

Structure and adaptation of the fauna in the black zone (littoral fringe) along rocky shores in northern Europe

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ABSTRACT: The black zone within the littoral fringe of world-wide rocky shores is overgrown with lichens (*Lichina pygmaea*, *Verrucaria maura*), and blue-green algae. The zone is inhabited by a few coenophil animals: *Hyadesia fusca* (Acari), *Telmatogeton japonicus* (Chironomidae), *Mniobia symbiotica* (Rotatoria), *Echiniscoidea sigismundi* (Tardigrada), and several aquatic or terrestrial intruders (Nematoda, *Littorina*, Copepoda-Harpacticoida, *Ligia*, Collembola, terrestrial mites and insects). The main adaptation of foundation species lies in their ability to reduce metabolism by anhydrobiosis or anaerobiosis and to survive unfavourable circumstances in quiescence. Faunal structure is influenced by unpredictably changing abiotic factors such as moisture, salinity, temperature and eutrophication, which influence quantitative rather than qualitative aspects.

INTRODUCTION

The boundary zone between sea and land along rocky shores is an environment characterized by abrupt change from marine to terrestrial conditions: salinity, light, and temperature alter gradually; submersion and emersion alter periodically and induce the development of a characteristic littoral zonation.

The shore edge above the high water mark is blackened by an overgrowth of blue-green algae and lichens and called the 'black zone' (Stephenson & Stephenson 1972). The black zone marks the margin between eulittoral and supralittoral. Here, living conditions are characterized by unpredictable changes in abiotic factors: spring tide and wave spray moisten this zone without clear periodicity and involve mechanical stress. Insolation leads to heating and evaporation, and hence tends to increase salinity; rain and dew lead to moistening with freshwater. Thus the black zone is an extreme environment with pronounced variations in moisture, salinity, temperature, light, and wave exposure.

The black zone is a common feature along most rocky shores including artificial shorelines (Stephenson & Stephenson 1972). Even in the Antarctic, littoral cyanophyte associations are found in the littoral fringe (Broady 1981).

The black zone consists of 3 different plant associations: (1) Cyanophyta (*Calothrix*, *Plectonema*, *Gloeocapsa*, *Chroococcus* etc.); (2) *Lichina pygmaea* Lightf. (Lecanorales, Lichenes); (3) *Verrucaria maura* Wahlenberg (Verrucariales, Lichenes).

The faunal part of the community remains practically unknown; only species of *Littorina*, *Ligia* and Chironomidae have been recorded (Southward 1958, Hedgpeth 1957, Stephenson & Stephenson 1972). The flora has been investigated by Lindstedt (1943), Umezaki (1961) and Little (1973).

The encrusting lichen *Verrucaria maura* grows preferentially along dry and wave-exposed shores. If crevices are available, they are inhabited by a terrestrial fauna composed of *Nanorchestes amphibius* and *Bdella septentrionalis* (Acarina), *Anurida maritima* (Collembola), *Strigamia maritima* (Chilopoda), *Petrobius brevistylis* (Archaeognatha), and by aquatic forms such as *Ligia oceanica* (Isopoda) and *Littorina neritoides* (Gastropoda). Small shrub-like lichens *Lichina pygmaea* grow in moister sites at the barnacle line, and are inhabited by thalassogen species, such as the isopod *Campecopea hirsuta* or the molluscs *Lasaea rubra*, *Mytilus edulis* (juvenile), *Littorina neritoides*, *L. saxatilis*, the mites *Hyadesia fusca*, *Ameronothrus* spp. and Limoniidae instars (*Geranomyia unicolor*).

Cyanophytes prefer sheltered shores with wet

conditions and show a high tolerance to freshwater influence, although they are replaced by mosses in pure freshwater sites. The fauna is composed of a few aquatic animals: *Hyadesia fusca* (Acarina), *Mniobia symbiotica* (Rotatoria), *Telmatogeton japonicus* (Chironomidae), *Echiniscoides sigismundi* (Tardigrada), *Littorina saxatilis* (Gastropoda), and several eulittoral and terrestrial intruders.

The black zone is therefore actually an intermediary between sea and land: the *Verrucaria maura* association belongs to the supralittoral, while cyanophytes and *Lichina pygmaea* belong, strictly speaking, to the littoral. According to Lewis (1964), the black zone can be attributed to the littoral fringe (Fig. 1).

	WOMERSLEY & EDMONDS 1952	DEN HARTOG 1959	LEWIS 1964	STEPHENSON & STEPHENSON 1972	FLETCHER 1973	SCHULTE 1977	
					Halophobad		
					Halophilic		
					Xenic		
					Submesic		
					Mesic		
Supralittoral zone	Supralittoral region	Upper supralittoral region	Supralittoral zone	Supralittoral zone	Supralittoral region	Supralittoral	
		Lower supralittoral region	Littoral fringe	Supralittoral fringe	Littoral fringe	Translittoral	Black zone
Littoral zone	Upper littoral		Littoral zone	Littoral zone	Littoral zone		
	Mid-littoral	Eulittoral region	Eulittoral zone	Midlittoral zone	Eulittoral	Eulittoral	
	Lower littoral			Littoral zone			
Upper sub-littoral zone	Sublittoral fringe		Sublittoral zone	Intralittoral fringe	Sublittoral zone	Sublittoral	
Lower sub-littoral zone		Sublittoral region		Intralittoral			

Fig. 1. Comparison of different littoral schemata (adapted from Hedgpeth 1957)

Littoral cyanophytes have been known since the Precambrian (Laporte 1968, Remane 1979) and have continuously provided a potential habitat for animal colonization. The inhabiting fauna, however, consists of few species with high densities, and special adaptations are rare. This is a community structure regarded typical for extreme environments (Thienemann 1939). The present paper investigates the structure and stability of this low diversity community and the influences of salinity, moisture, eutrophication and biotic factors. It also illustrates how animals have adapted to abiotic factors with respect to protection, locomotion, reproduction, development and ingestion.

MATERIALS AND METHODS

Sampling. Samples were obtained by scraping the rock surface with a knife. For quantitative analysis, 10 square sampling units of 10 or 20 cm² each, taken at random, formed 1 sample. Samples were stored at -18°C until analysis or were fixed with 4% formaldehyde. Faunal inhabitants of the overgrowth were

studied with a stereomicroscope. Representiveness of samples was tested using similarity area curves which assigned a minimal area of 100 cm² to include 74 to 100% of the species and an accuracy of ±10% for abundance data. Only in seasons when few animals are present were 200 cm² samples necessary in order to obtain the same degree of accuracy (Kronberg 1987).

Sampling stations were situated mainly in the Baltic Sea and along the Kiel Canal (F.R. Germany). Qualitative samples were taken near Kristineberg (Sweden), Herdla (Norway), Penzance (Cornwall, UK), Sherkin Island (Ireland), and Helgoland (F.R. Germany). Quantitative samples were taken at the following sites:

(a) Two adjacent stations along the Kiel Canal (Landwehr, salinity 8.2‰) were checked twice a month in 1979. One of the stations had a slope of 10°, the other of 45°. Six units of 10 cm² made up 1 sample which proved representative for the 3 dominant species. The width of the black zone was recorded and compared with watermarks in the Holtenau canal office. The samples were used to investigate the influence of moisture and exposition.

(b) Two stations at Friedrichsort (Kiel Bight, slope 35°): one was protected from rain influence by a bridge, the other exposed to rain. Twenty samples of 10 cm² were taken from each station in October 1980. These samples served to investigate the influence of moisture and freshwater. The role of insolation was negligible during this season.

(c) Eleven stations along the Kiel Canal (slope 30 to 50°; salinity: at Brunsbüttel, 3.6‰; Burg, 3.5‰; Hohenhörn, 3.4‰; Fischerhütte, 3.2‰; Oldenbüttel, 3.0‰; Breiholz, 3.6‰; Rendsburg, 5.3‰; Sehestedt, 6.6‰; Landwehr, 8.2‰; Levensau, 10.4‰; Holtenau, 11.9‰) and in the Kiel Bight (Friedrichsort) 13.4‰. Ten sample units of 20 cm² were taken from each station in September 1979. Salinity was determined by titration (Mohr-Knudsen method). These samples were used to investigate the influence of salinity.

(d) Eight stations in Bülk (Kiel Bight, slope 30 to 50°, salinity 15‰), located at different distances from the sewage duct at breakwaters. Ten sample units of 10 cm² were taken monthly from each station from 1980 to 1982. In winter, stations were visited every second or third month because they were only scarcely inhabited. One station was abandoned in 1982 owing to construction work at the duct. Samples were used to investigate the influence of eutrophication.

Ecological parameters were: *Z*: number of species; *Z_p*: number of species in sample *p*; *Z_{pq}*: number of species common to samples *p* and *q*; *C* (species density): average number of species per defined area (10 cm²); *N*: number of individuals of all species per sample; *W* (living density): average number of indi-

viduals of all species per defined area (10 cm²); A_i (abundance): average number of individuals of species i per defined area (10 cm²); A_{ip} : abundance of species i in sample p ; D_i (dominance): percentage of individuals of species i per sample; M : total station number; m_i : number of stations containing species i ; P_i (presence): number of stations containing species i related to total station number.

Diversity: Rarefaction diversity (Sanders 1968) is a graphical method which estimates the theoretical species number of smaller samples starting out from the whole number of individuals; it is a size-independent method. The steepness of the curve represents the evenness; and the level of saturation indicates the number of species. The original method allows a rough comparison of communities, though it tends to overestimate the interpolated expected number of species (Hurlbert 1971).

Similarity: $0 \leq I \leq 1$

$$\text{Sørensen } I_S = \frac{2 Z_{pq}}{Z_p + Z_q}$$

$$\text{Kulczynski } I_K = \frac{2 \sum_{i=1}^z \min(A_{ip}, A_{iq})}{\sum_{i=1}^z (A_{ip} + A_{iq})}$$

Statistics were compiled with SPSS-programs at the Computer Center in Kiel; ecological parameters were calculated by a TURBO PASCAL 4.0 program. To calculate similarity area curves, a FORTRAN program (Weinberg 1978, Kronberg 1987) was used. (Programs are available from the author upon request; please enclose a 5.25" disk.)

RESULTS AND DISCUSSION

Faunal composition

To record the inhabitants of the black zone, cyanophytes and *Lichina pygmaea* associations in different climatic regions were investigated. The *Verrucaria maura* association was considered only briefly, as the animals living here do not belong to the phytal, but to the crevice fauna (Kronberg 1983).

A total of 67 species was recorded: 17 Nematoda, 13 Acarina, 11 Insecta and 8 Copepoda-Harpacticoida; but most of these species were represented by only a few individuals (Table 1).

The most abundant species were Rotatoria (*Mniobia symbiotica*), Tardigrada (*Echiniscoides sigismundi*), Acarina (*Hyadesia fusca*), Collembola (*Anurida maritima*, *Hypogastrura viatica*), and Chironomida

(*Telmatogeton japonicus*). None of the species showed a restriction to the black zone, all live in other biotopes as well. *M. symbiotica*, *E. sigismundi*, *H. fusca* live in the *Enteromorpha* zone (Marcus 1927, Otto 1936), in eu- and supralittoral rockpools (*H. fusca*: Ganning 1970); in the barnacle zone (*E. sigismundi*: Morgan & King 1976, Kristensen & Hallas 1980); and in lichens and mosses (*M. symbiotica*: Remane & Schlieper 1958, Donner 1965). *Campecopea hirsuta* (Isopoda) and *Lasaea rubra* (Bivalvia) not only live in the *Lichina pygmaea* zone but also between barnacles in the trottoir, in the Mediterranean *Enteromorpha* zone, and in similarly patterned interstices (Woodward 1851, Wieser 1959, Schuster 1962, Nordsieck 1969). Thus the indigenous species of the black zone are coenophil, but not coenobiont. In the Baltic Sea, *H. fusca*, *T. japonicus* and *M. symbiotica* are 'foundation species' sensu Dayton (1972), their population dynamics being characteristic of the community.

The black zone is an open biotope accessible to terrestrial, marine, limnic and brackish species, as well as to subterranean and flying animals which find, at least for a short time, adequate conditions here. Some actively enter the black zone; for example, from the eulittoral, *Littorina saxatilis* and, in the Atlantic region, *Patella vulgata* which feeds here during dampness. During low water, terrestrial animals enter from the supralittoral for feeding, e.g. *Anurida maritima*, *Hypogastrura viatica*, *Bdella septemtrionalis*, *Abrolophus rubripes*.

A large number of species appear occasionally in high densities; they are not, however, a permanent part of the community: under extreme conditions they withdraw or die, and then the population must replenish itself from similar environments (Nematoda, Copepoda-Harpacticoida, Ostracoda).

Typical trespassers searching for crevices are *Petrobius brevistylis* (Insecta), *Strigamia maritima* (Diplopoda) and *Ligia oceanica* (Isopoda). From the air, *Fucellia* spp. and Ephydriidae (Insecta) visit the black zone. Several terrestrial (Oribatei) and eulittoral mites (*Rhombognatus* spp.) as well as Nematoda are seen frequently, but more irregularly, in the black zone. *Enchytraeus albidus* is a subterranean visitor.

Many species living in the black zone are cosmopolitans, i.e. are present in many climatic regions of the world, both at the species and/or genus level. For example, *Telmatogeton remanei* from the Baltic Sea turned out to be synonymous to *T. japonicus* from the Pacific Ocean (Kronberg 1986). *Echiniscoides sigismundi* has been reported from the Baltic Sea, the Mediterranean (Wieser 1959), the Galapagos Islands (McKirdy et al. 1976), the Caribbean and China (Green 1950). This spectrum of species is influenced by several micro- and macroclimatic factors.

Table 1. Fauna list for the black zone in northern Europe. L: Lichina pygmaea association; C: Cyanophyta association. O: eastern coastline of Schleswig-Holstein (FRG); K: Kiel Canal (FRG); W: western coastline of Schleswig-Holstein; S: Sweden (Kristineberg); N: Norway (Herdla); G: UK (Penzance); I: Ireland (Sherkin Island)

Assoc.	Taxa		O	K	W	S	N	G	I
Nematoda									
C	<i>Rhabditis marina</i> Bastian	(Rhabditidae)	x	-	x	-	-	-	-
C	<i>Aphelenchoides</i> sp.	(Aphelenchoididae)	-	x	-	-	x	-	-
C	<i>Monhystera parva</i> Bastian	(Monhysteridae)	x	x	-	x	-	-	-
C	<i>Monhystera disjuncta</i> Bastian	(Monhysteridae)	x	x	-	-	-	-	-
C	<i>Monhystera</i> sp.	(Monhysteridae)	-	-	x	-	x	x	-
C	<i>Gammarinema</i> sp.	(Monhysteridae)	x	-	-	-	-	-	-
C	<i>Theristus pertenuis</i> Bresslau & Stekhoven in Stekhoven	(Xyalidae)	x	x	-	-	-	-	-
C	<i>Araeolaimus</i> sp.	(Diplopeltidae)	x	-	-	-	-	-	-
C	<i>Chromadora nudicapitata</i> Bastian	(Chromadoridae)	x	-	-	-	-	-	-
C	<i>Chromadora macrolaima</i> de Man	(Chromadoridae)	x	x	-	-	-	-	-
C	<i>Chromadora supralitoralis</i> Lorenzen	(Chromadoridae)	-	x	-	-	-	-	-
C	<i>Dichromadora cephalata</i> Steiner	(Chromadoridae)	-	x	-	-	-	-	-
C	<i>Plectus</i> sp.	(Plectidae)	-	x	-	x	x	-	-
C	<i>Anaplectus</i> sp.	(Plectidae)	-	x	-	-	-	-	-
C	<i>Enoplus</i> sp. (<i>brevis</i> or <i>communis</i>)	(Enoplidae)	x	-	-	-	-	-	-
C	<i>Adoncholaimus fuscus</i> de Man	(Oncholaimidae)	x	-	-	-	-	-	-
C	<i>Anticomma acuminata</i> Eberth	(Anticomidae)	x	-	-	-	-	-	-
Rotatoria									
L, C	<i>Mniobia symbiotica</i> Zelinka	(Bdelloidea)	x	x	x	x	x	x	-
Bivalvia									
L	<i>Lasaea rubra</i> Montagu = <i>L. adansonii</i> Gmelin	(Leptonidae)	-	-	-	-	-	x	x
L, C	<i>Mytilus edulis</i> L. (juv.)	(Mytilidae)	x	-	x	-	x	x	-
Gastropoda									
C	<i>Littorina neritoides</i> L.	(Littorinidae)	-	-	-	-	-	x	x
L, C	<i>Littorina saxatilis</i> Olivi	(Littorinidae)	x	x	x	x	x	x	x
C	<i>Patella vulgata</i> L.	(Patellacea)	-	-	-	-	-	x	x
Oligochaeta									
L, C	<i>Enchytraeus</i> sp.	(Enchytraeidae)	-	x	-	-	-	-	x
Tardigrada									
L, C	<i>Echiniscoidea sigmundi</i> Schultze	(Echiniscoidea)	-	-	x	x	x	-	-
Ostracoda									
C	<i>Cytherura gibba</i> O. F. Müller	(Cytheridae)	-	x	-	-	-	-	-
C	<i>Cytheromorpha fuscata</i> Brady	(Cytheridae)	x	-	-	-	-	-	-
Copepoda-Harpacticoida									
C	<i>Harpacticus gracilis</i> Claus	(Harpacticidae)	x	-	-	-	-	-	-
C	<i>Harpacticus flexus</i> Brady & Robertson	(Harpacticidae)	x	-	-	-	x	-	-
C	<i>Leptomesochra</i> sp.	(Ameiridae)	-	-	-	-	x	-	-
C	<i>Nitocra typica</i> Boeck	(Ameiridae)	-	x	-	-	-	-	-
C	<i>Heterolaophonte strömi</i> Baird	(Laophontidae)	-	-	-	x	-	-	-
L	<i>Heterolaophonte</i> sp.	(Laophontidae)	-	-	-	-	-	x	-
C	<i>Tachidius</i> sp.	(Disaccidae)	x	-	-	-	-	-	-
C	<i>Mesochra rapiens</i> Schmeil	(Canthocamptidae)	-	-	-	-	x	-	-
Amphipoda									
L, C	<i>Orchestia gammarella</i> Pallas	(Talitridae)	x	-	-	-	-	-	x
Isopoda									
C	<i>Ligia oceanica</i> Fabr. (juv.)	(Ligiidae)	-	-	x	x	x	x	x
L	<i>Campeopea hirsuta</i> Montagu	(Sphaeromatidae)	-	-	-	-	-	x	x

Table 1 (continued)

Assoc.	Taxa		O	K	W	S	N	G	I
Acarina									
L, C	<i>Hyadesia fusca</i> Lohmann	(Hyadesidae)	x	x	x	x	x	x	-
C	<i>Hermannia nodosa</i> Michael	(Oribatei)	-	-	-	-	-	-	x
C	<i>Hermannia</i> sp.	(Oribatei)	x	-	-	-	-	-	-
L	<i>Ameronothrus maculatus</i> Michael	(Oribatei)	-	-	-	-	-	-	x
L	<i>Ameronothrus bilineatus</i> Michael	(Oribatei)	-	-	-	-	-	-	x
L, C	<i>Nanorchestes amphibius</i> Tops & Tr.	(Nanorchestidae)	x	-	x	x	-	-	x
C	<i>Bdella septemtrionalis</i> Atyeo & Tuxen	(Bdellidae)	-	-	-	x	-	-	x
L	<i>Abrolophus rubripes</i> Trou.	(Erythraeidae)	x	x	-	-	-	-	-
L	<i>Hydrogamasus</i> sp.	(Eugamasidae)	-	-	-	-	-	x	x
C	<i>Rhombognathus setosus</i> Lohmann	(Rhombognathidae)	x	-	-	x	-	-	x
C	<i>Rhombognathus notops</i> Gosse	(Rhombognathidae)	x	-	-	-	-	-	-
L	<i>Agauopsis</i> sp.	(Halacaridae)	-	-	-	-	-	-	x
C	<i>Halacarellus basteri</i> Johnston	(Halacaridae)	x	-	-	-	-	-	-
Insecta									
C	<i>Anurida maritima</i> Guerin	(Neanuridae)	-	-	x	-	x	x	x
C	<i>Hypogastrura viatica</i> Tullberg	(Hypogastruridae)	x	-	-	-	-	-	-
C	<i>Petrobius brevistylis</i> Carpenter (juv.)	(Machilidae)	-	x	-	x	x	x	x
C	<i>Telmatogeton japonicus</i> Tokunaga = <i>T. remanei</i> Remmert	(Chironomidae)	x	x	x	x	-	-	-
C	<i>Halocladus variabilis</i> Staeger = <i>Trichocladus vitripennis</i> sensu Otto	(Chironomidae)	x	-	-	-	x	x	x
L	<i>Geranomyia unicolor</i> Haliday	(Limoniidae)	-	-	-	-	-	-	x
C	<i>Fucellia</i> spp.	(Anthomyiidae)	x	x	-	-	-	-	-
C	<i>Scatella</i> sp.	(Ephydriidae)	x	x	-	-	-	-	-
C	<i>Scatophila</i> sp.	(Ephydriidae)	x	x	-	-	-	-	-

Structure and modifying factors

Moisture

The degree of moisture of the thin algal layer in the black zone is primarily determined by the littoral level and slope, wave exposure, tidal influences, amount of precipitation (rain and dew), air humidity, insolation, and water capacity of the substratum. Den Hartog (1959) and Nienhuis (1969) investigated the influence of substratum water capacity on the zonation of littoral plants and found that the upper limit of eulittoral zones is higher on soft than on hard rocks. In the present paper, the influence of moisture was determined by looking at the effect of littoral slope and rain.

Fig. 2 shows the density of dominant species at 2 adjacent sites in the Kiel Canal (Landwehr) with 10 or 45° angle; these are *Telmatogeton japonicus*, *Hyadesia fusca* and *Mniobia symbiotica*. The SL-line (sea level) characterizes the margin between more or less desiccation-tolerant species (Kronberg 1983). The higher moisture at the flatter site leads to a more diverse fauna, traceable to intruders such as *Monhystera parva*, *M. disjuncta*, *Chromadora macrolaima*, *Anaplectus* sp., *Dichromadora cephalata*, *Nitocra*

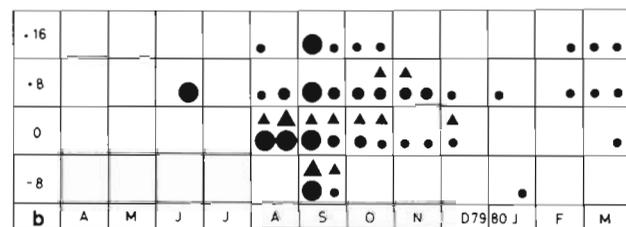
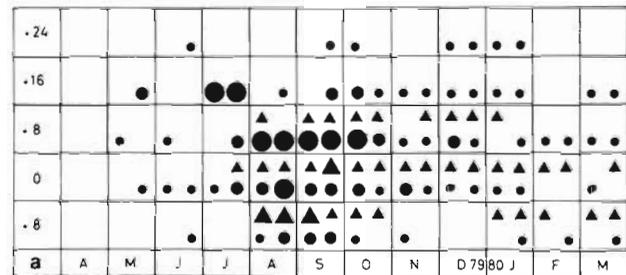


Fig. 2. Density of foundation species in the black zone of Kiel Canal (Landwehr, 8.2‰) with a slope of (a) 10° (b) 45°. 0: sea level (SL); -8: 8 cm below SL; +8/+16/+24: 8/16/24 cm above SL. Density of *Hyadesia fusca*: large circle: ≥ 50 ind. 10cm^{-2} ; medium sized circle: ≥ 10 ind. 10cm^{-2} ; small circle: < 10 ind. 10cm^{-2} . Density of *Telmatogeton japonicus* instars: large triangle: ≥ 10 ind. 10cm^{-2} ; small triangle: < 10 ind. 10cm^{-2} .

typica and *Cytherura gibba*. Moreover, there are obvious differences in the abundance of the common species *H. fusca* and *T. japonicus*: the flatter shore is inhabited more densely and for a longer seasonal period. The aquatic *M. symbiotica* is absent at the dryer 45° shore.

Rainfall brings freshwater and moisture to the black zone. Faunal composition was compared at 2 adjacent sites in Friedrichsort (Kiel Bight), one protected from rain by a bridge, the other exposed to rain. As shown in Fig. 3 no differences in the abundances of the dominant

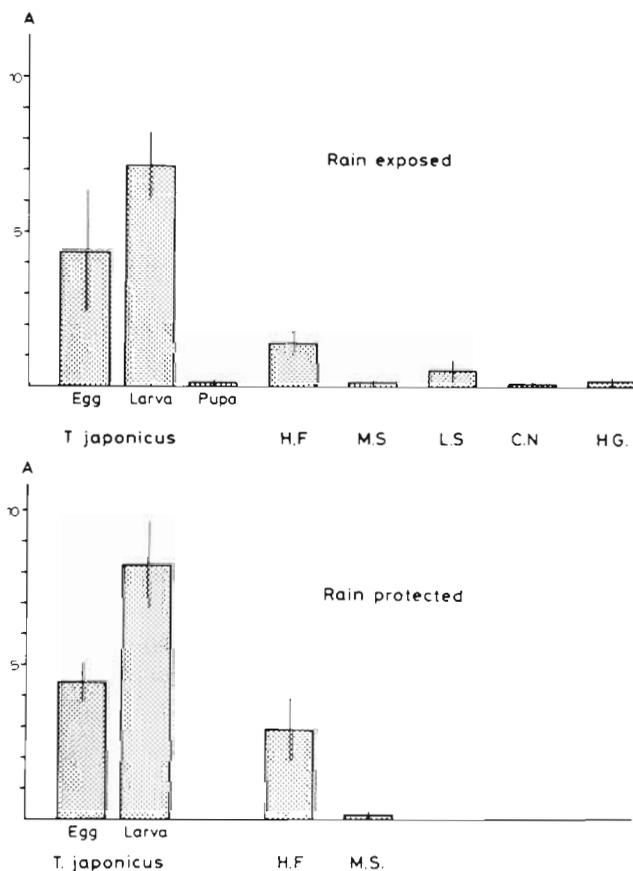


Fig. 3. Abundance of the fauna in the black zone of Kiel Bight (Friedrichsort) at a rain-exposed and rain-protected station. H.F.: *Hyadesia fusca*; M.S.: *Mniobia symbiotica*; L.S.: *Littorina saxatilis*; C.N.: *Chromadora nudicapitata*; H.G.: *Harpacticus gracilis*; A: abundance (ind. 10cm⁻²); bar: ±1 SE

species *Hyadesia fusca*, *Telmatogeton japonicus* and *Mniobia symbiotica* (*U*-test, $\alpha = 0.05$) could be detected, but the moister algal layer was inhabited by several eulittoral intruders not found at the rain-protected site: *Littorina saxatilis*, *Chromadora nudicapitata* and *Harpacticus gracilis*. Thus humidity, more than freshwater influenced by rainfall, changed the faunal composition in the black zone.

In conclusion: dryer living conditions narrow the species inventory, lower faunal diversity, and enhance the abundance of the remaining species.

Salinity

Salinity of the interstitial water in the black zone is influenced by contact with seawater, rain and evaporation. The Kiel Canal shows a more or less continuous decrease in salinity from 12 to 3 ‰ and hence is an ideal site for studying the influence of salinity on faunal structures. Fig. 4 shows the abundance values of

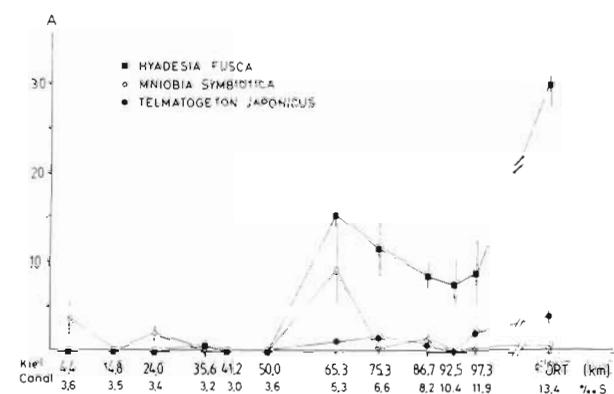


Fig. 4. Abundance of foundation species (*Hyadesia fusca*, *Mniobia symbiotica*, *Telmatogeton japonicus* instars) in the black zone along Kiel Canal and Kiel Bight. F.ORT: Friedrichsort; km: canal distances, from Brunsbüttel to Kiel; S: salinity; A: abundance (ind. 10cm⁻²); bar: ±1 SE

dominant species: the eastern marine brackish part of Kiel Canal (11.9 to 5.3 ‰) is densely populated with *Hyadesia fusca* and *Telmatogeton japonicus* instars. These species are nearly absent in the western limnetic brackish part (3.6 ‰ and lower); *Mniobia symbiotica* and the nematode genera *Aphelenchoides* and *Plectus* appear only irregularly. The density of *H. fusca* and *T. japonicus* instars is significantly correlated with salinity ($\alpha = 0.05$, Rank-Spearman), though in *T. japonicus* this influence is intermixed with the initial outspread of the midge in the Baltic Sea (Kronberg 1986). In 1982, *T. japonicus* instars were also found near Brunsbüttel (3.6 ‰), and near Helgoland (30 to 35 ‰); the salinity tolerance would thus appear greater than estimated in the first survey. In the laboratory the salinity tolerance of *H. fusca* was 0.05 to 40 ‰ (Ganning 1970).

For comparison, poly- and euhaline stations near Kristineberg (Sweden), Herdla (Norway) and Helgoland were investigated. Here *Echiniscoides sigismundi* is an additional member of the faunal inventory and an exceptional occurrence of *Littorina neritoides* was reported (Lewis & Tambs-Lyche 1962, Ziegelmeier 1966).

The influence of salinity on the faunal structure in the black zone can be summed up as follows: the species inventory is displaced, diversity remains nearly constant, and the abundance of species changes.

Temperature, light, and wave exposure

These abiotic factors further influence faunal composition in the black zone. The higher the littoral level, the greater is the importance of air temperature compared with water temperature; this results in more daily and seasonal variation than occurs in the lower littoral zones.

Light reflection from rocks elevates temperature in the immediate vicinity of the black zone: 25 °C air and 23 °C water temperature (August 1982, Bülk) resulted in 35 °C above the stones. Wave spray cools the air quickly to 29 °C, and not only thermal causes but also mechanical stress to the organisms.

Extremely low temperatures result in mechanical damage from floating ice; this may destroy the whole environment and result in a bare zone, as in the Scandinavian area (Lewis 1964). Frost resistance may be a function of cell physiology as in *Mniobia symbiotica*, which survived experimental freezing at -18 °C, or of behaviours as in *Littorina saxatilis* which retreats to the ice-free eulittoral, or as in *Telmatogeton japonicus* which survives in tubes built in small crevices.

Along exposed shores, the upper limit of littoral communities is displaced landwards; biological zonation thus shows a greater discrepancy to hydrographical zonation (Lewis 1964). The extension of the black zone serves as an indicator for the degree of wave exposure (Ballantine 1961, Lewis 1964). The *Lichina pygmaea* and *Verrucaria maura* associations prefer exposed shores, while cyanophytes prefer sheltered shores. The resulting changes are followed by altered faunal settlement as described below in 'Biotic factors'.

Eutrophication

The influence of eutrophication on the structure of the fauna in the black zone was investigated in Bülk (north-western exit of Kiel Bight) where domestic sewage from Kiel discharges into the Baltic Sea. The sewage is composed of organic materials, i. e. materials with high content of P, N and Si (Horstmann 1971, Anger 1975), which are less dense than seawater, and which thus drift at the surface. During easterly winds the sewage extends along the beach in a northwesterly direction (Horstmann 1971), resulting in different influences for each of the investigated stations. Eight (in 1981) or 7 (in 1982) breakwaters served as sample stations. Differ-

ences in the composition of the overgrowth did not reveal any significant influence on the faunal structure (Rank-Spearman correlation; Kronberg 1983).

Again, the animals most abundant were *Hyadesia fusca*, *Telmatogeton japonicus*, *Mniobia symbiotica*, and occasionally *Hypogastrura viatica*. These species have the main impact on the living density. Fig. 5 shows the living density (10cm⁻²) at 8 or 7 stations in Bülk in

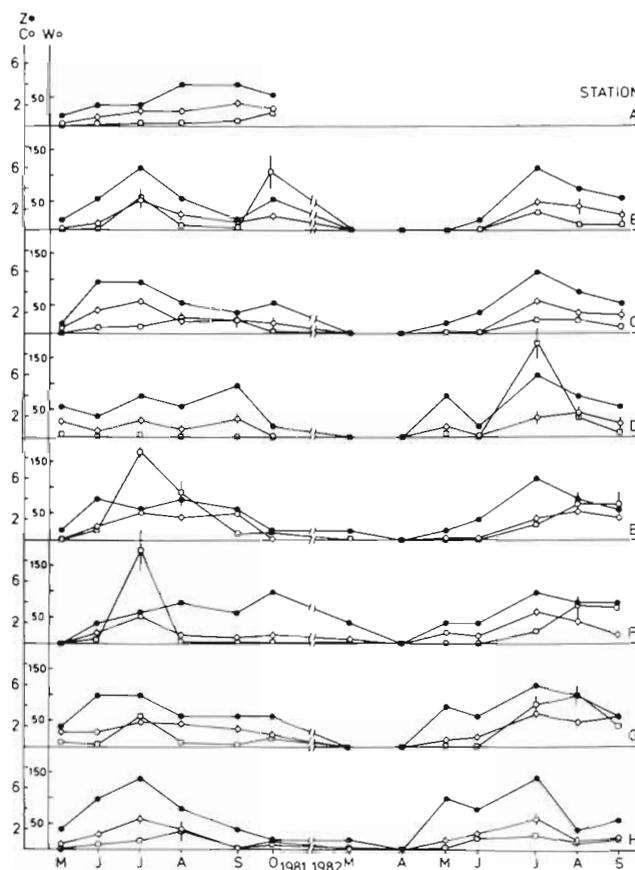


Fig. 5. Species number (Z), species density (C) and living density (W) per 10 cm² in the black zone of differently eutrophicated adjacent breakwaters in Bülk (Stns A to H, Kiel Bight; bar: ± 1 SE)

1981 and 1982, respectively. The black zone is most densely inhabited from June to September. In the cold season, almost no fauna at all was recorded, and a quantitative analysis was not possible. Remarkable is the repeated occurrence of sudden increases in living density, due to the reproduction of *H. fusca* and *M. symbiotica*. Population dynamics of *M. symbiotica* do not show a high synchrony between stations, in contrast to the situation for *H. fusca* and *T. japonicus* instars which are most abundant in July and August. In addition to these typical phytal organisms, aquatic intruders are present, such as Nematoda, Copepoda-Harpac-

ticoidea, Ostracoda, Acarina (Rhombognathidae), *Littorina saxatilis*, *Mytilus edulis* (juvenile) and terrestrial intruders such as *Abrolophus rubripes*, *Ameronothrus* spp. and *Nanorchestes amphibius*. However, their density is not important. An exception is *Hypogastrura viatica* (Collembola) which may reach such high densities (200 ind. 10cm⁻² in July 1982) that the black zone appears blue. *H. viatica* is saprophagous and known to appear at sewage filters. Species density is more uniform and never greatly exceeded 3 species 10cm⁻², which concurs with the number of dominant species. Total number of species per month reached 8 in summer (Fig. 5).

The eutrophication effect of sewage cannot be quantified but can be ranked and thus correlated to diversity, species density, living density, and abundance of species (Rank-Spearman correlation; Kronberg 1983). In 1981 no significant correlation could be found; in 1982, only singular correlations could be detected: species density and living density decreased in June 1982 with increased eutrophication, due to the preference of *Mniobia symbiotica* for cleaner breakwaters. The same behaviour was observed in Nematoda in July 1982. *Hypogastrura viatica* was found more often in the neighbourhood of the outfall (July and August 1982) since it feeds on decomposing organic materials. No further correlations could be detected and, as the correlation appears only temporarily the dependency of faunal structure on eutrophication appears small or hidden by other microclimatic factors.

The abundance of foundation species (*Hyadesia fusca*, *Telmatogeton japonicus*, *Mniobia symbiotica*) at different stations showed significant differences (Kruskal-Wallis-Test; Kronberg 1983). Population dynamics were thus not uniform at differently eutrophicated breakwaters. Only during scarce settlement were no differences detectable. Quantitative similarity (Kulczynski index) is slight (Fig. 6). Identity of community structure ($I_k \geq 0.80$; Kronberg 1987) was achieved only once in 1981 and 1982 at 2 adjacent stations. In 29 % of comparisons, the index was less than 0.1. Faunal structure at adjacent breakwaters revealed considerable differences.

Qualitative similarity between stations was never less than 50 %; in summer it often reached values greater than $I_s = 0.85$, i.e. identity according to the accuracy of the species minimal area. Qualitative similarity thus far exceeded quantitative (Fig. 7). The presence of foundation species reached values of nearly 100 % in summer (Fig. 8), diminishing towards winter.

Sewage in Bülk caused no detectable disturbance to the fauna in the black zone. Quantitative parameters reacted appreciably to regional and seasonal changes, but no particular microclimatic causality was found. Compared to the unstable abundance values, faunal

1981 1982	A	B	C	D	E	F	G	H
A		*	*	*	*	*	*	*
B			*	*	*	*	*	*
C			*	*	*	*	*	*
D					*	*	*	*
E						*	*	*
F							*	*
G								*
H								

Fig. 6. Quantitative similarity (Kulczynski-Index, I_k) of the fauna in the black zone at differently eutrophicated adjacent breakwaters during densest settlement in July 1981 and July 1982 (Stns A to H, Bülk, Kiel Bight; I_k : large star: 1.0 to 0.86 (identity); medium sized star: 0.85 to 0.41; small star: 0.40 to 0)

1981 1982	A	B	C	D	E	F	G	H
A		*	*	*	*	*	*	*
B			*	*	*	*	*	*
C				*	*	*	*	*
D					*	*	*	*
E						*	*	*
F							*	*
G								*
H								

Fig. 7. Qualitative similarity (Sørensen-Index, I_s) of the fauna in the black zone at differently eutrophicated adjacent breakwaters during densest settlement in July 1981 and July 1982 (Stns A to H, Bülk, Kiel Bight; I_s : large star: 1.0 to 0.81 (identity); medium sized star: 0.80 to 0.41; small star: 0.40 to 0)

composition remained nearly unchanged – even extreme density variation did not lead to a collapse of the community. The diversity-stability-hypothesis (MacArthur 1955), which predicts low stability in communities of low diversity, is not supported in the black zone.

Biotic factors

Besides abiotic factors, biotic factors such as plant substratum character may control the settlement of the fauna in the black zone. To compare the faunal composition in different associations of the black zone,

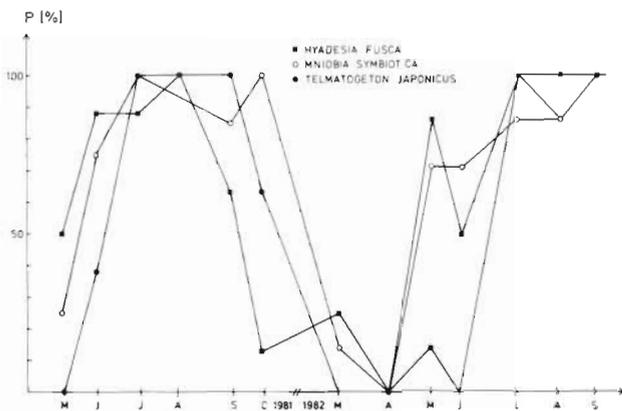


Fig. 8. Presence (P) of foundation species (*Hyadesia fusca*, *Mniobia symbiotica*, *Telmatogeton japonicus* instars) in the black zone of differently eutrophicated adjacent breakwaters in Bülk (Stns A to H: 1981; Stns B to H: 1982)

Lichina pygmaea (shrub-like lichen) and Cyanophyta in different climates were analysed. As the samples were not of the same size, rarefaction diversity (Sanders 1968) was chosen to compare the fauna (Fig. 9). Lichina and Cyanophyta associations show a gradual approximation to saturation level because there were only 2 or 3 dominant species but a few rare species; species evenness in both environments is therefore low. Species richness, designated by height of the curve, is a little higher in the Lichina association than in blue-green algae.

Adaptation

Since the extremely variable living conditions proved exacting on fauna adaptation, different responses from terrestrial and aquatic intruders were to be expected.

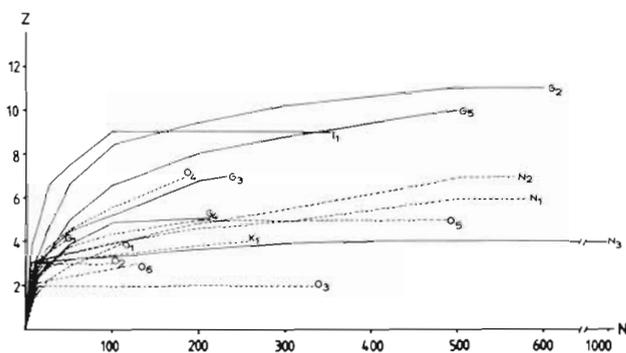


Fig. 9. Rarefaction diversity of the fauna in *Lichina pygmaea* associations (—) and Cyanophyta associations (---) in the black zone of different climatic regions. Z : number of species; N : number of individuals; O_1 to O_6 : eastern coastline of Schleswig-Holstein (F. R. Germany); K_1 : Kiel Canal (F. R. Germany); N_1 to N_3 : Herdla (Norway); G_1 to G_5 : Penzance (Cornwall, UK); I_1 : Sherkin Island (Ireland)

Protection

Protection was primarily directed against abiotic factors such as desiccation, submersion, exposure and heat; predators were not important.

The tubes of *Telmatogeton japonicus* instars, where pupation subsequently takes place, are built in small crevices and represent protective adaptations of foundation species in the black zone. The pupa bears cuticular structures (respiratory horns, terminal abdominal disk) which close these tubes.

Physiological adaptations were more important than morphological patterns. Tardigrada, Nematoda and Rotatoria are predisposed to tolerate an extremely variable environment by their ability to survive through anhydrobiosis; this ability is best developed in moss organisms. In the quiescent stage, these Tardigrada are able to withstand several days or even months of desiccation or other extreme abiotic factors such as cold (-271.9°C for 20 mo) or heat (100°C for 6 h), O_2 absence, vacuum, X-rays and radium radiation (Marcus 1928). No measurable metabolism occurs (Keilin 1959, Crowe & Madin 1974, Kronberg 1983 for *Echiniscoides sigismundi*). Anhydrobiosis is 'life in the absence of water': free water in the cells is substituted by glycerol (Crowe & Madin 1974). Trehalose serves as a carbohydrate store (Crowe & Madin 1974, Womersley & Smith 1981). *Mniobia symbiotica* survived freezing at -18°C in the contracted stage for several months.

The shell of gastropods presents a predisposition for surviving in temporarily drying environments. The influence of different shell globosity and sculpture on littoral level was investigated by Vermeij (1973). The colour of snails may serve as a protection from predators such as seabirds and crustaceans (Heller 1975). Littorinids close their shell using their operculum, such that isolating air between body and substratum prevents heat conduction from the substratum. Also in littorinids, changes in energy metabolism occur during air exposure: they change to a low anaerobic homeostasis e. g. 41 % of active metabolism (heat dissipation) in *Littorina saxatilis*, and 25 % in *L. neritoides* (Kronberg 1983).

Aquatic and terrestrial intruders – such as Rhombognathidae, Ostracoda, Copepoda-Harpacticoida, Oribatei and Collembola – remain in moist or dry refuges respectively. Many terrestrial species wear a hydrophobic integument (Cheng 1976).

Locomotion

Mobility in the black zone includes the possibility of retreating into crevices, but also a risk of being washed out of the overgrowth by waves. The foundation

species thus tend to a haptic behaviour with suction tubes, mucous secretion, or claws. *Hyadesia fusca* possesses a third claw between the lateral claws with a long muscular connecting piece. This claw serves as an elastic anchor. Instars of *Telmatogeton japonicus* are unable to swim in open water, but crawl by attaching with their mandibles and anterior and posterior parapods. When disturbed, they discharge a large amount of adhesive saliva to attach themselves to the substrate or to build a girdle around the thorax. The rotifer *Mniobia symbiotica* also avoids swimming and moves like a leech. The foot contains glands secreting agglutinant to adhere to algal thalli.

Littorinids use their suction foot as long as they are moistened: they retract into their shell during desiccation. The shell is then anchored by dried mucus. Many intruding species, conversely, show high vagility, often linked with the ability to jump, as in the case of *Ligia* spp., Talitrida, *Petrobius maritimus*, Collembola and *Nanorchestes amphibius*. This enables them to retreat into crevices.

Reproduction and development

Adaptation of adults to extreme conditions ensures survival of the population only if the delicate development stages such as the ovular, juvenile and desquamation stages are protected too. In the black zone, the sensitivity of these stages is often reduced by shortening their duration; ovoviviparity and a short pupation stage make this possible.

Hyadesia fusca is ovoviviparous, and juveniles appear in July (black zone, Baltic Sea) or June (rock-pools, Great Britain; Ganning 1970). The imago of *Telmatogeton japonicus* is short-lived (24 to 36 h; 20 h, Wirth 1947); the female abdomen containing 200 to 300 eggs which are laid separately into the moist overgrowth. Instars moult 4 times until pupation. The 4th instar shows a fully developed genital tract, even eggs and sperm are differentiated. Imaginal disks show the shape of legs and the terminal abdominal disk is recognizable. Pupation takes place in the web tube, obviously initiated by dry conditions; in wet turf no pupae were found. Under dry conditions, significantly smaller instars revealed maturity (Kronberg 1983). Quiescence during pupation therefore only serves the sclerotisation of imaginal organs already formed.

Mniobia symbiotica propagates parthenogenesis which leads to a high variability between populations. Its occurrence in fresh water and marine habitats is possibly an indicator of species separation (Otto 1936). Unlike some moss-dwelling species, *Echiniscoides sigismundi* does not lay eggs in the exuvium for protection (Kronberg 1983).

Among the littorinids, ovoviviparity occurs in *Littorina saxatilis*. The higher-zoned *L. neritoides* is oviparous like eulittoral *Littorina* species. Even within the *L. saxatilis* complex there are species which lay eggs, for example *L. arcana* (Hannaford-Ellis 1978). Therefore no correlation exists between tidal level and the mode of reproduction of littorinids – even 'reproductive effort' sensu Hughes & Roberts (1980) is independent of littoral zonation.

Ingestion

Food availability in the black zone includes epilithic blue-green and green algae, lichens and detritus. Cyanophytes were identified by fluorescent microscopy and were found in the stomach of all foundation species and of some intruders: *Telmatogeton japonicus* instars, *Hyadesia fusca*, *Mniobia symbiotica*, *Echiniscoides sigismundi*, *Littorina saxatilis*, *L. neritoides*, *Anurida maritima*, *Rhombognathus setosus*, *R. notops*, *Campeopea hirsuta*, *Ligia oceanica* (juv.) (Kronberg 1983). A massive number of *L. saxatilis* may destroy the environment in the lower regions as observed at Bülk in August–September 1981 and 1982. Predators are found only as intruders from neighbouring environments: small arthropods such as *A. maritima*, chironomid instars and *Nanorchestes amphibius* are prey for mites such as *Neomolgus litoralis* and *Bdella longicornis* (Alberti 1973). *T. japonicus* adults are eaten by some flies (Chopodidae, Anthomyiidae; Wirth 1947). *Littorina* spp. are prey for seabirds and crabs (Raffaelli 1978), for blennioid fishes, for predatory snails (*Nucella* sp.) and even rats (Pettitt 1975). Moreover, they are hosts for parasitical trematodes (family Microphallidae), which may lead to oversized growth by sterilization (McManus & James 1975, Elnor & Raffaelli 1980, Irwin & Irwin 1980).

Thus the foodweb in the black zone is very simple, consisting of some phytophagous, seldom omnivorous-saprophagous, species which are occasionally consumed by predatory intruders.

CONCLUSIONS

The black zone in wave spray regions of rocky shores is an extremely variable environment with cosmopolitan characteristics. Moisture, salinity, and temperature fluctuate within a wide range. In addition to lichens (*Verrucaria maura*, *Lichina pygmaea*), blue-green algae create the blackish colour. As littoral cyanophytes are phylogenetically rather old, the environment appears to represent ancient conditions.

Faunal composition. The fauna consists of thalasso-

gen (*Echiniscoides*, *Littorina*, *Lasaea*, *Campecopea*) and limnio-terrestrial genera (*Hyadesia*, *Telmatogeton*, *Mniobia*) and corresponds with the topographic position between marine littoral and terrestrial supralittoral. An obvious relationship exists to the fauna in mosses.

Diversity is very low: there are no coenobiont and only 3 to 5 coenophile species. Most animals are intruders from neighbouring environments that only live or feed here temporarily. Low diversity corresponds to the low heterogeneity in the environment. Competition for crevices is strong, and in general only 1 species occupies a defined size class (length/width): *Telmatogeton japonicus* instars (10/0.8 mm), *Hyadesia fusca* (0.5/0.3 mm), *Mniobia symbiotica* (0.4/0.05 mm), each needing a particular crevice size.

Adaptation. Foundation species are haptic forms, most intruders are vagile and often retreat into refuges by jumping. The duration of sensitive development stages may be shortened by ovoviviparity or short pupation. The foodweb is simple; foundation species are phytophagous. Predators occur only occasionally, and come from neighbouring environments. Protection is thus more against abiotic than biotic factors. Shells, cuticular structures, and web tubes protect against desiccation, washing out, and heat. The most important adaptation lies in the ability to survive unfavourable circumstances in stages of quiescent life. Metabolism is reduced to a level which satisfies an extremely low homeostasis. Tardigrada, Rotatoria and Nematoda choose anhydrobiosis for this purpose; littorinids, anaerobiosis. This behaviour often makes further adaptations superfluous – adaptation to active terrestrial life does not take place.

Faunal structure. The influence of abiotic factors on the structure of the biocenosis can be interpreted as follows: moisture changes species composition, whereas salinity influences the density of species. Only in freshwater associations are new faunal elements added; often blue-green algae are displaced by mosses. Biotic factors are not very important: the shrub-like lichen *Lichina pygmaea* accommodates only a few more species than cyanophytes, which is apparently due to the higher spatial heterogeneity and accompanying higher crevice availability. Fauna is bound not so much to the quality of overgrowth but to the littoral level with its special moisture conditions.

Though the community shows high seasonal and regional variations in density caused by microclimatic factors, species composition remains nearly unchanged. The community is qualitatively stable, which contradicts the diversity-stability-hypothesis (MacArthur 1955). For many species in the black zone high variability is reported (Otto 1936 for *Mniobia symbiotica*; Kristensen & Hallas for *Echiniscoides sigismundi*; Smith 1981, Janson 1985 for *Littorina saxatilis*). Thus it is

supposed that polymorphism in low diversity and species diversity in high diversity environments ensures the resilience of communities. Artificially poor systems, such as man-made monocultures, do not show diversity in either respect and are more susceptible to external disturbance. In an unpredictable environment such as the black zone, polymorphous communities have a selective advantage over monomorphous ones (Grassle 1972). Thus the small species inventory in the black zone is not an artifact but the result of natural selection.

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