

THE ECOLOGY OF MICRO- AND MEIOBENTHOS

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INTRODUCTION

While the existence of protozoa and minute metazoa has been known for a long time, it was during the 1930s that the concepts of microbenthos and benthic microfaunal communities were first recognized. Recognition was due particularly to the work of the Kiel school of marine biology in Germany (109, 115). What stimulated zoologists to study this fauna was the discovery of new and morphologically aberrant forms between the sandgrains of littoral and sublittoral sediments, such as the medusa *Halamohydra*, less than 1 mm in diameter, and a solitary bryozoan, *Mono-bryozoon*. Previously unknown or very poorly known taxonomic groups (e.g. macrodasyoid gastrotrichs, gnathostomulids, and mystacocarids) were discovered. Easily accessible habitats (such as beach sand) in otherwise faunistically well-known parts of the world yielded a wealth of new species, of which many represented new types of animal organization (e.g. 5, 6, 103, 108, 110, 118). This exploratory phase naturally gave rise to a number of faunistic and taxonomic monographs.

Morphological adaptations of the newly discovered fauna quickly drew attention. In particular, it was shown how convergent evolution in unrelated taxonomic groups had led to a number of morphological and behavioral features that could be interpreted as adaptations to the movement of life in the interstices of sand grains. Also the relation between small size and organization was studied, namely, how organisms belonging to groups characterized by a complex organization (holothurians, ascidians, polychaetes, and molluscs) are built when they measure only between 0.5 and 5 mm (6, 113, 128).

Early attempts were also made to classify microfaunal communities (biocoenoses) and to correlate these with environmental factors, in particular with salinity and the mechanical properties of the sediment (39, 101, 102, 109). Of special interest was the discovery of microfaunas characteristic of coastal and of terrestrial ground water (21, 115).

Krogg & Spärck (81) and Mare (90) were the first to consider the quantitative role of the benthic microfauna. Since then, the quantification of microbenthos and

its role in the carbon flow and food chains of aquatic ecosystems have attracted increasing interest; these problems are central to the reviews by McIntyre (94) and Gerlach (41). The various techniques developed for the study of microfauna, and not least for its quantification, were compiled by Hulings & Gray (68).

The last decade has witnessed an increasing interest in meio- and microbenthos. Their energetic significance has been emphasized most, but new aspects have also been examined. The study of the meiobenthos of the deep sea has begun; zoogeographical and evolutionary aspects play an increasing role in "meiobenthology." Most interesting, perhaps, have been recent attempts to approach microbenthic communities in the light of modern ecological ideas on resource partitioning, niche packing, and species richness. The breadth of the contemporary approach to the study of the small animals of the sea bottom is evident from the titles in the proceedings of a recent symposium on meiofauna (126).

Against the background of earlier reviews, in particular the important papers by Swedmark (128) and by McIntyre (94), which were published in 1964 and 1969 respectively, the present review emphasizes the developments in meiofauna research during the last 10–15 years. The potential value of this fauna to the study of the general aspects of community ecology is stressed. Little reference is made to the microbenthos of freshwaters. This is due in part to the experience of the author, and in part to the fact that, compared to its marine counterparts, this fauna has received little attention in the literature.

THE FAUNA

The Concepts of Micro- and Meiobenthos

Micro- and meiofauna are generally defined as "small animals." The term *microfauna* was originally used to describe the fauna living interstitially in sand. Most authors now follow the terminology of Mare (90), who used the term *meiofauna* to designate the metazoan fauna that passes through a sieve with a given mesh size (most authors use 1 or 0.5 mm sieves to retain the "macrofauna"). The term microfauna is thus reserved for the protozoa (although foraminiferans are often included in the meiofauna and some ciliates may be larger than the smallest metazoa, such as rotifers. Other authors (31, 98) have defined the meiofauna as the metazoans that weigh less than 10^{-4} g (wet weight). These authors have considered the protozoans to comprise the microfauna. None of these definitions has any special taxonomical or ecological significance. The meiofauna also includes juvenile stages of the macrofauna. On the surface of noncapillary sediments, the whole range of body sizes is found, from the smallest protozoans to very large invertebrates. The size-range from 10^{-5} to 10^{-4} g includes, for example, many oligochaetes, small polychaetes, and some large nematodes. Most nematodes, gastrotrichs, turbellarians, and harpacticoid copepods range in weight between 10^{-6} and 10^{-5} g, while some very small metazoans such as rotifers and chaetonoid gastrotrichs weigh only between 10^{-7} and 10^{-6} g. Ciliates are found within the weight-range between 10^{-10} and 10^{-6} g, while the smallest protozoa (zooflagellates) weigh on the order of 10^{-11} g. Organisms classified as meio- and microfauna thus span seven orders of weight

magnitude and consequently exhibit great variations in organizational level and in other physiological and ecological properties. Practically all major metazoan groups have representatives among the meiofauna, but a more restricted number of taxa dominate with respect to numbers of species and individuals.

A special fauna is found in the interstices between the sand grains of capillary sediments; this fauna was termed the *interstitial fauna* by Nicholls (99) while Remane (112) coined the word *mesopsammon*. From an ecological viewpoint this fauna comprises a natural group: the animals found swimming or gliding in the interstices, as opposed to those that burrow in the sediment. In some sandy sediments there is a clear hiatus with respect to body sizes between these two groups of infauna (31).

Adaptation to life in the interstices of sand has resulted in the independent evolution of a number of morphological features within many taxa. One of these is size. The body length of interstitial animals is typically between 0.2 and 3 mm; ciliates are often among the longest representatives, a few forms attaining a length of more than 3 mm. Swedmark (128) has discussed the organizational consequences of the reduction in body size among the more complex forms, such as annelids. Among these consequences is the loss of several organs and the retention of various larval features. Another typical adaptation of the interstitial fauna is an oblong shape usually accompanied by external ciliation and a gliding movement. Some of the large ciliates have attained a flat, ribbon-like shape rather than a thread-like one. The presence of attachment organs, for example in turbellarians and the gastrotrichs, is another typical feature; in interstitial tardigrades adhesive pads have replaced the claws typical of other forms (Figure 1). Interstitial ciliates have special fields of haptic cilia with which they can cling to smooth surfaces. Eyes have been lost in most forms, whereas statocysts occur in some species. Sessile animals are absent among the interstitial fauna; the one bryozoan genus known from the interstitial fauna is solitary and motile.

An interstitial fauna exists not only in coastal groundwater but also in sandy sediments of lakes and river beds, where representatives of ciliates, turbellarians, nematodes, rotifers, and other groups are found. However, these forms show a degree of morphological adaptation to the interstitial life considerably smaller than that of marine forms. The ciliates that show the most extreme morphological adaptations to interstitial life (*Tracheloraphis*, *Geleia*, *Remanella*, and others) belong to groups that are only very sparsely represented, if at all, in freshwater where less extreme morphological types are found in sands (31, 102).

The presence and nature of an interstitial fauna depend, of course, on the size of the interstices. In well-sorted sands, the average size of the interstices is determined by the median grain size. In more poorly sorted sands, or in the presence of a small percentage of clay and silt, the interstices become clogged. In well-sorted sands a true interstitial fauna disappears when the median grain size is less than $\sim 100 \mu\text{m}$. In sand with median grain sizes of between 100 and 200 μm , ciliate protozoans outnumber other individuals and species, although representatives of harpacticoids, turbellarians, and gastrotrichs occur as well. In sand with grain sizes exceeding 200 μm , ciliates may still be common, but they are accompanied

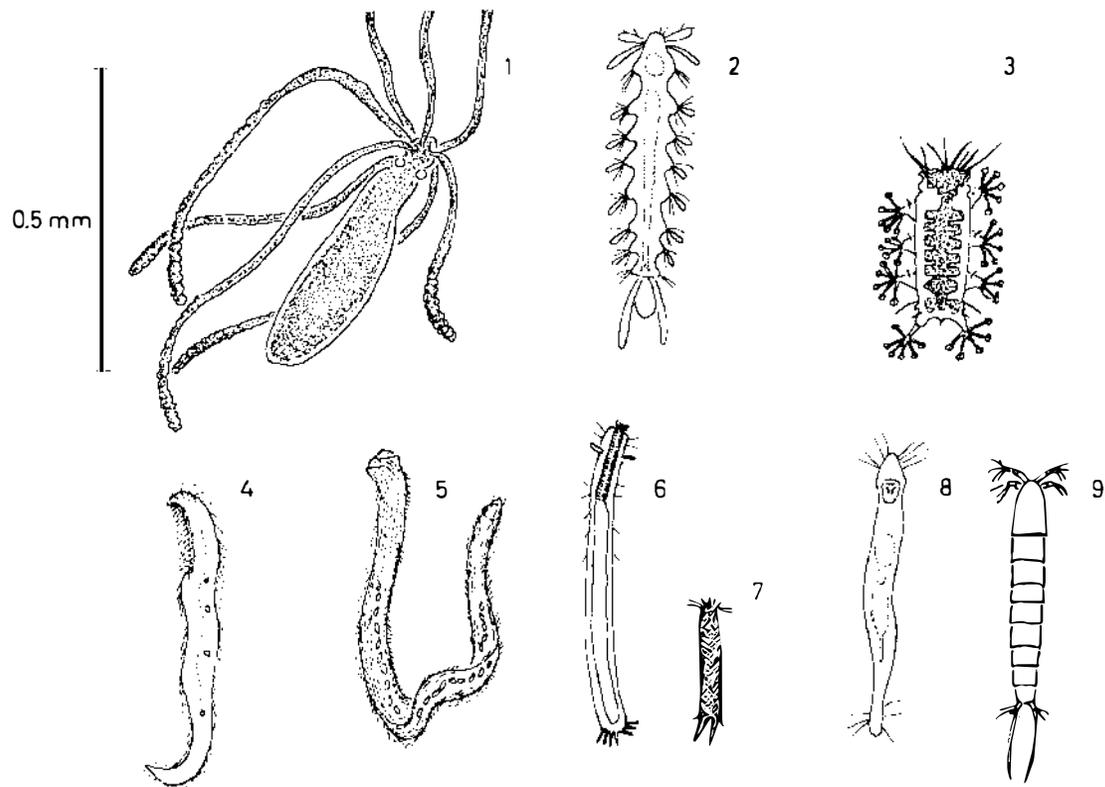


Figure 1 Typical genera of the interstitial fauna belonging to seven different phyla and exemplifying the uniformly small size and oblong shape. 1. *Halamohydra* (coelenterate); 2. *Nerillidium* (archiannelid); 3. *Batillipes* (tardigrade); 4, 5. *Remanella* and *Helicoprordon* (ciliates); 6. *Paradasys* (macrodasypod gastrotrich); 7. *Aspidophorus* (chaetonotid gastrotrich); 8. *Gnathostomula* (gnathostomulid); 9. *Arenopontia* (harpacticoid copepod).

by a rich fauna of metazoan forms: tardigrades, turbellarians, gastrotrichs, oligochaetes, archiannelids, harpacticoids, ostracods, and others. The coarsest sands ("amphioxus-sand") harbor a number of forms not found in fine-grained sands (31, 72, 128, 143).

A very rich interstitial fauna exists in the coastal ground water of sandy beaches (21, 33, 76, 122, 123). A special community of interstitial animals is found in the splash zone of beaches (109).

In silty and clayey sediments the character of the meiobenthos changes totally. Nematodes, which are usually also found in large numbers in sands, absolutely dominate in noncapillary sediments since they, in contrast to the groups mentioned above, are capable of burrowing. The loose, water-sediment interface of clays and silty sediments may contain a rich fauna with representatives of foraminifers, nematodes, kinorhynch, ostracods, harpacticoids, polychaetes, and juvenile specimens of macrofaunal species. This fauna lacks the morphological features characteristic of the interstitial fauna; with respect to size distribution, it blends gradually into the macrofauna. Special micro- and meiobenthic communities develop on sediments covered by algal mats or layers of sulfur bacteria (31).

The Major Taxonomic Groups Constituting the Micro- and Meiobenthos

PROTOZOA The unicellular organisms are represented by all major, free-living groups. Of these, the ciliates are taxonomically and ecologically by far the best studied. They are present within capillary sediments and on the surface of all types of sediment; they reach their maximum importance in relatively fine sands and in mats of sulfur bacteria. Dragesco (24) listed more than 300 species of interstitial forms; the number actually present is much higher. Other important contributions to the taxonomy and ecology of ciliates are found in (25, 28–31, 59, 60). Amoebae and heliozoa occur in and on marine sediments, but have attracted hardly any interest yet. Foraminifera, long considered only as potential fossils, have more recently been the subject of ecological studies (54, 85, 86, 92, 97, 141). The small zooflagellates have so far been neglected almost entirely, although it was early suggested (90) that they are of great importance in marine sediments. Plentiful in the detrital sediments of a freshwater pond, they constitute the single most important group of bacterial consumers in the system (32).

TURBELLARIA The turbellarians constitute an important component of the meiofauna of sand and also occur in detrital sediments. Some important references to their taxonomy and ecology are (1–4, 10, 11, 23, 79, 80, 87, 88, 127).

GNATHOSTOMULIDA Some twenty years ago this remarkable group of worms with a mastax resembling that of rotifers was described as an aberrant type of turbellarian. It has turned out to be a separate taxon with several unique features. This group of exclusively interstitial organisms now includes nearly 100 known species (6, 26, 118, 124).

NEMATODA These animals (a very large number of species) surely constitute the quantitatively most important component of the meiofauna, especially in noncapil-

lary sediments. Some representative references are (38, 65, 133, 135–137, 142). Gerlach & Riemann (44) give a complete bibliography of this important group.

ROTIFERS These animals play a modest role in the marine meiobenthos; they are more important in brackish water and become a very important group in freshwater (129).

GASTROTRICHA Of the two orders of this group, the chaetonoids are well-known from fresh- as well as seawater, occupying various habitats, including sediments. The macrodasyoids, on the other hand, occur nearly exclusively in marine sands and in coastal groundwater (12, 22, 69–70, 111, 130).

TARDIGRADA The tardigrades comprise a number of marine interstitial forms and are also a component of the benthos of the deep sea (95, 104–106, 117).

KINORHYNCHA This relatively species-poor group is found in and on the surface layers of noncapillary marine sediments (67, 111).

ANNELIDA The oligochaetes, though primarily a limnetic group, play a considerable role in the sea as well, especially in estuarine sediments and in coastal groundwater. The “archiannelida” (now believed to be a polyphyletic group deriving from various polychaete families as the result of regressive evolution in connection with the attainment of a small body size) comprise many typical interstitial forms. The polychaetes also contain forms that must be classified as meiofauna, including species that have adapted to the life in interstices, in particular the Syllidae, Hesionidae, Pisionidae and Psammodrilidae (47–49, 82–84, 100, 128).

CRUSTACEA Representatives of the crustaceans are quantitatively important in or on most types of sediments and some groups are very rich in species. This especially applies to the harpacticoids, which occur interstitially and in detrital sediments. Ostracods seem to be more important in detrital habitats. The mystacocarids, first discovered in 1943, constitute a special group of crustaceans and are confined to interstitial life (17, 19, 21, 101, 131).

OTHER GROUPS While practically all major groups of invertebrates are represented in among the meiobenthic fauna, many are rarely met or are very poor in species. Several have not attained sufficiently small body sizes to occur in fine or medium sand and are found as interstitial animals only in coarse sands. Among these invertebrate groups are coelenterates, priapulids, loxosomatids, bryozoans, halacarids, gastropods, holothurians, and ascidians (9, 66, 96, 119, 120, 128).

THE FAUNA OF ANOXIC, REDUCING SEDIMENTS

Beneath an oxidized zone of variable thickness practically all aquatic sediments are completely anoxic. The thickness of the oxidized layer is a function of the input of organic material, the permeability of the sediment, the degree of water turbulence,

and the light intensity at the sediment surface. The depth of the transition zone between the oxidized and the reduced layers of the sediment is determined by the balance between, on the one hand, the downward diffusion of oxygen from the overlying water or of oxygen produced photosynthetically at the sediment surface, and, on the other hand, the consumption of oxygen in the sediment. In the anoxic zone, organic material is fermented into volatile fatty acids by bacteria. Other bacteria mineralize these low molecular-weight organic compounds further through anaerobic respiration. The dominant process in marine sediments is sulfate reduction. The resulting sulfide (really HS^- at the prevailing pH) may occur in the interstitial water in concentrations of up to 20 mmole. Part of it is bound as iron sulfides, which lend the black color to anoxic sediments. The sulfide poises the redox potential, E_h , of the interstitial water to values between -100 and -220 mV. There is a net upward diffusion of sulfide from the anoxic layer. In the surface layers it is oxidized, either spontaneously or by chemolithotrophic bacteria, and is responsible for more than half of the total oxygen demand of a typical marine sediment. The sulfide may also be oxidized photosynthetically by purple or green sulfur bacteria in shallow-water sediments (31, 34, 78).

The consequence of this vertical biological and chemical zonation of sediments for the meio- and microbenthos in general is discussed later. Here we consider only the very specialized fauna that is confined to the strictly anoxic and reducing layers of the sediment. This zone was earlier believed to be essentially azoic; however, although this part of the sediment is dominated by prokaryote life, a characteristic fauna develops whenever the interstices of the sediment are sufficiently large (31, 35, 36).

The ciliates are the best-studied component of this fauna. They belong mainly to three orders, Trichostomatida, Heterotrichida, and Odontostomatida. The last order, which can be derived phylogenetically from heterotrichs, seems only to contain anaerobic species; the other orders are represented by only a few families. In addition, a few ciliates belonging to other groups may be found as a part of the "sulfide fauna." These ciliates are always confined to anaerobic and usually sulfide-containing environments; being sensitive to oxygen, and lacking both mitochondria and cytochrome oxidase activity, they are true obligate anaerobes. A characteristic feature of these ciliates is their association with ecto- as well as endosymbiotic bacteria. It has been conjectured that the bacteria utilize lactate or succinate (the typical endproducts of eukaryotic anaerobic metabolism) as a substrate for energy metabolism through a further fermentation or through anaerobic respiration (35).

Zooflagellates are also a constituent of the anaerobic fauna, but they have not yet been studied in detail. Some metazoans, e.g. some nematodes, turbellarians, gnathostomulids, rotifers, and gastrotrichs, are sometimes found in the anoxic zone in the field (13, 31, 36, 89). It is not known whether this is due to occasional excursions from the oxic zone or whether they are found there permanently. The exact chemical environment experienced by an animal in the transition zone of the sediment may be difficult to establish, since this zone may be very patchy with respect to oxidizing

and reducing conditions (77). It has been shown that some of the species can survive and even grow under anaerobic conditions (31, 146), but obligatory anaerobicity in free living metazoa has been established in only one species of nematodes (147). Some nematodes frequently found in the reducing zone of sediments have ectosymbiotic prokaryotes (described as blue-green bacteria) similar to those found in ciliates (144).

The existence of the sulfide fauna has stimulated some phylogenetical speculations in the literature (13, 36). The presence of only primitive eukaryotes in anaerobic environments has been considered suggestive in view of the current belief that an anoxic atmosphere prevailed in the first part of Precambrian times. However, the eukaryotes must have arisen at a time when the earth's atmosphere contained some oxygen. All the representatives of the sulfide fauna (with the possible exception of flagellates) can be derived phylogenetically from aerobic forms; viability under anaerobic conditions must have been acquired subsequently. The sulfide fauna is comparable to the protozoan fauna found in the intestinal tract of many higher animals; in both cases a few groups of simple eukaryotes have filled the ecological niche as phagotrophs in an environment where eukaryotes otherwise have an inefficient energy metabolism as compared to many forms of bacteria.

THE MICRO- AND MEIOBENTHOS OF THE DEEP SEA

The study of micro- and meiobenthos was long confined to littoral and shallow sublittoral habitats. During the last decade their study has been extended to the deep sea. Such studies are complicated by the fact that most of the "soft bodied" meiofauna are identifiable only if they can be taken alive. A number of works have treated the qualitative as well as quantitative aspects of meiobenthos (e.g. 17, 18, 117, 132, 134, 139).

The presence of all the major groups of meiofauna (turbellarians, gastrotrichs, tardigrades, gnathostomulids, harpacticoids, kinorhynchs, nematodes, and foraminiferans) has been established down to depths exceeding 5000 m. Nematodes and foraminiferans dominate the fauna; turbellarians, gastrotrichs, tardigrades and gnathostomulids are often limited by the absence of sandy sediments. Coull et al (18) studied a transect off North Carolina between depths of 400 and 4000 m; the greatest number of individuals (about 90 cm⁻²) was found at 800 m; at 4000 m the number was reduced by more than a factor of 10. In a review on the quantitative composition of the deep sea benthos, Thiel (132) found evidence that the well-known reduction in population density and biomass with depth is less-pronounced for the meiofauna than is the case for the macrofauna.

The microfauna (i.e. protozoans other than foraminiferans) have so far attracted little attention, but their presence in deep sea sediments has been established (14).

Coull (17) studied the species diversity of benthic copepods along a transect from 14 m to more than 5000 m depth and used Sanders' "rarefaction method" to analyze the data. In accordance with what has previously been found for the macrofauna, meiofauna diversity is higher in the deep sea than on the shelf; these data support the hypothesis that a predictable "climate" favors a high species richness.

REPRODUCTIVE BIOLOGY

The reproductive biology of the meiofauna has been studied and reviewed by several authors (1, 7, 50, 113, 128). Only very few forms (e.g. the archiannelid genus *Polygordius* and some species of *Protodrilus*) have pelagic larvae, and these forms produce a relatively large number of eggs at a time (up to 200). The great majority of the meiofauna produce only a few gametes and typically release from 1 to 10 eggs at a time. The eggs are either released directly into the water or are deposited in a cocoon attached to sand grains. Benthic larvae develop from the eggs or else development is direct. A number of forms exhibit brood protection or viviparity.

Mechanisms that increase the probability of fertilization are common. In crustaceans copulation occurs; many forms have spermatophores, and hermaphroditism has been established in several groups.

COMMUNITY STRUCTURE AND SPECIES RICHNESS

Next to the astonishing morphological adaptations of the meio- and microfauna, the most remarkable thing about it is perhaps its richness in species. Few environments would seem more homogeneous than the sand making up beaches or sublittoral sediments. Yet samples of only a few cubic centimeters may yield a wealth of species. Fenchel et al (33; see also Figure 2) extracted five cores, of 10 cm² each, from a transect perpendicular to the water's edge on a Danish beach. The samples yielded nearly 3000 individuals of metazoan meiofauna belonging to 71 species, of which 43 were nematodes. Fenchel (31) found that core samples of 1 cm² and 20 cm long from sublittoral sands typically yielded 30–50 species of ciliates in addition to several unidentified forms and species of metazoans. In many respects the meiobenthos offers unique possibilities for studying resource sharing and niche overlap in natural communities. A large body of information has already been collected. Here we treat the subject in terms of the three main dimensions of the ecological niche: habitat, time, and food resources.

Habitat Niches

Many studies have been carried out on the distribution patterns of meiofauna in beach sands and on the environmental factors that govern these patterns. Sections through beaches perpendicular to the water's edge will show vertical and horizontal gradients in grain size, temperature, water contents, salinity, and oxygen. In general, of course, salinity will decrease landwards and the water content upwards, but complications arise due to rainfalls, tidal action, and the layering of different grain sizes. The gradients also move according to tidal and annual patterns—for example, in response to strong rainfalls.

Characteristic zonation patterns of the species populations are correlated with these environmental gradients. Due to the low oxygen tension, only a few species and individuals are found below the water table, but in the moist sand above it, a rich fauna is found, with the various species distributed according to salinity, grain size, water contents, and oxygen. There are many examples showing how different,

related forms have subdivided the habitat (Figure 2). Annual changes in the environmental gradients lead to movements of the whole zonation patterns of the organisms (27, 33, 55–57, 72, 74–76, 104, 105, 107, 116, 122, 123).

The ability of the species to detect and move along the environmental gradients have been studied intensively, using tolerance and preference experiments, by Gray (51, 52) and Jansson (73, 76; and papers cited therein). In general, the experimental results accord with the field distribution and show that the animals are capable of finding their preferred habitats. Tolerance limits, and to a lesser extent preference optima, do not tend to change after habituation to suboptimal conditions. Wieser (145) showed that distribution in the field often fills out an organism's entire tolerance range. His examples show the period for which a species can endure anoxia corresponds to the time during which it is exposed to this condition in the tidal cycle. It seems beyond doubt that the high species richness characteristic of somewhat sheltered beaches is based to a large extent on a high degree of habitat selection along environmental gradients. In strongly exposed beaches climatic predictability is smaller and the meiofauna is poorer in species (70).

In sublittoral sediments the important small-scale gradients are vertical. Variations in exposure to water turbulence, input of organic material, and grain-size distribution (factors that are highly correlated) occur over greater horizontal distances. As previously discussed, these give rise to differences in faunal composition. Diversity is generally higher for the interstitial fauna of sands than for that of noncapillary sediments. This has been directly shown for communities of nematodes. Species numbers are higher in sandy sediments than in silt, and sandy sediments contained more "specialist" species than did silty (65).

The vertical zonation of sublittoral sediments is clearly reflected in the zonation of the fauna. The interpretation of this zonation may be difficult since it reflects preferences for certain chemical factors as well as for certain foods. In a generalized sediment the surface layer is oxidized and the uppermost layer (about 5 mm) sustains photosynthesis by diatoms, dinoflagellates, blue-green bacteria and other organisms. If the anoxic layer is close to the surface, photosynthetic bacteria will also be found here (37). Beneath the oxidized zone are layers characterized by a low oxygen tension and "reduced microniches" (i.e. detrital particles or faecal pellets within which anoxic and reducing conditions prevail). Under this layer again the reducing and completely anoxic sulfide layer is found. The extents of these zones vary according to external factors. In sheltered habitats with a high productivity or input of organic material the anaerobic layer may reach to the surface—at least during the night in the absence of photosynthetic activity. In exposed beaches the oxidized zone may extend several meters down.

The interstitial fauna shows clear and reproducible vertical zonation patterns correlated with the mentioned chemical zonation. Several groups besides the anaerobic fauna already discussed (e.g. the Loxodiidae among the ciliates) are confined to the zone between the aerobic and the anaerobic zones. This transition zone is characterized by a high productivity of bacteria. Other forms are confined to the oxic layer or to the photic surface layer. This has been particularly well documented in the case of ciliates, but similar patterns are also evident for other, metazoan groups (31, 47, 48, 145, 147).

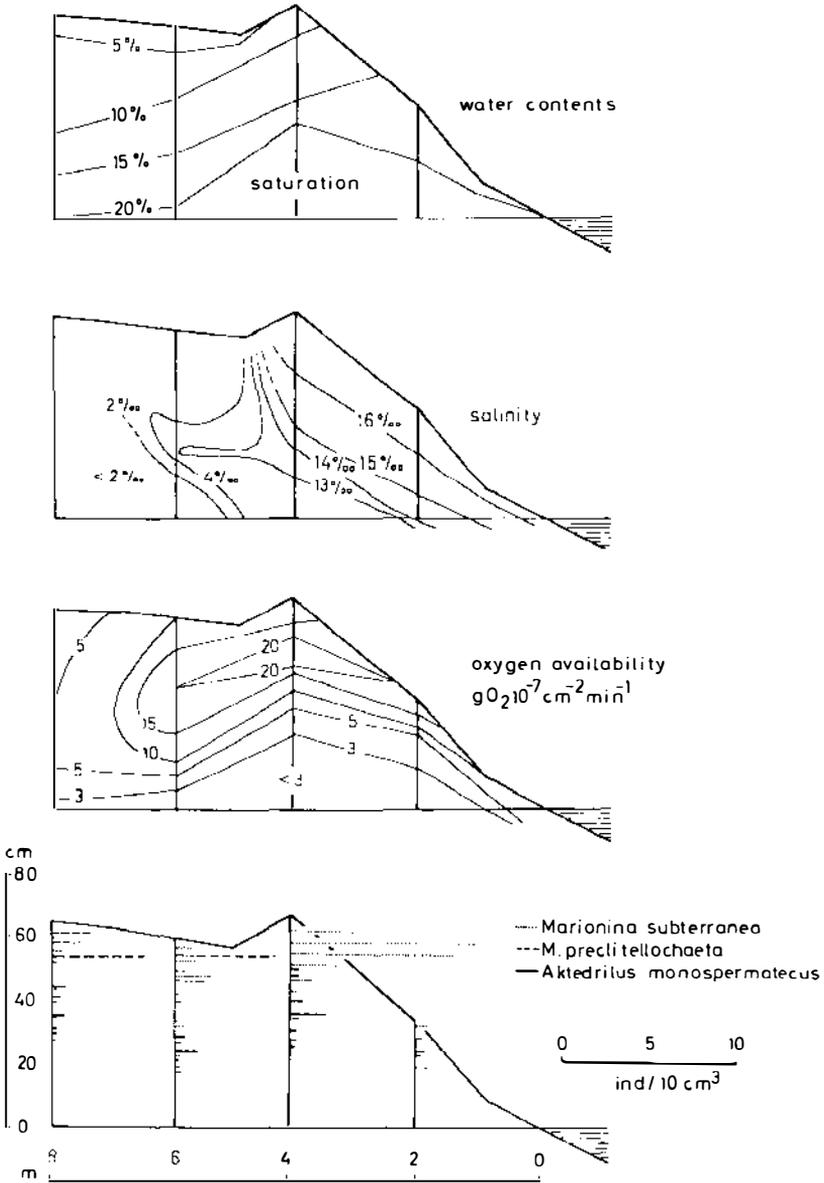


Figure 2 A transect through a sandy beach in northern Oresund, Denmark showing gradients of some environmental factors and the distribution of three related oligochaetes. [Redrawn from (33)]

Time Niches

It was long believed, perhaps due to the low egg production of meiofaunal species, that reproduction took place throughout the year. Consequently, not much attention was given to temporal variations in the faunal composition. Recently, however, more detailed studies based upon field work outside the summer season have revealed the temporal structures of meiofaunal communities. In temperate shallow estuarine communities there is a clear annual pattern in the succession of maximum densities: Copepods are followed by oligochaetes, nematodes, ostracods, and finally turbellarians; there is sometimes a second peak of harpacticoid copepods. This pattern is largely controlled by the increase in photosynthetic production in the spring, the reproductive potential of the different groups, and predation.

The most important predator in these habitats is the coelenterate *Protohydra*, whose maximum density correlates with the beginning of the decline of the harpacticoid and oligochaete populations (61, 127, 133). Similar patterns have been found in other habitats for foraminifera and ciliates: The population sizes of different groups or species vary strongly and predictably during the year, following successional changes of the abundance of certain microalgae or bacteria (31, 92). Communities of nematodes also show distinct annual successional patterns (133, 148). Coexisting harpacticoid copepods show displaced reproductive cycles, which have been related to resource sharing between the species (20, 58, 63).

Food Niches

In contrast to the earlier generalization that this fauna "feeds on detritus and diatoms" [see e.g. (128)], recent studies have revealed distinct and often very specialized food niches in many species of the micro- and meiobenthos. Studies on a large number of species of turbellarians and rotifers (127, 129) show a high degree of food specialization. Species may specialize in diatoms, blue-green bacteria, euglenoid flagellates, etc or in other members of the meiofauna, such as nematodes, oligochaetes, or rotifers. Fenchel (29) assembled information on the food and feeding of 260 species of benthic ciliates. These could be classified according to various kinds of feeding mechanisms: filter feeding, which is rare among interstitial forms; browsing; hunting; scavenging; or attacking injured animals. This diversity corresponds to the diversity of ciliate feeding organelles. Specialists can be found that feed only on items such as purple sulfur bacteria, filamentous white sulfur bacteria, blue-green bacteria, diatoms, and other ciliates. Many species, such as feeders on diatoms or bacteria, also specialize in prey of a certain size. In certain habitats whole guilds of coexisting species were found to subdivide a given resource according to particle size. These findings are in accordance with the theory of limiting similarity—i.e. equal distances between the niche modes (the optimum food particle size) and with niches displaced by about one standard deviation. This was found for four species of the genus *Remanella* coexisting in the deeper part of the sediment and also in a guild of less closely related ciliates living in the surface sediments in an estuarine environment (15, 29; see also Figure 3). Nematodes may also show a high degree of food specialization (136, 137), a fact which correlates with mouth morphology (137, 142). The

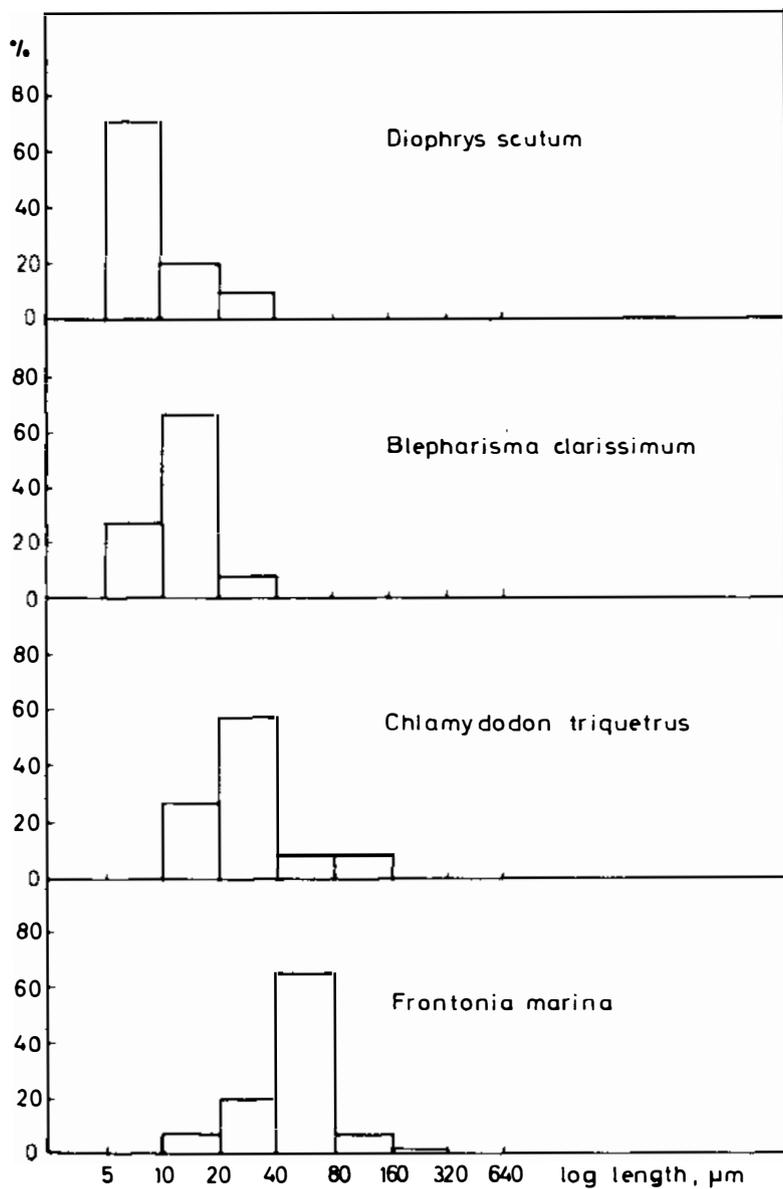


Figure 3 The size distributions of diatoms ingested by four species of ciliates coexisting in the surface layers of estuarine sediments. [Data from (29)]

use of mouthpart morphology in harpacticoids as a measure of food specialization (71) has recently been attempted. Evidence from other groups such as oligochaetes and foraminiferans (49, 85, 86) has given additional evidence of the importance of food selectivity for the understanding of meiobenthic communities.

DISTRIBUTION, DISPERSAL, AND SPECIATION

Large-Scale Geographical Variation in Diversity

One of the most striking of zoogeographical patterns is the "latitudinal diversity gradient": Within most major taxonomic groups the number of species increases with decreasing latitude. While evident for the littoral and sublittoral macrofauna (121), this trend seems to be less pronounced and may be absent in the case of the meio- and microfauna. Gerlach (40) studied the beach meiofauna in the intertidal zone of the arctic Svalbard Islands and found it very rich compared to the impoverished macrofauna. More recent studies of the meiofauna in lower latitudes do not indicate a species richness much higher than that known from temperate localities. It is, however, difficult to obtain a clear picture. The temperate meiofauna is still by far the best known, and the difference in species richness between different, closely situated habitats is quite high. It can, however, be postulated that the unpredictability in physical factors and in food resource availability that is characteristic of higher latitudes and that gives rise there to greater niche widths, higher extinction rates, and thus a lower number of coexisting species, may be less important for the meiofauna than for the macrofauna. The interstitial fauna within a sandy beach lives in a relatively protected habitat where the environmental factors characteristic of the arctic intertidal (changing salinity, ice scouring) are less extreme. The food chains of the meiofauna are to a large extent based on the microbial decomposition of slowly degradable detrital particles derived from macrophytes—a less seasonal source than, for example, phytoplankton production.

There is a clear difference in species richness between the macro- and the meiofauna of brackish water. There are far fewer macrofauna species in the Baltic Sea, which has a low, constant salinity of 6–7‰, than in the surrounding Inner Danish Waters and the North Sea, which are more saline (114). Within the meiofauna, some taxonomic groups are absent in the Baltic; however, there is no obvious overall reduction in species richness. This difference between the macro- and the meiobenthos is easily explained. The modern Baltic Sea is of very recent origin (about 3000 years). The macrofauna is made up of a few freshwater species, but mainly of estuarine, euryhaline species that can tolerate low salinity and that have colonized the Baltic from the surrounding seas. Such an estuarine fauna is relatively poor in species because its habitats are widely scattered and small. On the other hand, a very species-rich, true brackish-water meiofauna exists. The reason for this is not only that estuaries can harbor larger population sizes of meiofauna and thus also a higher species numbers but also that a brackish-water meiofauna develops in the coastal ground water along all marine coasts. Therefore, there existed a very large pool of species that could invade the Baltic when it developed as a brackish-water sea.

Zoogeography and Speciation

Only recently have zoogeographic patterns emerged from meiofauna studies. Due in part to the fact that until recently only European and North American coasts had been studied in detail, the meiofauna was long believed to be cosmopolitan. Also, descriptions of species have not always been adequate and have often been based on "soft" characteristics. Permanent preparations are often difficult to make and there are often no type specimens. Consequently it has been difficult to discuss large-scale distribution patterns on the basis of the existing evidence.

It is now evident that meiofauna species do not always have a cosmopolitan distribution. For example, Coull & Herman (19) demonstrated several faunal provinces for meiofaunal copepods and showed that different representatives of the same genera formed "parallel communities" in similar habitats in different parts of the world. Sterrer (125) has provided a thorough discussion of the zoogeography of the meiofauna based on the literature and on his own studies of gnathostomulids. He found that although several meiofauna species seem to have a cosmopolitan distribution, in some cases this impression may be due to inadequate morphological criteria for the distinction between species. There are a number of examples of allopatric distribution of species belonging to the same genus. The mystacocariid genus *Dereilocharis* has been found in coastal sands of Europe, North and South America, and Africa. It comprises several species; but with the exception of the Mediterranean coast of Israel where two species coexist (91), the different species never overlap, and this distribution pattern can probably be explained as the result of allopatric speciation maintained by competitive exclusion. Within the Gnathostomulida there are many genera but no species in common between the east and the west side of the Atlantic Ocean. A similar pattern can be found in many turbellarian families.

Ax & Schmidt (8) studied the interstitial fauna of the Galapagos Islands. Among the turbellarians, gnathostomulids, nemerteans, gastrotrichs, archiannelids, polychaetes, and tardigrades, between 50 and 100% of the species, but practically none of the genera, are endemic. The authors took this as a measure of the rate of meiofauna speciation on these isolated islands believed to be about 2 million years old.

Thus it can be concluded that the meiofauna shows a large-scale zoogeographic pattern on the specific level, whereas most genera are cosmopolitan. Sterrer (125) interprets his findings on gnathostomulids from the two sides of the Atlantic as the result of the isolation of littoral faunas following the opening of the Atlantic Ocean during the Triassic period some 200 million years ago. However, comparison with the much younger Galapagos Islands, which seem to harbor an equally or even more differentiated meiofauna, would indicate that the isolation between the meiofauna on both sides of the Atlantic is not complete.

Any discussion of these findings—for example, of whether they indicate a slow rate of speciation—must take the possibilities of dispersal into account. This has most recently been discussed by Gerlach (43). With very few exceptions, the meiofauna has no planktonic larval stages. Dispersal along coastlines due to the animals'

own movements or through current-driven transport of sediment must, of course, take place. However, small suitable stretches of coastline isolated by long stretches of unsuitable coastline and isolated islands also harbor rich littoral meiofaunas. The general absence of cysts or desiccation-resistant eggs should minimize aerial transport by seabirds, for which there is in fact little direct evidence. (In Northern Germany, some inland saline waters formed during salt mining have been found to contain representatives of a marine meiofauna; this can only be explained by aerial transport.) There is evidence that drifting materials (algae, coconuts, driftwood) contain sediment; objects that must have been floating in the ocean for a long period of time harbored several species of benthic meiofauna species. Gerlach (43) concludes that although long-distance (transoceanic) dispersal in this way may not be a frequent event it will consistently take place over long periods. In the light of this evidence, the zoogeographic distribution of the meiofauna as we know it (some cosmopolitan species, some species endemic to the coasts of continents or to oceanic islands, and practically no endemic genera) must be interpreted as the dynamic balance between speciation and dispersal in conjunction with competitive exclusion. There is no reason to infer, as does Sterrer (125), that meiofauna dispersal is low and that the process of speciation is slower among the meiofauna than among macrofauna species.

With respect to the protozoan microfauna (excluding foraminifera), all the evidence based on morphological criteria points to a cosmopolitan distribution [for ciliates, see for example (16, 31)]. However, the previously mentioned precautions with respect to the interpretation of existing fauna lists also apply here, and further studies may well reveal some endemisms.

The Origin of Freshwater and Soil Fauna

The existence of an uninterrupted habitat for interstitial fauna from the sandy littoral through coastal groundwater to the subterranean groundwater, may explain the origin of at least several elements of the freshwater and soil fauna (e.g. nematodes, turbellarians, annelids, harpacticoids, amphipods, gastrotrichs). The coastal groundwater contains a large number of brackish-water or euryhaline forms of marine origin. Many representatives of the subterranean fauna (and cave fauna) have very close marine relatives and must have descended from forms that have relatively recently colonized the nonmarine habitats (114).

THE CARBON FLOW THROUGH THE MEIO- AND MICROBENTHOS

The base of the food chains that support benthic animals can be divided into three categories. Material suspended in the water over the sediments (phyto-, zoo-, and bacterio-plankton) is utilized by the filter-feeding macrofauna but must play a negligible role for the meio- and microbenthos except where large water masses are filtered through sand (e.g. the splash zone of beaches). Another food source is the benthic microalgae (diatoms, phytoflagellates). The third is the bacterial production

based on dissolved or particulate dead organic matter (detritus). The conversion of this material into a bacterial biomass accessible to the fauna may be complex and may involve several different metabolic types of bacteria (34). The bacteria are utilized by the "detritus-feeding" macrofauna. These resources also support the meio- and microbenthos. The representatives of the latter form complex food webs, and a species population may belong to one or several trophic levels. However, one may still ask how much of the carbon from the above-mentioned sources flows through the meio- and microbenthos, and how this flow compares to that through the macrofauna.

Several studies [e.g. (28, 31, 41, 42, 53, 93, 94, 132, 133) and papers cited therein] have explored the quantitative importance (by numbers and weight per unit area) of the micro- and meiobenthos and compared it with that of the macrofauna. In spite of the technical problems involved in the enumeration of small benthic animals, a fairly consistent and reliable picture has emerged. A large range of sublittoral sandy sediments with more or less silt yields between 200 and 10,000 individuals m^{-2} of macrofauna, which corresponds to a wet weight of 10–300 $g m^{-2}$. The values for the meiofauna are 10^5 – 10^6 individuals m^{-2} , and 0.2–5 $g m^{-2}$, to which the nematodes typically contribute by more than 50%. The number of ciliates found is usually between 10^6 and $5 \times 10^7 m^{-2}$, which corresponds to between 0.1 and 2 $g m^{-2}$. In estuarine sediments, numbers are usually higher for all categories but the meiofauna may be relatively more important; this is also the case in sandy beaches. In the deep sea the number of individuals in the macrofauna is reduced more than that in the meiofauna, so that here the two biomasses are about the same.

The figures do not directly reveal the importance of meiobenthos in the carbon flow. It is well known that the metabolic rate per unit weight of animals of various sizes can be compared by means of the power function $M = aW^{b-1}$, where M and W are the metabolic rate per unit weight and the body weight, respectively, and where a and b are constants, the latter taking the value 0.75. Thus the metabolic rate per unit weight increases by a factor of about 1.77 for a reduction in body weight by a factor of 10. Using this relationship and supported by measurements of the metabolic rates of individual species, some authors have attempted to estimate the energetic significance of the meiobenthos. Gerlach (41, 42) found that the meiobenthos has an average metabolic rate about 5 times higher per unit weight than that of the macrofauna. He concluded that on a silty, sublittoral sandbottom, the carbon metabolized by the metazoan meiofauna is about 15% that of the macrofauna. Using the quantitative data of Fenchel (31), Vernberg & Coull (140) estimated the ratio of the metabolic activities of ciliates to metazoan meiofauna to macrofauna as follows: 1:0.5:2.1 for a sandy, sublittoral sediment; 1:3.4:1.9 for an estuarine sediment; and 1:0.54:0.04 for an exposed beach (where the metabolic rate of the ciliates has arbitrarily been assigned the value of unity). Another approach has been to compare the reproductive potentials of the different groups in order to give a picture of the turnover of the populations (30, 46, 62, 64, 138). Much like the metabolic rate, the reproductive potential of animals tends to increase with decreasing body size. In both cases there is a large variance in the data, in particular when varying environmental conditions are taken into account.

In any case, crude estimates do show that a considerable part of the animal production of the sea bottom is due to the meio- and microbenthos. It would, therefore, be of interest to consider the importance of the micro- and meiobenthos as food for the macrofauna. Information on this is still scattered and largely anecdotal, and some authors (49) have suggested that the meiofauna largely represent a final link in the food chains. One reason for this impression may be that the remains of most micro- and meiobenthic species are hard to detect in the gut contents of animals. Detritus- and sediment-ingesting animals may consume considerable quantities of this fauna. It certainly comprises a larger portion of the biomass per unit volume of sediment than do the bacteria that are usually stressed as the food of detritus feeders (34). A detailed study of the shrimp *Crangon* has shown that it is capable of extracting nematodes from sand and of growing, albeit slowly, on this diet alone (45). The importance of the meiofauna as food for juvenile fish and for crustaceans that migrate into estuaries during summer has also been demonstrated (98).

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