Succession of marine epipelagic communities

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ABSTRACT: The changes occurring in the structural-functional characteristics of plankton communities (assemblages) in the course of their development have been repeatedly described and modelled for various oceanic regions. However, the tracing of a particular community through the whole course of its successional development is practically unattainable and the comparison of the serial stages in different communities reflects neither the duration of each separate stage nor their strict sequence. We propose here a method of ranging of the communities observed according to the value of $\Theta = \lg D/P_p$ (maturity index); this makes it possible to follow changes in the community's characteristics in the course of its quantitatively assessed development. The scale comprises designated intervals corresponding to different community-development stages and their coincidence with the trophicity gradations of the waters that these communities inhabit. The influence of frontal zones on the development of plankton communities is discussed and a comparison is given of the quantitative characteristics of communities at different stages of development in the eastern tropical Pacific Ocean and in the Black Sea.

INTRODUCTION

The concept of regular development of ecosystems and communities with time – succession – has a paramount importance in modern ecology, equal to that of evolution in general biology (Margalef, 1968). Succession is inherent in a process of self-organization in an ecosystem. According to its own peculiar characteristics and the duration of life cycles of its elements, succession goes through its initiation state and finally attains its quasi-stationary (climacteric) stage. The duration of this process varies from a few weeks up to several centuries (Margalef, 1968; Odum, 1971, Frontier, 1978; Pérès, 1982).

During the succession the quantity of information (stratification, complexity, diversity, etc.) accumulating in the system gradually increases. Concurrent successional changes occur in the amount of energy incorporated within the community (total biomass and its distribution among the elements of the community that form a food web), as well as in a number of other structural and functional characteristics. The generalized pattern of these changes has been discussed repeatedly in the literature and requires no further comment in this paper.

The development (succession) of pelagic communities differs from the development of terrestrial or benthic communities in a number of peculiarities (Vinogradov, 1977, 1979; Frontier, 1978; Vinogradov and Voronina, 1979). Owing to the mobility of the habitat itself (aquatic environment), vertical mixing and its horizontal transport of waters, pelagic ecosystems are far more 'open' than their terrestrial counterparts. In regard to the changes of abiotic components of an ecosystem, hydrodynamic factors play a significant role; to a lesser extent, these changes result from biological activities of the developing community.

Nevertheless, several parameters important for life are influenced by biological processes; for example, transparency of water, which depends on the thickness of the photic layer, or the rate of nutrient utilization and secretion of metabolites within it. Thus, some changes in the physical and chemical environment are directly related to the development of biotic system components. This manifests itself also in the change of ratio of nutrient salts utilized by a community at different stages of succession. The share of the initial primary production, ensured by a direct supply of nutrient elements carried upward from the deep-water layers into the euphotic zone (the so-called 'new production'), decreases from 80 to 90 % in young communities formed during the 'bloom' to 4 to 5 % and even less in mature communities. In contrast, the share of production formed by the release of nutrients in the process of biotic regeneration rises from 10 to 20 % to 95 to 96 % (Eppley and Peterson, 1978; Harrison, 1980; Eppley, 1980, 1981). This situation is quite analogous to that observed in terrestrial ecosystems where plant produc-

tion in young communities is almost entirely ensured by the nutrient elements already available (or added by agriculture) in the soil, whereas in mature climactic systems, such as for instance the tropical rain forests, where the soil is practically devoid of nutrient salts, plant production subsists on the nutrients released by disintegrating plants, i.e. in the process of biotic regeneration.

Exploitation, i.e. partial removal from the total biomass of the community (Margalef, 1968), is, as a rule, far more intense in pelagic systems than in terrestrial ones. Transportation of organisms from the layer of their basic habitat into depths with adverse living conditions, deportation by currents beyond their optimum range of distribution, removal by consumers – all these processes exert huge pressure on the populations, often involving the bulk of them. Enhanced exploitation leads to a regression of the system in its ecological sequence (succession) impeding maturation and even affecting the community's rejuvenation. It also precludes a characterization of the ultimate state of succession (its climax) (Margalef, 1968), since the highest degree of maturity is achieved by the communities only in stratified water, e.g. in the anticyclonic halistases of the central part of the ocean where the removal of phytoplankton cells from the euphotic layer is reduced to a minimum.

The store of energy (biomass) accumulating in pelagic communities attains its maximum at a certain intermediate stage of succession, then it gradually diminishes, and biomass maxima shift to higher trophic levels (Vinogradov et al., 1973; Vinogradov, 1977; Vinogradov and Menshutkin, 1977).

The period during which the developing community accumulates energy (production prevailing over heterotrophic respiration-destruction of organic matter) may be termed its 'productive phase' and the period of energy expenditure – its 'destructive phase' (decrease of the system's biomass). The value of net production of the community (P_o), determined as the difference between primary production (P_p) and heterotrophic destruction of organic matter (D), is positive during the first phase and negative during the second one. Pelagic communities are characterized by a far longer duration of the destructive phase as compared with the productive phase.

CRITERIA FOR THE EVALUATION OF STAGES IN THE DEVELOPMENT OF PLANKTON COMMUNITIES

To uncover the laws underlying the development of pelagic ecosystems, criteria had to be found by which separate stages could be determined quantitatively, in order to facilitate the tracing of changes in the structural-functional characteristics associated with any particular stage (serial states of successions).

Margalef (1965), for example, suggested as criterion the pigment index of phytoplankton, i.e. the ratio of various pigments subject to regular concentration changes in the development of phytoplankton communities and other diversity indices. Margalef (1968) and Odum (1971) thought it possible to use for this purpose the ratio P_p/B_o (where $B_o = \Sigma B_i$ represents the total biomass of the community), i.e. the value of the primary energy flow per unit of community's biomass (in other words, the intensity of biomass renovation).

Highly informative is the quotient $K_{3p} = P_p/D$, i.e. the ratio primary production to total heterotrophic destruction of organic matter in the community. This value reflects the production-destruction activity of the community and permits the dividing of productive and destructive phases as well as the degrees of prevalence of production and destruction. The value K_{3p} or its reciprocal are often used to characterize the community's state.

The reciprocal of K_{3p}, increasing along with the community's maturation, varies widely in different regions of the ocean. In our data from the eastern part of the Pacific Ocean it was less than 0.2 in communities forming in the patches of ascending waters (i.e. during the earliest stages of the Peruvian upwelling) whereas in old, degrading communities in the southeastern ultra-oliogotrophic waters it reached 250, that is an increase by 3 orders of magnitude. It is convenient, therefore, to operate with the logarithms of D/P_p, rather than with absolute values. The ratio reflects the successional development of the communities and may be adopted as *index* of their *maturity*:

$$\Theta = \lg D/P_p = \lg \Sigma R_i/P_p$$

where: $D = \Sigma R_i$ is the metabolism (respiration) of all heterotrophic elements of the community from bacteria to mesoplankton. The value of the index Θ is negative during the productive phase, nil at equilibrium of production and destruction, and rises with the prevalence of destruction over production.

Total destruction of plankton communities comprises the destruction of bacteria, protozoans (zooflagellates, infusorians), multicellular microplankton, meso- and macroplankton. However, an experimental evaluation of the share contributed by the various elements is rather laborious; it is achievable only during large-scale expeditions recruiting experts in various branches of science with special apparatus and techniques.

During expeditions of research ships of the Institute of Oceanology (Academy of Sciences, USSR) the function of plankton communities was investigated. Micro-

bial respiration was calculated on the basis of data on the production of bacteria measured in the experiments employing the C^{14} method of measuring dark CO_2 assimilation, and accepting the K_{2b} coefficient to be equal to 0.33 (Sorokin, 1971, 1975; Sorokin and Mamaeva, 1980). It was stated that the microbial respiration comprised ca. 60 % of the total heterotrophic respiration (destruction). Respiration of zooflagellates was calculated after having estimated their production by experimental measurements of their generation time, using $K_2 = 0.3$. Respiration of ciliates was measured directly. Respiration of the total heterotrophic microplankton, including bacteria and microzooplankton, comprised 80 to 90 % of the total heterotrophic respiration (Pomeroy and Johannes, 1968; Sorokin, 1971; Shushkina et al., 1980). However, it is natural that under different conditions and at different stages of community development this share may vary considerably. Respiration of mesoplankton was determined experimentally according to oxygen consumption rates.

STAGES OF DEVELOPMENT OF PLANKTON COMMUNITIES

The communities encountered in different regions of the ocean may be ranged according to the maturity index, i.e. this index may be used as a scale of community development. On this scale, intervals may be defined corresponding to consecutive stages of development characterized by definite structural and functional pecularities. Of course, the values of these intervals are not proportional to the time during which the community is maintained at a given stage of development. Moreover, the stages may be extended or shortened in time depending on the definite conditions of the area and its general hydrological regime.

Our analysis of the state of epipelagic plankton communities in various regions of the Pacific Ocean, in part described earlier (Vinogradov et al., 1976, 1980; Vinogradov and Shushkina, 1978; Shushkina et al., 1978, 1980), as well as numerous data from the literature, permit us to define 5 successional stages in the development of epipelagic plankton communities (Table 1):

Initial state. Short phase emerging immediately with conditions required for community development (e.g. ascent of deep 'blue' water in upwelling of the Peruvian shelf; Strickland et al., 1969; Barber et al., 1971) or, in temperate latitudes, just before the commencement of vernal phytoplankton vegetation. There are no definitive values of Θ during this stage.

Juvenile state. Relatively short phase including the burst of phytoplankton. Photosynthetic production attains its highest values and thus provides for maximum net production of the community. Algae biomass increases rapidly up to its maximum values, thus contributing to a maximum total (phyto-, zoo- and bacterioplankton) biomass of the community. The biomass of zooplankton is relatively low. The maturity index varies from -0.7 to -0.2; in our data it averages -0.5.

Balanced state. The production phase is superseded by the phase of destruction, both processes being roughly balanced. The biomass of phytoplankton diminishes, that of zooplankton is still below its maximum. The total biomass of the community is high, but may be lower than at the juvenile stage. The maturity index is close to zero varying from -0.2 to $+0.2$.

Developed state. Phytoplankton biomass continues to decrease, bacterioplankton biomass remains relatively high. The biomasses of all zooplankton and of various groups of mesoplankton approach their maximum values. Maturity index averages 0.6, varying from 0.2 to 1.

Mature state. Greatest length of trophic chains and highest values of species diversity, low total biomass and low biomasses of lower trophic levels. This phase is thus near the climacteric state. The maturity index lies between 1 and 2.

Degrading state. Further reduction of biomass on all trophic levels. Impoverishment of species composition proceeds. Extremely low photosynthetic production. Maturity index >2.

Peculiarities of real succession

This description of development of an isolated community from the initial to the degrading state is an ideal case. In a real environment the pattern will always prove to be far more complicated and far less distinctly expressed owing to various external influences. It is usually impossible to trace the entire course (from start to finish) in any particular community. To begin with, it is seldom possible to observe a true primary succession, i.e. the formation of a community in 'pure', practically uninhabited waters. Such situations sometimes may arise on the Peruvian shelf in the so-called 'blue' water but in the usual course of events we have to deal with secondary succession. The water enriched by nutrients in which the community is formed, usually already contains its own populations and its own fairly well developed community. Such a situation is clearly expressed for instance in the equatorial upwelling (Vinogradov and Semenova, 1978). However, the flow of nutrient salts through the pycnoclyne occurs consistently or occasionally during the whole existence of ecosystems, thus playing a role in their succession (Vinogradov et al., 1970).

The water with its own community comes into contact with other water masses carrying communities of different ages; these intermix and interact with each other. The intensity and duration of intermixing is of paramount importance: for example, interaction of frontal zones may cause profound reorganization, affecting the production and biomasses of various trophic levels, impeding the development of younger communities and accelerating the quantitative development of the most mature ones (Shushkina et al., 1978; Frontier, 1978; Owen, 1981).

Nevertheless, any community may be assigned to a definite successional state of the 'ideal' community by its maturity index, so that it becomes possible to assess its production, destruction and other structural-functional characteristics, and, hence, to predict the next stages of its development.

SUCCESSIONAL CHANGES IN THE STRUCTURAL-FUNCTIONAL CHARACTERISTICS OF DEVELOPING COMMUNITIES

Evaluations of the structural-functional characteristics of a community, or of its elements, are usually no more than quantitative descriptions of one or another stage of development (Vinogradov et al., 1976; Vinogradov and Shushkina, 1978), or are based on the results of model simulations (Vinogradov et al., 1972;

Vinogradov et al., 1973; Vinogradov and Menshutkin, 1977). Ranging of communities according to their maturity index makes it possible to categorize them on a general scale and to assess changes in their quantitative characteristics with progressing development.

To illustrate this statement let us consider certain characteristics which we regard essential for evaluating the state of a community. We have examined the plankton communities of the productive layer (0 to 200 m) at 70 stations in the eastern tropical part of the Pacific Ocean, mainly off Peru and adjacent waters, as well as in the halistases of the central part of the ocean (Fig. 1; Cruises 17 and 34 of 'Akademik Kurchatov' and Cruise 20 of 'Dmitryi Mendeleev'). All samples represented the successional stages of the communities, from the initial (in the centres of local patches in the Peruvian upwelling) to the degrading (in the halistases of the southeastern Pacific). The area investigated and especially its coastal waters are generally considered to be the most productive ones in the World Ocean; hence our estimates of production and biomasses should be regarded as the highest values attainable at a definite state of successional development.

Owing to local differences in the intensity of production processes (depending on the region and period of observation, as well as on the accuracy of the determinations of primary production and heterotrophic destruction) a rather wide spread of points was to be expected. The curves were corrected by using the moving average method over 3 points.
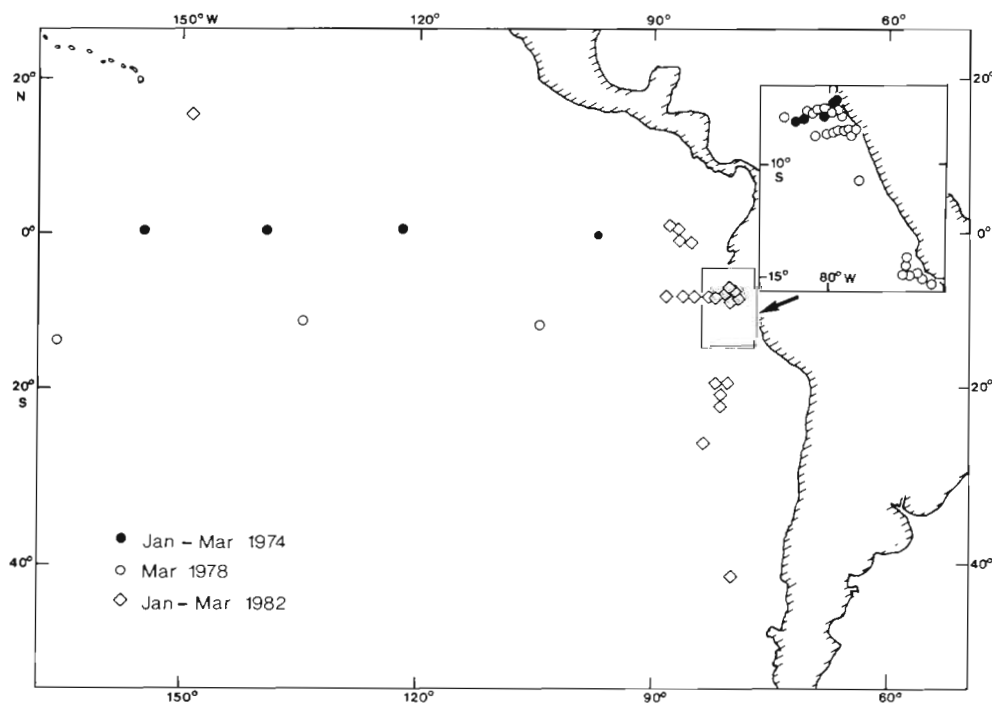

Fig. 1. Location of stations

Changes in primary production values (P_p) and biomass of phytoplankton (B_p)[*] (Fig. 2 and 3)

Biomass and production of phytoplankton in the upwelling of the Peruvian shelf are, at first, rather low in the patches of recently ascended 'blue' water, but
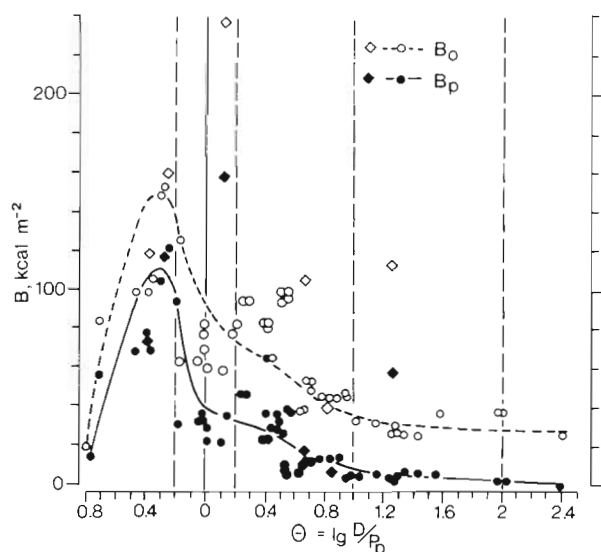

Fig. 2. Changes in phytoplankton biomass (B_p) and total biomass (B_o) of the community during its development (kcal m^{-2}). Rhombi: biomass values characteristic of frontal zones (filled – phytoplankton, open – whole community)

primary production rapidly increases, and at $\Theta = -0.7$ to -0.6 attains its highest value which in the Peruvian upwelling may attain 100 to 170 kcal m^{-2} d^{-1} (Table 1).

Simultaneously, specific production P_p/B_p attains 2 to 3.8 and even up to 7 to 8 (Sorokin and Kogelshatz, 1980). With further increase of the maturity, but still within the interval termed 'juvenile state' of successional development ($\Theta = -0.7$ to -0.2), phytoplankton production decreases to 30 to 70 kcal m^{-2} and specific production falls to about 1. The latter value, after a further slight decrease to 0.4 to 0.8, remains practically unchanged within $\Theta = -0.2$ to 1. The biomass of phytoplankton accrues at a slower rate and reaches its maximum at $\Theta = -0.4$, -0.3. In the Peruvian upwelling its peak may amount to 200 kcal m^{-2}. At $\Theta = 0$, i.e. at the border line between the production phase and that of destruction, the maximum has already been passed; with further increase of the maturity index P_p and B_p continue to decrease. In mature communities, at $\Theta > 1$, they drop to less than 5 kcal m^{-2} (Table 1). In degrading communities, at $\Theta > 2$, the values not only of P_p and B_p, but also of specific production (P_p/B_p), are still lower. Unfortunately, data available on the communities in this state of development are very scarce.

Each definitive state of the communities corresponds to a definite values of primary production so that it may
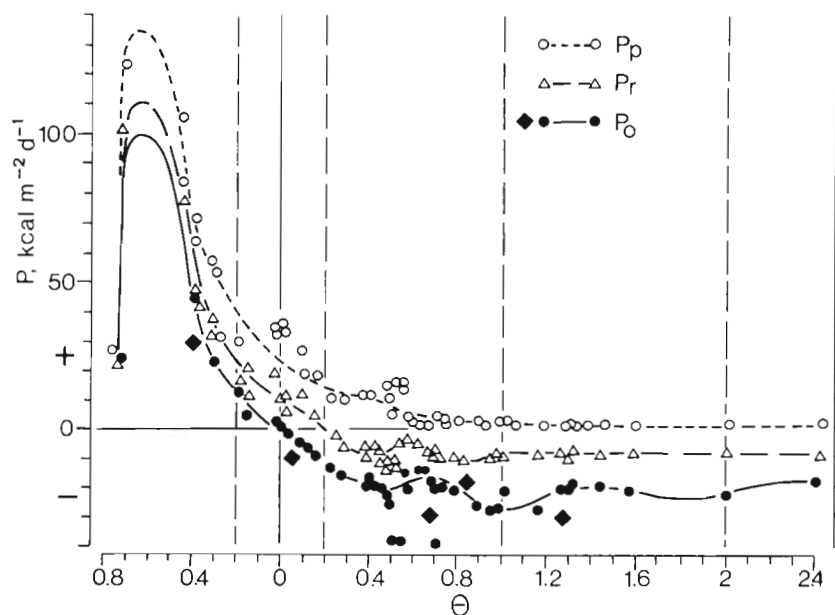

Fig. 3. Changes in primary production (P_p), net production (P_o) and real production (P_r) of the community during its development (kcal m^{-2}d^{-1}). Rhombi: net production at frontal stations

be characterized by the means of P_p and B_p. Comparison of the mean values of P_p and the range of its fluctuations in communities of different maturities reveals that they are in good agreement with the generally accepted gradation of waters in terms of trophicity, especially in freshwater and, to a lesser degree,

[*] Primary production was determined by the carbon method in series *in situ* or in incubators (Koblentz-Mishke, 1977; Sorokin, 1960). Phytoplankton biomass was determined by direct counting and measuring of cell sizes in fresh samples concentrated on nuclepore filters (Sorokin et al., 1975; Vedernikov and Sukhanova, 1979). All values cited refer to diel production.

Table 1 States of plankton communities in the south-eastern Pacific Ocean

Range of maturity index Θ	State of community	Θ	K_{3p}	P_p kcal m^{-2}	B_p kcal m^{-2} d^{-1}	P_p/B_p	P_p/B_o	Number of variants
− 0.7 to − 0.2	Juvenile	−0.47 ± 0.07	3.2 ± 0.6	77 ± 20	79 ± 25	1.43 ± 0.44	0.96 ± 0.31	7
− 0.2 to + 0.2	Balanced	−0.01 ± 0.04	1.06 ± 0.08	27.3 ± 5.8	25.7 ± 5.4	1.04 ± 0.16	0.45 ± 0.07	10
0.2 to 1.0	Developed	0.61 ± 0.04	0.20 ± 0.02	8.2 ± 1.2	19.3 ± 4.5	0.71 ± 0.11	0.14 ± 0.02	26
1.0 to 2.0	Mature	1.30 ± 0.06	0.05 ± 0.007	0.8 ± 0.29	4.8 ± 1.0	0.32 ± 0.10	0.04 ± 0.007	8
> 2.0	Degrading	2.15 ± 0.13	0.006 ± 0.002	0.17 ± 0.06	1.7 ± 0.5	0.31 ± 0.2	0.004 ± 0.0006	3

Table 2. Comparison of maturity index and diel primary production (P_p, mg C m^{-2}) in waters of different trophicity in the south-eastern Pacific Ocean and other marine and freshwater basins

State of Community	Index of maturity	Own data S.-e. Pacific P_p	Level of water trophicity	P_p in ocean after Koblentz-Mishke 1967	1977	1983	P_p in freshwater After Winberg (1960) and Bulyon (1983)	After Likens (1975)
Juvenile	−0.7 to −0.2	3000 to 15 000 and more (mean 7700)	Hypertrophic				> 2000	600–8000
Balanced	−0.2 to 0.2	1500 to 6500 (mean 2700)	Eutrophic	> 650	> 500	650 to 7000 (mean 1000)	700–2000	
Developed	0.2 to 1.0	200 to 2500 (mean 800)	Mesotrophic	150–650	150–500	70 to 550 (mean 300)	200–700	250–1000
Mature	1.0 to 2.0	20 to 200 (mean 80)	Oligotrophic	< 150	< 100	1 to 110 (mean 90)	70–200	50–300
Degrading	> 2.0	10 to 30	Ultraoligotrophic				< 100	< 50

also in marine basins (Table 2). Therefore, it seems likely that according to the degree of trophicity of the waters it is possible to judge the maturity degree of the communities inhabiting these waters.

The relations indicated above (Table 1) were obtained in the highly productive eastern tropical part of the Pacific Ocean. In other, less productive regions the relation between Θ and P_p will probably be somewhat different, the values of P_p will be lower, their scale showing some shift in respect to the maturity index.

Developmental changes in the biomass of zooplankton (B_m) and its trophic groups: fine filter-feeders (B_f), omnivores (B_v) and carnivores[*] (B_s) in the 0 to 200 m layer (Fig. 4)

As could be expected from theoretical and model notions of the development of plankton communities, the various groups of zooplankton reach their max-

imum concentrations (biomass) at a later stage than the phytoplankton. In the tropical communities of the eastern Pacific the nannophagous animals – fine filter-feeders – reach a maximum biomass (up to 10 kcal m^{-2}) in young communities at $\Theta = 0$ to 0.2, while the highest biomasses of omnivores are recorded in more mature communities at $\Theta = 0.2$ to 0.6. At about the same time the biomass of carnivorous zooplankton reaches its maximum, nearly equalling in values the maximum of omnivores. As a result, the period of abundance of mesoplankton is rather extended with its peak at $\Theta = 0.2$ to 0.6. This period, which we termed the 'developed state of the community', is confined mainly to mesotrophic water.

This proximity of biomass maxima and their nearly equivalent values in omnivores (coarse filter-feeders) and carnivores follows also from the model output (Vinogradov et al., 1975; Vinogradov and Menshutkin, 1977). At a maturity index above 1, at mature and degrading states of the communities in the area confined to oligotrophic and ultra-oligotrophic water, no biomass maximum is attained in any of the large trophic groups. In ultra-oligotrophic waters the biomass of zooplankton diminishes to less than 5 kcal m^{-2}.

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[*] From samples taken with a 150 l water bottle. For accepted divisions of plankton into trophic groups consult Vinogradov and Shushkina (1978) and Vinogradov et al. (1980)
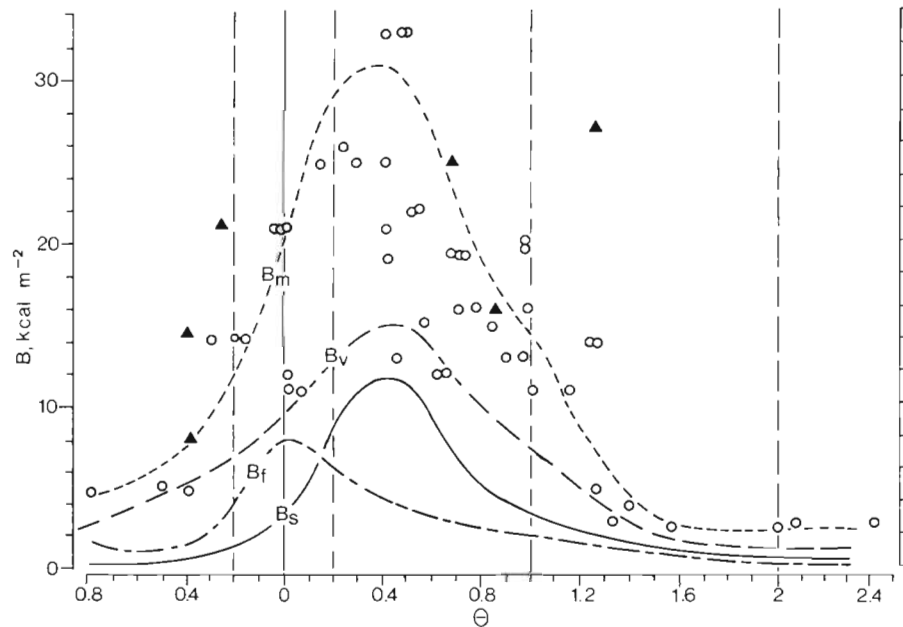
Fig. 4. Changes in biomass of mesoplankton (B_m) and its trophic groups: herbivores (B_p), omnivores (B_v) and predators (B_g) (kcal m^{-2}). Circles: total biomass of mesoplankton; triangles: biomass at frontal stations

The production of various groups of multicellular zooplankton follows the same trend as does the position of maxima of their biomasses while the absolute values of the diel production of fine filter-feeders and omnivores proves to be slightly under 3 kcal m^{-2}.

Developmental changes in net production (P_o) and real production (P_r) of the community and its total biomass (B_o) (Fig. 2 and 3)

The pattern of changes occurring in the net production of the whole community (P_o)[*] is depicted in Fig. 3. Soon after the beginning of its formation, when the community is still in the juvenile state of development, its net production reaches the maximum, followed by an abrupt drop.

In the communities of the Peruvian upwelling this peak (at $\Theta = -0.6$) exceeded 100 kcal m^{-2}. At $\Theta = 0$ the production processes in the communities maintain balance with the processes of destruction so that, naturally, the net production also is reduced to zero.

In more mature communities destruction prevails over production; hence net production is negative. In the region investigated, at $\Theta = 0.5$, during the period of maximum development of mesoplankton, its absolute value attained 30 kcal m^{-2} and remained practi-

cally unchanged at $\Theta > 0.5$ (20 to 30 kcal m^{-2}), both in mature and in degrading communities.

Mature pelagic communities may subsist at negative net production by utilizing previously accumulated energy reserves (decrease in B_o) as well as the energy of allochthonic organic matter, either introduced into the community from without or formed during the preceding production stages. Indeed, the evaluation of real production, inclusive of allochthonic DOM consumption by bacteria and protozoans ($P_r = P_p - D + A_b$; where A_b = allochthonic organic matter assimilated by the bacteria and protozoans)[**], shows also that although in this case the production of mature communities turns out to be negative, the value of its module no longer exceeds 5 to 10 kcal m^{-2} (Fig. 3). Possibly, this residual imbalance results from insufficient assessment of primary production in the oligotrophic waters of the ocean (Eppley, 1980).

The pattern of changes in total biomass (B_o) – comprising the biomasses of phytoplankton, bacteria, protozoans and multicellular micro- and mesoplankton (Fig. 2) – is determined by the energy balance of the community; biomass attains its maximum during the juvenile stage at $\Theta = -0.5$ to -0.2. The peak, accounted for mainly by mass production of phytoplankton, is followed by a rapid decrease so that in the young communities during the period of their equilized state, when production is balanced by destruction ($\Theta = 0$), the phase of maximum biomass has already been passed. The fact that this maximum does not occur at the end of the productive phase of succession is explained by lack of balance between the processes of production and consumption. Some portion of

[*] For method used in estimating net production consult Shushkina (1977) and Vinogradov and Shushkina (1978)
[**] For method of real production calculation consult Vinogradov et al. (1980) and Shushkina et al. (1980)

the biomass produced (especially of phytoplankton) is not utilized in the community but carried away. The better the balance between production and destruction in the community of a given region, the nearer the maximum of its biomass will approach the end of the production phase.

At the stage of developed community the decrease in biomass becomes less intense because it probably coincides with a maximum development of meso-plankton, i.e. of species with longer life cycles than species of young communities. The rate of energy flow through the community likewise slows down. After attaining a certain low level (in our data from 25 to 55 kcal m^{-2}) the biomass changes little and very slowly. Mature communities characterized by complex structures spend their inner resources economically.

Changes in some other characteristics

Fig. 5 shows changes in the Odum index – the ratio of primary production to total biomass of the community (P_p/B_o) – with progressing development of the com-
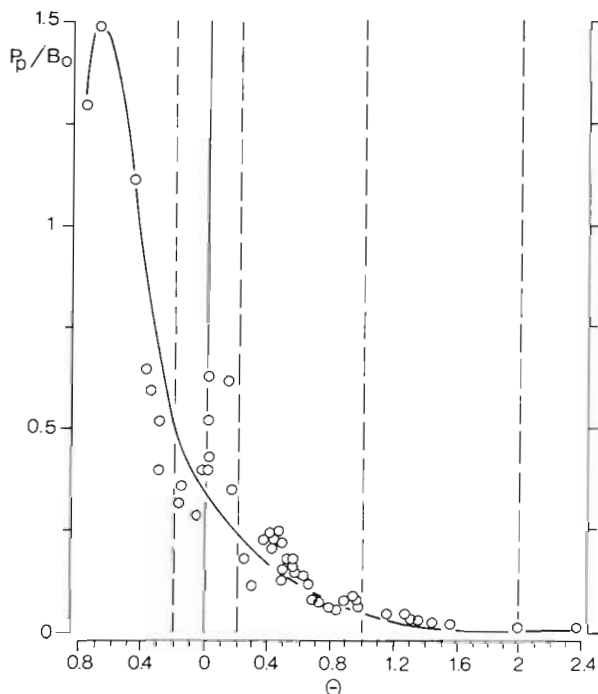

Fig. 5. Changes in the ratio between primary production and total biomass during community development

munities. The index is highest (> 1) in juvenile communities; it drops abruptly with their maturing to 0.3 to 0.6 in the balanced state, to no more than 0.25 in the developed state and to 0.1 in mature communities with

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* For method of estimation consult Vinogradov et al. (1976)

$\Theta > 1$. In communities with $\Theta > 2$ P_p/B_o is often reduced to less than 0.01.

Trophic characteristics of developing communities likewise are subject to successional changes. Thus the degree of satisfying the food requirements of their elements

$$\delta_i = \frac{C_i}{C_i^{max}}$$

where C_i = the element's real ration; C_i^{max} = ration ensuring maximum production*, varies in mesoplankton herbivores (Fig. 6) from 0.95 in juvenile communities (production being near maximum) to 0.75 to 0.65 in mature and degrading ones. It is somewhat higher in omnivores; in predators it is usually about 0.9 to 1.0 at all stages of community development (Vinogradov et al., 1976).

It is of interest to trace the changes in the share of phytoplankton and bacteria in the food ration of zooplankton (Fig. 7). During the productive phase ($\Theta < 0$) phytoplankton still prevails in the ration, although its role decreases along with the development of the community. In contrast, the share of bacterioplankton increases and during the destructive phase of the communities where it accounts for 50 to 70 % of the total ration of the zooplankton.

COMMUNITIES IN FRONTAL ZONES

Above we have considered the generalized course of changes in the characteristics of a developing community. It is obvious that in a series of real communities, ranged according to their maturity index, the real values of their characteristics will be influenced by the local singularities inherent in the communities examined at each given point, as well as by the accuracy of the determination of their initial values, so that the points will be found to be widely dispersed around the generalized curve. These deviations may be more important in some characteristics and less in others.

However, in some cases they were exceptionally strongly expressed so that an analysis was made of the stations at which the characteristics of the communities did not conform to the general pattern. These stations, as a rule, were found to be confined to frontal zones.

In these zones an abrupt replacement of communities takes place, usually caused by the partition of colder waters inhabited by young communities and warm waters with more mature communities. It is known (Fedorov, 1983) that the water masses in frontal zones undergo a complicated process of interpenetration and interaction, facilitating and securing the interaction of the communities they carry. The more mature communities begin to exploit the younger ones.
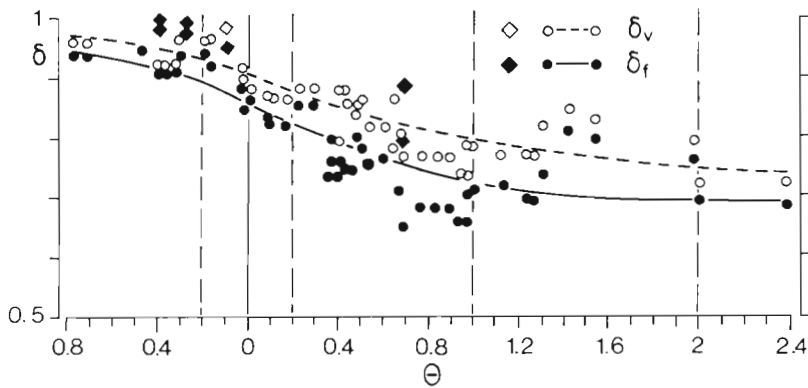
Fig. 6. Changes in satisfying food requirements ($\delta = \dfrac{C}{C^{max}}$) for herbivores ($\delta_f$ and omnivores (δ_v) of mesoplankton, during the development of the community. Rhombi: values at frontal stations
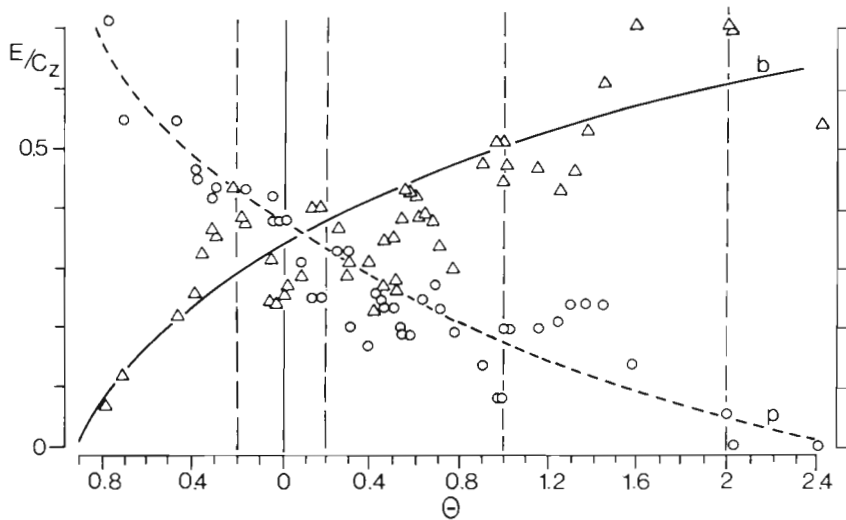

Fig. 7. Changes in the share of phytoplankton and bacterioplankton in the ration of zooplankton (micro- und mesoplankton) during community development

This leads, on the one hand, to the impediment of development and even a rejuvenation of less developed communities and, on the other hand, to a rapid rise of production (and biomass) at the higher levels of more developed communities (e.g. Margalef, 1968; Odum, 1969; Vinogradov, 1977, 1979; Frontier, 1978).

Thus in frontal zones the communities undergo abrupt changes which do not conform to the pattern of common successional development. These changes may vary greatly, depending on the gradients of the hydrophysical characteristics at the frontal partition and on structure, age and other specific features of the contacting communities.

The changes affect both contacting communities involved, but for each of them they are expressed in different ways. In the young communities from the cold side of the front the changes are not distinctly expressed, but the young community with a loose structure seems to acquire some dynamic stability that compensates for the export of biomass into more mature communities. In the communities from the warm side of the front a sharp increase is observed in the zooplankton

biomasses (filter-feeders and predators) (Fig. 2 and 4) and in nekton which actively concentrates here to feed on zooplankton (Knauss, 1957; Vinogradov and Voronina, 1964; Murphy and Shomura, 1978; Laurs and Lynn, 1977). At the same time the net production of the entire community may drop abruptly (Shushkina et al., 1978; Vinogradov and Shushkina, 1978; Vinogradov et al., 1980) due to intensive grazing on phytoplankton and to intensive predation.

There are, however, some important characteristics – such as the share of primary production in proto-food production (P_{p+b}) – that do not deviate in the frontal zones from their normal trend of development.

COMPARISON OF STRUCTURAL-FUNCTIONAL CHARACTERISTICS OF DEVELOPING COMMUNITIES IN THE SOUTH-EASTERN PACIFIC OCEAN AND OTHER REGIONS

Are these pecularities of successional development of the communities in the Eastern Pacific Ocean typical also for communities inhabiting other regions? In other

Table 3. Structural-functional characteristics of communities in the mesotrophic waters of Pacific Ocean and Black Sea. [B] kcal m^{-2}; [P] kcal m^{-2} d^{-1}. Averages from our observations

Region	Index of maturity	Biomass (B)			Share of total biomass (%)					Production (P)		Role in hetero-trophic destruction (%)	
		Total plank-ton	Phyto-plank-ton	Zoo-plank-ton	Phyto-plank-ton	Bac-teria	Proto-zoans	Zoo-plank-ton	Carni-vorous zoo-plankton	Phyto-plank-ton	Bacte-ria	Bacte-ria	Zoo-plank-ton
Southeastern part of Pacific Ocean	0.61	77	26	27	35	20	12	33	8	8	9	58	22
Black Sea	0.57	30	13	10	40	18	9	30	6	3	4	60	27

words, are they of general or of merely regional importance? To answer this question the characteristics of the south-eastern communities were compared with the characteristics of the communities investigated in the western tropical part of the Pacific Ocean during the cruises of the R/V 'Vitjaz', 'Akademik Kurchatov' and 'Dmitryi Mendeleev'. They were found to be in good agreement. It must be noted, however, that western communities have been examined in less detail than the eastern ones, so that thorough comparison among them caused serious difficulties. Still, we were able to compare the communities of such far apart regions as the Pacific Ocean and the Black Sea, as in both cases the same methods were used.

Estimates on Black Sea communities are based on seasonal-succession data obtained in 1978 in the region of Gelendjik (Sorokin and Vedernikov, 1983). Comparison with data on the spatial succession of plankton communities in the coastal waters of Peru revealed some distinct features of similarity in the dynamics of a number of structural-functional characteristics, such as phytoplankton production and biomass.

The mean seasonal parameters of the Black Sea plankton from waters that are mesotrophic during the summer months ($\Theta = 0.57$) were compared with corresponding parameters of developed communities in the mesotrophic waters of the Pacific Ocean and found to differ strikingly in regard to biomass and production of their elements but to have no less strikingly similar relative values (Table 2). Thus, for instance, the contribution of the biomass of each essential element to the total biomass of plankton, or the share of each separate component in the heterotrophic destruction of the entire community proved to be practically equivalent.

It is noteworthy that in freshwater basins (e.g. lake Naroch in Byelorussia or Kuibyshev water reservoir) the relative values of the characteristics are about the same as those recorded in marine communities at corresponding stages of maturity. Thus the contribution of

bacteria to total heterotrophic destruction (R_b/D) is 0.65 (Winberg, 1971), i.e. it very nearly approaches the corresponding values characteristic of mesotrophic waters of Black Sea and Pacific Ocean (Table 3).

Thus it may be assumed that many of the structural-functional characteristics of communities passing through the same stages of successional development and inhabiting waters of similar trophicity, are actually similar, despite the different composition and habitats of these communities.

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