869, 894, 895, 913, *1041, 1070*  
 CHRISTOPHERSEN, J., 727, *1070*  
 CLARIDGE, C. A., 695, *1063*  
 CLARK, A. E., 951, *1041*  
 CLARK, H. W., 1183, *1190*  
 CLARKE, F. W., 825, *1041*  
 COHEN, E., 1164, *1190*  
 COKER, R. E., 1183, *1190*  
 COLBY, B. R., 1157, *1190*  
 COLE, W. H., 889, 895, *1041*  
 COLLIER, H. O. J., 945, *1037*  
 COLMAN, J., 810, *1041*  
 COLOMBO, G., 1031, *1041*  
 COMFORT, A., 977, *1041*  
 CONKLIN, D. E., 950, 961, *1071*  
 CONNER, R. L., 885, *1041*  
 CONOVER, J. T., 804, 805, *1041, 1096-1098, 1150, 1179, 1190*  
 CONOVER, R. J., 687, *1041*  
 CONTE, F. P., 998-1000, 1032, *1041*  
 CONWAY, E., 816, *1041, 1112, 1117, 1150*  
 CONWAY, E. J., 825, *1041*  
 COOPER, L. H. N., 974, *1041*  
 COPELAND, D. E., 894, 913, 988, 1031, *1042*  
 CORDIER, D., 1001, 1021, *1042*  
 CORDONE, A. J., 1181, *1190*  
 COSTERTON, J. W., 703, *1079*  
 COSTLOW, J. D., JR., 842-845, 868, 879-882, 908, 909, 913, *1042, 1056*  
 COTRONEI, G., 948, *1042*  
 COTTON, A. D., 1112, *1150*  
 COX, R. A., 831, *1042*  
 CRAGG, J. B., 868, 871, 872, 895, 913, *1036*  
 CRAIG, H., 825, *1042*  
 CRAIGIE, J. S., 772, *1037*  
 CREPY, D., 1018, *1033*  
 CREUTZBERG, F., 1024, *1042*  
 CRIMSON, J. M., 876, *1082*  
 CRISP, D. J., 845, 851, *1042, 1126, 1150, 1177, 1190*  
 CROGHAN, P. C., 868, 869, 884, 913, *1042, 1043*  
 CRONKLIN, R. E., 870, 941, *1043*  
 CROZIER, W. J., 926, *1034*  
 CURRA, R. A., 884, *1043*  
 CURWAY, E., 816, *1040*  
 CYRUS, B. S., 714, *1045*  
 CZIHAK, G., 1129, *1150*  
 DAHL, E., 822, *1043*  
 DAKIN, W. J., 868, *1043*  
 DALES, R. P., 899, 904, 913, 915, 926, *1055*  
 DALL, W., 885, *1043*  
 DALTON, A. J., 1031, *1042*  
 DAMBOVICEANU, A., 910, *1043*  
 DANIELLI, J. F., 885, *1039*  
 DARLINGTON, P. J., 974, *1043*  
 DART, M. C., 1188, *1191*  
 DARWIN, C., 1123, 1148, *1150*  
 DAVIES, P. S., 847, 973, *1043*  
 DAVIS, C. C., 944, *1043*  
 DAVIS, H. C., 835, 883, 953, *1040, 1043, 1186, 1190*  
 DAY, J. H., 822, *1043*  
 DEBYSER, J., 1179, *1190*  
 DECLER, W., 897, 898, *1043*  
 DEGENS, E. T., 825, *1043*  
 DEHNEL, P. A., 847, 868, 875, 884, 892, 894, 913, 924, 925, 929-931, 941, 974, *1043, 1075*  
 DEKHUYZEN, M. C., 900, *1043*  
 DELAUNAY, H., 910, *1043*  
 DELF, E. M., 1113, *1150*  
 DELLA CROCE, N., 969, *1043*  
 DEMETROPOULOS, A., 1120, *1151*  
 DENISOVA, A. I., 825, 828, *1033*  
 DENNERT, A. L., 950, 974, *1044*  
 DENNERT, H. G., 950, 974, *1044*  
 DENNIS, M., 925, *1050*  
 DENSMORE, C. D., 821, *1039*  
 DENTON, E. J., 888, *1044*  
 DERJUGIN, K. M., 954, *1044*  
 DIAMOND, J. M., 894, *1044*  
 DIANOVA, E., 894, *1044*  
 DICK, D. A. T., 885, *1041*  
 DIETRICH, G., 686, 687, 821, *1044, 1085, 1141, 1150, 1167, 1188, 1190*  
 DILLON, J. R., 1125, 1131, *1155*  
 DISKUS, A., 711, *1053*  
 DITTMER, D. S., 1000, *1034*  
 DJATLOVITSKA, F. J., 825, 828, *1034*  
 DOMMASNES, A., 1144, *1150*  
 DONALDSON, E. M., 1013, *1054*  
 DOFLEIN, F., 983, *1053*  
 DORNHEIM, H., 974, *1044*  
 DOTY, M. S., 810, *1044, 1101, 1188, 1190*  
 DOTY, M. W., 1125, 1134, *1150*  
 DOYLE, W. L., 1031, *1044*  
 DRAGENDORFF, O., 900, *1051*  
 DRAPEAU, G. P., 896, 897, *1044*  
 DREVS, P., 761, *1044*  
 DREW, G. H., 1169, *1190*  
 DROOF, M. R., 687, 699, *1071*  
 DRUEHL, L. D., 787-789, *1044*  
 DUBROW, D. L., 969, *1079*

- DUBUISSON, M., 896, 1044  
 DUCHATEAU-BOSSON, C., 913, 1044, 1055  
 DUDNIKO, V. F., 898, 1044  
 DUNBAR, C. O., 825, 1075  
 DUNBAR, M. J., 974, 1044  
 DUNCAN, A., 878, 934, 935, 1044  
 DUNHAM, P. B., 885, 886, 899, 1044, 1056  
 DUNN, A. E. G., 1029, 1055  
 DUTRIEU, J., 950, 1045  
 DUVAL, M., 868, 885, 886, 913, 930, 1045  
 DYBERN, B. I., 825, 835, 842, 974, 1045  
  
 EAGLESON, P. S., 1086, 1150  
 EBASHI, S., 932, 1045  
 EBLING, F. J., 1115, 1149, 1150  
 EDIPIDIS, T. A., 1162, 1190  
 EDMONDS, E., 868, 1043, 1045  
 EDNEY, E. B., 862, 872, 988, 1045, 1077  
 EIBL-EIBESFELD, J., 1137, 1150  
 EISMA, D., 982, 983, 1045  
 EKMAN, S., 822, 974, 1045, 1086, 1141, 1150  
 ELIASSEN, E., 875, 1045  
 ELLIS, W. G., 834, 835, 840, 899, 1045  
 ELTRINGHAM, S. K., 875, 1045  
 EMERIT, M., 1028, 1065  
 EMERSON, A. E., 974, 1033  
 EMERSON, R., 698, 1045  
 EMERY, K. O., 821, 831, 1045, 1129, 1150, 1162, 1190  
 ENDO, M., 932, 1045  
 ENGLE, J. B., 939, 1048  
 ENGLUND, B., 795, 1045  
 EPPLEY, R. M., 714, 1045  
 ERCEGOVIĆ, A., 700, 812, 1045, 1046, 1117, 1150  
 EVANS, D. H., 1003, 1049  
 EVANS, J., 870, 917, 1059  
 EVANS, R. G., 810, 1000, 1046  
 EWER, D. W., 904, 1046  
 EWER, R. F., 904, 1046  
 EWING, J., 1177, 1190  
 EWING, M., 1165, 1177, 1190  
  
 FALLS, C. P., 1170, 1190  
 FARINA, T. D. W., 1186, 1191  
 FARMER, J. B., 785, 1046  
 FAURÉ-FREMIET, E., 1179, 1191  
 FAY, P., 693, 1046  
 FELDMANN, G., 819, 1046  
 FELDMANN, J., 717, 790, 800, 819, 1046  
 FERGUSON, J. C., 911, 1046  
 FESSLER, J., 998-1000, 1041  
 FIELD, J., 876, 1082  
 FIGUERAS, A., 846, 1046  
 FINLAYSON, D. M., 851, 875, 1035  
 FISCHER, B., 689, 1046  
 FISCHER-PIETTE, E., 825, 973, 1046  
 FISHER, F. M., 941, 1063  
 FITTING, H., 728, 1046  
 FLEMING, R. H., 825, 831, 974, 1061, 1078, 1085, 1140, 1150, 1155  
 FLEMISTER, L. J., 868-870, 875, 895, 1046  
 FLEMISTER, S. C., 868, 869, 875, 895, 1046  
 FLOODGATE, G. D., 1177, 1190  
 FLOREY, E., 900, 1046  
 FLORKIN, M., 885, 910, 913, 1044, 1046, 1055  
 FLÜGEL, H., 836, 868, 908, 913, 923, 925, 974, 1046, 1074  
 FOERSTER, R. E., 1005, 1046  
 FOYNE, B., 802, 1038  
 FOGG, G. E., 693, 698, 840, 885, 1046  
 FOLLET, B. K., 1018, 1036  
 FONTAINE, A. R., 911, 1046  
 FONTAINE, M., 1019, 1047  
 FORCH, C., 686, 1059  
 FORD, E., 1027, 1047  
 FORD, P., 1032, 1047  
 FORD, T. B., 969, 1074  
 FORSMAN, B., 974, 1047  
 FORSTNER, H., 1086, 1087, 1140, 1144, 1146, 1147, 1150, 1154  
 FOSTER, B. A., 842, 852-858, 860-862, 875, 905, 920, 926, 937, 938, 941, 942, 973, 1047  
 FOX, D. L., 825, 862, 1047, 1069  
 FRANKENBERG, D., 875, 924, 1047  
 FRASER, J. H., 827, 1047, 1103, 1150, 1151  
 FREDERIQ, L., 913, 1047  
 FREEMAN, R. F. H., 941, 1047  
 FRETTER, V., 904, 913, 915, 1047  
 FRIEDMANN, I., 784, 1047  
 FRIEDRICH, H., 875, 974, 1047, 1140, 1151  
 FRIES, N., 691, 1051  
 FRITZSCHE, H., 871, 1047  
 FROMAGEST, C., 741, 1047  
 FRY, F. E. J., 876, 1003, 1020, 1047  
 FUGELLI, K., 1019, 1029, 1061  
 FUJIIYA, M., 883, 951, 1047  
 FUKUDA, M., 1159, 1165, 1191, 1192  
 FULLER, J. L., 899, 1079  
 FULTON, C., 864, 1047  
  
 GAARDER, K. R., 1102, 1103, 1150  
 GAJEWSKI, N., 983, 1047  
 GALKINA, L. A., 1027, 1047, 1048  
 GALLI, M. G., 820, 1079  
 GALTSOFF, P. S., 939, 1048, 1186, 1189, 1191  
 GALUN, E., 787, 1079  
 GEHRINGER, J. W., 1164, 1190  
 GEINRIKH, A. K., 975, 1048  
 GERASIMOV, V. V., 1028, 1056  
 GERLACH, S. A., 1134, 1151  
 GESSNER, F., 705, 706, 717, 735, 741-743, 746,

- 760, 765-767, 780, 781, 789, 795, 797, 798,  
807, 808, 816, 1048, 1085, 1087, 1091, 1095,  
1098-1100, 1103-1106, 1109, 1112, 1114,  
1151, 1179, 1191
- GETMAN, H. C., 1031, 1048
- GHIRETTI, F., 897, 1048
- GIBSON, M. B., 1005, 1048
- GIERE, O., 955, 959, 960, 962, 1048
- GIESE, A. C., 902, 910, 1079
- GIFORD, C., 925, 1052
- GILCHRIST, B. M., 875, 883, 1048
- GILLBRICHT, M., 969, 1048, 1170, 1191
- GILPIN-BROWN, J. B., 888, 1044
- GITELZON, I. I., 975, 1081
- CLAUS, K. J., 939, 1048
- GLEASON, H. A., 955, 1048
- GLOVER, R. S., 974, 1048
- GLYNN, P. W., 849-851, 1049
- GNOSE, G., 998-1000, 1041
- GOHS, L., 1177, 1191
- GOLD, H. S., 700, 1049
- GOLDBERG, E. D., 683, 684, 687, 1041, 1049
- GOLDSCHMIDT, E., 983, 1049
- GOLDSTEIN, S., 698, 1049, 1076
- GOLIKOV, A. N., 842, 843, 954, 955, 1049
- GOMPEL, M., 835, 1049
- GORBUNOV, G. P., 954, 1049
- GORDON, C. M., 974, 1049
- GORDON, M. S., 1003, 1049
- CORECKI, D., 1031, 1044
- COSELCK, F., 980, 981, 1049
- GRAHAM, J. M., 690, 695, 701, 1049
- GRAHAM, M., 1028, 1049
- GRAINGER, E. H., 954, 1049
- GRAINGER, F., 851, 1049
- GRAN, H. H., 810, 1049, 1103, 1151
- GRAND, Y. LE, 1161, 1191
- GRAY, I. E., 988, 1049
- GRAY, T. R. G., 700, 1049
- GREEN, J. W., 868, 869, 894, 895, 913, 1049,  
1070
- GREENFIELD, L. J., 1169, 1190, 1191
- GRENAGER, B., 1120, 1151
- GRESENS, J., 825, 835, 1049
- GREVE, W., 976, 1050
- GRIFFIN, T. B., 690, 1064
- GRØNTVED, J., 1102, 1103, 1150
- GROSCH, D. S., 950, 995, 1050, 1061
- GROSCH, O. P., 995, 1061
- GROSS, F., 734, 735, 983, 994, 1050
- GROSS, W. J., 847, 862, 868, 869, 873, 875,  
878, 894, 895, 899, 900, 902, 909, 913, 921,  
925, 930, 932, 1050
- GRUBB, V. M., 810, 811, 1050
- GRUFFYDD, Ll. D., 953, 1050
- GUILLARD, R. R. L., 756, 757, 1050
- GUNTER, G., 821, 825, 872, 892, 974, 976,  
1000, 1050, 1069, 1077, 1183, 1191
- GUPTA, B. L., 911, 1062
- GURJANOVA, E. F., 954, 1051, 1118, 1119,  
1151
- GURNEY, R., 822, 1051
- GUSTAFSSON, V., 691, 1051
- GUTKNECHT, J., 714, 760, 1051
- HAACKER, U., 1130, 1152
- HAAHTELA, I., 974, 1066
- HAAS, H., 778, 779, 834, 923, 984, 1051
- HAERTEL, L., 955, 956, 1051
- HAGEN, G., 977, 985, 1051
- HAGMEIER, E., 1177, 1191
- HAHN, H., 1086, 1151
- HALL, W. E., 876, 1082
- HALLIK, R., 797, 1051
- HAMMER, L., 746, 764, 766, 767, 780, 781,  
1043, 1051, 1114, 1151
- HAMPSON, G. R., 830, 963, 964, 1074
- HANKS, J. E., 939, 940, 1051
- HANSEN, H. J., 989, 1051
- HANSEN, K. W., 969, 1051
- HAPPOLD, F. C., 695, 1070
- HARDEN-JONES, F. R., 1022, 1051
- HARDER, R., 771, 815, 1051
- HARDER, W., 969, 971, 972, 1039, 1051
- HARMS, J. W., 900, 988, 1051
- HARNISCH, O., 885, 923, 984, 1051, 1052
- HARRISON, A. D., 1186, 1191
- HARRISON, F. M., 889, 1064
- HARSCH, M., 868, 869, 894, 895, 1049
- HARTENSTEIN, R., 873, 1052
- HARTNOLL, R. G., 1129, 1151
- HARTOG, C. DEN, 707, 822, 1052
- HARVEY, E. N., 693, 701, 1052
- HASS, H., 1131, 1151
- HASSELBACH, W., 896, 1052
- HATCHETT, G. L., 1161, 1190
- HATZIKAKIDIS, A. D., 1162, 1190
- HAUG, A., 750, 1052
- HAUPT, J., 920, 1038
- HAYES, F. R., 825, 1052
- HAYS, E. E., 821, 1045
- HEDGPETH, J. W., 804, 822, 824, 974, 1052,  
1134, 1151
- HEEREBOUT, G. R., 960, 1052
- HEINCKE, F., 822, 1065
- HELA, I., 1185, 1191
- HELFF, O. M., 876, 1052
- HELLE, J. H., 998, 1052
- HELLER, H., 1018, 1052
- HEMMERT, D. VAN, 1168, 1193
- HEMPEL, G., 1028, 1032, 1033, 1039, 1052
- HENDERSON, I. W., 1018, 1041

- HENSEL, H., 727, 1070  
 HENTIG, R. VON, 883, 927, 928, 950-952, 1052  
 HERBERT, D. W. M., 1182, 1188, 1189, 1191  
 HERREID, C. F., 925, 1052  
 HERRMANN, F., 870, 871, 930, 932, 1052, 1074  
 HERZ, R., 896, 1081  
 HESS, G., 1031, 1052  
 HESS, N. N., 1015, 1040  
 HESSE, R., 954, 983, 1052, 1053  
 HETHERINGTON, W. M., III, 832, 833, 936, 937, 1072  
 HEUTS, M. J., 840, 1025, 1030, 1053  
 HIJATT, R. W., 913, 1053, 1137, 1151  
 HICKMANN, C. P., 1002, 1003, 1013, 1018-1020, 1053  
 HIDAKA, T., 689, 695, 1053  
 HIESTAND, W. A., 876, 1053  
 HILL, S. E., 694, 701, 1053  
 HILL, T. G., 778, 779, 1051  
 HILTERMANN, H., 822, 1053  
 HIND, G., 747, 1053  
 HIRST, B., 1005, 1048  
 HOAR, W. S., 1017, 1019, 1020, 1027, 1053, 1063  
 HOBSON, L. A., 1177, 1190, 1191  
 HODGKIN, A. L., 894, 1053  
 HÖFKEN, U., 977, 1053  
 HÖFLER, K., 708-711, 730, 732, 734, 735, 1053  
 HOEK, C. VAN DEN, 1114, 1151  
 HOFFMANN, C., 735, 791, 1053, 1121, 1151  
 HOHENDORF, K., 835, 912, 913, 974, 1053  
 HOLDREIDE, W., 770-773, 815, 816, 1078  
 HOLLAND, P. V., 895, 921, 925, 1050  
 HOLLE, H., 730, 1053  
 HOLLIDAY, F. G. T., 997, 998, 1000-1002, 1009-1013, 1025-1029, 1031, 1037, 1053-1055  
 HOLMES, W. N., 1003, 1004, 1013, 1018, 1041, 1054  
 HOLST, E. VON, 899, 913, 1036  
 HÖLZ, G. G., JR., 885, 886, 899, 1056  
 HOOD, D. W., 687, 1073  
 HOOP, M., 983, 994, 1053  
 HOPKINS, H. S., 877, 1054  
 HORI, A., 695, 1063  
 HORNE, R. A., 687, 1054  
 HOSOI, K., 886, 1060  
 HOUSE, C. R., 1000, 1054  
 HOUSTON, A. H., 1001, 1020, 1021, 1031, 1054, 1079  
 HOWARD, A. D., 1183, 1190  
 HUBER-PESTALOZZI, 1109, 1151  
 HUF, E., 899, 913, 1036, 1054  
 HUGHES, D. A., 968, 969, 1054  
 HUKUDA, K., 894, 1054  
 HULBURT, E. M., 855, 1054  
 HUMBOLDT, A., 1124, 1148, 1151  
 HUNT, J. M., 821, 1045  
 HUSMANN, S., 822, 1054  
 HUSTEDT, F., 707, 808, 809, 817, 1054  
 HUSTON, M. J., 889, 1064  
 HYMAN, L. H., 935, 1054  
 HYNES, H. B. N., 946, 947, 1054  
 ILJIN, W. S., 721, 730, 820, 1054, 1055  
 INOUE, N., 1159, 1165, 1191, 1192  
 ISAAC, W. E., 785, 810, 815, 1055  
 ISAACS, J. D., 1086, 1151  
 ISAWA, S., 747, 1053  
 ISELIN, C., 1086, 1151  
 ISSEL, R., 833, 1055  
 JANNASCH, H. W., 1175, 1191, 1192  
 JANSEN, K. P., 841, 846, 847, 849, 1055  
 JANSSON, B. O., 831, 832, 941, 965-968, 1055  
 JELISAVCIĆ, O., 913, 1062  
 JENIK, J., 815, 1055  
 JERLOV, N. G., 1161, 1162, 1177, 1191  
 JEUNIAUX, C., 913, 1055  
 JOB, S. V., 1003, 1055  
 JØRGENSEN, C. B., 899, 904, 913, 915, 926, 1055, 1126, 1151, 1165, 1184, 1191  
 JOHANSEN, A. C., 822, 1055  
 JOHNSON, D. S., 810, 815, 1055  
 JOHNSON, D. W., 1135, 1151  
 JOHNSON, M. A., 1157, 1191  
 JOHNSON, M. W., 825, 974, 1078, 1085, 1125, 1151, 1155  
 JOHNSON, R. F., 1169, 1190  
 JOHNSON, T. W., JR., 691-693, 1055  
 JOHNSTON, R., 683, 831, 1055  
 JONES, A. E., 969, 1079  
 JONES, F. W., 1123, 1151  
 JONES, L. G., 1102, 1153  
 JONES, L. L., 847, 868, 913, 1055  
 JONES, M. P., 1009-1011, 1013, 1029, 1053-1055  
 JONES, W. E., 1117, 1118, 1120, 1151  
 JOHNSON, H., 816, 1055  
 JORDE, I., 800-803, 1055  
 JOSEPH, J., 1086, 1151  
 JOSHI, G. V., 752, 753, 1069  
 KÄHLER, H. H., 834, 835, 864-866, 1055  
 KALBER, F. A., 908, 909, 1055, 1056  
 KALLE, K., 683, 685-687, 1044, 1056, 1085, 1141, 1150, 1167, 1190  
 KALMUS, H., 876, 1056  
 KALTWASSER, J., 719-721, 774, 776, 1056  
 KAMEMOTO, F. I., 886, 900, 902, 1056  
 KAMYSHLOV, M. M., 1028, 1056  
 KANESHIRO, E. S., 886, 899, 1056

- KANT, P., 950, 974, *1044*  
 KANWISHER, J. W., 1146, *1151*, 1178, *1191*  
 KARANDJEVA, O. G., 900, *1056*  
 KARPEVICH, A. F., 834, 912, *1056*  
 KARSTEN, G., 1109, *1151*  
 KATO, S., 778-780, *1081*  
 KATYS, G. P., 1086, *1152*  
 KATZ, B., **945**, *1056*  
 KEHLENBECK, E. K., 885, *1056*  
 KELLEY, D. W., 1162, 1181, *1190*, *1191*  
 KEMP, H. A., 1182, *1191*  
 KENSLEER, C. B., 847, 852, 856, *1056*  
 KERKUT, G. A., 897, *1056*  
 KERLEY, D. E., 885, *1056*  
 KESSEL, R. G., 1031, *1056*  
 KESSELER, H., 733, 735, 758, 759, 763, *1056*,  
*1057*  
 KESSLER, H., 977, *1067*  
 KEUNEN, D. J., 862, *1057*  
 KEYS, A. B., 1031, *1057*  
 KHLEBOVICH, V. V., 822, 827-829, 866, 867,  
 875, *1057*  
 KHMELEVA, N. N., 928, *1057*  
 KING, E. N., 877, 884, *1057*  
 KINGSBURY, J. M., 1117, 1118, *1152*  
 KINNE, E. M., 739, 1025, 1026, *1059*  
 KINNE, O., 687, 735, 821, 822, 825, 826, 830,  
 832, 836, 840, 846, 864, 866-868, 872, 874,  
 875, 879, 883, 885, 906, 907, 913, 924, 927-  
 929, 939, 946, 948-950, 953, 965, 974-981,  
 984-994, 1001, 1003, 1006-1010, 1016,  
 1017, 1025, 1026, 1029, 1033, *1057-1059*,  
*1075*, *1078*, 1123, 1141, *1152*, 1178, *1191*  
 KIRCHNER, W.-P., 908, *1059*  
 KIRSCH, M., 827, 828, *1059*  
 KISCH, B., 910, *1059*  
 KITCHING, J. A., 1115, *1149*, *1150*  
 KJELLMAN, F. R., 1121, *1152*  
 KLAVESTAD, N., 800-803, *1055*, *1059*  
 KLEKOWSKI, K. Z., 878, *1044*  
 KNIEP, H., 771, 784, 815, *1059*  
 KNUDSEN, M., 686, *1059*  
 KOBJAKOVA, Z. I., 954, *1059*  
 KOCH, H. J., 870, 917, 923, 984, *1059*  
 KOCHWOLLA, N., 691, *1037*  
 KOIZUMI, T., 886, 895, 905, *1059*, *1060*  
 KOLBE, R. W., 809, 817, 818, *1060*  
 KOLLER, G., 899, 900, 902, *1060*  
 KORINEK, J., 690, *1060*  
 KORNAS, J., 1121, *1152*  
 KORNMANN, P., 1106, *1152*  
 KORRINGA, P., 1134, *1152*, 1183, 1184, *1191*  
 KOSKE, P., 1172, *1192*  
 KOTTE, H., 732, *1060*  
 KOWALSKI, R., 834, 836, 839, 840, 974, *1074*  
 KRATZ, W. A., 698, *1060*  
 KRAUSE, G., 821, *1044*, 1092, *1152*  
 KREBS, E. M., 926, *1038*  
 KREEB, K., 770, *1081*  
 KREY, J., 1177, *1192*  
 KRISHNAMOORTHY, B., 835, 889, 890, 899,  
 900, 907, 909, 936, *1060*,  
 KRISHNAMOORTHY, R. V., 932, 933, *1060*,  
*1081*  
 KRISHNAN, G., 904, *1060*  
 KRISHNASWAMY, S., 835, 889, 890, 899, 907,  
 909, 910, 936, *1060*  
 KRISTENSEN, I., 726, 819, 820, *1060* 1113,  
*1152*  
 KROGH, A., 835, 870, 872, 875, 885, 895, 905,  
 917, 941, *1043*, *1060*, 1168, *1192*  
 KRUMM, H., 1172, *1192*  
 KRYZHANOVSKY, S. G., 1029, 1032, *1061*  
 KÜHL, H., 955, 974, *1061*  
 KÜKENTHAL, W., 1123, *1152*  
 KUENEN, D. J., 983, *1061*  
 KÜNNE, C., 976, *1064*, 1103, *1152*  
 KÜNZENBACH, R., 730, 790, *1061*, *1066*, 1113,  
*1153*  
 KUDO, T., 1159, 1165, *1191*  
 KUFFLER, S. W., 917, *1067*  
 KURATA, H., 998, 1000, *1061*  
 KYLIN, H., 789, 790, *1061*  
 LACHMANN, G. V., 1086, *1152*  
 LAEVASTU, T., 831, *1061*, 1185, *1191*  
 LAGERSPETZ, K., 835, *1061*  
 LAKOWITZ, K., 791, *1061*, 1111, *1152*  
 LA MARCHE, P. H., 995, *1061*  
 LAMOUREUX, J. V. F., 810, *1061*  
 LANCE, J., 969, *1061*  
 LANDERS, W. S., 934, 936, *1061*  
 LANE, C. E., 884, *1071*  
 LANGE, O., 717, *1061*  
 LANGE, R., 877, 878, 1019, 1029, *1061*  
 LARSEN, B., 750, *1052*  
 LARSEN, H., 690, *1061*  
 LARSON, E. J., 886, 900, *1056*  
 LASIEWSKI, R. C., 925, *1050*  
 LASKER, R., 1001, 1002, 1029, *1053*, *1061*  
 LASSIC, J., 836, 838, 839, 946, 947, *1061*, *1079*  
 LAUCKNER, G., 982, 983, *1061*  
 LAUFF, G. H., 974, 976, *1061*  
 LAWSON, G. W., 815, *1055*  
 LEATHERLAND, J. F., 1023, *1062*  
 LEDINGHAM, I. C., 936, *1082*  
 LEE, B. D., 892, 897, *1062*  
 LEERSNYDER, M. DE, 870, 917, *1062*  
 LEGENDRE, R., 741, 835, *1049*, *1062*  
 LEHTORANTA, L., 761, 762, *1062*  
 LELOUP, J., 1019, *1062*  
 LEMAIRE, J., 897, 898, *1043*

- LENHOFF, H. M., 864, 1062  
 LENZ, J., 1177, 1192  
 LERCHE, W., 757, 1062  
 LEVITT, J., 717, 1062  
 LEWIN, R. A., 739, 1062  
 LEWIS, C. M., 698, 1045  
 LEWIS, J. R., 973, 1062, 1108, 1115-1117,  
   1152, 1179, 1184, 1187, 1192  
 LIENEMANN, L. J., 871, 1062  
 LILLY, S. J., 886, 1062  
 LINDER, H. P., 691, 1035  
 LINKE, O., 1178, 1192  
 LIPMAN, C. B., 699, 1062  
 LITTLE, C., 911, 1062  
 LLOYD, J. I., 1184, 1188, 1192  
 LLOYD, R., 1189, 1191  
 LOBZA, P. G., 825, 927, 1062  
 LOCKWOOD, A. P. M., 825, 835, 868, 870, 872,  
   884, 885, 890, 891, 894, 895, 913, 1043,  
   1062, 1072  
 LODGE, S. M., 816, 1040, 1117, 1150  
 LOFTS, B., 875, 1062  
 LOOMIS, W. F., 864, 1062  
 LOOSANOFF, V. L., 934, 1062, 1183, 1184,  
   1186, 1192  
 LORENZ, J. R., 1135, 1152  
 LOUIS, C., 948, 1062  
 LÜNEBURG, H., 1177, 1192  
 LÜNING, K. O., 1178, 1192  
 LUCU, C., 913, 1062  
 LUKANIN, V. S., 898, 1063  
 LUMBYE, J., 875, 1063  
 LUMLEY, J. L., 1086, 1152  
 LUND, S., 1121, 1152  
 LUNZ, G. R., 1183, 1192  
 LUTHER, H., 792, 793, 1063  
  
 McALISTER, R. O., 941, 1063  
 MACALLUM, A. B., 886, 1063  
 MCCARTHY, R., 1003, 1049  
 MCFARLAND, W. N., 875, 878, 892, 897, 913,  
   945, 1062, 1063  
 MCGARY, J. W., 1158, 1192  
 MACHAN, R., 1086, 1154  
 MCKEE, J. E., 1183, 1192  
 McLAUGHLIN, J. J. A., 687, 799, 1071  
 McLEESE, D. W., 835, 1063  
 MACLEOD, R. A., 689, 690, 694-697, 701-703,  
   1039, 1044, 1063, 1064, 1079, 1083  
 McLUSKY, D. S., 831, 875, 890, 962, 1063  
 McMYNN, R. G., 1027, 1063  
 MAETZ, J., 1001, 1013, 1017, 1018, 1063, 1064  
 MAGARIA, R., 913, 1064  
 MAGNUS, D., 1127-1130, 1152  
 MAISTRENKO, J. G., 825, 828, 1034  
 MAKINOSE, M., 896, 1052  
  
 MALOEUF, N. S. R., 875, 1064  
 MANGELSDORF, P. C., JR., 830, 963, 964, 1074  
 MANN, H., 955, 974, 1061  
 MANTEL, L. H., 873, 885, 988, 1037, 1064  
 MANZI, J. J., 939, 1064  
 MARSHALL, E. K., 1032, 1064  
 MARSHALL, J. M., 885, 1064  
 MARSHALL, L. A., 869, 899, 913, 1050  
 MARSHALL, S. M., 876, 1064  
 MARTIN, A. W., 889, 1064  
 MARTIN, E. G., 832, 913, 1064  
 MATSUI, T., 743, 744, 746, 755, 778, 783, 784,  
   1064, 1067  
 MATSUMOTO, F., 1098, 1152  
 MATULA, T. I., 696, 697, 701, 702, 1044, 1063,  
   1064, 1079  
 MAURICE, A., 1001, 1020, 1042  
 MAXIMOV, N. A., 728, 1064  
 MAYER, A. G., 1125, 1152  
 MAYER, N., 1001, 1017, 1018, 1063, 1064  
 MAYERSON, H. S., 876, 1034  
 MEDWEDEWA, N. B., 913, 1064  
 MEIJERING, M. P. D., 835, 1064  
 MENZEL, D. W., 1159, 1192  
 MENZIES, R. J., 1129, 1153  
 MERKEL, J. R., 690, 1064  
 MERKENS, J. C., 1182, 1189, 1191  
 METCALF, M. M., 975, 976, 1064  
 MEYER, A., 759, 1064  
 MEYER, H., 975, 1064  
 MICHENER, H. D., 690, 1083  
 MIELCK, W., 976, 1064  
 MIKHIEEV, V. P., 898, 1044  
 MILEIKOVSKY, S. A., 954, 1064, 1065, 1141,  
   1153  
 MILLER, R. L., 1087, 1153  
 MITCHELL, C. T., 1102, 1153  
 MIYAWAKI, M., 948, 1065  
 MODLINGER, G., 988, 1065  
 MODY, B. N., 691, 1037  
 MÖBIUS, K., 822, 1065  
 MÖHNSON, T., 1028, 1065  
 MONNIOT, C., 1131, 1153  
 MONROE, R., 842, 843, 845, 879-882, 909, 1042  
 MONSI, M., 711, 712, 739, 747, 748, 1066  
 MONTEROSSO, B., 851, 1065  
 MONTFORT, C., 717, 719, 731, 739, 741, 743,  
   774, 815, 1065  
 MOORE, D. R., 1120, 1155  
 MOORE, H. B., 825, 974, 976, 1065  
 MOORHOUSE, F. W., 1125, 1153  
 MORDUCHAI-BOLTOVSKOI, F. D., 866, 1065  
 MÖRITA, R. Y., 690, 1077  
 MORITZ, P. M., 897, 1056  
 MORRIS, E. O., 692, 693, 1073  
 MORRIS, R., 1000, 1013-1016, 1030, 1065

- MOSEBACH, G., 732, 733, 1065  
 MOSS, B. L., 1112, 1153  
 MOSTAD, A., 877, 1061  
 MOTAIS, R., 1001, 1015, 1017, 1018, 1064, 1065  
 MOTHES, K., 778, 1066  
 MOTODA, S., 1125, 1153  
 MRAK, E. M., 691, 1069  
 MUDRAK, A., 694, 1066  
 MÜLLER-STOLL, W. R., 730, 1066, 1113, 1153  
 MUNSCHER, W. L. C., 723, 724, 810, 812, 813, 816, 1066  
 MUKHERJEE, B. B., 690, 1064  
 MUNDA, I., 749-752, 1066  
 MUNDAY, K. A., 877, 897, 1056, 1066  
 MUNNS, R., 821, 1039  
 MURPHY, G. I., 1185, 1192  
 MURRAY, J. F., 695, 1063  
 MUSE, L., 687, 1073  
 MUUS, B. J., 912, 974, 1066, 1087, 1153  
 MYERS, J., 698, 1060  
 MYKLESTAD, S., 756, 757, 1050
- NAGABHUSHANAM, R., 937, 938, 1066  
 NAGEL, H., 868, 869, 899, 913, 1066  
 NAKANISHI, M., 711, 712, 739, 747, 748, 1066  
 NASSONOW, D. N., 884, 1066  
 NATH, E., 735, 739, 740, 1066  
 NATH, H., 1099, 1100, 1153  
 NAUMANN, E., 1110, 1153  
 NAUMIN, G. G., 1164, 1192  
 NAYLOR, E., 974, 1066  
 NEEDHAM, P. R., 1184, 1188, 1192  
 NEFF, J. M., 937, 1066  
 NELLEN, U. R., 743-745, 818, 1066, 1099, 1153  
 NELSON, B. W., 831, 1067  
 NELSON, T. C., 969, 1067  
 NEMENZ, H., 895, 921, 922, 924, 1067  
 NESIS, K. N., 954, 1067  
 NEUGEBAUER, F. L. M., 847, 848, 1038  
 NEUMANN, D., 832, 834, 896, 921-923, 974, 984, 1067, 1078  
 NEUMANN, G., 1164, 1192  
 NEUSUHL, M., 1113, 1120, 1150  
 NEWCOMBE, C. L., 977, 1067  
 NEWELL, G. E., 851, 1049  
 NEWMAN, W. A., 926, 1067  
 NICHOLLS, J. G., 917, 1067  
 NICOL, J. A. C., 825, 885, 897, 944, 1067  
 NICOLL, C. S., 1018, 1036  
 NIENBURG, W., 1112, 1153, 1178, 1192  
 NIKULICHEVA, E. N., 828, 1057  
 NIPKOW, 1109, 1151  
 NISHIZAWA, S., 1159, 1191, 1192  
 NITTA, J. Y., 900, 902, 1056  
 NODDACK, I., 683, 1067
- NORTH, W. G., 1102, 1153  
 NULTSCH, W., 1179, 1180, 1192  
 NYGREN, S., 752, 1067
- ODUM, E. P., 974, 1067, 1125, 1153  
 ODUM, H. T., 1125, 1153  
 OGATA, E., 719, 735-739, 743, 744, 746, 755, 768, 769, 773, 774, 778, 783, 784, 1067  
 OGLESBY, L. C., 836, 862, 885, 886, 889, 899-906, 910, 912, 913, 974, 1003, 1049, 1068  
 OGURI, M., 1032, 1068, 1101, 1150  
 OHNO, M., 728, 729, 752, 754, 1068  
 OLIPHAN, V. I., 1027, 1068  
 OLIVEREAU, M., 1019, 1047, 1068  
 OLMSTED, J. M. D., 913, 1035  
 OLSON, R. A., 1165, 1192  
 OLTMANN, F., 708, 717, 781, 785, 815, 816, 818, 1068, 1110, 1111, 1153  
 ONOFREY, E., 690, 694, 695, 1063  
 OOSTEN, J. V., 1182, 1192  
 OPPENHEIMER, C. H., 1171, 1175, 1192  
 ORR, A. P., 877, 1064, 1125, 1153  
 ORTON, J. H., 1117, 1155  
 OSADČICH, V. F., 912, 1056  
 OSTENFELDT, C. H., 793, 1068  
 OSTERBERG, C., 955, 956, 1051  
 OTT, J., 1137, 1153  
 OTTO, L., 1177, 1192  
 OUTRAM, D. M., 1025, 1068  
 OVERBECK, J., 731, 782, 1068, 1107, 1108, 1112, 1153  
 OWEN, H. M., 831, 1068  
 OXNER, N., 686, 1068
- PACKARD, G. L., 1159, 1193  
 PAFFENHÖFER, G. A., 879, 948, 949, 1059  
 PAGAST, F., 984, 1068  
 PALMER, M. F., 875, 1068  
 PALMER, R. F., 896, 1068  
 PANCER, E., 1121, 1152  
 PANDIAN, T. J., 927, 951, 1068  
 PANIKKAR, N. K., 868-870, 872, 913, 969, 1068, 1069  
 PANNIER, F., 735, 1048  
 PANTIN, C. F. A., 834, 839, 899, 903, 913, 945, 1069, 1073, 1081  
 PARAMONOV, A. N., 1164, 1192  
 PARK, O., 974, 1033  
 PARK, T., 974, 1033  
 PARKER, J., 728, 1069  
 PARR, A. E., 1105, 1106, 1153  
 PARRY, G., 825, 840, 847, 868-872, 878, 884-886, 888, 889, 894, 904, 905, 914, 915, 917, 918, 926, 1000, 1013, 1015, 1017, 1031, 1054, 1069, 1070  
 PARSONS, T. R., 1177, 1193

- PARVATHESWARARAO, U., 1032, 1081  
 PATIL, B. A., 752, 753, 1069  
 PAVLOV, V. M., 1162, 1193  
 PAYNE, W. J., 694, 695, 697, 1069, 1072  
 PEARSE, A. S., 821, 825, 872, 897, 976, 987, 988, 1069  
 PEEBLES, F., 862, 1069  
 PEQUEGNAT, W. E., 1126, 1153  
 PERNAUER, S., 702, 703, 1069  
 PETERS, H., 987, 1069  
 PETERS, N., 1109, 1153  
 PETTIT, G., 822, 1069  
 PHAFF, H. J., 691, 1069  
 PHILLIPS, J. G., 1017-1019, 1041, 1070  
 PHILLIPS, R. C., 811, 1069  
 PIATIGORSKY, J., 851, 875, 1035  
 PICARD, J., 976, 1069  
 PICKENS, P. E., 875, 878, 1063  
 PICKFORD, G. E., 1017, 1019, 1034, 1064, 1070  
 PIERSON, W. J., 1164, 1192  
 PIGNATTI, S., 734, 1070  
 PILGRIM, R. L. C., 836, 1070  
 PINKSTER, S., 950, 974, 1044  
 PINNER, I. J., 693, 698, 1070  
 PLATTNER, F., 913, 1070  
 POMPE, E., 795, 796, 1070  
 PORA, A. E., 832, 833, 835, 1070  
 POSEY, V. A., 896, 1063  
 POST, E., 717, 820, 1070  
 POSTMA, H., 1177, 1193  
 POTTS, W. T. W., 825, 840, 868, 870, 871, 878, 884-886, 888, 889, 894, 904, 905, 914, 915, 917, 918, 926, 1000, 1070  
 POWELL, H. T., 1117, 1150  
 POWELL, S. M., 816, 1040  
 PRANDTL, L., 1086, 1147, 1153  
 PRATT, D. B., 689, 690, 694, 695, 701, 1070, 1080  
 FRECHT, H., 727, 1070  
 PRESCOTT, J. M., 690, 1064  
 PRINGSHEIM, E., 819, 1070  
 PRINZ, H., 1099, 1153  
 PRIOU, M. L., 815, 819, 1070  
 PRITCHARD, A. W., 868, 886, 1056, 1079  
 PRITCHARD, D. W., 960, 1070  
 PROSKIN, V. N., 1164, 1192  
 PROSSNER, C. L., 825, 868, 869, 885, 893-895, 913, 932, 1000, 1013, 1034, 1049, 1070  
 PROVASOLI, L., 687, 693, 698, 699, 832, 950, 951, 1033, 1070, 1071  
 PRYTMERCH, H. F., 939, 1048  
 PURAJOKI, K. J., 974, 1071  
 PURCHON, R. D., 1115, 1149, 1150  
 QUINN, D. J., 884, 1071  
 QUINTON, R., 900, 1071  
 RABEN, K. VAN, 988, 1071  
 RAFFY, A., 875, 1003, 1071  
 RAMAMURTHI, R., 875, 1071  
 RAMSAY, J. A., 921, 923, 1071  
 RANADE, M. R., 833, 1071  
 RANDALL, D. J., 1017, 1053  
 RANKAMA, K., 825, 1071  
 RANKIN, J. C., 1018, 1041  
 RANSON, G., 825, 1071  
 RAO, K. P., 875, 1071  
 RAO, K. V., 825, 875, 1071  
 RAUSCHELBACH, H., 1086, 1154  
 RAYMOND, P. E., 825, 1071  
 REDEKE, H. C., 809, 822, 1071  
 REEVE, M. R., 927, 950, 1071  
 REID, D. M., 830, 831, 1071, 1072  
 REINKE, J., 1096, 1111, 1154  
 REISH, D. J., 832, 833, 835, 911, 936, 937, 939, 1072  
 REISS, I., 896, 1081  
 REMANE, A., 791, 802, 822-825, 827, 866, 885, 895, 905, 922, 946, 947, 974-977, 1072  
 REMMERT, H., 906, 1072  
 RENEFRO, N. C., 998, 1072  
 RENTZ, G., 985, 1072  
 RESTHÖFT, K., 836, 974, 1072  
 RHEINHEIMER, G., 1167, 1170, 1172, 1173, 1175, 1192, 1193  
 RHODES, M. E., 697, 1072  
 RICHARD, A., 897, 898, 1043  
 RICHARDS, F. A., 683, 1072  
 RICHARDSON, W. D., 1120, 1155  
 RICHTER, O., 694, 1072  
 RIED, A., 717, 722, 726, 727, 770, 777, 782, 815, 1072  
 RIEDL, R., 1085-1087, 1092, 1123-1126, 1129-1147, 1154  
 RIEGEL, J. A., 890, 894, 913, 1062, 1072  
 RIEMANN, F., 974, 1072  
 RIETZ, E. G. DU, 1117, 1154  
 RIGLER, F. H., 941, 1047  
 RILEY, G. A., 1168, 1193  
 RILEY, W. H., 701, 1070  
 RITCHIE, D., 692, 700, 1072, 1073  
 ROBERTSON, J. D., 825, 840, 845, 868, 869, 871, 885-888, 890, 891, 894-896, 910, 913, 926, 944, 945, 988, 989, 997, 1013, 1073  
 ROBINS, R. C., 1188, 1193  
 ROCH, F., 834, 864, 1073  
 ROCH, S. LE, 976, 1069  
 ROCKWELL, J., 998, 1073  
 RONA, E., 687, 1073  
 ROSCA, D. I., 832, 835, 1070

- ROSENTHAL, H., 1187, 1191  
 ROSENVINGE, L. K., 1106, 1154  
 ROSS, D. A., 825, 1043  
 ROSS, D. M., 945, 1073  
 ROSS, S. S., 692, 693, 1073  
 ROTHSCHILD, LORD, 895, 1073  
 ROTTGARDT, D., 822, 1073  
 ROTTHAUWE, H.-W., 868, 907, 913, 924, 1059  
 RUBEY, W. W., 825, 866, 1073  
 RUDJAKOV, J. A., 943, 1073  
 RUDOLF, J., 836, 974, 1074  
 RUDY, P. P., JR., 913, 925, 1050, 1073  
 RUETZLER, K., 1086, 1135, 1148, 1150, 1154  
 RUSSELL, F. S., 1103, 1154  
 RUSSELL-HUNTER, M., 943, 1073  
 RUSSELL-HUNTER, W. D., 943, 1073  
 RUŽIĆ, I., 913, 1062
- SABBADIN, A., 977, 1073  
 SAHAMA, T. G., 825, 1071  
 ST. AMANT, L. S., 969, 1074  
 SAITO, Y., 726, 785, 1074  
 SAMUELSSON, G., 792-795, 1074  
 SANDERS, H. L., 830, 963, 964, 1074  
 SANDOW, A., 896, 1074  
 SARÁ, M., 1148, 1154  
 SAROJINI, R., 937, 938, 1066  
 SASTRY, A. N., 868, 909, 1042  
 SATYANARAYANA RAO, T. S., 1163, 1193  
 SAVVATEEV, V. B., 842, 1074  
 SAWYER, W. H., 1001, 1064  
 SAYLES, L. P., 835, 1074  
 SCARLATO, O. A., 842, 843, 1049  
 SCHACHTER, D., 822, 1074  
 SCHALLER, F., 921, 1074  
 SCHEER, B. T., 885, 1046  
 SCHELTEMA, R., 1141, 1154  
 SCHICKS, E., 870, 917, 1059  
 SCHIFFMAN, A., 1087, 1154  
 SCHILLER, J., 807, 816, 1074, 1108, 1154  
 SCHINSKE, R. A., 910, 1078  
 SCHLICHTING, H., 1147, 1148, 1154  
 SCHLIENZ, W., 822, 973, 1074  
 SCHLIEPER, C., 822, 823, 825, 827, 834, 836, 839, 840, 868, 870, 871, 875, 877, 878, 885, 899, 905, 906, 913, 917, 922, 931, 947, 974, 976, 977, 1037, 1072, 1074, 1080  
 SCHMANKEWITSCH, W. J., 983, 1074  
 SCHMIDT, H., 948, 1075  
 SCHMIDT, K. P., 954, 974, 1033, 1052  
 SCHMIDT-NIELSON, S., 1013, 1075  
 SCHNEIDER, D. E., 836, 974, 1080  
 SCHÖNE, H., 1110, 1154  
 SCHOFFENIELS, E., 840, 885, 921, 1075  
 SCHOLLES, W., 870, 871, 895, 913, 917, 1075
- SCHRAMM, W., 705, 719, 721-723, 725, 727, 728, 730, 731, 755, 775-777, 815, 1067, 1075, 1094, 1154  
 SCHREIBER, E., 785, 1075  
 SCHUCHERT, C., 825, 1075  
 SCHÜCKING, A., 900, 1075  
 SCHÜTZ, L., 946, 974, 1075  
 SCHÜLTZ-GRUNOW, F., 1147, 1148, 1155  
 SCHULTZ, L. P., 833, 948, 1040  
 SCHULZ, S., 974, 1075  
 SCHUMANN, F., 834, 1075  
 SCHUTZ, D. F., 687, 1075  
 SCHWABE, E., 868, 870, 875, 913, 917, 926, 929, 930, 987, 1075  
 SCHWARTZ, F. J., 1000, 1075  
 SCHWARZ, S., 969, 1075  
 SCHWENKE, H., 712, 713, 1075, 1091, 1095, 1100, 1107, 1116, 1121, 1155  
 SCOTT, W. J., 876, 1034  
 SCOTT, W. W., 1159, 1193  
 SCULTHORPE, C. D., 1180, 1193  
 SECK, C., 890, 895, 913, 1075  
 SEELEMANN, U., 825, 834, 1075  
 SEGAL, E., 847, 907, 912, 924, 941, 1075  
 SEGERSTRÅLE, S. C., 822, 867, 946, 974, 976, 1076  
 SEILING, F. M., 1158, 1192  
 SEKI, H., 1174, 1175, 1193  
 SERTORIO, T., 969, 1043  
 SETON, E., 910, 1076  
 SEURAT, L. G., 925, 1076  
 SHARMA, M. L., 910, 1076  
 SHAW, J., 825, 835, 868, 870, 871, 885, 886, 894, 913, 915-918, 921, 923, 926, 1036, 1076  
 SHAW, T. I., 888, 1044  
 SHELDON, R. W., 1177, 1193  
 SHIRA, A. F., 1183, 1190  
 SHOEMAKER, W. S., 1163, 1193  
 SHOUP, C. S., 875, 1076  
 SHULGINA, E. F., 825, 828, 829, 1080  
 SIEBURTH, J. McN., 780, 1076, 1169, 1193  
 SIEGENTHALER, P. A., 698, 1076  
 SIEPMANN, R., 691, 1076  
 SIMONSEN, R., 707, 1048, 1077  
 SIMPSON, D. C., 1000, 1077  
 SKUTCH, A. F., 810, 1055  
 SLANINA, K., 1181, 1193  
 SLEIGH, M. A., 941, 1034  
 SMITH, D. C. W., 1019, 1077  
 SMITH, H. W., 997, 1032, 1064, 1077  
 SMITH, R. I., 822, 831, 835, 868, 885, 899, 912, 913, 974, 1077  
 SÖRENSEN, S. P. L., 686, 1059  
 SORKINA, N. A., 1164, 1192  
 SOROKIN, Y. I., 975, 1081

- SOUTHGATE, B. A., 830, 1033  
 SOUTHWARD, A. J., 851, 911, 1042, 1077,  
 1117, 1126, 1150, 1155  
 SOUTHWARD, E. C., 911, 1077  
 SPARROW, F. K., 691, 1055  
 SPENCER, J. O., 862, 1077  
 SPOONER, G. M., 977, 1077  
 SRIVASTAVA, V. S., 696, 1064  
 STADELMANN, E. J., 703, 1077  
 STÄLFELT, M. G., 779, 1077  
 STANIER, R. Y., 690, 1077  
 STANLEY, R. J., 821, 1039  
 STANLEY, S. O., 690, 1077  
 STEEMANN NIELSEN, E., 898, 1077, 1099,  
 1101, 1155  
 STEELE, J. H., 1180, 1193  
 STEIN, W. D., 885, 1039  
 STEINBACH, H. B., 886, 896, 1077  
 STEPHENS, G. C., 910, 911, 913, 1072, 1077,  
 1078  
 STEPHENSON, A., 1134, 1155  
 STEPHENSON, T. A., 847, 848, 1038, 1134,  
 1155  
 STEVENSON, R. E., 831, 1045, 1162, 1190  
 STEWART, D. M., 889, 1064  
 STEWART, W. D. P., 693, 699, 1078  
 STICKNEY, A. P., 835, 1078  
 STIEVE, H., 969, 1078  
 STOBART, R. H., 895, 921, 1078  
 STOCK, J. H., 950, 974, 1044  
 STOCKER, O., 717, 770-773, 779, 815, 816,  
 1078  
 STONE, D., 868, 894, 913, 924, 929, 1043  
 STONER, L. C., 885, 1044  
 STOSCH, H. A. VON, 1178-1180, 1193  
 STOTT, G. H., 1003, 1004, 1054  
 STRASBURG, D., 1137, 1151  
 STRENZKE, K., 834, 896, 984, 1051  
 STRUCK, B., 1092, 1152  
 STUART, T. A., 1187, 1193  
 SUNDENE, O., 800, 1078  
 SUTCLIFFE, D. W., 835, 868, 870, 910, 913,  
 921-923, 1076, 1078  
 SUZAKI, K., 778-780, 1081  
 SVEDKLIVS, N., 1112, 1155  
 SVENDSEN, P., 1121, 1155  
 SVERDRUP, H. U., 825, 974, 1078, 1085, 1155,  
 1158, 1193  
 SVOBODA, A., 1130, 1155  
 SWEET, J. G., 1029, 1078  
 SWENSON, H. A., 1157, 1193  
 SZKIELDA, K. H., 1172, 1192  
  
 TABE, D. C., 969, 1079  
 TACA, N., 1174, 1175, 1193  
 TAIT, J. B., 1104, 1155  
  
 TAKACS, F. P., 701, 1079  
 TAKADA, H., 735-739, 768, 769, 1067  
 TAMUKAI, K., 1159, 1165, 1191  
 TATEDA, H., 1022, 1079  
 TECHET, K., 708, 1079  
 TESCH, F.-W., 832, 1079  
 THEEDE, H., 825, 836-839, 846, 863, 865, 868,  
 875, 893, 911, 913, 974, 1074 1079  
 THEILACKER, G., 1001, 1061  
 THIEL, M. E., 974, 1079  
 THIEMANN, K., 1104, 1105, 1155  
 THOMAS, L. P., 1120, 1155  
 THOMPSON, B. D., 877, 1066  
 THOMPSON, J., 703, 1079  
 THOMPSON, L. C., 868, 1079  
 THORADE, H., 1086, 1155  
 THORNDIKE, E. M., 1165, 1190  
 THORSON, G., 1186, 1193  
 THREADGOLD, L. T., 1029, 1031, 1061, 1079  
 TIETJENS, O., 1147, 1153  
 TOMMERS, F. D., 1183, 1184, 1192  
 TONER, R. C., 934, 936, 1061  
 TOPPING, F. L., 899, 1079  
 TORMEY, J. MCD., 894, 1044  
 TORREY, J. G., 787, 1079  
 TOWLE, A., 902, 910, 1079  
 TRAGANZA, E. D., 690, 1064  
 TRAMER, P. O., 732, 733, 1079  
 TRAUT, W., 953, 1079  
 TRAVIS, D. M., 910, 1079  
 TREHERNE, J. E., 921, 1079  
 TRESSLER, W. L., 1165, 1192  
 TREZZI, F., 820, 1079  
 TROSHIN, A. S., 884, 885, 1079, 1080  
 TRUMP, B. F., 1013, 1053  
 TSCHUGUNOVA, M. N., 875, 877, 1036  
 TSURIKOV, V. L., 825, 828, 1080  
 TSURIKOVA, A. P., 825, 828, 829, 1080  
 TUREKIAN, K. K., 687, 1075  
 TYLER, M. E., 689, 690, 695, 701, 1080  
 TYNEN, M. J., 866, 1080  
  
 URL, W., 711, 1053  
 UESPRUNG, A., 768, 1080  
 USMAKOV, P. V., 954, 1080  
 USSINO, H. H., 885, 894, 1034, 1080  
 UTERMÖHL, H., 1109, 1155  
  
 VACCARO, R. F., 1159, 1192  
 VALIKANAS, I., 792, 797, 809, 822, 1080  
 VALENTIN, H., 1135, 1155  
 VANDEL, A., 862, 872, 1080  
 VASILESCU-MARINESCU, E., 800, 1080  
 VENKATRAMIAH, A., 932, 933, 1060  
 VERHOEFF, K. W., 988, 1080  
 VERNBERG, F. J., 836, 974, 1080

- VERNBERG, W. B., 974, 1080  
 VERWEY, J., 925, 969, 973, 1080  
 VEVEERS, H. G., 1129, 1155  
 VICKERS, T., 1031, 1050  
 VIKHRENKO, N. M., 1164, 1194  
 VINETSKAYA, N. I., 825, 828, 1080  
 VINOGRADOV, A. P., 866, 1080  
 VINOGRADOV, M. E., 975, 1081  
 VIOLANTE, U., 897, 1048  
 VIRABHADRACHARI, V., 1032, 1081  
 VIRKAR, R. A., 900, 910, 1081  
 VISHNIAC, H. S., 691-693, 697, 700, 1081  
 VISWANATHAN, R., 868, 913, 1069  
 VOLLENWEIDER, R. A., 699, 1081  
 VOLODIN, V. M., 1027, 1081  
 VORONINA, N. M., 975, 1081  
 VOROSHILOVA, A., 694, 1044  
  
 WÄLSHE-MAETZ, B. M., 876, 1081  
 WAERN, M., 790, 791, 1081, 1111, 1121, 1155  
 WAGNER, H. H., 998-1000, 1041  
 WAINWRIGHT, S. A., 1125, 1131, 1146, 1151, 1155  
 WALD, C., 1032, 1081  
 WALFORD, L., 974, 1081  
 WALKER, F. T., 1120, 1155  
 WALLEN, I. E., 1183, 1194  
 WALTER, H., 732, 770, 1081  
 WALTHER, J., 825, 1081  
 WANGERSKY, P. J., 1168, 1193  
 WARD, H. B., 1182, 1194  
 WATANABE, T., 778-780, 1081  
 WATERMAN, T. H., 876, 945, 1081, 1083  
 WATERING, W. P. M. VAN DE, 1086, 1150  
 WEBB, D. A., 889, 895, 913, 1073, 1081  
 WEBER, A., 896, 1081  
 WEBER, F., 709, 1081  
 WEIL, E., 834, 899, 903, 1081  
 WEISEL, G. F., 1025, 1082  
 WELCH, P. S., 1157, 1194  
 WELLS, G. P., 936, 945, 1082  
 WELLS, H. W., 974, 1082  
 WELLS, J. W., 1125, 1155, 1156  
 WENDELL, B. J., 1016, 1082  
 WERTZ, H. O., 868, 913, 1082  
 WESTERHAGEN, H. VON, 998, 1026, 1082  
 WEYMOUTH, F. W., 876, 1082  
 WHATLEY, F. R., 747, 1038  
 WHITE, E. I., 997, 1082  
 WHITE, J. J., 862, 1082  
  
 WIDMANN, E., 868, 1082  
 WIEGHARDT, K., 1147, 1156  
 WIESER, W., 897, 1082  
 WIGGLESWORTH, V. B., 921, 922, 984, 1082  
 WILBER, C. G., 1157, 1181  
 WILBER, G. C., 910, 1076, 1082  
 WILBUR, B. C., 832, 913, 1064  
 WILBUR, K. M., 883, 983, 1082  
 WILCE, R. T., 1121, 1156  
 WILLIAMS, A. B., 913, 1082  
 WILLIAMS, J., 1157, 1194  
 WILLIAMS, J. C., 785, 1046  
 WILLIAMS, O. B., 691, 1069  
 WILLIAMSON, R. S., 998, 1052  
 WILLMER, E. M., 1031, 1057  
 WILSON, D. P., 834, 1082  
 WINBERG, G. G., 1003, 1082  
 WINGE, Ö., 1105, 1156  
 WINKLE, W. VAN, JR., 876, 877, 939, 1082  
 WINTER, J. E., 937, 1082, 1184, 1194  
 WITIG, H., 825, 827, 828, 1082  
 WIUM-ANDERSEN, S., 898, 1077  
 WOHLBERG, E., 1179, 1194  
 WOJTCZAK, A., 899, 913, 1038  
 WOLF, H. W., 1183, 1192  
 WOLVEKAMP, H. P., 876, 1083  
 WONG, P. T. S., 696, 697, 1083  
 WOOD, E. J. F., 1170, 1194  
 WOODHEAD, A. D., 1031, 1083  
 WOODHEAD, P. M. J., 1031, 1083  
 WORK, R. C., 1120, 1155  
  
 YANAGIMACHI, R., 1025, 1083  
 YONGE, C. M., 883, 1082  
 YORK, H. H., 810, 815, 1055  
 YOSHIDA, T., 1106, 1156  
 YOLLE, P. V., 843, 880, 1038  
  
 ZAITSEV, J. P., 998, 1083  
 ZALKINA, A. V., 975, 1083  
 ZANEVELD, J. S., 810, 819, 820, 1083  
 ZAR, J. H., 862, 1082  
 ZEGLER, J. M., 1087, 1153  
 ZEITZSCHEL, B., 1177, 1194  
 ZENKOVICH, L. A., 822, 825, 866, 912, 913, 974, 1083, 1140, 1156  
 ZHIRMUNSKY, A. V., 836, 1083  
 ZOBELL, C. E., 689, 690, 700, 1083, 1169, 1170, 1194  
 ZUCKERKANDL, E., 897, 1083



## TAXONOMIC INDEX

- Abramis brama*, 1027, 1068  
*Acanthocyclops viridis*, 830  
*Acanthomyxis macropsis*, 957  
*Acanthophora spicifera*, 806  
*Acartia*, 962  
*A. clausii*, 957, 970  
*A. longiremis*, 957  
*A. tonsa*, 957  
*Acetabularia crenulata*, 805  
*Achnanthes*, 812  
*A. brevipes*, 810  
*A. curvirostrum*, 808  
*A. taeniata*, 797  
*Acmaea limatula*, 846, 941, 1075  
*Acrosiphonia*, 814  
*A. centralis*, 790  
*Acrosiphonia-Polysiphonia* association, 814  
*Actinia equina*, 1083  
 actinians, 948  
*Actinocyclus ehrenbergii*, 797  
*A. oceanicus*, 808  
 Actinozoa, 1073  
*Aedes*, 870  
*A. aegypti*, 895, 921, 922, 1068, 1078  
*A. detritus*, 921-923, 1036  
*Aequoria* sp., 956  
*Aeromonas proteolytica*, 690, 1064  
*Aeschna*, 921  
*Agardhiella tenera*, 715, 806  
*Agarum*, 1110  
*Aglaophenia*, 1143  
*A. elongata*, 1143, 1145, 1146  
*A. pluma*, 1138, 1141, 1142, 1145  
*A. pluma dichotoma*, 1142, 1145, 1146  
*A. pluma octodonta*, 1142, 1145  
*A. pluma typica*, 1142, 1143  
*A. septifera*, 1143, 1145  
*A. tubulifera*, 1145  
 Aglaopheniidae, 1146  
 Aglaopheniinae, 1145  
*Agropyron junceum boreo-atlanticum*, 1064  
*Agrostis alba*, 796  
*Ahnfeltia plicata*, 801  
*Aktedrilus monospermatecus*, 1055  
*Alaria*, 814, 1095, 1110, 1116, 1118, 1187  
*A. esculenta*, 801  
*A. valida*, 813  
 albacore, 1192  
*Alderia modesta*, 875, 1047  
 algae, 705ff, 898, 968, 1036, 1037, 1039, 1044, 1048, 1053, 1059-1062, 1065, 1068, 1071, 1072, 1074, 1076, 1078, 1081, 1083, 1091ff, 1124, 1149-1156, 1177ff  
 algae, blue-green, 689ff, 797, 807, 808, 812, 1034, 1046, 1060, 1089, 1117, 1167ff  
 algae, brown, 711, 739, 741, 778, 789, 790, 792, 1066, 1153  
 algae, green, 711, 739, 741, 747, 792, 797, 808, 1066, 1112, 1125, 1153  
 algae, mangrove, 711  
 algae, red, 707-713, 732, 741, 789, 790, 792, 800, 1037, 1053, 1107, 1155  
*Alona costata*, 957  
*A. quadrangularis*, 956  
*Ambloplites rupestris*, 1183  
*Amphidinium höfleri*, 711  
*A. cf. operculatum*, 756  
*A. sp.*, 712  
*Amphipleura rutilans*, 810  
*Amphipoda*, 872, 873, 875, 883, 970, 1082  
*Amphiprora alata*, 808  
*A. paludosa*, 810  
*Amphiroa fragilissima*, 805  
*Amphisphaeria maritima*, 691  
*Amphitrite*, 889  
*Amphora commutata*, 810  
*A. gigantea*, 808  
*A. turgida*, 808  
*Amphoroidea media*, 846, 847, 849  
*Anabaena baltica*, 792  
*A. cylindrica*, 693, 698, 1033, 1046  
*A. variabilis*, 698  
*Anabolia nervosa*, 921, 922  
*Anacystis nidulans*, 698  
*Anadonta* sp., 958  
*Anadyomene stellata*, 766  
 Ancestrulac, 1147  
 anemones, 948  
*Anemonia sulcata*, 948, 1062  
 angiosperms, 707, 1034  
*Anguilla anguilla*, 1000, 1001, 1041, 1047, 1063  
*A. rostrata*, 1048  
*A. vulgaris*, 1024, 1042  
*Anisogammarus confervicolus*, 957  
*Ankistrodesmus falcatus*, 699, 808  
 Annelida, 889, 898, 910, 956, 1046, 1068, 1076, 1078  
*Anondonta cygnaea*, 878, 926, 1070  
*Antho involvens*, 1139  
*Anthopleura stellula*, 948, 1075  
 Anthozoa, 1130, 1135, 1149  
*Antithamnion cruciatum*, 707

- A. plumula*, 718  
*Aphrodite aculeata*, 889  
*Apium graveolens*, 796  
*Aporrhais*, 1144  
 Appendicularia, 970, 1105  
*Archaeomysis grebnitzkii*, 957  
*Archidoris pseudoargus*, 886, 887  
*Arctica islandica*, 1082, 1184, 1194  
*Arenicola*, 889, 905, 906, 938, 1082  
 Armadillidiidae, 862, 988  
*Armadillidium*, 988  
*Armeria vulgaris* var. *maritima*, 796  
*Artemia*, 1033, 1034, 1050, 1064, 1071  
*A. franciscana*, 1038  
*A. mülhausei*, 1074  
*A. salina*, 823, 826, 827, 832, 868, 869, 875, 883, 913, 921, 927, 928, 931, 950-952, 972, 976, 983, 994, 995, 1038, 1042, 1043, 1045, 1047-1050, 1052, 1057, 1061, 1064, 1070, 1074  
 Ascidia, 1135, 1153  
 Ascomycetes, 691, 700, 1049  
*Ascophyllum*, 814, 1106, 1112, 1116, 1118  
*A. nodosum*, 750, 752, 779, 780, 782, 783, 785, 786, 801, 810, 819, 820, 1052, 1099, 1112, 1113, 1120  
*Astellus aquaticus*, 830, 835, 870, 872, 1062  
*A. sp.*, 871, 958  
*Aspergillus*, 692  
*Asplanchna* sp., 956  
*Assimineca grayana*, 1075  
 Astacidae, 871  
*Astacus*, 875  
*A. astacus*, 871, 876, 913, 930, 932, 987, 1044  
*A. fluviatilis*, 835, 870, 1039  
*A. pallipes*, 835, 1076  
*Aster tripolium*, 796  
*Asterias*, 875  
*A. forbesi*, 1046  
*A. rubens*, 894, 895, 913, 946, 1037, 1055, 1064  
*Asterionella*, 1103  
*A. japonica*, 1103  
*A. sp.*, 800  
*Asterocystis racemosa*, 792  
*Atriplex hastata*, 780  
*Atropis maritima*, 1178  
*Aulacodiscus* sp., 1180  
*Aurelia aurita*, 946  
*A. flavidula*, 886, 1063  
*A. sp.*, 956  
*Australorbis glabratus*, 834  
*Australoplax tridentata*, 912, 974  
*Austropotamobius pallipes*, 1043  
*Azinella*, 1142, 1144  
*A. damicornis*, 1142, 1143  
*A. polypoides*, 1142, 1143  
*A. (poriferans)*, 1143  
*A. verrucosa*, 1143  
  
*Bacillaria paradoxa*, 797  
 Bacillariales, 1054  
*Bacillus subtilis*, 1175  
 Bacteria, 689ff, 1036, 1039, 1044, 1046, 1049, 1052, 1053, 1061-1063, 1066, 1069, 1070, 1072, 1077, 1080, 1083, 1089, 1167ff, 1190-1193  
*Bacterium vulgare*, 1175  
 Balanidae, 1126, 1139  
*Balanus*, 825, 1132, 1135  
*B. amphitrite amphitrite*, 845, 846  
*B. balanoides*, 842, 852-862, 875, 905, 926, 937, 938, 941, 973, 1038, 1049, 1074, 1119  
*B. balanus*, 905, 926, 941  
*B. crenatus*, 858-862, 926, 941, 1038, 1119  
*B. eburneus*, 845  
*B. improvisus*, 905, 926, 941  
*B. perforatus*, 1124, 1126  
*B. tintinnabulum*, 970  
*Bangia*, 814, 1095, 1116  
*B. fuscopurpurea*, 717, 770, 805, 1081  
*Bangia-Urospora* association, 814  
 barnacles, 830, 851-853, 859, 920, 973, 1034, 1035, 1042, 1047, 1049, 1061, 1150, 1155  
*Batophora oerstedii*, 805  
*Bellerochea malleus*, 1103  
*Bellis perennis*, 796  
*Beneckea*, 1175  
*Biddulphia*, 1104  
*B. regia*, 808  
*B. sp.*, 1103  
*B. titania*, 1053  
 Biddulphiaceae, 706  
*Bifurcaria*, 1116, 1187  
*Biomphalaria pfefferi*, 1186  
*Birgus*, 988  
*B. latro*, 868, 873, 925, 1051  
 bivalves, 836, 974, 1074, 1079, 1082, 1135, 1192  
*Blennius pholis*, 1000, 1054  
*Blidingia*, 1095, 1116  
*B. minima*, 790, 1117  
*Bosmina* sp., 957  
*Bostrychia*, 717, 807  
*B. scorpioides*, 779  
*B. sp.*, 707  
*B. tenella*, 711  
*Botryllus schlosseri*, 977, 1073  
*Botryocladia pseudodichotoma*, 716  
*Botryoglossum farlowianum*, 716  
*B. ruprechtianum*, 715  
*Brachiomonas submarina*, 804  
*Brachionus calyciflorus*, 956  
*B. plicatilis*, 956

- Brachyrhyncha*, 944  
*Brachyura*, 870, 1037, 1071  
*Branchidontes recurvus*, 937, 938, 1066  
*Branchipus*, 872, 1074  
*B. schaefferi*, 872  
*Breslailla relicta*, 823  
*Brissus unicolor*, 849-851  
 brittle stars, 1129  
*Bronniartella byssoidea*, 708  
*Brunella vulgaris*, 796  
*Bryocampus hiemalis*, 957  
*Bryocladia cuspidata*, 806  
*Bryopsis duplex*, 734  
*B. hypnoides*, 759, 805, 1097  
*B. plumosa*, 733, 1097  
 bryozoans, 1119, 1135, 1144, 1147  
*Buccinum undatum*, 886, 887  
*Bulinus globosus*, 1186  
*Bupleurum tenuissimum*, 796  
  
*Carnia fumosa*, 1037  
*Calanus*, 1049  
*C. finmarchicus*, 876, 957  
*Callinassa*, 868, 1079  
*Callinectes sapidus*, 843-845, 879, 880, 893, 909, 932, 1042, 1064  
*Callithamnion*, 814  
*Callitriche autumnalis*, 793  
*C. tetragonum* var. *brachiatum*, 707, 708, 710  
*Callophyllis flabellulata*, 715  
*C. heanophylla*, 715  
*C. laciniata*, 801, 803  
*C. violacea*, 716  
*Caloglossa adnata*, 717  
*C. leprieurii*, 711, 717  
*C. ogasawaraensis*, 707  
*Caloneis amphiboema*, 809, 817, 818  
*C. formosa*, 810  
*Calothrix parietina*, 693  
*C. scopulorum*, 693  
*Cambarus clarkii*, 1062  
*C. immunis*, 1052  
*Campanopsis*, 1140  
 Campanulariidae, 1146  
*Cancer antennarius*, 887  
*C. magister*, 958  
*C. pagurus*, 905, 944, 945  
*Candida*, 691, 692  
*Canuella canadensis*, 957  
*Carassius auratus*, 1009, 1022  
*Carcharinus leucas*, 1032  
*Carcinides maenas* (Syn: *Carcinus maenas*), 1039, 1079  
*Carcinus*, 1076  
*C. maenas*, 825, 829, 868, 869, 875, 890, 893-895, 899, 911, 913, 915-918, 924, 926, 930, 944, 945, 950, 1037, 1046, 1056, 1062, 1066, 1072, 1073, 1076, 1079, 1081  
*C. mediterraneus*, 1062  
*Cardisoma carnifex*, 870, 925  
*C. guanzhoui*, 880, 909, 1042, 1052, 1056, 1071  
*Cardium edule*, 836-839, 846, 981-983, 994, 1035, 1045, 1061  
*C. edule* var. *lamarcki*, 982  
*C. lamarcki*, 982, 983, 1061  
*Carex distans*, 796  
*C. goodenoughii*, 796  
*Carpophyllum moschatocarpum*, 772  
*Caspiolosa volgensis*, 1026, 1068  
*Catenella repens*, 711  
 catfish, 1079  
*Caudina*, 1060  
*C. chilensis*, 895, 905, 1059, 1060  
*Caulerpa*, 1112  
*C. crassifolia*, 805  
*Centrocercas clavulatum*, 711, 806  
*Centropages memmrichi*, 957  
 cephalopods, 886-888, 897, 910, 944, 945  
*Ceramium*, 1107  
*C. ciliatum*, 708-710, 730, 734  
*C. diaphanum*, 712, 713, 792  
*C. durum*, 712, 713, 759, 801, 1099  
*C. sp.*, 735, 736, 1100  
*Cerataulina bergoni*, 800, 1104  
*C. pelagica*, 712  
*Ceratia*, 1153  
*Ceratium*, 800, 1109  
*C. farca*, 712, 756  
*C. fusus*, 712, 756  
*C. lineatum*, 756  
*C. sp.*, 1104  
*C. tripos*, 756  
*Ceratophyllum demersum*, 761, 763  
*Ceriosporopsis halima*, 691  
*C. maritima*, 691  
*Chaetoceros*, 800, 1103  
*C. curvisetus*, 1110  
*C. danicus*, 1103  
*C. debilis*, 1103  
*C. elmorei*, 712  
*C. radians*, 712  
*C. similoides*, 808  
*C. sp.*, 747  
*C. tenuissimus*, 1104  
*Chaetognatha*, 970, 1103, 1150  
*Chaetomorpha aerea*, 732  
*C. brachygena*, 805  
*C. canabina*, 714, 1037  
*C. licentia*, 733, 759, 763-765, 1056, 1107  
*C. melagonium*, 790  
*C. tortuosa*, 732  
*Chama cornucopia*, 836

- Chanos chanos*, 1006  
*Chaos chaos*, 1041, 1064  
*Chara baltica*, 733  
*Chelonobia patula*, 845, 846  
*Chirocephalus diaphanus*, 872, 1069  
*Chironomus*, 834, 870, 923, 1067  
*C. halophilus*, 823, 832, 921, 922  
*C. salinarius*, 823, 832, 921, 922  
*C. thummi*, 832, 896, 984, 1051  
*C. thummi thummi*, 921, 922  
*Chiton*, 1034  
*C. tuberculatus*, 926  
 chitons, 926  
*Chlamydomonas*, 707  
*Chlorella*, 707, 735  
*C. ellipsoidea*, 747, 748  
*Chlorocella*, 806  
*Chlorogloea fritschii*, 693  
 Chlorophyceae, 790, 791, 798, 800, 802, 814  
 Chlorophyta, 705, 766  
*Chondria atropurpurea*, 806  
*C. sedifolia*, 806  
*C. tenuissima*, 806  
*Chondrus*, 1116  
*C. crispus*, 779, 1097, 1100  
*Chorda*, 1112, 1116  
*C. flum.*, 792, 1099, 1111, 1121  
*Chroococcus*, 698, 1045  
*Chrysaora quinquecirrha*, 833, 948, 1040  
 Chrysophyta, 705, 806  
 chthamaliids, 1126  
*Chthamalus*, 1132  
*C. depressus*, 851, 1035  
*C. stellatus*, 861, 862, 905, 926, 941, 1065  
*Chyocladia verticillata*, 801  
*Chydorus globosus*, 957  
 ciliates, 917, 949, 1034  
*Ciona intestinalis*, 825, 842  
*C. intestinalis* f. *typica*, 1045  
 Cirripedia, 851, 874, 941, 957, 970, 1035, 1042, 1049, 1132  
*Citharichthys stigmaeus*, 1003  
 Cladocera, 1064  
*Cladocora cespitosa*, 1141, 1142  
*C. cespitosa aestreaaria*, 1142  
*C. cespitosa typica*, 1142  
*Cladonema*, 1140  
*Cladophora*, 730, 812, 1100, 1107  
*C. aegagropila*, 1111  
*C. fascicularis*, 805  
*C. gracilis*, 718  
*C. luteola*, 805  
*C. refracta*, 805  
*C. rupestris*, 718, 790, 1116  
*C. sp.*, 710, 968  
*C. trichotoma*, 715, 716  
*Cladophoropsis macromeres*, 805  
*C. membranacea*, 805  
*Cladostephus*, 1116  
*C. spongiosus*, 766  
 clams, 830, 939, 1043, 1054, 1186  
*Claudea elegans*, 1111  
*Clausocalanus arcuicornus*, 957, 970  
*Clava multicornis*, 879, 948, 949, 1059  
*Cletocampius* sp., 823, 827  
*Clione limacina*, 1065  
*Clunio marinus*, 921  
*Clupea harengus*, 997, 998, 1000-1002, 1006, 1010-1012, 1025-1029, 1032, 1039, 1052, 1053, 1055, 1191  
*C. harengus membras*, 1029, 1032, 1061  
*C. pallasii*, 1000, 1026, 1027  
 clupeids, 1025, 1037  
*Clymenella torquata*, 910, 911, 1078  
 cnidarians, 910, 976, 1069, 1141  
 coccolithophorids, 799, 800  
*Coccolithus huxleyi*, 1104  
*C. (=Pontosphaera) huxleyi*, 1103  
*Cocconeis pensacolatae*, 808  
 cockles, 982  
*Codium*, 1116  
*C. bursa*, 766  
*C. fragile*, 758, 759  
*C. tomentosum*, 766, 1115  
*Coelastrum microsporium*, 808  
*C. reticulatum*, 808  
 Coelenterata, 886, 898, 905, 956, 978, 1058  
*Coelopa frigida*, 921, 923  
*Coenobita*, 988  
*C. brevimanus*, 873, 925  
*C. clypeatus*, 895  
*C. perlatus*, 873, 925, 1076  
*Colpomenia sinuosa*, 813  
*Colurella adriatica*, 823  
*C. colurus*, 823  
*Cominella cincta*, 847, 848, 934  
*Conchocelis*, 707  
*Convoluta roscoffensis*, 1049  
 Copepoda, 833, 954, 970, 972, 974, 975, 1035, 1051, 1064, 1103  
*Corallina*, 811, 814, 1061, 1116  
*C. officinalis*, 803, 805, 1097, 1150  
*Coralllopsis opuntia*, 1112  
 corals, 1114, 1120, 1123, 1125, 1135, 1146, 1150-1153, 1155  
*Corbicula fluminea*, 958  
*Corbulomya maotica*, 829  
*Cordyllophora*, 1047, 1058  
*C. caspia*, 826, 834, 879, 928, 939, 947-949, 956, 976, 978-981, 984-994, 1049, 1058, 1073  
*Coregonus clupeaformis*, 1005

- Corethra*, 1051  
*C. dumicornis*, 921, 1074  
*Cosiphium salmonis*, 957  
*C. spinicorne*, 957  
*C. volutator*, 831, 875, 890, 962, 1063  
*Corycaeus affinis*, 957  
*C. anglicus*, 970  
*C. sp.*, 970  
 Crystoidea, 944  
*Coscinodiscus*, 800, 1104  
*C. eccentricus*, 808  
*C. oculus iridis*, 808  
*C. perforatus*, 808  
*C. wailesii*, 758, 1057  
*Cosmarium abbreviatum* var. *minor*, 808  
*C. phaseolus* var. *minutus*, 808  
 crab, wool-handed, 706  
 crabs, 847, 868, 869, 873, 880, 894, 907, 920, 925, 929, 932, 974, 987, 988, 1034, 1035, 1042, 1043, 1046, 1050, 1055, 1056, 1069, 1074, 1075, 1082  
 Cranchiidae, 888  
*Crangon crangon*, 868, 907, 908, 913, 924, 925, 1039, 1041, 1044, 1046  
*C. franciscorum*, 958  
*C. nigricauda*, 958  
 Craspedomonada, 806  
*Crassostrea gigas*, 883, 951, 985  
*C. virginica*, 829, 831, 876, 877, 939, 951, 1186, 1187  
 crayfish, 1053  
*Cricotopus vitripennis*, 921, 923  
 Crinoida, 1152  
 Crustacea, 826, 834, 835, 867, 868, 870-873, 876, 886, 889, 891, 897, 910, 915, 944, 951, 956, 976, 977, 983, 987, 988, 1036, 1037, 1040, 1043, 1048, 1050, 1051, 1058, 1061, 1062, 1067-1069, 1071, 1073, 1074, 1076, 1081-1083  
*Cryptomonas* sp., 712  
*Cryptopleura ramosum*, 708  
*C. violacea*, 716  
 Cryptophyta, 806  
 Ctenophora, 956, 970  
*Culex pipiens*, 921, 922  
*Cuspidella*, 1140  
 Cyanophyceae, 700, 798, 1045, 1046, 1069  
 Cyanophyta, 699, 700, 705, 806, 807  
*Cyathura*, 1040  
*C. polita*, 875, 907, 924, 1047, 1075  
 Cyclopoida, 1083  
*Cyclops vernalis*, 957  
 Cyclostomata, 1073  
*Cyclotella meneghiniana*, 809  
*C. nana*, 756, 1050  
*C. sp.*, 712  
*Cymodocea manitorum*, 805, 1097  
*Cymodocella egregia*, 849  
*Cyprinodon macularius*, 927, 997, 1006-1009, 1016, 1026, 1029, 1035, 1078  
*C. variegatus*, 997, 1000  
 cyprinodonts, 1059, 1077  
*Cystoseira*, 1116  
*C. abrotanifolium*, 766  
*C. barbata*, 733, 734  
*C. crinita*, 765  
*C. tamariscifolia*, 1116  
 Cytophaga, 694  
*Daphnia*, 1061  
*D. longispina*, 957  
*D. magna*, 871, 951, 1047  
*D. pulex*, 957  
*Dasya mollis*, 711  
*D. pedicellata*, 752, 1067  
*Debaromyces*, 692, 693  
*D. kloeckeri*, 692  
 decapods, 845, 879, 891, 893, 908, 910, 917, 925, 929, 949, 1055, 1071  
*Delesseria sanguinea*, 712, 713, 743, 801, 817, 818, 1066, 1095, 1100, 1106, 1153  
*D. sanguinea* f. *lanceolata*, 745  
*D. sp.*, 1119  
*Dendrostomum signifer*, 1056  
*D. zostericolum*, 1050, 1069  
*Desmarestia*, 814  
*D. aculeata*, 779, 813, 1106  
*D. foliacea*, 715  
*D. viridis*, 759  
 desmids, 808  
*Diadema antillarum*, 849-851, 1114  
*Diadumene luciae*, 948, 1065  
*Diaphanosoma brachyurum*, 956  
*Diaptomus ashlandi*, 957  
*D. franciscanus*, 957  
*D. novamexicanus*, 957  
*Diaschiza* sp., 823, 827  
 Diatomeae, 705, 712, 734, 735, 797, 798, 804, 808, 809, 812, 817, 968, 1033, 1039, 1040, 1048, 1051, 1054, 1060, 1077, 1103-1105, 1110, 1178-1180, 1190, 1192, 1193  
*Dictyopteris membranacea*, 741-743, 766, 1048  
*Dictyosiphon foeniculaceus*, 792  
*Dictyosphaerium pulchellum*, 808  
*Dictyota dichotoma*, 718, 734, 805  
*D. indica*, 805  
*Digenea simplex*, 806  
*Dikergammarus haemobaphus*, 834  
*Dinobryon*, 707  
 Dinoflagellata, 705, 735, 756, 798, 800, 802, 806, 807, 1178  
*Dinophilus gyrotilatus*, 953, 1079

- Dinophysis*, 800  
*Diplanthera*, 811  
*D. wrightii*, 805, 1097  
Diptera, 827, 907, 921-923, 1059, 1078  
*Ditylum brightwellii*, 734, 1050  
*D. sp.*, 800  
*Dniester liman*, 1034  
*Dreissena*, 1044, 1063  
*D. polymorpha*, 835, 898  
dogfish, spiny, 1040, 1082  
*Dromia vulgaris*, 890, 891, 944, 945  
Dromiacea, 944  
*Dumontia incrassata*, 1096, 1108  
*Dunaliella*, 756, 757, 1062  
*D. euchlora*, 757  
*D. magna*, 757  
*D. media*, 757  
*D. (Monas dunalii)*, 827  
*D. parva*, 757  
*D. parva f. eugameta*, 757  
*D. peircei*, 757  
*D. salina*, 757, 820  
*D. salina f. oblonga*, 757  
*D. tertiolecta*, 883, 952  
*Dynamenella cordiforaminalis*, 846, 849  
*D. hirsuta*, 846, 849  
*D. huttoni*, 849  
*Dynamenopsis varicolor*, 849  
  
*Ebria tripartita*, 797  
echinoderms, 834, 849, 894, 895, 898, 910, 976, 1038, 1046, 1144  
echinoids, 850, 851, 1049  
*Echinometra lucunter*, 849-851  
*Echinus esculentus*, 834, 894  
Echiura, 1046, 1068, 1154  
*Ectocarpus confervoides*, 805  
*E. duchassaingianus*, 805  
*E. siliculosus*, 805  
*Ectochaete leptochaete*, 790  
eel, 706, 1019, 1031, 1041, 1057  
eel-grass, 1180  
*Eisenia arborea*, 1113, 1150  
*E. bicyclis*, 729, 752, 754  
*Elachista*, 708  
*E. fucicola*, 718, 792  
elasmobranch, 1015, 1016  
*Eledone cirrosa*, 886-888  
*Eleutheria*, 1140  
*Elminius modestus*, 858-862, 905, 926, 937, 938, 941  
*Elodea canadensis*, 793, 1099  
*Emerita talpoida*, 868  
*Encentrum marinum*, 823  
*Enchelyopus cimbrius*, 997, 1027, 1029, 1035  
Enchytraeidae, 1080  
*Enchytraeus albidus*, 835, 864-866, 939, 985, 1017, 1055  
*E. sp.*, 956  
*Endocladia muricata*, 715, 716  
*Ensis ensis*, 887  
*Enteromorpha*, 735, 807, 814, 1107, 1116  
*E. clathrata*, 761, 790, 805, 1037  
*E. compressa*, 734, 790  
*E. flexuosa*, 805  
*E. intestinalis*, 779, 790, 805, 819  
*E. linza*, 715, 718, 771-774, 1096, 1108  
*E. marginata*, 819, 1046  
*E. plumosa*, 805  
*E. prolifera*, 790, 805  
*E. sp.*, 722  
*Entocladia viridis*, 790  
*Ephydatia fluviatilis*, 947  
*Ephydra*, 826  
*E. cinerea*, 895, 921, 922, 924, 1067  
*E. macellaria*, 823, 827, 922  
*E. micans*, 1037  
*E. riparia*, 921-923, 1037  
*E. strenzkei*, 921, 922  
*Epicladia flustrae*, 790  
*Epinebalia pugettensis*, 957  
*Eriocheir*, 894, 1043  
*E. sinensis*, 823, 830, 870, 875, 876, 894, 895, 917, 1041, 1059, 1062, 1076  
*Eriphia spinifrons*, 875  
*Erythraea pulchella*, 796  
*Erythrotrichia carnea*, 805  
*Etone sp.*, 956  
*Etroplus maculatus*, 1032, 1081  
*Eucampia zodiacus*, 1104  
Eudendriidae, 1145  
*Eudendrium*, 1131, 1143, 1145  
*E. racemosum*, 1143  
*E. rameum*, 1130, 1132, 1138, 1143, 1145  
*E. ramosum*, 1138, 1143, 1145  
*Eudesme zosterae*, 805  
*Eudorina elegans*, 808  
Euglenaceae, 802  
Euglenophyta, 705, 806  
*Eunicella*, 1131  
*E. cavolinii*, 1130, 1135, 1137, 1138, 1141, 1142, 1146  
*Eupagurus bernhardus*, 891, 944, 945  
*E. prideauxi*, 891, 944, 945  
*Eupleura caudata*, 939, 953, 1048, 1064  
*Eupomatus dianthus*, 937  
*Eurycercus lamellatus*, 956  
*Eurytemora*, 962  
*E. hirundo*, 970, 972  
*E. hirundoides*, 957  
*Euterpina acutifrons*, 970  
*Euthora cristata*, 801

- Evadne nordmanni*, 957  
*Exosphaeroma obtusum*, 849  
*E. planum*, 849  
*Exuviaella baltica*, 1103, 1104  
*E. cordata*, 800  
*E. sp.*, 712  
  
*Fabricia*, 1035  
*F. sabella*, 977  
*Fabriciella*, 1035  
*Fauchea laciniata*, 715  
*Festuca arundinacea* var. *baltica*, 796  
*F. distans*, 796  
*F. rubra*, 796  
fishes, 997ff, 1034, 1036-1041, 1044, 1047, 1050, 1053, 1054, 1057, 1059, 1065, 1068-1070, 1075, 1077, 1079, 1082, 1114, 1137, 1149, 1151, 1181, 1182, 1184, 1187-1189, 1192-1194  
Flagellata, 712, 756, 797-799, 806  
Florideae, 814  
flounders, 1019  
*Foshiella le jolisii*, 806  
*Fragilaria*, 812  
*F. sp.*, 800  
Fucaceae, 770, 772, 785, 814, 819, 1041, 1046, 1068, 1070, 1083, 1113, 1150  
Fucales, 730, 772  
fucoids, 1060, 1152  
*Fucus*, 731, 751, 752, 770, 784, 1047, 1059, 1065, 1070, 1079, 1107, 1108, 1111, 1112, 1121, 1149, 1150, 1153  
*F. ceranoides*, 749-751, 782, 783, 1066, 1116  
*F. distichus*, 726  
*F. distichus anceps*, 1116  
*F. evanescens*, 813  
*F. inflatus*, 814  
*F. mytili*, 1112  
*F. serratus*, 719, 720, 726, 735, 743, 744, 750, 765, 771, 773, 776, 781-783, 785, 786, 801, 810, 811, 819, 820, 1066, 1075, 1095, 1099, 1100, 1112, 1113, 1116, 1118-1120, 1153, 1155  
*F. sp. f. nanus*, 1116  
*F. spiralis*, 726, 770, 771, 773, 785, 786, 801, 811, 814, 819, 820, 1112, 1113, 1116, 1118  
*F. spiralis f. limitaneus*, 1112  
*F. vesiculosus*, 719-721, 723-728, 730, 731, 735, 740, 749, 750, 770-773, 775-783, 785-787, 792, 801, 810, 814, 815, 817, 819, 820, 1037, 1066, 1068, 1075, 1095, 1099, 1100, 1107, 1108, 1112, 1113, 1116, 1118, 1120, 1153, 1154  
*F. vesiculosus f. subecostata*, 816, 817  
*F. vesiculosus f. vadorum*, 749-751  
*F. vesiculosus f. volubilis*, 779  
  
*F. vesiculosus* var. *muscooides*, 781  
*F. vesiculosus-Ascophyllum* association, 814  
*F. virsoides*, 734, 741, 743, 766, 816, 1048  
*Fundulus heteroclitus*, 1000, 1001, 1017, 1018, 1034, 1040, 1042, 1056, 1064,  
Fungi, 689ff, 1035, 1049, 1050, 1055, 1072, 1073, 1089, 1167ff  
Fungi Imperfecti, 691, 1049  
*Fungia*, 1077  
*F. scutaria*, 1078  
Funiculinidae, 1144  
*Furcellaria*, 1107, 1116  
*F. fastigiata*, 719, 720, 776, 792, 1100, 1107  
*F. fastigiata f. aegagropila*, 1102, 1107, 1111, 1149  
Furcellarietum, 791  
  
*Gadus callarias*, 998, 1026, 1027, 1029, 1031,  
*G. morhua*, 998, 1026, 1082, 1083  
*Gaffkya homari*, 690, 695, 701, 1049  
*Galiteuthis*, 888  
gammarids, 834, 1075, 1082  
*Gammarus*, 868, 891, 911, 1057, 1077  
*G. duebeni*, 825, 832, 835, 868, 872, 875, 890, 895, 896, 906, 907, 911, 913, 924, 946, 947, 949, 950, 953, 976, 977, 1040, 1054, 1057, 1058, 1062, 1076  
*G. lacustris*, 870, 871  
*G. locusta*, 868, 875, 876, 911, 913, 977, 987, 1053, 1057  
*G. obtusatus*, 868, 913  
*G. oceanicus*, 913, 977, 1057  
*G. pulex*, 835, 870-872, 876, 911, 987, 1062  
*G. pulex pulex*, 1076  
*G. salinus*, 868, 911, 977, 1057  
*G. sp.*, 1036  
*G. zaddachi*, 868, 977, 1044, 1057  
*Garveia franciscana* (Syn.: *Perigonimus megas*), 1058  
*Gasterosteus aculeatus*, 1000, 1019, 1022-1025, 1029, 1030, 1053, 1061, 1062,  
gastropods, 834, 835, 847, 934, 939, 945, 1034, 1038, 1039, 1065, 1129  
*Gastrosaccus sanctus*, 832, 1070  
*Gecarcinus lateralis*, 847, 868, 870, 873, 894, 925, 988, 1042  
*Gelidium amansii*, 729, 738, 744, 752, 754, 1102  
*G. cornutum*, 806  
*G. crinale*, 806  
*G. robustum*, 716  
*Germo alalunga*, 1185  
*Giffordia mitchellae*, 805  
*Gigartina*, 1116, 1118, 1187  
*G. californica*, 716  
*G. corymbifera*, 716  
*G. mamillosa*, 813

- G. papillata*, 715, 716  
*G. stellata*, 801  
*Gillichthys*, 1082  
*G. mirabilis*, 1025  
*Glaucus* sp., 944  
*Glaux maritima*, 796  
*Glenodinium*, 800  
*Gloiopeltis furcata*, 735, 736, 784, 813, 1064  
*G. tenax*, 735, 736, 773, 774, 784, 1064  
*Glyceria*, 889  
*Gnorimosphaeroma oregonensis*, 958  
*Gobia baltica*, 792  
Gobiesocidae, 1144  
*Gobius flavescens*, 1022  
*G. microps*, 1032, 1052  
*Golfingia gouldii*, 1079, 1081  
*Gomphonema exiguum*, 810  
*G. parvulum*, 809  
*Goniada* sp., 956  
*Gonyaulax*, 800  
*Gorgonacca*, 1145, 1146  
*Gorgonaria*, 1141  
*Gorgonia*, 1131, 1146, 1155  
gorgonians, 1139, 1146, 1147, 1155  
Gorgoniidae, 1145  
*Gracilaria blodgettii*, 806  
*G. cornea*, 806  
*G. crassissima*, 806  
*G. foliifera*, 760, 806, 1051  
*G. foliifera* var. *angustissima*, 806  
*G. verrucosa*, 735, 736, 806, 1097  
*Grammatophora*, 812  
grapsoids, 974  
*Grateloupia filicina*, 806  
*G. gibbesii*, 806  
*Griffithsia flocculosa*, 710  
*G. opunticoides*, 709, 732  
*Guinardia flaccida*, 734  
*Gunda ulvae*, 834, 1036, 1069, 1081  
guppies, 1028, 1048  
*Gymnodinium* sp., 970  
*Gytratrix hermaphroditus*, 823
- Haematodinium gessneri*, 807  
*Halacarus basteri basteri*, 907, 1059  
*Halarachnion ligulatum*, 718  
*Halecium*, 1143  
*H. halecinum*, 1143  
*H. lancesteri*, 1143  
*H. mediterraneum*, 1143  
*Halidrys*, 814, 1112, 1116  
*H. siliquosa*, 779, 1099, 1115  
*Halimeda*, 1112  
*H. tuna*, 766  
*Haliotis*, 1135  
*Halliella casperi*, 827, 922
- Halocordyle disticha*, 1130, 1132  
*Halocynthia*, 1148  
*Halophila engelmannii*, 805  
*Halophiobolus opaca*, 691, 692  
*H. salina*, 691  
halophytes, 793, 795, 1070  
*Halosaccion glandiforme*, 813  
*H. ramentaceum*, 1119  
*Halymenia floresia*, 743, 766  
*Haminea* sp., 970  
*Hansenula*, 691  
*Hantzschia amphioxys*, 1191  
harpacticoids, 974, 1144  
*Hebellopis*, 1140  
*Helicocranchia*, 888  
*Helicoma salinum*, 691  
*Helodea canadensis*, 1149  
*Helodes*, 921, 1079  
*Heloccius cordiformis*, 868  
helophytes, 1048  
*Hemiaulis sinensis*, 734  
*Hemigrapsus nudus*, 875, 891, 913, 924, 929, 1043  
*H. oregonensis*, 868, 875, 891, 924, 929-932  
*Henricia sanguinolenta*, 1046  
*Hepatus epheticus*, 879, 908, 1042  
*Herpobdella atomaria*, 830  
herring, 1037, 1047, 1048, 1053, 1056, 1061, 1063, 1068, 1081, 1083, 1185  
*Heterometra savignyi*, 1127, 1128, 1152  
*Heteropanope tridentatus*, (Syn.: *Rhithropanopeus harrisii*), 1059  
*Heterosiphonia plumosa*, 708, 709, 710  
*Hildenbrandia*, 814  
*Himantalia*, 811, 814, 1106, 1116, 1118, 1187  
*H. elongata*, 801, 1111, 1115  
*H. lorea*, 779, 1179  
*Hirudo medicinalis*, 899, 917, 919, 920, 929, 1038  
*Holothuria*, 894  
*H. tubulosa*, 894  
holothurians, 1132  
Homaridea, 944  
*Homarus*, 1040  
*H. americanus*, 883, 889, 944, 951, 987  
*H. gammarus*, 1068  
*Hormathonema*, 700  
*Hormosira banksii*, 730, 817, 1036  
*Hyas araneus*, 867, 891, 905, 944, 945  
*H. coarctatus*, 890, 944, 945  
*Hydra*, 1062  
*H. (Pelmatohydra) oligactis*, 886  
*Hydrobia*, sp., 958  
Hydrocharitaceae, 706, 707  
Hydroidea, 1047, 1058, 1119, 1125, 1130-1132, 1135, 1137, 1139-1146, 1154

- Hydroides brachyacantha*, 937  
 hydrophytes, 1048, 1079, 1091, 1096  
*Hydrosera triquetra*, 706, 1077  
 hydrozoans, 826, 917  
*Hymenomonas carterae*, 712  
*Hypnea cornuta*, 806  
*H. musciformis*, 711, 806  
  
*Ictalurus melas*, 1183  
*Ichthyophthirius multifiliis*, 832, 1079  
*Ilea fascia*, 1108  
*Ilyocryptus sordidus*, 956  
 insects, 872, 895, 917, 921, 923, 1053  
*Iridaea heterocarpa*, 715  
*I. laminarioides*, 813  
*Ishige okamurai*, 738  
 Isididae, 1145  
*Isidella elongata*, 1138, 1146  
*Isocladus armatus*, 841, 849  
*I. calcareus*, 849  
 isopods, 847, 849, 862, 872, 873, 897, 924,  
 988, 1045, 1057, 1065, 1082,  
  
*Jaera albifrons*, 1066  
*Jassa falcata*, 958  
*Juncus gerardi*, 796  
  
 killifish, 1070  
*Kjellmania sorifera*, 792  
 kormophytes, 1111, 1112  
  
*Labrus bergylata*, 1068  
*Labyrinthula*, 692, 697, 699, 1081  
 Labyrinthulales, 691, 692, 697  
*Lactuca sativa*, 884, 984  
*Laomedea loveni*, 946, 1058  
*Laonereis culveri*, 912  
*Lagenidium chthamalophilum*, 692, 693, 1055  
 Lamellibranchia, 835, 836, 917, 937, 962, 994,  
 1061, 1065, 1072, 1135  
*Lamellidens marginalis*, 875  
*Laminaria*, 785, 787, 811, 814, 1044, 1120,  
 1150  
*L. agardhii*, 1097  
*L. cloustoni*, 1155  
*L. digitata*, 719, 720, 735, 772, 776, 778, 779,  
 781, 785, 801, 814, 1055, 1113, 1115, 1116,  
 1118, 1120  
*L. digitata* f. *stenophylla*, 801  
*L. faeroensis*, 814  
*L. groenlandica*, 787-789  
*L. hyperborea*, 801, 814, 1106, 1115, 1116,  
 1155  
*L. saccharina*, 765, 767, 772, 787-789, 801,  
 1106, 1110, 1111, 1115, 1116, 1118, 1119  
 Laminariales, 707  
  
 laminarians, 1120  
*Lampetra fluviatilis*, 1000, 1014, 1016, 1030,  
 1031, 1036, 1065  
 lampreys, 1014, 1015  
*Lar*, 1140  
*Lates calcifer*, 1005  
*Lauderia borealis*, 734  
*Laurencia*, 811  
*L. obtusa*, 766  
*L. pinnatifida*, 1116  
*L. poitei*, 806  
*Laurencia-Corallina* association, 811  
*Lebistes reticulatus*, 1005, 1028, 1065  
*Lemna trisulea*, 793  
*Leontodon autumnalis*, 796  
 Lepadidae, 1141  
*Leptocylindrus danicus*, 712, 800  
*Leptograpsus variegatus*, 868  
*Leucosolenia*, 1148  
*Leydigia acanthocercoides*, 956  
*L. quadrangularis*, 956  
*Libellula*, 921  
*Libinia emarginata*, 908  
 lichens, 717, 770, 814  
 lichens, black, 1118  
 lichens, orange, 1118  
*Lichina*, 1118  
*Licmophora*, 812  
*Ligia oceanica*, 1069  
 Ligiidae, 862, 988  
*Limacina retroversa*, 969, 970, 972  
*Limapontia capitata*, 825, 1064, 1075  
*L. depressa*, 825, 1075  
*Limnaea stagnalis*, 835  
*Limnephilus affinis*, 910, 921, 923, 1078  
*L. stigma*, 921, 922, 1078  
*Limnoria*, 832, 833, 937, 1045, 1072  
*L. lignorum*, 832, 833, 936, 937  
*L. quadripunctata*, 832, 833, 936, 937  
*L. tripunctata*, 832, 833, 936, 937  
 limpets, 1062, 1129, 1144  
*Lithoderma*, 814  
*Lithodes maia*, 890, 944, 945  
*Lithothamnia*, 1116  
*Littorina knysnaënsis*, 847, 848, 934  
*L. littorea*, 825, 977  
*L. sp.*, 941, 969, 970  
 lobster, American, 1063  
*Loligo forbesi*, 886, 887  
*Lomentaria clavellosa*, 801  
*Lophopanopeus heathii*, 868  
*Lotus tenuifolius*, 796  
*Lucernaria quadricornis*, 946  
*Lucioperca lucioperca*, 1027, 1068  
*Lumbricillus reynoldsoni*, 1080  
*Lycastis indica*, 904

- Lymnaea natalensis*, 1186  
*L. stagnalis*, 884, 984  
*Lyngbya confervoides*, 806  
*L. sp.*, 827  
*Lytechinus variegatus*, 849-851  
*Lytocarpia*, 1145  
*L. myriophyllum*, 1138, 1145, 1146  
  
*Macoma baltica*, 836, 838, 839, 846, 958, 977, 994  
macrocrustaceans, 867, 974  
*Macrocystis*, 1112, 1153  
*M. integrifolia*, 716  
*M. pyrifera*, 1102  
*Macrophthalmus crassipes*, 974  
*M. setosus*, 923, 974, 1035  
*Macropipus puber*, 867  
*Macrostomum appendiculatum*, 823  
Madreporaria, 1141  
*Maia squinado*, 890, 891, 905, 944, 945  
*M. verrucosa*, 867, 929  
*Manayunkia*, 1035  
*Marinogammarus finmarchicus*, 913  
*Marionina preclitellochaeta*, 1055  
*Marphysa graveleyi*, 889, 890, 898-900, 907, 909, 910, 936, 1060  
*Marthasterias*, 894  
*Mastagloia pumila*, 808  
medusae, 1060, 1103  
*Melosira*, 800, 812  
*M. mammuloides*, 800, 810  
*M. subcaeta*, 1103  
*Membranipora*, 1038  
*M. crustulenta*, 977  
*Membranoptera alata*, 708, 712, 713, 718, 1100  
*Mercenaria mercenaria*, 876, 877, 1186, 1187  
*M. (Venus) mercenaria*, 1186  
*Mesidea entomon*, 958  
*Mesomysis kowalevskyi*, 834, 1056  
*Metapenaeus dobsoni*, 868, 913  
*M. monoceros*, 868, 875, 913, 1069, 1071  
*Metridium marginatum*, 875  
*Miamiensis avidus*, 886, 899, 1056  
*Microcladia borealis*, 715  
*M. coulteri*, 716  
*Microcophi aerucinosa*, 1153  
*Microcosmus vulgaris*, 1131  
*Microcystis aeruginosa*, 1110  
*Mietzius longicarpus*, 974  
*Miniacina miniacina*, 1139  
*Modiolus auriculatus*, 836  
*M. demissus*, 876, 877, 939  
*M. modiolus*, 1082, 1184, 1194  
Mollusca, 826, 835, 838, 874, 883, 886, 887, 898, 910, 926, 943, 945, 958, 970, 976, 977, 981, 983, 1034, 1037, 1040, 1041, 1043, 1064, 1073, 1080, 1082, 1152  
*Monas dunalii*, 823  
*Monochrysis lutheri*, 712  
*Monospilus dispar*, 956  
*Monostroma*, 814, 1107  
*M. baltica*, 792  
*M. grevillei*, 814  
*M. nitidum*, 729, 752, 754  
*M. zosterioloa*, 715  
*Monostroma-Enteromorpha* association, 814  
mosquito, 984, 1036, 1071, 1082  
mudskipper fish, 1049  
*Mulinia lateralis*, 883, 937, 1040, 1066  
*Muraena helera*, 1068  
*Murrayella pericladus*, 711  
mussels, 939, 962, 1047, 1054, 1079, 1183, 1190  
*Mya arenaria*, 836, 838, 839, 846, 887, 939, 940, 977, 990, 1067  
*Myriogramme pulchra*, 715  
Mysidacea, 970  
mysids, 969  
*Mysis oculata*, 823  
*Mytilus*, 1036, 1043, 1153  
*M. californianus*, 825  
*M. edulis*, 823, 834, 836-840, 846, 863, 865, 875-878, 883, 886, 887, 895, 905, 930, 939, 941, 994, 1038, 1048, 1061, 1070, 1072, 1074, 1112, 1119  
*M. edulis* var. *galloprovincialis*, 1038  
*M. galloprovincialis*, 886, 887, 1083  
*Myzine*, 1073  
*M. glutinosa*, 1013, 1065  
Myxinoidea, 1013  
Myxophyceae, 1033, 1078  
  
*Najas marina*, 793  
*Nassarius* sp., 958  
naticids, 943  
*Nautilus*, 944  
*Navicula arenicola*, 808  
*N. gregaria*, 810  
*N. longirostris*, 810  
*N. maculata*, 808  
*N. pygmaea*, 810  
*Neamthes arenaceodentata*, 911, 1072  
*N. brandti*, 956  
*N. bimaculata*, 956  
*Nematium*, 1116  
*N. lubricum*, 717  
Nematoda, 956, 1153  
*Nemertesia*, 1145  
*N. antennina*, 1138  
*Nemopsis beschei*, 1079  
*Neomysis kadiakensis*, 957  
*N. mercedis*, 957

- N. rayii*, 957  
*Nephrops*, 894  
*N. norvegicus*, 890, 894, 896, 944  
*Neptunea antiqua*, 887  
*N. despecta*, 1049  
Nereidae, 889, 1060  
*Nereis*, 1045  
*N. diversicolor*, 825, 830, 832, 834, 875, 899, 903, 904, 912-915, 926, 1036, 1038, 1045, 1047, 1053, 1070, 1077  
*N. (lighti) limnicola*, 913  
*N. limnicola*, 899, 904, 910, 912, 1068  
*N. pelagica*, 905  
*N. vexillosa*, 904  
*N. virens*, 899, 904, 1074  
*N. (Neanthes) succinea*, 904, 910, 912, 1056  
*Nereocystis leutkeanae*, 813  
*Neritina*, 975  
*N. virginea*, 977, 1034  
*Nienburgia andersoniana*, 716  
*N. borealis*, 715  
*Nitophyllum punctatum*, 708  
*Nitzschia*, 1103  
*N. apiculata*, 810  
*N. closterium*, 810  
*N. delicatissima*, 1103  
*N. filiformis*, 808  
*N. frustulum*, 810  
*Notiluca*, 1043  
*N. miliaris*, 758, 944, 962, 1057  
*N. sp.*, 970  
*Notholca bipalium*, 823  
*N. striata*, 823  
*Nostoc*, 693  
*N. entophyta*, 693  
*Nuphar luteum*, 793  
  
Octocorallia, 1152  
*Octopus hongkongensis*, 888  
*O. vulgaris*, 1048  
*Octosporea effeminans*, 953  
*Ocyropode*, 988  
*O. (albicans) quadrata*, 868, 869, 875, 895, 1046  
*Odonthalia dentata*, 1119  
*Odontites litoralis*, 796  
*Oedogonium sp.*, 1098  
*Oikopleura labradoriensis*, 970  
*Oithona similis*, 957, 970  
*Oithonina nana*, 970  
*Oligochaeta*, 827, 977, 985, 1051  
*Olithodiscus sp.*, 712  
*Oncorhynchus gorbusha*, 998, 1022, 1032, 1047, 1073  
*O. keta*, 998, 1020-1022, 1054, 1073  
*O. kisutch*, 998, 999, 1006, 1007, 1022-1024, 1041  
  
*O. nerka*, 1006, 1022, 1023  
*O. nerka kennerlyi*, 1005, 1046  
*O. nerka nerka*, 1005  
*O. sp.*, 1023  
*O. tshawytscha*, 1003, 1039  
Oniscidae, 862, 988  
*Oniscus*, 988  
*O. asellus*, 873, 1052  
Onisoidea, 1080  
*Ophiocoma scolopendria*, 1129, 1152  
*Ophiothrix fragilis*, 1129  
*O. quinquemaculata*, 1150  
Ophiura, 1152  
*Ophiura albida*, 946  
*Orchestia mediterranea*, 876  
*Orconectes immunitis*, 876  
*O. rusticus*, 910, 1076  
*O. virilis*, 876  
*Orthopyxis*, 1140  
*Oscillatoria peneta ad int.*, 702, 703  
*O. rubescens*, 699  
*Osmerus mordax*, 1005, 1006  
Osteichthyes, 1073  
Ostracoda, 957  
*Ostrea edulis*, 836, 846, 887, 1070  
*O. madrasensis*, 1071  
*Ovatella myosotis*, 826  
Oxyrhyncha, 944  
*Oxyrrhis marina*, 711  
*Oxystele sinensis*, 847, 848, 934  
*O. tigrina*, 847, 848, 934  
*O. variegata*, 847, 848, 934  
oysters, 831, 934, 939, 951, 953, 1040, 1041, 1043, 1046, 1047, 1059, 1062, 1067, 1068, 1082, 1183, 1184, 1186, 1187, 1191, 1192  
  
*Pachydriulus (Lumbricillus) lineatus*, 823  
*Pachygrapsus crassipes*, 847, 868, 869, 890, 893, 895, 899, 913, 925, 1053, 1070, 1073  
*P. marmoratus*, 890, 891, 944  
*Pacifastacus leniusculus*, 1056  
*P. trowbridgii*, 958  
*Padina pavonia*, 766  
*P. vickersiae*, 805  
Paguridea, 944  
*Pagurus longicarpus*, 868  
*Palaemon longirostris*, 869  
*P. squilla*, 868, 913  
*P. serratus*, 868, 913  
*Palaemonetes antennarius*, 870, 871, 1069  
*P. varians*, 868, 869, 875, 913, 1062, 1068, 1069  
*P. sp.*, 876  
*P. vulgaris*, 1063  
Palinura, 944  
*Palinurus elephas*, 868

- P. sp.*, 944  
*Panopeus herbstii*, 845, 879, 1042  
*Paludina viviparus*, 835  
*Paracalanus parvus*, 957  
*Paracentrotus lividus*, 834  
*Paracleistostoma mcneilli*, 974  
*Paracyclops fimbriatus*, 957  
*Paramysis lacustris kowalevskyi*, 1056  
*Paraphoxius milleri*, 958  
*Parasilurus asotus*, 1022  
*Parastenocaris vicesima*, 832, 941, 966-968  
*Parophrys vetulus*, 1003  
*Parazoanthus axinellae*, 1140  
*Parerythropodium sp.*, 1139  
*Patella*, 1043, 1135  
*P. aspersa*, 847  
*P. vulgata*, 847, 941, 973, 1034  
 Patellaceae, 1144  
*Pecten maximus*, 887, 953, 1050, 1129, 1151  
*Pediastrum clathratum*, 808  
*P. duplex* var. *reticulatum*, 808  
*P. duplex* var. *rotundatum*, 808  
*P. simplex*, 808  
*P. tetras*, 808  
*Pelmatohydra oligactis*, 830  
*Pelvetia*, 1116, 1118  
*P. canaliculata*, 717, 722, 731, 776, 778, 779, 785, 801, 815, 818, 820, 1055, 1112, 1113  
*P. canaliculata* f. *libera*, 779  
*Penaeus*, 1082  
*P. aztecus*, 892, 913, 969, 1074  
*P. carinatus*, 868, 913  
*P. duorarum*, 968, 1054, 1079  
*P. indicus*, 868, 913  
*P. setiferus*, 892, 913  
*Penicillus*, 1112  
*P. capitatus*, 805  
*Pennatularia*, 1146, 1152  
 Pennatulidae, 1144  
*Pennatulina penniformia*, 1146  
*P. verticillata*, 1146  
*Percursaria percursa*, 790  
 peridineans, 1104  
*Peridinium*, 800  
*P. pellucidum*, 797  
*P. triquetrum*, 712, 756  
*P. trochoideum*, 756, 1104  
*Perigonimus megas* (Syn: *Garveia franciscana*), 1058  
*Perinereis cultrifera*, 905, 912, 1047  
*P. nuntia*, 904  
*Periophthalmus sobrinus*, 1003  
*Peritrichospora integra*, 691  
 periwinkle, 1052  
*Petalonia fascia*, 805, 1096  
 Pertromyzontidae, 1014  
*Peyssonnelia rubra*, 766  
*P. squamaria*, 766  
*Phaeocystis sp.*, 1104  
*Phaeodactylum tricornutum*, 927  
 Phaeophyceae, 790, 791, 800, 802  
 Phaeophyta, 705, 766  
 phanerogams, 707, 717, 732, 746, 773, 792, 793, 812, 1048, 1106, 1107  
*Phascolosoma*, 886, 1033, 1077  
*P. agassizii*, 1079  
*P. japonicum*, 899, 900  
*Phascolopsis gouldii*, 900  
*Pherus fucicola*, 876  
*Phoma*, 692  
*Phormidium persicinum*, 693, 698, 1070  
*Photobacterium fischeri*, 696  
*Phragmites communis*, 796  
*Phycocoeles floridana*, 805  
*Phycodrys rubens*, 708, 801, 1100  
*P. sinuosa*, 713, 1095  
 Phycomycetes, 690-693, 697, 700, 703, 1081, 1170  
*Phyllophora*, 800  
*P. brodiaei*, 792, 800  
*P. membranifolia*, 801  
*P. nervosa*, 800  
*Phymatolithon*, 814  
*Physalia*, 944  
*Physcosoma japonicum*, 1060  
*P. lurco*, 1051  
*Picea excelsa*, 760  
*Pichia*, 692  
 plaice, 1039  
 planarians, 874  
*Planaxis sulcatus*, 1129, 1152  
*Plantago coronopus*, 796  
*P. maritima*, 796  
*Platichthys flesus*, 1001, 1019, 1066  
*P. flesus flesus*, 1065  
*P. stellatus*, 1002, 1003, 1018-1020, 1053  
*Platymonas sp.*, 712  
*Pleurobrachia pileus*, 970, 976, 1050  
*P. sp.*, 956  
*Pleurobranchus membranaceus*, 887  
*Pleurocera sp.*, 958  
*Pleuronectes flesus*, 997, 998, 1001, 1018, 1026, 1029, 1061, 1082  
*P. flesus luscus*, 1083  
*P. platessa*, 998, 1000, 1003, 1009-1013, 1025-1029, 1054, 1071, 1082  
*Pleuroaris denticulatus*, 956  
 Plexauridae, 1145  
*Plocamium*, 1095, 1116  
*P. coccineum*, 719  
*P. coccineum* var. *pacif.*, 715, 716  
*P. tenue*, 715

- Plotozus, anguillaris*, 1003, 1055  
*Plumularia*, 1130  
*P. setacea*, 1138, 1145  
 Plumulariinae, 1145  
*Podocoryna*, 1140  
*Podon leuckarti*, 957  
 Pogonophora, 1062, 1077  
*Polinices duplicata*, 939, 940, 943, 1051  
*P. heros*, 939, 940, 1051  
*Pollachius virens*, 1017, 1018  
*Pollicipes polymerus*, 970, 972  
 Polychaeta, 835, 874, 889, 898, 900, 904, 907,  
 912, 962, 969, 970, 1035, 1036, 1045, 1055,  
 1060, 1068, 1077, 1124, 1135, 1140  
*Polyides rotundus*, 726, 727, 801, 1119  
*Polyneura latissima*, 715  
*Polysiphonia*, 708, 814, 1107  
*P. elongata*, 801  
*P. ferulacea*, 806  
*P. fracta* (Syn: *P. echinata*), 806  
*P. harveyi*, 1097  
*P. havanensis*, 806  
*P. hendrii* var. *gardneri*, 715  
*P. lanosa*, 1102  
*P. macrocarpa*, 806  
*P. nigrescens*, 718, 792, 801  
*P. urceolata*, 708, 710, 737, 759  
*P. violacea*, 792, 801  
*Pomolobus pseudoharengus*, 1006  
*Pontogammarus maeoticus*, 832, 1070  
 Porcellidiidae, 1144  
*Porcellio*, 1080  
*P. scaber*, 1082  
 Porcellionidae, 862, 988  
 poriferans, 1135, 1140, 1142, 1147, 1148, 1154  
*Porphyra*, 707, 714, 755, 768, 769, 783, 811,  
 814, 820, 1081, 1095, 1111, 1116, 1118  
*P. atropurpurea*, 771-773  
*P. fucicola*, 715  
*P. laciniata*, 718, 719, 735  
*P. leucosticta*, 717, 805  
*P. perforata*, 716, 719, 813, 1045  
*P. sp.*, 714  
*P. tenera*, 729, 735, 744, 752, 754, 768, 769,  
 778-780, 1067, 1098, 1152  
*P. umbilicalis*, 719, 755, 774, 1067, 1117  
*P. yezoensis*, 755, 783, 784  
*Portunus depurator*, 891, 944  
*P. puber*, 890, 891, 944  
*Posidonia*, 1111, 1112  
*Potamobius astacus*, 1052  
*Potamogeton natans*, 793  
*P. pectinatus*, 793  
*P. vaginatus*, 793, 795  
 Potamogetonaceae, 706, 707  
*Potamon edulis*, 870-872, 875  
*P. johnstoni*, 835  
*P. niloticus*, 835, 870-872, 923, 1076  
*Potamopyrgus jenkinsi*, 934, 935, 1044, 1063  
*Potentilla anserina*, 796  
*P. reptans*, 796  
*Prasiola crispa*, 814  
*P. stipitata*, 784, 790, 814, 1047  
 prawn, 1068, 1069  
 Primnoidae, 1145  
*Pringsheimiella scutata*, 790  
*Prionotis australis*, 716  
*P. lanceolata*, 715, 716  
*Proales reinhardti*, 823  
*Procambarus clarkii*, 871  
*Procerodes ulvae*, 899, 904  
*P. (Gunda) ulvae*, 903  
*Proceronema micans*, 756, 800  
 Prosobranchia, 887, 1152  
*Prostoma obscurum*, 946, 1061  
*Proteus vulgaris*, 1175  
 Protozoa, 825, 874, 885, 899, 905, 944, 956,  
 970, 1041, 1071  
*Pseudocalanus minutus*, 957  
*Pseudodendroclonium submarinum*, 790  
 pseudomonad, 690, 694-697, 701-703, 1039,  
 1044, 1064, 1069, 1079, 1083  
*Pseudomonas fluorescens*, 1175  
*P. natrigens*, 694, 697  
*P. stutzeri*, 1170  
*Pseudosphaeroma campbellensis*, 846, 849  
*Pterosiphonia baileyi*, 716  
*Ptilota elegans*, 718  
*P. pectinata*, 1119  
*P. plumosa*, 708, 801  
*Pugettia producta*, 876  
*Pullularia*, 691  
*Purpura lapillus*, 825  
 Pyrrhophyta, 705  
*Pylaiella antillarum*, 805  
*P. littoralis*, 792  
*Pythium salinum*, 691  
  
*Ranunculus baudotii*, 793  
*R. circinatus*, 793  
*Raroia (Tuamotus)*, 1150  
 Reteporida, 1151  
*Rhabdonema*, 812  
*Rhithropanopeus harrisi*, 845, 868, 880-882,  
 907, 909, 924, 1042, 1056, 1077  
*Rhizoclonium*, 814  
*R. riparium*, 715, 790, 805  
*Rhizosolenia*, 800  
*R. alata*, 734  
*R. calcar avis*, 800  
*R. fragilissima*, 1103  
*R. hebetata*, 808

- R. imbicata* var. *shrubsolei*, 1104  
*R. shrubsolei*, 800  
*Rhodochorton*, 814  
*R. floridulum*, 718  
*Rhodoglossum affine*, 716  
*Rhodomela confervoides*, 801  
*R. larix*, 813  
Rhodophyceae, 709, 790, 791, 800, 802  
Rhodophyta, 705, 766  
*Rhodotorula*, 691, 692  
*Rhodymenia*, 814, 1116, 1187  
*R. californica*, 716  
*R. callophyllidoides*, 716  
*R. corallicola*, 766  
*R. pacifica*, 716  
*R. palmata*, 781, 801, 1119  
*R. pertusa*, 715  
*R. pseudopalmata*, 806  
*Rhynchonella psittacea*, 1119  
*Rissoa*, 1144  
Rotatoria, 985  
Rotifera, 956  
*Ruppia*, 811  
*R. maritima*, 793, 794, 805, 1097  
*R. spiralis*, 793  
*Rytiphlaea tinctoria*, 733  
  
*Sabella pavonina*, 904, 1046  
*Sabellaria pavonina*, 905  
Sabellidae, 1035, 1124  
*Saccorhiza*, 1116  
*S. polyschides*, 1115  
*Sagina nodosa*, 796  
*Sagitta* sp., 970  
*Sagittaria sagittifolia*, 793  
*Salicornia europaea*, 760  
*S. herbacea*, 796, 1178, 1192  
*Salmo clarki clarki*, 1003, 1004, 1054  
*S. clarkii*, 1182  
*S. gairdneri* (i), 998, 1001, 1041, 1054, 1181, 1182, 1189  
*S. gairdnerii gairdnerii*, 1005  
*S. gairdnerii kamloops*, 1005  
*S. salar*, 1000, 1006, 1019, 1031, 1047, 1068, 1079  
*S. trutta*, 1019, 1188, 1193  
salmon, 706, 1023, 1039, 1181  
salmon, chum, 1054  
salmon, coho, 1054  
salmon, Pacific, 1023, 1034  
salmon, pink, 1052, 1054  
salmonids, 1031  
*Salvelinus fontinalis*, 1006  
*Sarcina lutea*, 1175  
*Sarcophyllis californica*, 813  
*Sardinops caerulea*, 1001, 1029, 1061  
  
Sargassaceae, 1153  
*Sargassum*, 1102, 1105-1107, 1153  
*S. filipendula*, 805  
*S. fluitans*, 1105  
*S. hystrix*, 1105  
*S. linifolium*, 733, 760  
*S. natans*, 805, 1105  
*S. polyceratium*, 1105  
*S. thunbergii*, 735, 736  
*Scenedesmus dimorphus*, 808  
*S. ecornis*, 808  
*S. quadricauda*, 808  
*Schizochytrium aggregatum*, 698  
*Schizonema grevillei*, 812  
*S. ramosissima*, 812  
*Scirpus lacustris*, 795  
*S. maritimus*, 793, 795  
*S. parvulus*, 793, 794  
*S. tabernaemontani*, 793  
*Scopulonema*, 700  
*Serobicularia plana*, 941, 1047  
*Scutuloidea maculata*, 846, 847, 849  
*Scylla serrata*, 932, 933, 1080  
*Scytalopsis djiboutensis*, 1129, 1130  
*Scytosiphon lomentaria*, 729, 752, 754  
sea anemone, 1076  
sea fans, 1125, 1131  
sea grass, 707, 1052, 1069, 1096, 1098, 1111, 1120, 1179  
sea horses, 886  
sea pens, 1129  
sea star, 875, 894, 913, 946, 1037  
sea urchins, 895, 898, 1073  
seaweeds, 1095, 1106, 1112, 1117, 1120, 1121, 1151, 1156, 1191  
seaweed, brown, 1113, 1149  
Sedentaria, 1154  
*Sepia officinalis*, 886-889, 897, 898, 1043  
Sernowic *phyllophora* meadows, 800  
serpulids, 937  
*Sesarma cinereum*, 845, 879, 1042  
*S. meinerti*, 870  
sharks, 1068  
shellfish, 1181, 1183  
shrimps, 691, 868, 892, 907, 927, 945, 1050, 1061, 1063, 1069  
*Sialis lutaria*, 921, 1036, 1076  
*Siconina dorsalis*, 892  
*Sida crystallina*, 956  
*Siglingia decumbens*, 796  
*Siphonaria*, 1033  
*S. aspersa*, 847  
*S. capensis*, 847  
*S. deflexa*, 847  
*S. pectinata*, 941, 1063  
Siphonocladiales, 709

- siphonophores, 944, 1035  
*Sipuncula*, 1046, 1068  
 sipunculids, 886, 898, 900, 902, 910, 1043, 1154  
*Sipunculus nudus*, 1043  
*Sirolpidium*, 1081  
*S. zoophthorum*, 692  
*Skeletonema costatum*, 712, 747, 797, 800, 1103, 1110  
 snails, 884, 943, 1073, 1130, 1140, 1186, 1191  
*Solentia*, 700  
*Spartina alternifolia*, 795  
*S. stricta*, 795  
*S. townsendii*, 795  
*Speocarcinus californiensis*, 868  
*Spermatochmus*, 1116  
*Spergularia salina*, 796  
*Sphacelaria furcigera*, 805  
*S. plumosa*, 801  
*S. racemosa*, 792  
*Sphaeroma*, 988  
*S. hookeri*, 896, 1057  
 Sphaeromidae, 846, 849, 1051, 1055  
*Spirula*, 944  
*Spisula solida*, 836, 837  
 sponges, 826, 874, 1119, 1125, 1135, 1148  
*Spyridia aculeata*, 806  
*S. filamentosa*, 711, 733  
 squid, 1043  
*Squilla empusa*, 892, 1062  
*S. mantis*, 891, 944  
*Staurastrum manfeldtii*, 808  
 sticklebacks, 1023  
*Stictyosiphon*, 814  
*S. spp.*, 805  
*S. tortilis*, 792  
*Stilophora rhizoides*, 1097  
 Stomatopoda, 891, 944  
*Strongylocentrotus droebachiensis*, 1061  
*S. lividus*, 899  
*Stylochus ellipticus*, 934, 936, 1061  
 sucker fishes, 1144  
*Sycon*, 1148  
*Synechococcus cedrorum*, 698  
*Synedra tabulata*, 808  
*Sypharochiton pelliserpentis*, 905, 926, 1038  
*Syracosphaera carterae*, 712  
*Syringia vulgaris*, 760  
*Syringodium*, 811  
*Systilus*, sp., 956  
*Taraxacum officinale* var. *palustre*, 796  
 teleosts, 825, 997, 998, 1015, 1017, 1024, 1026, 1034, 1039, 1042, 1053, 1054, 1061, 1064, 1066, 1080  
*Temora*, 962  
*T. longicornis*, 970, 972  
*Teredo diegensis*, 969, 970, 972  
*Tersipnoe americana*, 808  
*Tetraedron caudatum*, 808  
*T. limneticum*, 808  
*T. muticum* var. *punctulatum*, 808  
*Tetrahymena*, 1044  
*Thais dubia*, 847, 848, 934  
*Thalassia*, 811  
*T. testudinum*, 805, 1097  
*Thalassionema nitzschioides*, 800  
*Thalassiosira decipiens*, 712  
*T. fluviatilis*, 810  
*T. gessneri*, 808  
*T. gravida*, 1103  
*T. nordenskiöldi*, 1103  
*T. sp.*, 800  
*Thalassiothrix frauenfeldii*, 808  
*T. longissima*, 800  
*Themiste dyscritum*, 836, 886, 899-903, 905, 906, 1068  
*T. zosteriolum*, 862, 899, 900  
*Themisto abyssorum*, 970, 972  
*Theodorus fluviatilis*, 832, 875, 947, 1063, 1067  
*Thraustochytrium*, 698, 1049  
*T. roseum*, 698  
*Thysanozssa longipes*, 957  
*Tigriopus californicus*, 970, 972  
*T. fulvus*, 823, 827, 833, 1047, 1071  
*T. japonicus*, 951  
*Tinca vulgaris*, 1001, 1042  
*Tintinnopsis* sp., 970  
*Tisbe*, 974, 977, 1035  
*T. furcata*, 833, 841, 842, 892  
*T. reticulata*, 833, 890, 892  
*T. reticulata* f. *trifasciata*, 833, 892  
*T. reticulata* f. *violacea*, 833, 892  
*T. trifasciata*, 974  
*T. violacea*, 974  
*Tolypeutes*, 988  
*Torulopsis*, 691, 692  
*Tracheoniscus*, 1080  
*T. rathkei*, 862  
*Trachypeneus similis*, 892  
*Trailliella intricata*, 718, 719  
 Trichoniscidae, 862, 988  
 Trichoptera, 910  
*Trichosporon*, 691  
*Trifolium fragiferum*, 796  
*T. repens*, 796  
*Triglochin maritima*, 796  
*Triops*, 1069  
*T. cancriformis*, 872  
*Tripaneustes ventricosus*, 849-851

- trout, 1077, 1181, 1182, 1189, 1191  
 trout, brown, 1189  
 trout, rainbow, 1182  
*Tubifex tubifex*, 1068  
 tuna, 1184  
 Tunicata, 835, 1073  
 Turbellaria, 835, 883, 903, 1154  
 turtle-grass, 1120, 1155
- Uca*, 988  
*U. crenulata*, 868  
*U. minax*, 868  
*U. pugilator*, 868, 869, 895, 1049  
*U. pugnax*, 868, 869, 895, 1049  
*U. spp.*, 875  
*Udotea desfontainii*, 766  
*Ulothrix*, 707  
*Ulva*, 811  
*U. fasciata*, 805  
*U. lactuca*, 715, 718-721, 734, 746, 752, 753, 766, 776, 813, 1069, 1107  
*U. lactuca* var. *latissima*, 805  
*U. lactuca* var. *rigida*, 805  
*U. latissima*, 779  
*U. pertusa*, 729, 735-737, 744, 752, 754, 768, 769, 773, 774, 1067  
*Undaria pinnatifida*, 726, 735, 736, 1074  
*Unio pictorium*, 835  
 Unionidae, 830  
*Upogebia*, 1079  
*U. affinis*, 868  
*U. pugettensis*, 868  
 urchins, 850  
*Uronema*, 1056  
*U. filificum*, 885
- Urosalpinx cinerea*, 939, 953, 1048, 1064  
*Urospora*, 814  
*U. penicilliformis*, 717
- Valonia*, 759  
*V. macrophysa*, 733  
*V. utricularis*, 733, 1064  
*V. ventricosa*, 759, 760, 766, 767, 1037, 1048, 1051  
*Varuna litterata*, 870  
*Velella*, 944  
*Venus (Mercenaria) mercenaria*, 1190  
*Verrilliteuthis*, 888  
*Verruca stroemi*, 1119  
*Vibrio*, 694, 695  
*V. marinus*, 690, 1077  
*Vidalia volubilis*, 766  
*Volvox* sp., 956
- worms, 835, 862, 866, 900-902, 910, 913, 936, 939, 1054, 1055, 1066, 1068  
*Wrangelia bicuspidata*, 711
- Xanthophyta, 806
- yeasts, 690-692, 1037, 1069, 1073
- Zanardinia collaris*, 766  
*Zannichellia palustris*, 793  
*Z. palustris* var. *major*, 793  
*Zea mais*, 760  
*Zostera*, 814, 1112, 1178  
*Z. marina*, 739, 773, 774, 778, 792, 793, 1063, 1096-1098  
*Z. nana*, 744, 778, 793

# SUBJECT INDEX

- Abnormalities in structure—*see also* Growth forms  
salinity effects, 816, 817, 984-986, 1029
- Aburatsubo Inlet  
distribution of bacteria, 1174, 1175
- Acclimation—*see* Non-genetic adaptation
- Acclimatization—*see* Non-genetic adaptation
- Acidophil cells, 1031
- Active ion uptake, 885-898
- Active transport, 885-898  
amount of Na required, 696, 697  
of non-metabolizable amino-acid analogues, 696, 697
- Activity—*see also* Metabolism and activity fishes  
salinity effects, 1020-1024
- invertebrates  
salinity effects, 934-945
- micro-organisms  
salinity effects, 693-699
- plants  
salinity effects, 731-784
- Adaptation—*see also* Non-genetic adaptation and Genetic adaptation  
to environmental changes  
plants, 792, 793  
to salinity stress  
bacteria, 690  
fishes, 998, 999  
fungi, 693
- Adaptive specialization, 706
- Adjustments  
of crustaceans  
to life in fresh water, 870-872  
to life on land, 862, 872, 873
- of hydroids  
to osmotic stress, 994
- of insect larvae  
to osmotic stress, 921-923
- Adnate algae, 1107
- Adrenocorticosteroid hormones  
control of ion exchange in fishes, 1018
- aegagropila* growth type, 1111
- After-effects of desiccation  
plants, 774, 776-779
- Air exposure  
distribution of  
intertidal invertebrates, 973  
intertidal plants, 810-816]
- reproductive response of invertebrates, 953
- structural adjustments of crustaceans, 988
- tolerance of  
intertidal invertebrates, 846-862  
intertidal plants, 714-731
- Algae—*see* Plants
- Alkalinity, 685
- Amino acids  
osmoregulation, 909-911, 913, 923  
uptake, 910, 911
- Ammonium  
ion regulation, 758, 888
- Ammonotelic excretion, 873
- Analogy procedure  
water movement, 1087, 1088
- Anal papillae (mosquito)  
importance for ion regulation, 895  
salinity effects on structure, 984
- Animals—*see also* Invertebrates and Fishes  
tolerance to  
turbidity, 1181-1183  
water movement, 1124, 1125
- turbidity effects on  
distribution, 1187, 1188  
external structures, 1189  
internal structures, 1189  
metabolism and activity, 1184, 1185  
reproduction, 1185-1187  
size, 1188, 1189
- water movement effects on  
distribution, 1133-1141  
external structures, 1144-1148  
internal structures, 1148  
metabolism and activity, 1125-1132  
reproduction, 1132  
size, 1141-1144
- Antarctic Sea  
minimum salinities, 688
- Antennal gland  
organ involved in ion and osmoregulation, 869-873, 893
- Antennary gland—*see* Antennal gland
- Aquaculture, 879
- Architecture of cells  
salinity effects, 989-994
- Artificial sea water  
preparation of, 687  
recipe, 687
- Artificial seaweeds, 1121
- Asexual reproduction of invertebrates  
salinity effects, 947-949
- Askö Laboratory  
horizontal distribution of mesopsammon, 965-968

- Asphyxiation, 1001, 1020  
 due to water stagnation, 1124
- Assemblages of  
 animals  
 water movement, 1135-1138  
 plants  
 water movement, 1113-1121
- Associations of algae  
 vertical distributions near Faeroes, 814
- Atlantic Ocean  
 distribution of pelagic invertebrates, 954  
 maximum/minimum salinities, 688  
 optical characteristics, 1164  
 turbidity, 1164
- Atlantic Trench  
 turbidity, 1164, 1165
- ATPase activity  
 under salinity stress, 932, 933
- ATP-balance  
 role in desiccation of algae, 779, 780
- Attachment organs (plants)  
 different types, 1112  
 forces required for detachment, 1112, 1113
- Attachment of mollusc spat  
 turbidity, 1186  
 attenuation coefficient, 1158
- Automixis, 983
- Avoidance of desiccation, 717
- Azores  
 turbidity, 1164
- Azov Sea  
 number of marine algae, 800
- Bacteria—*see also* Micro-organisms  
 cytorrhysis, 702, 703  
 distribution  
 salinity effects, 699, 700  
 halophylic, 689, 690  
 luminescence  
 salinity effects, 693-697  
 marine, 689, 690  
 metabolism and activity  
 salinity effects, 693-697  
 reproduction  
 salinity effects, 699  
 structure  
 salinity effects, 701-703  
 terrestrial, 689, 690  
 tolerance  
 to salinity, 689-691
- Baltic Sea  
 benthonic algae distribution, 789-792  
 dwarf forms of algae, 1108  
 invertebrates  
 salinity effects on reproduction, 946  
 minimum salinities, 688  
 number of marine algae, 790  
 plants  
 distribution, 789-797  
 endemisms, 791, 792  
 transportation, 1107  
 structural instability of vegetations, 1120, 1121
- Barents Sea  
 distribution of littoral organisms, 1119
- Bay of Bengal  
 turbidity, 1163
- Behaviour  
 changes due to turbidity, 1184, 1185  
 of fishes  
 salinity effects, 1022  
 of invertebrates  
 reduction of osmotic stress, 926  
 salinity effects on activity, 934-945  
 supporting osmoregulation, 925
- Bending properties of plants, 1113
- Benthonic (benthic)  
 algae  
 distribution in Baltic Sea, 789-792  
 plants  
 water movement effects on  
 distribution, 1104-1108  
 external structures, 1110-1113  
 vegetation  
 water movement effects, 1114-1121
- Bergmann's rule, 976
- Biocoenosis  
 salinity effects, 842, 843
- Biocoenotic background, 843
- Biomass  
 laminarians, 1120
- Black Sea  
 minimum salinities, 688  
 number of marine algae, 800  
 phytoplankton, 800  
 plant distribution, 799, 800
- Blood  
 plasma  
 ionic constituents, 888, 891  
 -protein, 910  
 serum  
 ionic concentration, 892
- Blue-green algae—*see also* Micro-organisms  
 cytorrhysis, 703  
 salinity effects on  
 distribution, 700  
 metabolism and growth, 698, 699  
 reproduction, 699  
 structure, 702, 703  
 salinity requirements for  
 growth and nitrogen fixation, 693  
 tolerance to salinity, 693

- Body  
 appendages  
 salinity effects, 983, 984  
 cavity fluids, 885  
 ionic composition, 885-898, 1017-1020  
 osmoconcentration, 906-926, 1010-1016  
 shape  
 salinity effects, 978-983, 1029, 1030  
 size  
 salinity effects, 816, 817, 975, 976, 1028, 1029
- Bosphorus  
 salinity and temperature distributions, 799
- Bottom biocoenosis  
 salinity effects, 842, 843
- Boundary layer  
 water movement, 1140, 1144, 1146-1149
- line  
 critical salinity, 827  
 —see also *Horohalium*
- Brackish water  
 definition, 822  
 pauperization, 975, 976  
 submergence, 802-804
- Branching of body parts  
 water movement, 1144
- Breeding season  
 salinity effects, 947
- Brine water  
 definition, 822  
 occurrence of invertebrates, 826, 827
- Bromide  
 ion regulation, 886
- Buffering capacity  
 of sea water, 685, 686
- Byssal thread formation  
 salinity effects, 939
- Calcification  
 salinity effects, 977
- Calcium  
 ciliary activity, 840  
 content (ambient) as function of salinity, 827  
 importance for plants, 714  
 ion regulation, 714, 759, 885-896  
 permeability, 712  
 requirements  
 bacteria, 694, 695  
 blue-green algae, 698, 699  
 fungi, 697, 698  
 survival of invertebrates, 834, 835  
 tissue survival, 839, 840
- Calcium carbonate  
 in brackish water, 828  
 in sea water, 686
- Calcium-protein complexes, 894, 910
- Calculation procedure  
 water movement, 1087
- Calorific requirements—see Energy requirements
- Cape Sorrento  
 hydroid zones, 1139
- Carbohydrate consumption  
 under salinity stress, 927, 928
- Carbon  
 ion regulation, 897
- Causes  
 of death due to salinity  
 fishes, 998, 1000  
 invertebrates, 874  
 of salinity effects on respiration  
 invertebrates, 878
- Caves, 1125, 1126, 1131, 1136, 1137, 1146
- Cell  
 dimensions  
 salinity effects, 989-994  
 division  
 rates under salinity stress, 752-757  
 salinity effects, 949  
 envelope of bacteria  
 release of material, 701, 702  
 fluids  
 ion ratios, 897  
 osmoconcentration, 909  
 number  
 salinity effects, 988, 989  
 size of gills  
 turbidity effects, 1189  
 structures  
 salinity effects, 819, 820, 987-995, 1030-1032  
 wall  
 thickness in intertidal plants, 820, 1113
- Cells  
 tolerance to salinity, 836-840
- Chain length of diatoms  
 water movement effects, 1110
- Chemical composition  
 of algae  
 salinity effects, 749-752  
 of body fluids  
 animals, 885-897, 1013, 1021  
 of cell fluids  
 plants, 758-760
- Chemical properties of sea water, 685, 686  
 alkalinity, 685  
 anions, 684, 685  
 buffering capacity, 685  
 cations, 684, 685  
 pH, 685

- Chesapeake Bay Institute  
turbidity data, 1158
- China-clay wastes, 1188, 1189
- China Sea  
turbidity, 1159, 1165
- Chloride  
critical lower concentration, 834, 835  
exchange rates, 914, 915  
excreting cells, 1030  
excretion via gills, 1015  
fluxes, 889, 914, 915  
in urine, 1016  
ion regulation, 759, 885-897  
loss  
algae, 765-767, 780, 781  
requirement  
bacteria, 694, 695  
blue-green algae, 698, 699  
fungi, 697, 698
- Chlorinity, 687  
correlation with salinity, 828, 829  
tolerance of wood-boring isopods, 832, 833
- Chlorosity, 687
- Chromosome numbers  
salinity effects, 983, 994, 995
- Ciliary activity  
criterion  
of non-genetic resistance adaptation, 863, 865  
of salinity tolerance, 836-840
- Circulation  
ideal ocean, 1140
- Cirral activity  
salinity effects, 937, 938
- Classification  
geographical  
of littoral zones, 1140  
of estuarine waters, 959-961  
of waters with different salinities, 822, 823  
water movements, 1092-1094
- Coelomic fluid  
ionic constituents, 889  
lower critical concentrations, 912
- Cold resistance  
as function of salinity acclimation, 866
- Colony shape (hydroids)  
salinity effects, 978  
water movement, 1146
- Colour forms  
differential tolerances to salinity, 841
- Columbia River estuary  
distribution of plankton, 955-958
- Combined effects of salinity and temperature  
development of invertebrates, 880-883  
tolerance of invertebrates, 841, 845, 846
- Commercial oyster plants  
salinity effects on production, 831
- Communities  
definition, 842  
drifting seaweed, 1106  
pennate diatoms, 1179  
salinity effects on  
benthos, 842, 843  
diatom, 812  
phytoplankton, 797, 798  
*Sargassum*, 1105-1107  
water movement effects on  
distribution, 1103, 1104  
plants, 1096-1098
- Community diversity  
salinity effects, 791, 843
- Complexation, 898
- Composition—see Chemical composition
- Conclusions  
ion regulation of invertebrates, 897  
non-genetic capacity adaptation of invertebrates, 931  
responses of  
animals to water movement, 1148, 1149  
fishes to salinity, 1032, 1033  
micro-organisms to salinity, 703
- Conditioning  
discrimination between salinities, 1022
- Contours of mortality, 843-845
- Contractile vacuole, 885, 899
- Conversion efficiencies  
salinity effects, 1016, 1017
- Copper, 897, 898  
effects on invertebrates, 834
- Coral reefs  
water movement, 1125
- Coriolis force  
effects on salinity distribution in estuaries, 960
- Correlation salinity: chlorinity, 828, 829
- Coulter counter, 1177
- Crimean Sivash  
maximum salinities, 821
- Critical depths, 1137, 1138
- Critical minimum  
water movement, 1114
- Critical partial pressure  
oxygen, 876
- Critical salinities  
in the laboratory, 832-836  
in the sea, 826-831
- Critical saturation deficit, 775, 776
- Cross-acclimation, 863, 865  
—see also Non-genetic adaptation
- Cruising speed  
salinity effects, 1020-1022

- Currents—*see also* Water movement, 1092, 1093  
     importance for animal dispersal, 1123, 1139–1141  
 Current meters, 1086  
 Current speeds  
     maximum values, 1088  
 Current zone, 1142  
 Cyclones, 1120  
 Cytology  
     salinity effects, 701–703, 819, 820, 987–995, 1030–1032  
 Cytorrhysis  
     as function of salinity  
         bacteria, 702, 703  
         blue-green algae, 703  
         fungi, 703  
     definition, 702  
 Danish Wadden Sea  
     turbidity, 1165  
 Death due to salinity stress  
     causes, 874, 998, 1000  
 Deep sea  
     transparency, 1161  
 Deformation (structural)  
     due to salinity  
         in fish larvae, 1029  
         in hydroids, 984–986  
 Deformities—*see* Deformation  
 Dehydration—*see* Desiccation  
 Den Helder  
     vertical seaweed distribution, 810  
 Density, 685, 686  
     changes  
         invertebrates, 943, 944  
     discontinuities, 969–972  
     gradients, 972  
     interfaces, 969–972  
     of sea water, 683, 685, 686  
 Dermal differentiations  
     salinity effects, 977  
 Deplasmolysis  
     bacteria, 703  
     blue-green algae, 703  
     plants, 710, 711  
 Desiccation  
     adjustments of plants, 717  
     definition, 846  
     distribution  
         of intertidal invertebrates, 973  
         of intertidal plants, 810–816  
     lethal limits of plants, 717–730  
     metabolic responses of plants, 770–784  
     plants, 706  
     potential, 856, 857  
     reproduction of  
         invertebrates, 953  
         plants, 784–787  
     structural adjustments in  
         crustaceans, 988  
         plants, 816–820  
     tolerance  
         invertebrates, 846–862, 872, 873  
         plants, 714–731  
 Deterioration of climate, 1124, 1125  
 Development  
     of fish eggs  
         tolerance to salinity, 997, 998  
     of invertebrate larvae  
         salinity effects, 880–883  
         tolerance to salinity, 843–845  
 Dialysis, 885  
 Diatomaceous earth, 1182  
 Differentiation processes  
     salinity effects, 976–995, 1028–1032  
 Diffusion  
     of light, 1161  
     speed in water, 1085, 1091  
 Discontinuity layers, 969–972, 1177  
 Dislocations, 1092  
 Dissolved organic matter  
     uptake, 910  
 Distribution  
     endogenous properties, 974, 975  
     salinity effects on  
         bacteria, 699, 700  
         blue-green algae, 700  
         fishes, 1028  
         fungi, 700  
         invertebrates, 954–975  
         plants, 787–816  
     turbidity effects on  
         animals, 1187, 1188  
         micro-organisms, 1170–1175  
         plants, 1179, 1180  
     water movement effects on  
         animals, 1133–1141  
         plants, 1102–1108, 1115, 1116, 1119  
 Diurnal migrations  
     plankton, 943, 944  
 Donnan  
     effects, 910  
     equilibrium, 894  
     ratio, 894, 910  
 Drift, 1086  
 Drift ice—*see* Ice formation  
 Drifting seaweed communities, 1106  
 Drinking  
     crustaceans, 925  
 Drinking rate  
     fishes, 1015

- Drinking rate—*continued*  
 invertebrates, 891
- Drought  
 avoidance, 813  
 resistance, 813  
   in thallus parts of plants, 726, 727
- Duration of larval stages  
 salinity effects, 880–883
- Durham  
 turbidity effects on animal zonations, 1188
- Dwarf forms  
 algae, 781  
 invertebrates, 975, 976  
 plants, 803, 817, 1108
- Dynamic viscosity, 1086
- D<sub>2</sub>O permeability, 895
- Ecological  
 master factor, 847  
 master factors  
   affecting plant distribution, 787, 788  
   potential, 835, 836, 841
- Economical aspects  
 water movement, 1120
- Ecophysiological salinity barrier, 959
- Ecosystems  
 definition, 842  
 salinity effects, 842, 843
- Eddies, 1147
- Efficiency of metabolism  
 salinity effects, 927, 928
- Egg  
 production  
   salinity effects, 953  
 survival  
   turbidity effects, 1186
- Eggs  
 of fishes  
   oxygen uptake under salinity stress, 1001  
   tolerance to salinity, 997, 998  
 sensitivity to turbidity, 1186, 1187
- Ekenäs  
 salinity limits of hydrophytes, 793
- Elbe estuary  
 plankton distribution, 955, 959, 962  
 salinity distribution, 960
- Electrical conductivity, 685, 686, 828
- Elements in sea water, 683, 684
- Embryonic development  
 salinity effects, 950, 951, 953, 1025–1027  
 turbidity effects, 1186
- Emergence—*see* Desiccation
- Emersion—*see* Desiccation
- Endemisms  
 Baltic Sea, 791, 792  
   sea and brackish waters, 822
- Endocrine glands of fishes  
 salinity effects, 1017–1020
- Energy requirements  
 for chloride regulation, 926  
 for development under salinity stress, 927, 928  
 for ion regulation, 878, 926  
 for metabolism under salinity stress, 927, 928  
 for osmoregulation, 763, 765, 878, 926, 1002, 1003
- Errant algae, 1107
- Errors in ionic analyses, 896
- Estuaries  
 plankton distribution, 955, 959, 962, 1104, 1105  
 turbidity, 1162, 1165  
 water movement, 1104, 1105
- Estuarine zones, 959–961
- Exchange of water volume, 1086
- Euryhaline  
 algae, 707  
 crustaceans, 868–870  
 fishes, 997  
 osmoregulators, 913–917
- Euryhalinity, 823, 961
- Eurysaline—*see* Euryhaline
- Evaporation, 857, 862, 873  
 distribution of intertidal invertebrates, 973
- Evolution  
 effect of extreme salinity conditions, 823  
 of brackish-water fauna, 822, 823  
 of ion regulation, 897
- Evolutionary adjustments of crustaceans  
 to life in fresh water, 870–872  
 to life on land, 872, 873  
 to salinity variations, 867–873
- Excised  
 gill tissue  
   salinity tolerance, 836–840  
 tissue pieces  
   respiration under salinity stress, 876–878
- Excretion  
 ammonia, 873  
 ammonotelic, 873  
 nitrogenous wastes, 873
- Exosmosis, 765, 766
- Expatriation, 1141
- Expositiophile plants, 1114
- Expositiophobe plants, 1114, 1115
- Exposure index, 1120
- External structures—*see also* Structures  
 salinity effects on  
   fishes, 1029, 1030

- invertebrates, 976-987
- micro-organisms, 702
- plants, 817, 818
- turbidity effects on
  - animals, 1189
- water movement effects on
  - animals, 1144-1148
  - plants, 1109-1113
- Extinction, 1157
- Extinction coefficient, 1158, 1161, 1185
  - definition, 1161
- Extrarenal chloride excretion, 1031
- Extravascular salt pools, 894
  
- Facultative halophytes, 793, 795
- Faeroes
  - vertical algal distribution, 814
- Fat consumption
  - under salinity stress, 927, 928
- Fe (iron) uptake, 896
- Feeding activity
  - salinity effects, 939, 940
- Fertilization
  - salinity effects, 1024, 1025
- Filter-feeders
  - turbidity effects, 1184, 1187
  - water movement effects, 1125-1131, 1135, 1138-1140, 1144
- Final body length—*see* Size
- Finnish Bay
  - phytoplankton species composition, 798
- Fin ray counts
  - salinity effects, 1030
- Fisheries
  - importance of turbidity, 1184, 1185
- Fishes—*see also* Animals
  - salinity effects on
    - distribution, 1028
    - external structures, 1029, 1030
    - internal structures, 1030-1032
    - metabolism and activity, 1001-1024
    - reproduction, 1024-1027
    - size, 1028, 1029
  - tolerance to salinity, 997-1001
- Fishing
  - effects of turbidity, 1184, 1185
- Fission
  - salinity effects, 948
- Fjord effect, 804
- Fjords of Norway and Sweden
  - plant distributions, 800-802
- Floating processes—*see* Suspension processes
- Food
  - conversion
    - salinity effects
      - in fishes, 1006-1009
      - in invertebrates, 927, 928
  - intake
    - salinity effects
      - in fishes, 1006-1009
      - in invertebrates, 927
  - uptake
    - importance for ion regulation, 896
- Formations of algae
  - vertical distribution, 814
- Forms of water movement, 1131, 1137
- Free space (osmotic), 781
- Freezing-point depression of coll fluid
  - plants, 758
- Freezing points
  - crustacean body fluids, 870, 871
- Freezing tolerance, 846
- Fresh water
  - definition, 822
- Friday Harbor
  - algal resistance to emersion, 812, 813
  - salinity and heat tolerances of littoral algae, 715
- Fuller's earth, 1157, 1186, 1187
- Fungi—*see also* Micro-organisms
  - nutritional salt requirements, 691
  - salinity effects on
    - distribution, 700
    - metabolism and activity, 697, 698
    - reproduction, 699
    - structure, 702, 703
  - tolerance to salinity, 691-693
  
- Gamete
  - release
    - algae under desiccation, 785, 786
    - invertebrates under desiccation, 953
  - sensitivity
    - to desiccation, 785
    - to salinity, 951, 953
- Gas exchange
  - plants
    - under desiccation, 770-778
    - water movement effects, 1098-1101
- Gaula estuary
  - chemical composition of algae, 750
- Genetic capacity adaptation
  - to salinity, 932, 1016
- Genetic resistance adaptation
  - to desiccation, 731
  - to life in fresh water, 870-872
  - to life on land, 847, 862, 872, 873, 988
  - to salinity, 842, 866-873, 1016
  - examples among crustaceans, 867-873
- German Bight
  - phytoplankton species composition, 798

- Germination  
algae under desiccation, 785, 786
- Gill  
damage due to turbidity, 1189  
nets  
efficiency in turbid water, 1185  
—see also Nets  
organ involved in ion and osmoregulation,  
869–873, 890, 893, 894, 1014, 1015,  
1030, 1031  
tissue  
respiration under salinity stress, 876–878  
salinity effects, 1030, 1031  
salinity tolerance, 836, 840
- Glacial relicts, 867
- Glycine uptake, 910
- Gonophore production  
salinity effects, 949
- Grain size distribution, 967, 968
- Ground ice—see Ice formation
- Growth  
as function of desiccation, 781–784  
as function of salinity  
fishes, 1005–1009  
invertebrates, 878–884, 927, 928  
micro-organisms, 694–699  
plants, 752–757, 781–784  
as function of turbidity  
animals, 1183  
micro-organisms, 1168–1170  
plants, 1178  
as function of water movement  
corals, 1123  
plants, 1096, 1098
- Growth disharmony, 816, 817, 984–986, 1029
- Growth forms  
as function of salinity  
animals, 975–987, 1029, 1030  
plants, 816–818  
as function of turbidity  
animals, 1189  
micro-organisms, 1175  
plants, 1180  
as function of water movement  
animals, 1141–1147  
corals, 1123  
plants, 1108–1112
- Gulf of Mexico  
turbidity, 1163
- Gut  
organ involved in ion and osmoregulation,  
869–873, 893, 903, 904, 1014, 1032  
structure  
salinity effects, 1032
- Halobiont system of diatoms, 809, 810
- Haloclines, 969–972
- Halophytes  
facultative, 793, 795  
obligatory, 793  
terrestrial, 795
- Hardanger Fjord  
algae distributions, 800–802  
number of algae species, 802
- Hatching  
salinity effects, 1024–1026
- Heat  
resistance  
as function of salinity acclimation, 866  
tolerance of plants  
as function of salinity, 714–716
- Helgoland  
composition of algal cell fluids, 759  
effect of water stagnation on plants,  
1100  
storm effects on algae, 1120  
tolerance of benthonic algae to air ex-  
posure, 718  
Underwater Laboratory, 1141
- Helophytes  
marine forms, 795
- Hidden—see  
plant distributions, 796
- Hold fasts—see Attachment organs
- Holeuryhaline, 823, 961  
crustaceans, 870  
osmoregulators, 917  
species, 706
- Homeohydric plants, 812
- Homeo-osmosis, 925
- Homeo-osmotic, 908
- Homeo-osmoticity, 870
- Horizontal distribution  
invertebrates, 954–969  
plants under desiccation stress, 815, 816
- Horizontal migrations, 968, 969
- Hormones  
salinity effects in fishes, 1017–1020
- Horohalium, 827–829, 866, 867, 959
- Humidity  
effects on emerged plants, 719, 720, 722,  
723, 726, 729, 730, 770, 784  
tolerance of intertidal invertebrates, 847–  
862
- Hunnebrunnen  
phytobenthos distribution, 802  
phytoplankton distribution, 802
- Hurricanes, 1120
- Hydranth (hydroids)  
number  
salinity effects, 879  
water movement effects, 1146

- shape  
   salinity effects, 978-981  
 size  
   salinity effects, 978-981  
 Hydrochemistry of brackish waters, 827-829  
 Hydrodynamic drag, 1113, 1121  
 Hydrodynamic forces—*see* Water movement  
 Hydrodynamic pressure, 1086, 1147  
 Hydrogen  
   ion regulation, 759, 897  
 Hydroids  
   salinity effects on structure, 976-994  
 Hydrostatic pressure, 1086, 1087  
 Hyper-hypo-osmotic regulation, 868, 906-909, 921-923  
 Hyperosmotic regulation, 868, 869, 906-913  
   sites of water and salt exchange, 869, 871  
 Hyperosmoticity, 906  
 Hypersaline  
   rock pools  
     plant distributions, 804-807  
     water, 822  
   Hypo-osmotic regulation, 869, 870, 921-923  
     sites of water and salt exchange, 869  
   Hypo-osmoticity, 906  
   Hypophysectomy, 1017  
  
 Ice formation  
   destructive effects on vegetations, 1121  
 Ideal ocean  
   distribution of hydrological characteristics, 1140  
 Imbibition of water  
   invertebrate eggs, 951  
 Immigration  
   to terrestrial habitats, 795, 847, 862, 872, 873, 988  
   to waters with different salinity regimes, 706, 707, 867-873, 923  
 Incipient plasmolysis, 710, 732  
 Incubation period  
   salinity effects, 1026  
 Indian Ocean  
   maximum/minimum salinities, 688  
   transparency, 1162, 1163  
   turbidity, 1162, 1163  
 Indicators (plankton)  
   water body, 1103, 1104  
   water movement, 1103  
 Infauna  
   salinity effects, 964  
 Interchangeability of Mg and Ca, 695, 698, 699  
 Intermediary metabolism  
   desiccated plants, 778-780  
  
 Internal structures—*see also* Structures  
   salinity effects on  
     fishes, 1030-1032  
     invertebrates, 987-995  
     micro-organisms, 701-703  
     plants, 819, 820  
   turbidity effects on  
     animals, 1189  
   water movement effects on  
     animals, 1148  
     plants, 1113  
 International Indian Ocean Expedition  
   water transparencies, 1163  
 Interpopulational—*see* Intraspecific, Populations  
 Interspecific  
   differences  
     osmoregulative capacity, 911, 912  
     variation  
       water movement effects, 1142-1144  
 Interstitial salinities  
   effect on substrate-living invertebrates, 830, 831  
   fluctuations, 830, 831, 963, 964  
 Intracellular osmoconcentration, 909  
 Intraspecific  
   differences  
     ion transport, 892, 893  
     osmoregulative capacities, 911, 912  
     salinity tolerance, 826, 838, 841-843  
     sodium regulation, 892, 893  
   variation  
     water movement effects, 1141, 1142  
 Invertebrates—*see also* Animals  
   salinity effects on  
     distribution, 954-975  
     external structures, 976-987  
     internal structures, 987-995  
     metabolism and activity, 874-945  
     reproduction, 946-954  
     size, 975, 976  
     tolerance to salinity, 825-874  
 Ion  
   accumulation  
     in cell sap, 762  
   concentration  
     in cell fluids of plants, 759  
   effects on neuromuscular responses, 944, 945, 1020-1022  
   pumps, 760  
   ratios (ambient), 828  
   regulation  
     capacities in invertebrates, 885-895  
     definition, 885  
     energy requirements, 926  
     evolution, 897

- Ion, regulation—*continued*  
   in fishes, 1009, 1013–1016  
   in invertebrates, 884–898  
   in plants, 758–760  
   organs involved, 869–873, 888–890, 893–896, 899, 902–904, 910, 911, 1013–1015, 1017–1019, 1030–1032  
   transport, 885–898  
     activation, 917  
     role of sodium, 698  
 Ionic analyses  
   errors, 896  
   methods, 896  
 Ionic composition  
   effects on activity, 944, 945  
   tolerance of invertebrates, 827–830  
 Ionic gradients  
   muscle vs blood, 892  
 Irradiance meter, 1160, 1161  
 Isosmoticity, 906  
 Isotachs, 1148  
  
 Jackson Candle Method, 1159  
 James River  
   salinity distributions, 960  
  
 Kaolin, 1182–1184, 1186, 1187  
 Kidneys  
   organ involved in ion and osmoregulation, 1013, 1014, 1032  
   structure  
     salinity effects, 1032  
 Kiel Bay  
   effect of water stagnation on plants, 1100, 1101  
 Kiel Canal  
   salinity effects on reproduction, 946, 948  
 Kinematic viscosity, 1086  
 'Klimaverschlechterung'—*see* Deterioration of climate  
 Knudsen tables, 686  
  
 Lacerating water body, 1135  
 Lago Maracaibo  
   diatoms, 808  
   planktonic algae, 808  
   plant distributions, 807, 808  
 Lagoons  
   in the subtropics  
     plant distributions, 804, 805  
   of Texas  
     plant distributions, 804–806  
 Laguna Madre  
   maximum salinities, 821  
   plant distributions, 804  
 'Lake' Maracaibo—*see* Lago Maracaibo  
  
 Lake Pontchartrain  
   turbidity, 1183  
 Land  
   loss, 1121  
   reclamation, 795–797, 1121, 1178, 1179  
 Larvae  
   of fishes  
     osmoconcentration, 1010–1012  
     oxygen uptake under salinity stress, 1001  
     sensitivity to turbidity, 1187  
     tolerance to salinity, 997, 998  
     weight changes due to salinity, 1012  
   of insects  
     adjustments to osmotic stress, 921–923  
   of invertebrates  
     osmoregulative potentials, 908, 909  
     sensitivity to turbidity, 1186, 1187  
 Larval stages  
   salinity effects on duration, 880–883  
 Lateral plates  
   salinity effects, 1030  
 Law  
   of equifinality, 763  
   of poverty, 791  
 'Lebensformtypen', 1149  
 'Leitformen'—*see* Indicators  
 Lethal salinity effects  
   total osmoconcentration, 832–834  
   proportions of solutes, 834–836  
 Life on land  
   structural adjustments in crustaceans, 847, 862, 872, 873, 988  
 Light—*see also* Turbidity  
   refraction, 685  
   scattering, 1157, 1164  
   transmission, 1157, 1165  
 Limiting forces  
   water movement effects  
     animals, 1124, 1125  
     plants, 1095, 1096  
 Lithium  
   ion regulation, 896  
 Littoral zonations, 1117, 1118  
 Littoral zones  
   geographic classification, 1140  
 Locomotion  
   diatoms, 1179, 1180  
   ion effects, 944, 945  
   salinity effects, 934, 935  
 Long Island Sound  
   turbidity, 1165  
 Longitudinal effects, 948  
 Lough Ine Rapids  
   water movement effects on algal distributions, 1115

- Luminescence  
in bacteria, 693, 694
- Lysis as function of salinity  
bacteria, 701, 702  
blue-green algae, 702  
fungi, 702  
prevention of lysis by salts, 701
- Magnesium  
ciliary activity, 840  
effects on locomotory activity, 944, 945  
ion regulation, 759, 885-897  
requirements  
bacteria, 694-696  
blue-green algae, 699  
fungi, 697, 698  
tissue survival, 840  
tolerance of invertebrates, 834, 835
- Magnesium: calcium balance  
importance for locomotory performance, 945
- Mangrove algae  
salinity tolerance, 711
- Mantle tissue  
salinity effects, 994
- Marine helophytes, 795
- Mass spectrometry, 687
- Maximum salinities  
natural habitats, 700, 821, 826, 827, 1000
- May cast, 1120
- Median lethal times  
tolerance to desiccation, 854-860
- Mediterranean Sea (European)  
maximum salinities, 688  
number of marine algae, 800
- Meio-mesohaline zone, 809
- Meristic characters  
salinity effects, 977, 978, 1030, 1032
- Mesohaliniacum, 809
- Mesopsammon  
horizontal distribution, 965-968
- Metabolic  
cost  
ion and osmoregulation, 926, 1002, 1003  
efficiency of invertebrates  
salinity effects, 927, 928  
salt requirements  
micro-organisms, 693-699  
water and salt regulation  
fishes, 1010-1023, 1030-1032  
invertebrates, 884-926  
plants, 757-767
- Metabolism and activity  
salinity effects on  
bacteria, 693-697  
blue-green algae, 698, 699  
fishes, 1001-1024  
fungi, 697, 698  
invertebrates, 874-945  
plants, 731-784  
turbidity effects on  
animals, 1184, 1185  
micro-organisms, 1168-1170  
plants, 1178, 1179  
water movement effects on  
animals, 1125-1132  
plants, 1096-1102
- Methods  
ionic analyses, 896
- Micro-organisms—see also Bacteria, Fungi,  
Blue-green algae  
salinity effects on  
distribution, 699, 700  
metabolism and activity, 693-699  
reproduction, 699  
structure, 701-703  
tolerance to  
salinity, 689-693  
turbidity, 1167, 1168  
turbidity effects on  
distribution, 1170-1175  
metabolism and activity, 1168-1170  
reproduction, 1170  
structures, 1175
- 'Migration forms'  
in algae, 1107
- Migrations  
between different salinity regimes, 1000  
horizontal, 968, 969  
salinity effects, 1022-1024  
seasonal, 968, 969  
vertical, 973
- Mineral requirements  
bacteria, 693-697  
blue-green algae, 698, 699  
fungi, 697, 698
- Minimum velocity layer, 1145-1161
- Mitochondria  
salinity effects, 1031, 1032
- Mitochondrial pumps, 894
- Model oceans, 973
- Model system of water transport, 894
- Mode of filtration, 1126, 1127
- Mokelumne River  
turbidity, 1162
- Monstrosities  
due to salinity stress, 984-986
- Mortality contours, 843-845
- Motility  
salinity effects on  
blue-green algae, 703

- Motility, salinity effects on—*continued*  
 invertebrates, 943-945  
 unicellular algae, 711
- Mucilaginzation of fish gill  
 turbidity, 1181
- Multivariable conditions  
 salinity tolerance, 843-846
- Muscle  
 activity  
 ion effects, 944, 945  
 salinity effects, 936  
 efficiency, 932  
 ionic concentration, 892
- Mutual exclusion, 975
- Myotome counts in fish larvae  
 salinity effects, 1032
- Nematocyst size  
 salinity effects, 989, 991, 993
- Nepheloid layer, 1164, 1165
- Nephridia  
 importance for volume regulation, 902-904  
 organ involved in ion and osmoregulation,  
 888, 902-904
- Nets  
 catches as a function of turbidity, 1184,  
 1185
- Neuromuscular responses  
 ion effects, 944, 945, 1020, 1022
- Neutron-activation analysis, 687
- Newfoundland Slope  
 turbidity, 1164
- Ninhydrin-positive substances, 1019
- Nitrogen  
 balance  
 desiccated algae, 778, 779  
 fixation  
 blue-green algae, 693
- Niveau fluctuation, 1093, 1094
- Non-genetic capacity adaptation  
 to salinity  
 fishes, 1016, 1017  
 invertebrates, 928-933
- Non-genetic resistance adaptation  
 to desiccation stress  
 plants, 730, 731  
 to salinity  
 invertebrates, 863-866
- Non-sedentary animals  
 behavioural responses to water movement,  
 1127-1130
- Normal sea water, 686
- North Atlantic Current  
 turbidity, 1164
- North Sea  
 distribution of phytoplankton, 797
- turbidity, 1164  
 'turbidity screen', 1188  
 water body qualities, 1103, 1104
- Nucleus size  
 salinity effects, 989-992
- Number of species  
 in waters with different salinities, 823, 824
- Nutrition  
 effects on salinity tolerance, 693  
 importance for ion regulation, 896  
 requirements  
 of micro-organisms, 690-693  
 significance of amino-acid uptake, 911
- Obligate marine micro-organisms, 689
- Obligatory halophytes, 793
- Ocean-wide distributions  
 water movement, 1140, 1141, 1149
- Oligohaline, 961  
 osmoregulators, 917-920
- Oligostenohaline, 823, 961  
 crustaceans, 870-872
- 'Omnipresence' of elements, 683
- Optical density  
 in bacteria, 701
- Orbital water movement, 1131, 1137
- Organic compounds  
 in body cavity fluids, 910
- Organic matter exudation  
 littoral algae, 780
- Organs involved in ion and osmoregulation,  
 869-873, 888-890, 893-896, 899, 902-904  
 910, 911, 1013-1015, 1017-1019, 1030-  
 1032
- Orientation, 973  
 water currents, 1129-1131
- Origin of brackish-water species, 791
- Orthostenohaline, 823, 961  
 crustaceans, 867, 868
- Oscillating water body, 1135
- Oscillating water movement, 1131, 1137
- Oscillatory zones, 1142
- Osmoconcentration  
 as a function of desiccation, 770, 861  
 in fishes, 1009-1016, 1021  
 in invertebrates, 867-873, 904-926, 929-  
 932  
 in plants, 732-734, 761-770
- Osmoconformers, 758, 905, 906
- Osmolabile, 905
- Osmometer, 761
- Osmoregulation  
 as a function of age, 908, 909, 1013  
 capacities  
 in fishes, 1010-1015  
 in invertebrates, 906-912, 915-925

- in plants, 761-767  
 definition, 904  
 energy requirements, 926, 1002, 1003  
 in fishes, 1003, 1009, 1013-1016  
 in invertebrates, 868-873, 884, 885, 904-926  
 in larvae of invertebrates 908, 909  
 in plants, 732-735, 760-767  
 Osmoregulators, 758, 906  
 Osmotic climate  
   importance for desiccation, 728, 730  
 Osmotic independence, 870, 925  
 Osmotic space, 766, 781  
 Oviposition  
   salinity effects, 953  
 Oxygen  
   consumption  
     of isolated invertebrate tissues  
       salinity effects, 876-878  
     of fishes  
       salinity effects, 1001-1004  
     of plants  
       salinity effects, 735-740  
     of whole invertebrates  
       salinity effects, 874-876  
   content  
     effect on embryonic development, 1026,  
       1027  
   output  
     in plants under desiccation stress, 721-  
       725, 727, 728  
     in plants under salinity stress, 739-748  
 Pacific Grove  
   salinity and heat tolerance of littoral algae,  
     718  
 Pacific Ocean  
   maximum/minimum salinities, 688  
 Parameters of water movement, 1086  
 Parthenogenesis  
   salinity effects, 1027  
 Partial pressure  
   carbon dioxide, 876  
   oxygen, 876  
 Partial size  
   turbidity, 1157  
 Particle speeds (water movement)  
   maximum values, 1088  
 Particle velocity, 1124  
 Particulate carbon, 1158, 1159, 1161  
 Particulate matter—*see* Turbidity  
 Pendular water movement, 1131, 1137  
 Permeability, 731, 779  
   effect of Ca, 903  
   for D<sub>2</sub>O, 895  
   membrane theory, 884  
   sorption theory, 884  
 Persian Gulf  
   maximum salinities, 688  
 Peveril Point  
   distribution of algal associations, 811  
   vertical distribution of diatoms, 812  
 pH of invertebrate blood, 897  
 Phosphate  
   ion regulation, 759  
   requirements  
     bacteria, 694  
   uptake  
     fungi, 698  
 Photoperiod, 1024  
 Photosynthesis  
   importance for plant distribution, 787, 788  
   under desiccation stress, 717, 719-725, 730,  
     731, 770-778  
   under salinity stress, 739-749  
   water movement effects, 1099  
 Physical properties of sea water, 683, 685  
   density, 685  
   electrical conductivity, 685  
   light refraction, 685  
   speed of sound, 685  
   temperature and salinity, 685  
 Physiological potential, 836  
 Phytobenthos  
   effects of water movement, 1093, 1094  
 Phytoplankton  
   communities, 797, 798  
   distribution  
     in Baltic Sea and North Sea, 797-  
       799  
     in Black Sea, 800  
   effects of water movement, 1092  
   distribution, 1102-1104  
   external structures, 1109, 1110  
   photosynthesis under salinity stress, 748  
   salinity tolerances, 712  
 Pigmentation  
   salinity effects, 977, 1032  
 Pituitary gland, 1024  
   water balance in fishes, 1017, 1018  
 Planar body growth, 1145, 1146  
 Plankton  
   communities  
     water movement effects on distribution,  
       1103, 1104  
   definition, 1102  
   distribution in Elbe estuary, 955-959  
   diurnal migrations, 943, 944  
   feeding habits as ecological master factor,  
     976  
   horizontal distributions, 954-962  
   indicators of water bodies, 955  
   sequence, 1103

- Plankton—*continued*  
 succession, 1103  
 vertical distributions, 969-975
- Planktonic algae—*see* Phytoplankton
- Plant phyla  
 in sea, brackish and fresh water, 705, 706
- Plants  
 desiccation effects on  
 distribution, 810-816  
 external structures, 818  
 internal structures, 819, 820  
 metabolism and activity, 770-784  
 reproduction, 784-787  
 size, 816, 817  
 salinity effects on  
 distribution, 787-816  
 external structures, 817, 818  
 internal structures, 819, 820  
 metabolism and activity, 731-784  
 reproduction, 784-787  
 size, 816, 817  
 tolerance to  
 desiccation, 714-731  
 salinity, 707-731  
 turbidity, 1178  
 water movement, 1094-1096  
 turbidity effects on  
 distribution, 1179  
 metabolism and activity, 1178, 1179  
 reproduction, 1179  
 structures, 1180  
 water movement effects on  
 distribution, 1102-1108, 1115, 1116, 1119  
 external structures, 1109-1113  
 internal structures, 1113  
 metabolism and activity, 1096-1101  
 reproduction, 1102  
 size, 1108  
 supra-individual structures, 1113-1121
- Plasmatic exosmosis, 712-714
- Plasmatic viscosity  
 desiccated plants, 779
- Plasmolysis  
 bacteria, 703  
 blue-green algae, 703  
 plants, 708-711, 730, 732, 768
- Pleio-mesohaline zone, 809
- Plymouth  
 particulate matter in ocean water, 1165
- Pocasset River estuary  
 distribution of invertebrates, 963, 964  
 salinity regime, 830, 831, 963, 964
- Poikilohydric plants, 812
- Poikilosmoticity, 905, 906
- Pollution  
 effects on turbidity, 1162
- Potomac River, 1182
- Polyhaline, 961
- Polystenohaline, 823
- Population growth  
 dinoflagellates in different salinities, 756
- Populations—*see also* Intraspecific differences in salinity tolerances, 826, 841-843
- Porphyropsin, 1032
- Positioning  
 relative to currents, 1129-1131  
 water movement, 1146, 1147
- Possjet Bay  
 salinity effects on ecosystems, 842, 843
- Potassium  
 ciliary activity, 840  
 ion regulation, 759, 885-897  
 pump, 870  
 requirement  
 bacteria, 694-697  
 blue-green algae, 698, 699  
 fungi, 697, 698  
 survival of invertebrates, 834, 835  
 tissue survival, 840
- Potassium-sodium pump, 759, 760
- Potomac River  
 turbidities, 1182
- Pre-adaptations, 838, 839  
 to land life, 872, 873
- Preference experiments  
 salinity, 832, 1022-1024
- Primary distributional aspects  
 water movement, 1135-1140
- Primary limiting forces  
 water movement, 1095, 1124
- Primary production  
 water movement effects, 1101
- Prolactin, 1023  
 secretion, 1018
- Protein  
 consumption  
 under salinity stress, 927, 928  
 in blood, 910
- Pseudotracheae, 873
- Pumping rate  
 effect of turbidity, 1184
- Q<sub>0</sub> values  
 plants under salinity stress, 737-739
- Radial body growth, 1145
- Radial symmetry—*see* Symmetry of body
- Ram pressure, 1086, 1135
- Randers Fjord  
 salinity limits of hydrophytes, 793
- Reclamation of land—*see* Land reclamation

- Rectal gland  
 importance for ion regulation, 1015  
 salinity effects, 1032  
 —see also Organs involved in ion and osmo-  
 regulation
- Red algae  
 tolerance to artificial sea water, 713
- Red Bulack Lake  
 occurrence of invertebrates, 826, 827
- Red Sea  
 maximum salinities, 688, 821  
 responses of animals to water movement,  
 1127–1130
- Reduction of contact with adverse salinities,  
 939, 941, 942
- Regeneration  
 salinity effects, 948
- Regulatory organs  
 structural modifications due to salinity  
 stress, 987  
 —see also Organs involved in ion and osmo-  
 regulation
- Regulatory structures  
 fish larvae, 1013
- Rehydration  
 metabolic effects on plants, 774–779
- Re-immersion  
 metabolic effects on plants, 774,  
 775
- Release of material from bacteria cells  
 as function of salinity and temperature,  
 701, 702  
 pH effects, 702
- Renal sac fluid  
 ionic constituents, 888
- Renal salt excretion, 920
- Reproduction  
 desiccation effects on  
 invertebrates, 953  
 plants, 784–787  
 salinity effects on  
 fishes, 1024–1027  
 invertebrates, 946–954  
 micro-organisms, 699  
 plants, 784  
 turbidity effects on  
 animals, 1185–1187  
 micro-organisms, 1170  
 plants, 1179  
 water movement effects on  
 animals, 1132  
 plants, 1102
- Resistance adaptation—see Adaptation
- Resistance—see Tolerance
- Respiratory fever  
 plants, 776
- Respiratory rate—see also Metabolism and  
 Activity  
 importance for plant distribution, 787, 788  
 in fishes  
 salinity effects, 1001–1004  
 in invertebrates  
 salinity effects, 874–876, 878  
 in isolated invertebrate tissues  
 salinity effects, 876–878  
 in plants  
 desiccation effects, 770–778  
 salinity effects, 735–739, 742, 764  
 water movement effects, 1099–1101
- Response surface, 843–845, 880–882
- Resting stages  
 tolerance to salinity, 825, 826, 941
- Rhodopsin, 1032
- River Ythan  
 distribution of *Corophium*, 831, 962, 963  
 estuary  
 salinity regime, 831
- Rock pools  
 plant distributions, 804–807
- Sacramento River  
 turbidity, 1162
- Salinity  
 barrier ('Salzschranke'), 705, 706  
 chemical aspects, 685, 686  
 correlation with chlorinity, 828, 829  
 definition, 686  
 distribution  
 in oceans and coastal waters, 687, 688  
 ecological factor  
 in marine botany, 705, 706  
 in marine zoology, 821–825  
 ecological master factor, 705, 731, 822  
 functional responses  
 fishes, 997–1028  
 invertebrates, 825–975  
 micro-organisms, 689–700  
 plants, 797–816  
 general aspects, 683–686  
 interfaces, 969–972  
 measuring techniques  
 analytical methods, 687  
 colorimetric methods, 687  
 density, 686  
 electrical conductivity, 686  
 ionic composition, 686  
 mass spectrometry, 687  
 neutron-activation, 687  
 total salinity, 686  
 physical aspects, 683–685  
 structural responses  
 fishes, 1028–1032

- Salinity, structural responses—*continued*  
 invertebrates, 975–995  
 micro-organisms, 701–703  
 plants, 816–820  
 total range on earth, 821
- Salt—*see also* Sea salt  
 contents in oceans, 688  
 exchange  
 invertebrate eggs, 951  
 pools  
 extravascular, 894  
 receptor, 1022  
 regulation—*see* Ion, Volume, Osmoregulation  
 requirements  
 bacteria, 693–695  
 blue-green algae, 698, 699  
 fungi, 697, 698  
 secretion, 873  
 'Salzschranke' (salinity barrier), 705, 706
- San Joaquin River  
 turbidity, 1162
- Sarcoplasmic reticulum, 896
- Sargasso Sea, 1105–1107  
 transparency, 1161, 1164
- Saturation deficit  
 air humidity, 862
- 'Schwebefortsätze'—*see* Suspension processes
- SCUBA diving, 1123
- Sea balls, 1111
- Sea-grasses  
 sterility due to turbidity, 1179  
 zonation, 811
- Sea salt—*see also* Salt  
 constancy of composition, 685, 686  
 major elements, 683–686  
 minor elements, 683–686  
 trace elements, 683–686
- Seasonal changes  
 in desiccation tolerance, 726  
 in distribution  
 salinity effects, 968, 969  
 in inorganic and organic constituents of  
 algae, 753
- Seasonal migrations, 968, 969
- Seasonal successions, 815, 816
- Sea water  
 artificial, 687  
 calcium carbonate content, 686  
 chemical properties, 685, 686  
 composition, 684  
 definition, 686  
 major elements, 683–685  
 minor elements (trace elements), 683, 684,  
 686  
 normal, 686  
 physical properties, 683–685
- Seaweeds  
 desiccation effects on growth, 782, 783  
 zonation, 810
- Secchi-Disc, 1159
- Secondary distributional aspects  
 water movement, 1135–1140
- Secondary limiting forces  
 water movement, 1095, 1096, 1124–1126
- Sedentary animals  
 behavioural responses to water movement,  
 1130, 1131
- Sediment—*see also* Substrate  
 danger to fishes, 1181, 1182  
 salinity fluctuations, 830, 831, 963, 964  
 transport, 1152
- Sedimentation, 1177
- 'Seeknödel'—*see* Sea balls
- Selection of favourable salinities, 941
- Seston, 1067
- Settling of plant spores  
 water movement effects, 1102
- Sex ratio  
 salinity effects, 953
- Sexual reproduction of invertebrates  
 salinity effects, 949–953
- Shellfish  
 importance of turbidity, 1183, 1184, 1186,  
 1187
- Shell structures (molluscs)  
 salinity effects, 981–983
- Shell thickness  
 water movement, 1144
- Sight feeders, 1185
- Sites of ion and osmoregulation—*see* Organs  
 involved in ion and osmoregulation
- Size—*see also* Structures  
 salinity effects on  
 fishes, 1005, 1028, 1029  
 invertebrates, 975, 976  
 micro-organisms, 702  
 plants, 816, 817  
 turbidity effects on  
 animals, 1188, 1189  
 water movement effects on  
 animals, 1141–1144  
 plants, 1108
- Sodium  
 absorbing mechanisms, 870  
 concentration in blood, 916, 917  
 critical lower concentration, 834, 835  
 fluxes, 890, 891, 915, 918, 1001  
 ion regulation, 696–698, 759, 885–897  
 penetration mechanism, 697  
 requirements  
 bacteria, 694–697

- blue-green algae, 698, 699  
 fungi, 697, 698  
 indicator for obligate marine micro-organisms, 703  
 transport, 895  
 uptake, 916, 1003
- Sör Fjord  
 algae distributions, 801
- Spawning  
 salinity effects, 951, 953, 1024, 1025  
 turbidity effects, 1187
- Speciation  
 effect of extreme salinity conditions, 823
- Species  
 composition  
 of phytoplankton communities, 798  
 diversity  
 salinity effects, 791, 792, 795  
 numbers  
 in waters with different salinities, 823, 824
- Speed of water movement, 1086
- Sperm of fishes  
 viability as function of salinity, 1025
- Spillway (Bonnet Carre)  
 effects on oyster beds, 1183
- Spores of marine algae  
 tolerance to desiccation, 729
- Spray zone  
 maximum height, 1088
- Stagnation, 1124  
 water movement, 1094, 1095, 1099-1101
- Standing crop, 1097, 1098
- Stenohaline, 823, 961
- Stenohyperosmotic plants, 763
- Stenosaline, 823
- Sterility  
 due to salinity, 946  
 in drifting algae, 1107  
 sea-grasses under high turbidity stress, 1179  
 water movement effects, 1102
- 'Stoffgewinn', 739
- Storms  
 destructive effect on vegetation, 1120, 1121  
 effects on fisheries, 1185  
 turbidity, 1188
- Strategies  
 for maximum ecological success, 841
- Structures—*see also* Size, External structures, Internal structures  
 of fishes  
 salinity effects, 1028-1032  
 of invertebrates  
 salinity effects, 975-995  
 of micro-organisms  
 salinity effects, 701-703  
 turbidity effects, 1175  
 of plants  
 salinity effects, 816-820  
 turbidity effects, 1180
- Subindividual level  
 tolerance to salinity, 836-840
- Sublittoral water body types, 1135
- Submarine caves, 1125, 1126
- Submergence in brackish water, 802-804
- Substrate—*see also* Sediment  
 distribution as a function of water movement, 1133-1135  
 salinity fluctuations, 830, 831, 963, 964  
 water movement effects on distribution, 1096, 1135, 1136
- Subtropical lagoons  
 plant distributions, 804, 805
- Successions, 843
- Sulphate  
 ion regulation, 759, 885-897  
 requirements  
 bacteria, 694  
 blue-green algae, 699
- Supra-individual level  
 tolerance to salinity, 841-843
- Supra-individual structures  
 water movement effects in plants, 1113-1121
- Surf  
 action, 1093  
 effects  
 plants, 1117  
 phenomena, 1086  
 pressure  
 maximum value, 1088  
 zone, 1142
- Surface: volume ratio of cells  
 salinity effects, 990, 991
- Surface water movement, 1131, 1137
- Suspended material—*see* Turbidity
- Suspended solids  
 effects on fishes, 1181, 1182
- Suspension processes  
 plankters, 1109, 1110
- Swedish Deep Sea Expedition, 1161, 1177
- Swelling and shrinkage  
 algae, 768-770
- Swimming activity  
 salinity effects, 1020
- Symmetry of body  
 water movement effects, 1145
- Tampa Bay  
 sea-grass zonation, 811

- Temperature  
 ecological master factor, 1103  
 effects on  
   ATPase activity, 933  
   cell number, 988  
   desiccation tolerance, 727, 728, 849, 854-860  
   developmental rate, 880-883, 1027  
   energy expenditure, 928  
   growth under salinity stress, 1008  
   osmoregulation, 906-908, 923-925  
   salinity tolerance, 843-846  
   structural modifications due to salinity stress, 979-981, 991, 993, 994  
 'Temporalvariationen', 1109  
 Tentacle (hydroids)  
   dimensions  
     salinity effects, 979  
   numbers  
     salinity effects, 979  
 Terrestrial and semiterrestrial habitats  
   genetic adaptation of crustaceans, 847, 862, 872, 873, 988  
 Terrestrial halophytes, 795  
 Terrestrialization, 938  
 Tertiary distribution aspects  
   water movement, 1133-1135  
 Tertiary limiting forces  
   water movement, 1096, 1125  
 Texas lagoons  
   phytobenthos, 804-806  
 Thermal disharmonization  
   osmoregulative capacity, 925  
 Thermistor measurements, 1086  
 Thermoclines, 972  
 Thermodynamic work  
   osmoregulation, 926  
 Thiourea, 1019  
 Thiourocil, 1019  
 Thyroid  
   gland, 1018-1020, 1023, 1024  
   hormone, 1023  
   calorigenic action, 1019  
 Thyrotrophin, 1019  
 Thyroxin, 1019  
 Tidal currents  
   effects on plant zonation, 1118, 1119  
 Tidal rapids, 1115  
 Tide-level differences  
   maximum value, 1088  
 Time course  
   acclimation to salinity, 929  
 Tissues—*see* Subindividual level  
 Tolerance  
   correlation to activity, 840  
   to desiccation  
   invertebrates, 846-862  
   plants, 714-731  
   to salinity  
   bacteria, 689-691  
   blue-green algae, 693  
   fishes, 997-1001  
   fungi, 691-693  
   invertebrates, 825-874  
   plants, 707-731  
   to turbidity  
   animals, 1181-1183  
   micro-organisms, 1167, 1168  
   plants, 1178  
   to variations in ionic composition, 712-714, 827-830, 834, 835, 839, 840  
   to water movement  
   animals, 1124, 1125  
   plants, 1094-1096  
 Trace elements  
   gradients and exchange, 897, 898  
   in sea water, 683, 686  
 Transformation into salinity resistant stages, 941  
 Transmission of light, 1158, 1159, 1162-1164  
 Transmissometer, 1158, 1159  
 Transparency of (sea) water, 1161-1165  
   effect on fish catching, 1185  
   turbidity, 1157, 1158  
 Transportation of plants  
   water movement, 1102  
 Transverse fission  
   salinity effects, 948  
 Trimethylamine oxide, 1019  
 Troll catch—*see also* Nets  
   relation to gill net catch, 1185  
 tsp-diagrams, 954  
 Tube-building activities  
   salinity effects, 937  
 Turbidity  
   definition, 1157  
   distribution in oceans and coastal waters, 1161-1165  
   functional responses  
   animals, 1181-1188  
   micro-organisms, 1167-1175  
   plants, 1178, 1179  
   hindering settlement, 1184  
   importance for planktonic eggs and larvae, 1185, 1186  
   inhibition of feeding mechanism, 1183, 1184  
   methods of measuring, 1158-1161  
   modification of light penetration, 1161  
   practical value for fishermen, 1185  
   selected data, 1162-1165  
   standard unit, 1157

- structural responses  
 animals, 1188, 1189  
 micro-organisms, 1175  
 plants, 1180  
 variations in ocean water, 1159
- Turbidity meter, 1159  
 'Turbidity screen', 1188
- Turbulences, 1092  
 —see also Water movement
- Turgor  
 pressure deficit, 732  
 regulation, 760-767
- Two-dimensional water body, 1135
- Tyndall effect, 1177
- Ultrastructure of cells  
 salinity effects, 1031, 1032
- Underwater Laboratory 'Helgoland', 1141
- Underwater research  
 importance, 1123
- Underwater visibility, 1159, 1160
- Unidimensional water body, 1135
- Uptake of glucose and amino acids, 910, 911
- Ureotelism, 910
- Urinary bladder  
 role in osmoregulation, 893  
 —see also Organs involved in ion and osmoregulation
- Urine  
 flow, 903, 917, 920  
 rate, 915, 917  
 production, 871-873, 889, 890, 915, 917, 920, 1015, 1016
- Vascular plants  
 distribution in Baltic Sea, 792-797
- Vegetations  
 water movement, 1113-1121
- 'Verlandung', 795-797
- Vertebral counts in fish  
 salinity effects, 1032
- Vertical distribution  
 invertebrates, 969-974  
 plants, 802, 803, 810-815
- Vertical migration, 973
- Viscosity  
 ambient medium, 943, 944  
 dynamic, 1086  
 kinematic, 1086  
 plasma, 779
- Volume  
 conformers, 768, 898  
 ratio nucleus: cell  
 salinity effects, 992
- regulation  
 invertebrates, 884, 885, 898-904  
 plants, 768-770  
 regulators, 770, 898  
 regulatory devices, 903, 904—see also  
 Organs involved in ion and osmoregulation
- Water  
 economy, 732-734  
 exchange, 951—see also Osmoregulation  
 loss, 873  
 metabolic response of plants, 770-784  
 reproduction in littoral plants, 784-787  
 tolerance  
 of invertebrates, 846-862  
 of plants, 714-731  
 propulsion  
 salinity effects, 937, 938  
 regulation, 884-926—see also Osmoregulation
- Water body qualities, 1103, 1104
- Water movement  
 analysis of biological effects, 1085, 1086  
 critical minimum, 1114  
 definition, 1085  
 destructional effects on benthonic vegetation, 1120, 1121  
 fluctuation patterns, 1088  
 functional responses  
 animals, 1123-1141  
 plants, 1094-1108  
 general aspects, 1085, 1086, 1091, 1092  
 importance as ecological factor, 1085, 1091, 1123, 1124  
 intensities, 1088  
 measuring methods, 1086-1088  
 prerequisite and inhibitor of benthonic vegetation, 1114  
 structural responses  
 animals, 1141-1149  
 plants, 1108-1121  
 structure-formative effects on benthonic vegetation, 1114-1120  
 supra-individual structures of plants, 1113-1121  
 typology, 1092-1094
- Wave action, 1093
- Wave effects,  
 plants, 1117
- Wave lengths, heights, depths  
 maximum values, 1088
- Wave pressure, 1124, 1135
- Weight changes—see also Water loss  
 in fish larvae  
 salinity effects, 1012

- Weight changes—*continued*  
 in invertebrates  
   salinity effects, 900–902, 904  
 in lamprey  
   salinity effects, 1014, 1015  
 Weight gain of salmon  
   salinity effects, 1007  
 White Sea  
   distribution of littoral organisms, 1119  
 Wind—*see* Storms, Water movement  
 Winds prevailing in ideal ocean, 1140  
 Winter cast, 1120  
 Wood-boring isopods  
   activity under salinity stress, 936, 937  
   tolerance to chlorinity, 832, 833  
 Work performed  
   salinity effects, 934  
 Xenorheophily, 1139, 1140  
 Yeast—*see* Fungi  
 Yellow substance, 1161  
 Yolk sac larvae of fishes  
   tolerance to salinity, 998  
 Zonation  
   desiccation effects, 810–814  
   salinity effects, 959–961, 973  
   turbidity effects, 1188  
   water movement effects, 1114–1120, 1137,  
     1138  
 Zooplankton  
   distribution  
     in Atlantic Ocean, 954  
     in estuaries, 955–962  
   mutual exclusion, 975  
   response to salinity interface, 969–973