

Chapter 2

The Biotope: Factors and Study Methods

2.1 Abiotic Factors (Sediment Physiography)

2.1.1 *Sediment Pores and Particles*

When describing the habitats of meiofauna, grain size is a key factor since it directly determines spatial and structural conditions and indirectly determines the physical and chemical milieu of the sediment. Poorly sorted sediment particles (e.g., sand mixed with gravel and silt) become tightly packed and the interstitial pore volume is often reduced to only 20% of the total volume. Well-sorted (coarse) sediments contain up to 45% pore volume. According to Ruttner-Kolisko (1962), most field samples of unsorted freshwater sand have 40% pore volume.

Aside from pore volume, the external surface area of the sediment particles is an important determinant of meiobenthic life. It directly defines the area available for the establishment of biofilms (mucus secretions of bacteria, fungi, diatoms, fauna), which, under natural conditions, form the matrix into which the sediment particles are embedded. Thus, particle surface is an important parameter for microscopic animal life. This internal surface is unbelievably large: for a 1-m³ stream gravel it has been calculated to amount to about 400 m². One gram of dry fine sand with a median particle diameter of 63–300 µm may have a total surface area of 8–12.5 m²; if it consists mostly of diatom shells, this value can even exceed 20 m², whereas for 1 g of coarse-grained calcareous sand a value of just 1.8 m² was calculated (Suess 1973; Mayer and Rossi 1982).

In addition to size, the grain shape also determines the sorting of the sediment. Angular, splintery particles are packed tighter than spherical ones. A higher angularity leads to more structural complexity, less water permeability and usually higher abundance of meiofauna (Fig. 2.1; see Conrad 1976). A direct correlation between pore dimensions and body size of meiofaunal animals has been demonstrated experimentally (Williams 1972). In general, mesobenthic species moving between the sand grains prefer coarse sands, while endo- and epibenthic ones are

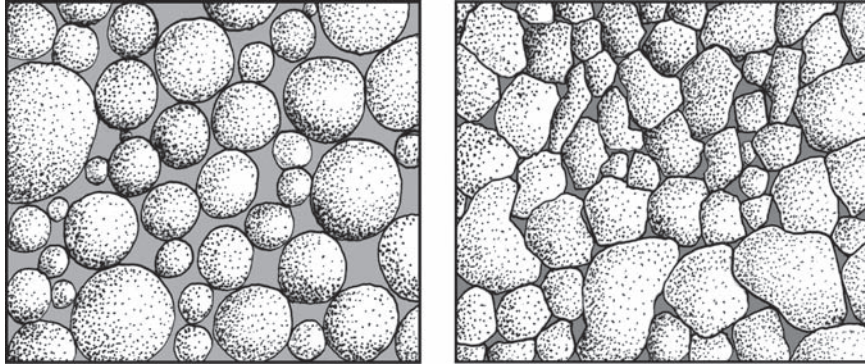
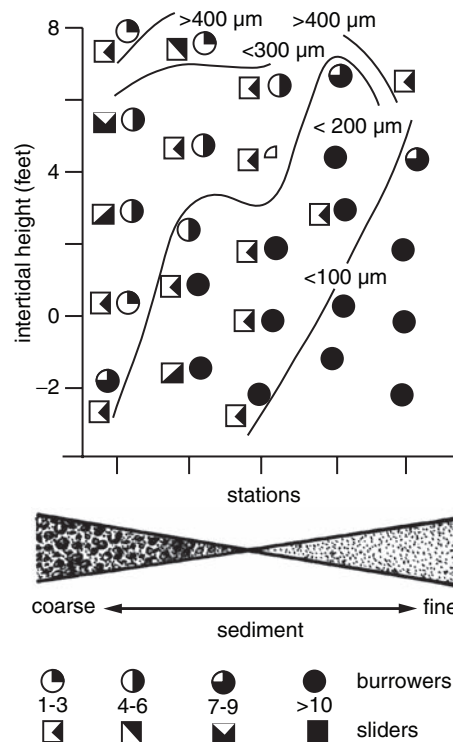


Fig. 2.1 The pore system in sediments consisting of grains with a round shape (glass beads; *left*) vs. natural grains of angular shape (*right*); note differences in pore space due to different packing. (After Conrad 1976; modified)

mostly encountered in fine to silty sediments. These sediment differences affect the two major groups of meiobenthos, nematodes and harpacticoids. The finer sediments are preferred by most nematodes, while coarser ones are often favored by harpacticoids (Coull 1985). Within the nematode taxon, the preference for a specific grain size was found to relate to certain ecological types (Wieser 1959a). “Sliders” live in the wide voids of coarse sand; below a critical median grain size of about 200 μm , the interstices become too narrow. Thus, fine sand and mud will be populated by “burrowers” (Fig. 2.2). The particle shape determines the colonization of the sediment by meiofauna through indirect action via water content and by permeability (Sect. 2.1.3).

The colonization of sand by meiobenthos is also determined by the grain structure, the roughness of edges, and the shapes of grain surfaces and cracks. These are important parameters that structure the microhabitats of different bacterial colonies (Meadows and Anderson 1966). Sand grains with diameters of $>300 \mu\text{m}$ frequently have more plain surfaces than smaller particles; they also have a different bacterial epigrowth. This diversification has been shown to attract different meiofauna (Marcotte 1986a, Watling 1988). Likewise, in comparative experiments, cores of different grain sizes have been colonized by different meiobenthos. This emphasizes the capacity of meiofaunal species to choose and “recognize” their preferred sediment (Boaden 1962; Gray 1965; Hadl et al. 1970; Vanreusel 1991). Although the direct structural impact of the sediment particles is mostly confounded by other factors, e.g., biofilms, water flow, etc. (see Table 2 in Snelgrove and Butman 1994), there are strong affinities of specific meiofauna for specific sediments (Schratzberger et al. 2004). The structure and dimensions of the pore system are also directly correlated with the anatomy of the inhabitants and the functions of their organs (Ax 1966; Lombardi and Ruppert 1982).

Fig. 2.2 Distribution pattern of meiofaunal locomotory groups in the intertidal of a sandy shore. Black areas in circles or squares relate to the number of species per sample (250 cm³) that belong to the same locomotor type; lines indicate areas of identical median grain size. (After Wieser 1959)



2.1.2 Granulometric Characteristics

2.1.2.1 Grain Size Composition

Grain size analysis is fundamental to all ecological aspects of meiobenthic work. Although the fractionation of the sediment into different size groups does not reflect the natural composition, it provides a basis for reference and an important comparative framework. Techniques of sediment analysis are well covered in Bale and Kenny (2005); only some additional practical hints are presented here. Granulometry is usually based on the rather tedious procedure of the fractionated sieving of a sufficiently large sample. Recently sieving has been replaced by electronic procedures (modified Coulter counters, laser diffraction counters) with higher accuracy and throughput. Inherent inaccuracies with sieving (underrepresentation in the finer fractions) are based on effects of the adhesion of particles to the mesh fibers (Logan 1993). Salt-containing marine samples are mostly wet sieved, especially when fecal pellets consolidate fine sediment. However, the faster technique of dry sieving is often preferred (80 °C, 24 h) and is sufficiently accurate if agglutination

is avoided and the salt content of the sample is corrected for. The inaccuracies involved in these procedures are acceptable for most ecological questions. The silt-clay fraction (“mud content”) passing through the 63- μm or 44- μm sieve is an important ecological parameter that determines the biological and mechanical properties of the sediment, but is usually not differentiated any further. After sieving, its proportion is determined by the loss of weight. However, it can be refined by performing a fractionated analysis of the settling velocity using elaborate soil science methods.

The mesh sizes of the sieve set usually follow a geometric series (Wentworth scale) with 1.0 or 0.5 ϕ (phi) intervals, where $\phi = \frac{-\log x}{\log 2}$ with x = particle size in mm (Wentworth 1922; Krumbein 1939). Commonly for meiofaunal studies a series of sieves are used with mesh sizes (mm) 1.0/0.5/0.25/0.125/0.063/0.044 (= 0/ + 1.0/ + 2.0/ + 3.0/ + 4.0/ + 4.5 ϕ units). Very small meiofauna (e.g., some nematodes) would even pass through the 0.044-mm sieve and can only be quantitatively retained using a 0.031- μm sieve (= + 5.0 ϕ). Some animals with a smaller diameter than the mesh width are always retained lengthwise on the screen despite the wide meshes. A correction factor has been calculated to account for this inaccuracy (Tseitlin et al. 2001). With the increasing use of electro-optical devices this problem is has reduced in importance. Electronic calculations and illustrations of particle size mean that the ϕ notation is losing relevance.

The simple process of sieving has some pitfalls that can render the procedure needlessly tedious or misleading:

- (a) It is important to weigh the whole sample as soon as possible to ensure the correct determinations of water content and salinity (see below). If this treatment is not possible shortly after sampling, care must be taken to keep the fresh core in a tight bag to minimize the outflow of water and evaporation.
- (b) Massive shaking of water-unsaturated cores during transport (e.g., due to motor vibrations on boats!) should be avoided because this can alter sediment structure and water saturation considerably.
- (c) If a sediment core contains a few coarse pebbles or shells in otherwise relatively homogeneous and fine sediment, these should be removed. Since calculations of character indices depend solely on weight, one or two massive particles can completely change the granulometric curve without having a relevant impact on the meiofauna. I believe that this alteration of conditions is justified in biological studies, provided that the manipulation is mentioned in the text.

Block histograms or ternary diagrams (triangular coordinates) are the usual methods used to illustrate particle size distribution (Krumbein 1939; Gray 1981; Bale and Kenny 2005). The relevant granulometric parameters can be computer-calculated using specific software (e.g., Gradistat; Blott and Pye 2001) or calculated by simple mathematical methods: the fractions are computed as cumulative percentages starting with the coarsest fraction. These values are listed for further mathematical treatment or plotted as cumulative frequency curves (Fig. 2.3). It is apparent

that the use of the ϕ notation (abscissa) has the advantage of giving relatively more detailed information on the important finer particles, and it also produces equidistant intervals that are relevant for the assessment of the following important statistical indices.

The grain size composition of a sample is characterized by a few statistical parameters (see Table 2.3 in Bale and Kenny 2005) which can be read directly from the diagram or calculated. These include the median (Md) and the first (Q_1) and the third (Q_3) quartiles. The Md value corresponds to the 50% point of the cumulative scale (ϕ 50), Q_1 to ϕ 25 and Q_3 to ϕ 75. These values indicate the average grain size and the spread (scatter) of the grain size fractions towards both ends. The spread distance is defined by the sorting coefficient and conveniently expressed by the

$$\text{Quartile Deviation } QD_{\phi} = \frac{\phi_{25} - \phi_{75}}{2}.$$

A homogeneous sediment with a small QD enclosing only a few phi-intervals between the quartiles is regarded as “well sorted” (Table 2.1). An ideally sorted sediment would consist just of one grain fraction and would thus have $QD = 0$.

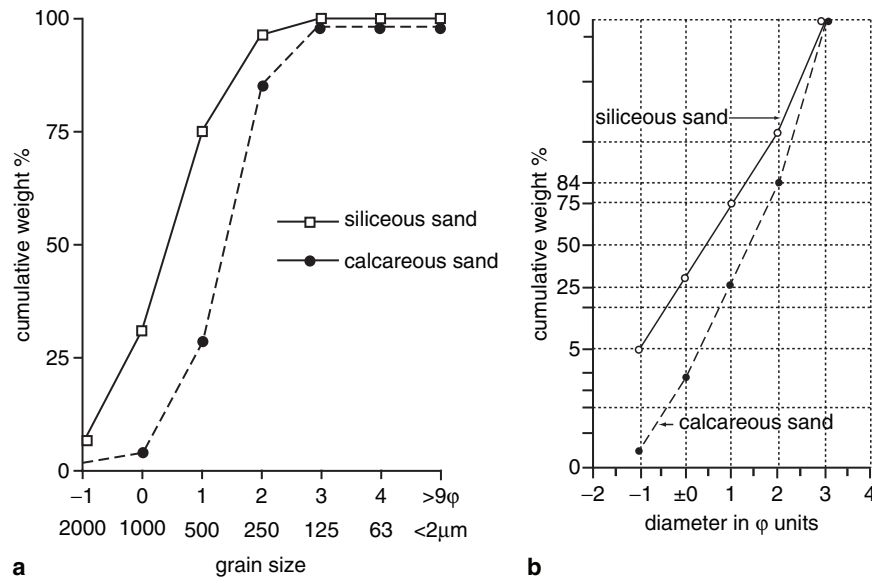


Fig. 2.3 a–b Granulometric analysis of two exposed Atlantic beaches. *Open squares*, Portugal; *solid circles*, Bermuda. **a** Cumulative frequency curves. **b** The same granulometric data plotted on probability paper

Table 2.1 Sediment sorting classes (Gray 1981)

Sorting class [ϕ]	Classification of sediment
<0.35	Very well sorted
0.35–0.50	Well sorted
0.50–0.71	Moderately well sorted
0.71–1.00	Moderately sorted
1.00–2.00	Poorly sorted
2.00–4.00	Very poorly sorted
>4.00	Extremely poorly sorted

The frequency curve will only attain a sigmoid shape if the sediment fractions tend to follow a normal distribution. However, it will become “skewed,” i.e., it will have an asymmetrical slope when certain fractions are over- or underrepresented. The degree of curve symmetry is measured by the

$$\phi \text{ Quartile Skewness: } Sk_{\phi} = \frac{(\phi Q1 + \phi Q3)}{2} - \phi Md.$$

The above indices are based only on very few ϕ values, and they tend to neglect the “tails” of the curve. More precise computations comprise a wider portion of the fraction, i.e., the mean,

$$M = \frac{(\phi 25 + \phi 75)}{2}$$

$$\text{the “graphic mean” } M_z = \frac{(\phi 16 + \phi 50 + \phi 84)}{3}$$

the “inclusive quartile deviation or “inclusive sorting coefficient:”

$$QD_1 = \frac{\phi 84 - \phi 16}{4} + \frac{\phi 95 - \phi 5}{6.6},$$

$$\text{or the “inclusive graphic skewness:” } Sk_1 = \frac{\phi 16 + \phi 84 - 2\phi 50}{2(\phi 84 - \phi 16)},$$

From the grain size composition analyzed above and plotted as curves in Fig. 2.3a,b, the characteristic granulometric values can be derived (Table 2.2).

All granulometric indices (e.g., the values for the median or quartiles) can also be computed mathematically (Hartwig 1973b) from the listed size frequencies by interpolation or by using computer software. In biological papers it is more illustrative to convert ϕ values into metric units. The use of a conversion chart (Page 1955; Fig. 3.2 in Buchanan 1971) or computer software is often recommended, although calculation is just as easy. The calculation of ϕ from x [mm]: $-\log x / \log 2$; calculation of x [mm] from ϕ : $x[\text{mm}] = 2^{-\phi}$.

Table 2.2 Characteristic granulometric indices for the sediment samples plotted in Fig. 2.3a,b

Granulometric index	Siliceous sand from Portugal	Calcareous sand from Bermuda
Median, Md	0.4 ϕ = 740 μm	1.3 ϕ = 410 μm
Lower quartile, Q_1	-0.2 ϕ = 1140 μm	0.9 ϕ = 528 μm
Upper quartile, Q_3	1.0 ϕ = 500 μm	1.8 ϕ = 285 μm
Inclusive sorting coefficient, QD_1	0.93 = moderately sorted	0.74 = moderately sorted
Inclusive graphic skewness, Sk_1	0.003	-0.089

The occurrence of certain sediment types varies depending on the local geological and physiographical conditions. In temperate and boreal regions siliceous sands prevail, while in the warmer regions and on seamounts inhomogeneous biogenic calcareous sediments with more complex surface structures dominate (see Sect. 8.2). Black basalt and lava sand can often be found in volcanic areas. The deep sea floor is usually muddy and fluffy (unconsolidated), often consisting of foraminiferan (mostly calcareous) or radiolarian (mostly siliceous) skeletons. In shallow seas, offshore bottoms will usually consist of medium sand while nearer to the shore currents attenuate and will allow fine sand and mud to settle. In areas where ripple marks indicate strong currents, crests contain coarser sediments than troughs, where fine sand and often flocculent surface layers with a higher content of organic material tend to accumulate. The fine sediment in seagrass beds, where currents are

Box 2.1 To See a World in a Grain of Sand

The size, shape and composition of sediment particles interact via the water flux with the physical and chemical regime of the sediment, the exposure to currents and waves as well as the general geological setting. In this network of abiotic factors that influence the habitat of meiobenthos, grain size plays a dominant role and can serve as the integrative key factor that characterizes the habitat of meiobenthos. Although we now know that communities and zones are not defined only by grain size composition, and that the differentiating factors are instead chemically and biologically controlled, granulometry remains an important foundation. Angular grains are packed tighter than round ones, but splintery, uneven surfaces are better for microbe colonization. Sediments with smaller grains offer less interstitial space and are preferred by different meiofaunal species to those in coarser sands. In general, the void system of sediments accounts for 20–45% of the total sediment volume. Careful granulometry should form the basis for every benthic ecological study. Modern data processing programs enable the relevant granulometric parameters, such as median, mean, quartiles, sorting coefficient and kurtosis, to be calculated automatically. These describe the granulometric basis for the living conditions of the biota and allow for abiotic structural comparisons.

weak, is enriched with leaf detritus. Near the shoreline the sediment structure may vary rapidly due to irregular water agitation, sedimentation and resuspension of shore vegetation and wrack material. These various sediment structures all represent different microhabitats for meiobenthic animals (Eckman 1979; Hogue and Miller 1981; Hicks 1989).

2.1.3 The Sediment–Water Regime

2.1.3.1 Exposure, Sediment Agitation, and Erosion

Largely determined by the impacts of waves and currents, the exposure of a habitat is of eminent importance for the agitation and sorting of sediment particles, the flow of sediment water and fluxes of nutrients. Current velocity, sediment agitation and sorting interact in a complex way with the weights and surface structures of the particles and determine particle deposition and packing. These factors, in combination, control the “exposure” of a site, but a direct measurement of exposure is too complicated mathematically and instrumentally to be used by most biologists. Thomas (1986) and Hummon (1989) estimated the exposures of sandy shores from a fetch-energy index which was calculated using wave height and shoreline configuration, parameters which can be extrapolated from maps and data sheets. Eleftheriou and Nicholson (1975), on the basis of granulometry, discriminated exposed beaches from sheltered and semi-exposed ones via a critical median grain size of 230 μm . McLachlan (1980, 1989) attempted to create a general rating system for beaches based on a set of parameters including the height of the incoming waves. Muus (1968) and Doty (1971) related exposure to the weight loss of plaster test blocks distributed in/on the sediment. The dissolution of calcium sulfate was considered to be proportional to the velocity of the surrounding water currents, thus reflecting the exposure of the habitat. Similarly, Craik (1980) tried to derive the relative degree of (massive) exposure from the long-term scouring of cement blocks. Valesini et al. (2003) based their assessment of exposure on a set of seven quantitative environmental variables (e.g., fetch, steepness of shore, width of beach), which they analyzed using multivariate statistics, and classified several groups of beaches. However, in practice and in studies dealing with heterogeneous sites and topics, this computer-based grouping appears rather complex. Exposure remains a more or less summative often even subjective factor. Hence, benthologists are well advised to include a significant amount of comparative experience when deriving any measurements of the rate of exposure.

Current velocity is not directly proportional to agitation and erosion. Turbulent water currents reduce particle suspension (McNair et al. 1997); particles with a diameter of approximately 180 μm are most easily eroded (Sanders 1958). A threshold of around 200 μm , earlier defined as a “critical grain size” for the occurrence of many animals (see Sect. 2.1.1), is of prime importance for the water contents of sediments. The lower average grain size threshold for the existence of an interstitial

assemblage is often reported to be 150 μm . In freshwater sediments, 250 μm has been considered the size limit for the circulation of interstitial water (Rutter–Kolisko 1961).

Neither tightly packed silt nor permanently agitated coarse sand offer favorable conditions for most meiofauna. In the rigid hydrographic regime of a North Sea estuary, increasing tidal ranges and current surges reduced nematode diversity in the sediment, while the biomasses of many species increased (Smol et al. 1994). Most but not all meiofauna react to strong currents and water surges by attempting to escape through downward migration (Steyaert et al. 2001; Sedlacek and Thistle 2006). Avoidance reactions of meiofauna to increasing currents and wave action, e.g., tidal wave fronts and concomitant vibrations of the sediment, have been documented and studied in experiments (Fig. 2.4; McLachlan et al. 1977; Meineke and Westheide 1979; Foy and Thistle 1991). Specialized species only will occur deep in the muds of sheltered flats or in the swash zones of exposed beaches (Menn 2002a, Gheskiere et al. 2005). Massive agitation of the sediment by storms apparently destroys the less agile meiofaunal groups.

The erosion, shear strength and settling velocity of the sediment are not just influenced by abiotic factors. Biogenic factors such as the reworking of the sediment by intensive burrowing and pelletization as a result of defecation contribute considerably to the physical and biological properties of the sediments. Fecal pellets covering the bottom surface, especially in tidal flats, may reduce sediment shear strength and enhance erodibility by water currents, but they also tend to increase settlement velocity (Rhoads et al. 1977; Andersen and Pejrup 2002). Protruding tubes and plant culms may cause water turbulences and erosive forces, sometimes with negative impact on meiofauna (Coull and Palmer 1984; Hicks 1989). Agglutination by mucus (produced by bacteria, microphytobenthos and

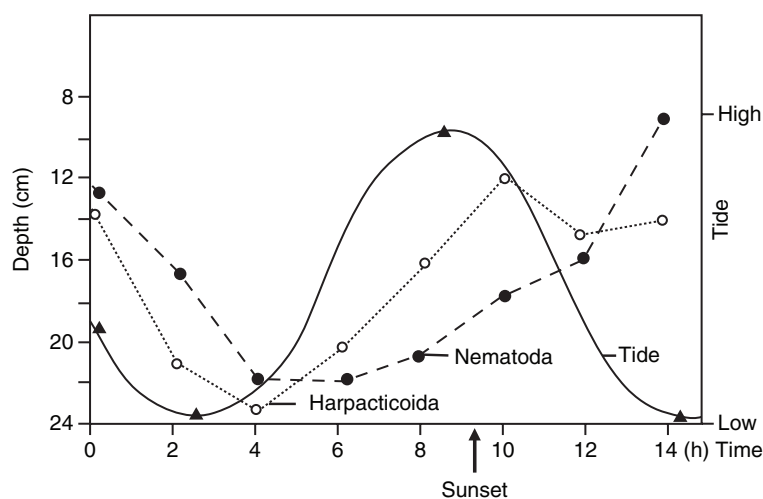


Fig. 2.4 Migration of beach meiofauna in relation to the tidal cycle. (McLachlan et al. 1977)

animals) as well as compaction in tube walls by small infauna will solidify the texture, increase sediment stability and diminish resuspension (Rhoads et al. 1978; Luckenbach 1986; Meadows and Tait, 1989; Decho 1990; Miller et al. 1996, Wiltshire 2000). When diatom populations became massively reduced by browsing so as to lower their mucus production, the shear strength and sediment cohesion decreased. There is a complex and dynamic correlation between the “biostabilizers” (mainly diatoms) and the “biodestabilizers” (mainly bivalves and polychaetes), between the “biosuspenders” (deposit feeders) and “bioirrigators” (tubicolous annelids and crustaceans) (Graf and Rosenberg 1997; Widdows et al. 2002; Meysman et al. 2006b).

2.1.3.2 Permeability, Pore Water Flow, Porosity, and Bioturbation

Permeability. Permeability denotes the potential speed of water flowing through the sediment (volume of water flow per time, $\text{cm}^3 \times \text{s}^{-1}$); in freshwater biology permeability is appropriately termed the “hydraulic conductivity.” It is calculated using a permeameter (see Fig. 5.4 in Giere et al. 1988). Directly influenced by the absolute size of the sand grains, it decreases as the proportion of small particles increases, especially those below 200 μm in diameter. The configurations of the individual pores and the structure and coherence of the void system all exert considerable influence on the permeability of the sediment, but permeability is not directly related to porosity (see below). Since water flow determines most chemical and physical factors in the sediment via the exchange rates of interstitial and supernatant water, permeability is responsible for supplying oxygen and dissolved and particulate nutrients, and so it largely controls the life conditions of meiofauna.

Nutrient fluxes caused by pore water drainage through the tides easily exceed diffusive or bioirrigative fluxes (Billerbek et al. 2006). In exposed sandy beaches, the “tidal pump” creates a “stormy interstitial,” exposing the interstitial animals to high flow velocities. In near-surface layers, the wave-induced advective transport of pore water ($>40 \text{ cm} \times \text{h}^{-1}$) exceeded diffusive transport by at least three orders of magnitude (Precht and Huettel 2003). Each lengthwise beach meter is percolated by several cubic meters of seawater each day. The yearly volume of the global shelf filtered (the “subtidal pump”) by the forces of percolation far exceeds the precipitation volume on land (Riedl and Machan 1972; Riedl et al. 1972). Berelson et al. (1999) calculated that within two hundred days the entire water column of Port Phillip Bay, Melbourne (Australia) passes through the sediment. In a tidal beach, 1 m^2 of coarse sand filtered 14 L of water each hour (Rusch and Huettel 2000), a value also confirmed for Mediterranean shores (Precht and Huettel 2004). Even the small-scale topography of sandy bottoms massively influences advective water flux and particle transport. On the exposed sides of sediment mounds or ripple marks, surface water and organic particles penetrated about seven times deeper into the sediment than on the sheltered sides (Ziebis et al 1996; Huettel and Rusch 2000). The small-scale topography also directs the water flow, with intrusion occurring mainly in the ripple troughs and release occurring after filtration at the crests (Precht and Huettel 2004).

The pore water velocity was first assessed by inserting heated thermistors into the sediment (Riedl and Machan 1972); microflowmeters based on minute thermistors were later used by researchers (LaBarbera and Vogel 1976; Davey et al. 1990). The cooling effect of the currents on a heated wire produces a voltage signal on a monitor, which, after calibration, indicates the microflow of water. Similarly, changes in the potential of a platinum wire used to measure the oxygen diffusion rate in sediments can be calibrated to record water microflows. Malan and McLachlan (1991) measured the pumping effects of waves and emphasized that most authors have underestimated wave-induced sediment water fluxes and their impact on the oxygen distribution. Long-term in situ records with oxygen microelectrodes have also indicated strong tide- and wave-dependent water pressure gradients (Weber et al. 2007). Precht and Huettel (2004) visualized the pore water flow in the field by applying fluorescent dye to the sediment and measuring it with an optical sensor (optode, see Sect. 2.1.4).

Porosity. The total pore volume of a sediment core, its porosity or void ratio, depends in a complex way on the shape, sorting and mixing of the particles, and not just on the pore size available to the animals. Thus, it is not directly predictable from sieving data alone, but it is, of course, of relevance for physicochemical fluxes in the sediment. For mechanical measurements of porosity see Buchanan (1984) or Bale and Kenny (2005). Porosity profiles can also be calculated using electrodes, by measuring the resistivity of the sediment lattice (Archer et al. 1989).

The velocity of the pore water flowing through the interstitial system does not depend solely on the hydrodynamics of the overlying water. The fluxes in the chemical milieu of sediments are strongly influenced by the sediment texture (see below). This, in turn, is controlled by bioturbation, sediment reworking, bioirrigation, and mucilage secretion of the benthic fauna (Graf and Rosenberg 1997; Pike et al. 2001; Berg et al. 2001; Murray et al. 2002; Meysman et al. 2006a,b), see below.

Bioturbation. The biological reworking of sediments by endobenthic organisms, termed “bioturbation,” affects all sediments, limnetic and marine, from shallow tidal flats to deep-sea bottoms. In modern ecology, bioturbation is considered a major factor in the engineering of all benthic ecosystems (Meysman et al. 2006a) and in the creation of three-dimensional sediment structure (Lohrer et al. 2004). Because of its numerous biogeochemical implications, bioturbation probably had a massive influence on the archaic evolution of life (Bottjer et al. 2000; Dornbos et al. 2005; see Chap. 7).

Among macrobenthos, bioturbation is mostly caused by the burrowing and digging of crustaceans and annelids. Bioturbative effects can extend to a sediment depth of >20 cm. Extrapolations suggest that in tidal flats the upper 10 cm of the sediment will become completely bioturbated once every three years. Depending on the population density, bioturbation can decrease compaction, and can even destabilize the bottom and increase its erodibility (Widdows et al. 2000). It provides a system of tubes and voids and enhances sediment mixing through particle exchange down to greater depths. Even sediment particles from a depth of 50 cm will be transferred to the surface. The burrows of the priapulid *Halicryptus*

spinulosus or the decapod *Trypea* (*Callianassa*) create a “secondary surface” of 0.7 m² per surface m² in muddy bottoms (Förster and Graf 1992; Powilleit et al. 1994). Transport rates of 40–50 g sediment per individual and day have been recorded through the burrow and void system. The subsequent increased water penetration accelerates the transport of solutes and gases more than diffusion (Diaz et al. 1994; Berelson et al. 1999; Berg et al. 2001). Twenty-five percent of the overall oxygen flux is attributed to the irrigational activity of burrowing animals (Booij et al. 1994). Bioirrigative water and solute transport into the sediment can exceed normal diffusion by a factor of ten (Aller 1988; Aller and Aller 1992; Kristensen 1988; De Deckere et al. 2001).

Thus, benthic fauna markedly increases the flux of particles and modifies the physical processes (Graf and Rosenberg 1997). This has both beneficial and aggravating effects: organic matter and pollutants can be removed from the surface and buried into deeper layers where degradation is slow. On the other hand, the export of contaminated pore water is enhanced by bioturbators (Green and Chandler et al. 1994; Levin et al. 1997). By altering the geochemical system with animal tubes, and particularly through the import of oxygenated water by irrigational fluxes into anoxic layers, heavy metal precipitates (sulfides) that are buried at depth will become dissolved and released into the surficial, oxygenated layers (Green and Chandler 1994). Also phosphates and ammonium compounds are released in considerable amounts from the sediment by bioturbation and bioirrigation. The result is (often undesirable) eutrophication with an enhanced production of microphytobenthos in the overlying water (Monaghan and Giblin 1994). Bioturbative effects have also been shown to cause an undersaturation of calcites in the surficial layers, leading to increased shell dissolution and mortality (Green et al. 1998).

Just as the sources of bioturbation are very diverse, their effects on meiobenthos are also very complex: negative impacts through disturbance and destabilization, positive ones through the oxygen and organic matter supplied (Green and Chandler 1994; Aarnio et al., 1998, Schratzberger and Warwick 1999; Thistle et al. 1999; Koller et al. 2006). Using radioactive isotopes and fluorescent dye as tracers, Bradshaw et al. (2006) found only minor chemical effects of bioturbation in Baltic Sea sediments compared to those of physical processes. On a general scale, the chemical impacts of the biogenic mobilization of buried chemical pollutants on meiofauna have not yet been sufficiently evaluated.

While macrofaunal burrows affect the sediment, even the dense net of mm-fine burrows of meiofauna can have a considerable influence on sediment structure and fauna colonization (Reichelt 1991, Fenchel 1996; Jensen 1996). Among meiobenthos, effective bioturbators are ostracods, nematodes and, particularly at the surface, harpacticoid copepods. Cullen (1973) experimentally demonstrated the bioturbative impact of meiofauna. He found that their burrowing activities alone eliminated all surface traces of macrofauna within 14 days. In average sandy sediment, the burrowing of meiofauna will completely displace the pore water in 1–3 years (Reichelt 1991). Because of meiofaunal bioturbation the transport of solutes with the subsequent stimulation of microbial mineralization was

increased up to threefold compared to molecular diffusion (Rysgaard et al. 2000). Meiofaunal activity induces considerable microscale oxygen dynamics along the chemoclines of sediments, as documented by online registration with 2D planar optodes (Oguri et al. 2006). Distribution patterns of meiofauna, especially their colonization of deeper, anoxic horizons, have been shown to be highly dependent on the burrow system providing favorable microhabitats (e.g., Thomson and Altenbach 1993).

Modern methods imaging the animal-made void system and bioturbative effects include the use of X-rays or fluorescence tracer techniques (Diaz et al. 1994, Powilleit et al. 1994). One (cost-intensive) method of analyzing the compositions of sediment cores and visualizing their biogenic tubes and burrows is computer-assisted tomography (Rosenberg et al. 2007). An indirect and elegant in situ method of demonstrating mixing processes due to animal activity on-line is the recording of oxygen changes by (expensive) optical sensors (Wenzhöfer and Glud 2004).

2.1.3.3 Water Content and Water Saturation

The water content (mass of water in relation to the wet mass of a sample) is linked to grain size and permeability. Fine-grained sediments saturated with water have higher water contents than coarse sands. Mud cores often contain >50 weight % of water, while medium sand will only hold about 25%. Water content is considered by Flemming and Delafontaine (2000) to be a universal master variable that is relevant to any other sediment parameter (attention: inaccuracies may arise from the incorrect use of “content” and “concentration;” content denotes the mass per unit mass, while concentration is the mass per unit volume!).

Water saturation and water flow play a dominant role in structuring meiofaunal settlement. If the water content fluctuates the pore water is replaced and the meiofauna are supplied with oxygen and nutrients, while in the deeper, permanently water-saturated layers the pore water flow is reduced. In tidal shores, the occurrence of meiofauna can become restricted because of insufficient water content. Moreover, because of their reduced capillary forces water-unsaturated surface layers cause steep gradients of many abiotic factors, such as temperature and salinity (see Sect. 2.1.4), often with negative impacts on the meiobenthos. Particularly in eulittoral shores at ebb tide, the degree of moisture or the desiccation stress often correlates with the distribution of meiobenthos. Lack of water in the surface horizons can force meiofauna into deeper horizons. Many eulittoral meiofauna species adapt to the regular tidal alterations of water content and concomitant salinity fluctuations with preference reactions and migrations (Fig. 2.4; see Sect. 7.3, 7.4).

McLachlan and Turner (1994), based on Delamare-Deboutteville (1960) and Salvat (1964), suggested a generalized stratification pattern of (South African) beaches and their meiofauna in relation to desiccation and water saturation (Fig. 2.5).

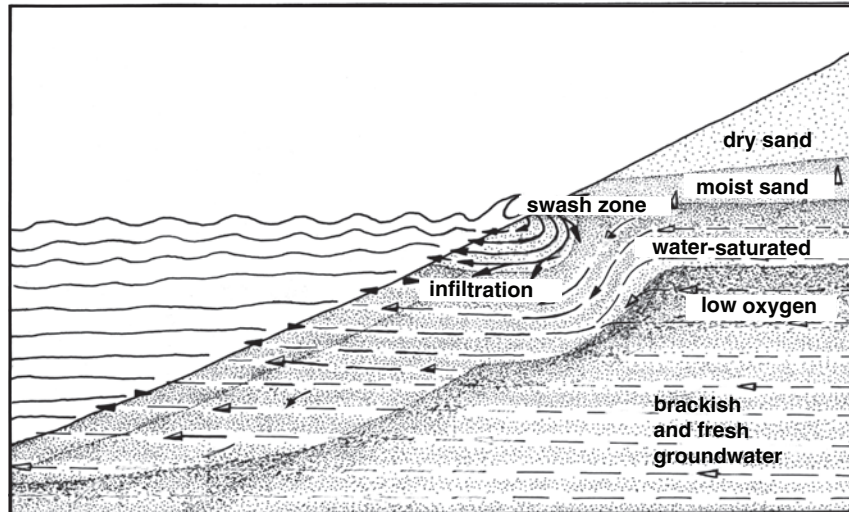


Fig. 2.5 Stratification of a beach profile related to water content. (Compiled from various authors)

- (a) An upper “dry sand stratum” is characterized by low water saturation and high fluctuations in temperature and salinity. Here, the prevalence of semi-terrestrial, specialized oligochaetes, mites and nematodes is contrasted with the scarcity of harpacticoids and turbellarians.
- (b) A partly underlying “moist sand stratum” (“zone of retention” in Salvat 1964) has an alternating water supply with fluctuations in temperature and salinity that decrease in the deeper strata. Due to the perpetually well-oxygenated conditions in this zone, meiofaunal abundance and diversity, particularly those of harpacticoids, increases.
- (c) In the “water table stratum” around the ground water layer, the sand is always water-saturated. In more sheltered beaches, restricted oxygen content and often brackish salinities lead to a reduced meiofaunal diversity and abundance.
- (d) The “low oxygen stratum,” where oxygen deficiency can extend down to a considerable depth, develops in beaches with a high content of organic matter; this zone can harbor meiofauna adapted to temporary oxygen depletion (see Sect. 8.4).

Variations in this four-strata pattern primarily depend on the beach slope and result in different patterns of wave energy, particle size and nutrient supply: reflective, dissipative and intermediate beaches (Fig. 2.6).

The tidal rhythm, local geography, high temperatures and different amounts of organic content will modify the above gradients. In flat-profiled and sheltered “dissipative” shores with medium-to-fine sand, the zonation is less developed.

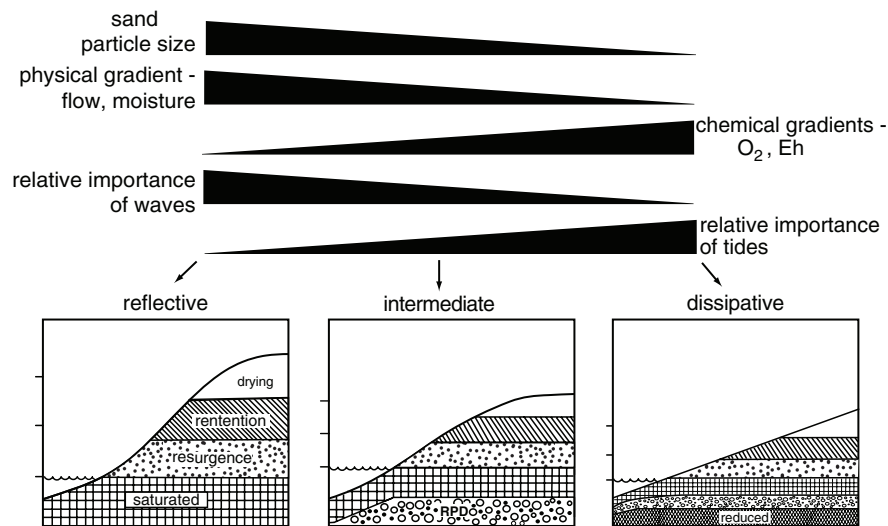


Fig. 2.6 Different beach types and their factor patterns. (After McLachlan and Turner 1994)

Conversely, in the exposed shore conditions of an “erosive” shore, the coarse-grained high-energy beaches have a “reflective” profile. Here, the waves prevent the occurrence of a low-oxygen stratum in the swash zone (“zone of resurgence,” Salvat 1964). This zone is characterized by intensive infiltration and circulation of interstitial water, and by a specialized interstitial fauna of reduced diversity and abundance. This physically controlled assemblage contrasts with the rich, often biologically controlled meiofauna of dissipative shores (Menn 2002b; see Sect. 9.4). Usually, moderately well-sorted medium sands provide the habitat with the most diverse meiofauna. In coarser sand, the species richness can be relatively high but population density may be low. Muddy sediments are more chemically controlled and often characterized by rich populations of a limited number of species restricted to the surface layer. In sublittoral sediments rich in organic matter, meiofaunal communities may be structured by the lack of pore water-flow and the resulting poor oxygen supply. In general, the correlation between hydrodynamic patterns, sediment structure and meiofaunal distribution is strong enough, particularly in littoral areas, to dominate all other factors. It often relates directly to the abundance and diversity of meiofauna, particularly nematodes (Vanreusel 1991, Menn 2002b, Gheskiere 2005).

More detailed reading: Hylleberg and Henriksen (1980); Yingst and Rhoads (1980); Gray (1981); Buchanan (1984); Aller (1988); Giere et al. (1988a); Kristensen (1988); Watling (1988); McCall and Tevesz (1982); Hall (1994); McLachlan and Turner (1994); Snelgrove and Butman (1994); Graf and Rosenberg (1997); Widdows et al. (2000); Pearson (2001); Cadée (2001); Murray et al. (2002); Reise (2002); Bale and Kenny (2005); Meysman et al. (2006a).

Box 2.2 The Sediment–Water Regime: Exposure, Permeability, Water Circulation, Bioturbation

The exposure of a habitat, which depends on the impacts of waves and currents, determines agitation, erosion, suspension, sorting of the sediment and flow of interstitial water. The degree of exposure, a complex parameter, is difficult to assess and is often only estimated. The erosion and permeability of the sediment are influenced by the hydrodynamic system, the sizes and shapes of the particles, and their material (quartz or biogenic calcium carbonate). The presence of organic matrices (biofilms, fecal pellets) is also important. The sediment represents a huge filter system of the water flow that provides the benthos with particulate organic matter from the water column and with dissolved nutrients. If saturated, the water content, determined by the capillary (adhesive) forces between the particles, is high in silt and mud (>50%) and low in sand (about 25%). In tidal shores, meiobenthic living conditions are influenced by pore water exchange. The sediment as a habitat is further complicated by biotic factors like bioturbation. This burrowing activity of animals massively reworks and irrigates the sediment and enhances pore water flow and primary production. Compounds bound to the sediment can become dissolved, resulting in eutrophication or polluting effects. Secretions and tubes compact the bottom. A complex web of particle mixing, in- and outflows, biosuspension and biocompaction links the sediment and water column. Various stratification patterns have been suggested for tidal shores. Based mainly on the beach slope, wave energy and tidal regime, dissipative accreting shores can be distinguished from reflective erosive beaches by grain size, water content, nutrients and oxygen supply. As meiofauna avoid strongly agitated sands, intermediate or dissipative beaches will be populated by more diverse and richer meiofauna.

2.1.4 *Physicochemical Characteristics*

2.1.4.1 **Temperature**

Meiofauna are present in polar ice and tropical coral reefs, in the constantly cold deep-sea and in the supralittoral fringe with frequent temperature fluctuations. Nevertheless, extremes of temperature can have a structuring impact on meiofauna, particularly in exposed tidal shores with their steep vertical thermal gradients. However, in sublittoral bottoms the influence of temperature on meiofaunal distribution is normally negligible. The steepness of the temperature gradient is strongly related to permeability (see Sect. 2.1.3). In water-saturated boreal mud flats of low permeability, surface and deeper layers can diverge widely in temperature, particularly at ebb tide. While summer temperatures can rise to >40 °C at the surface, those in the

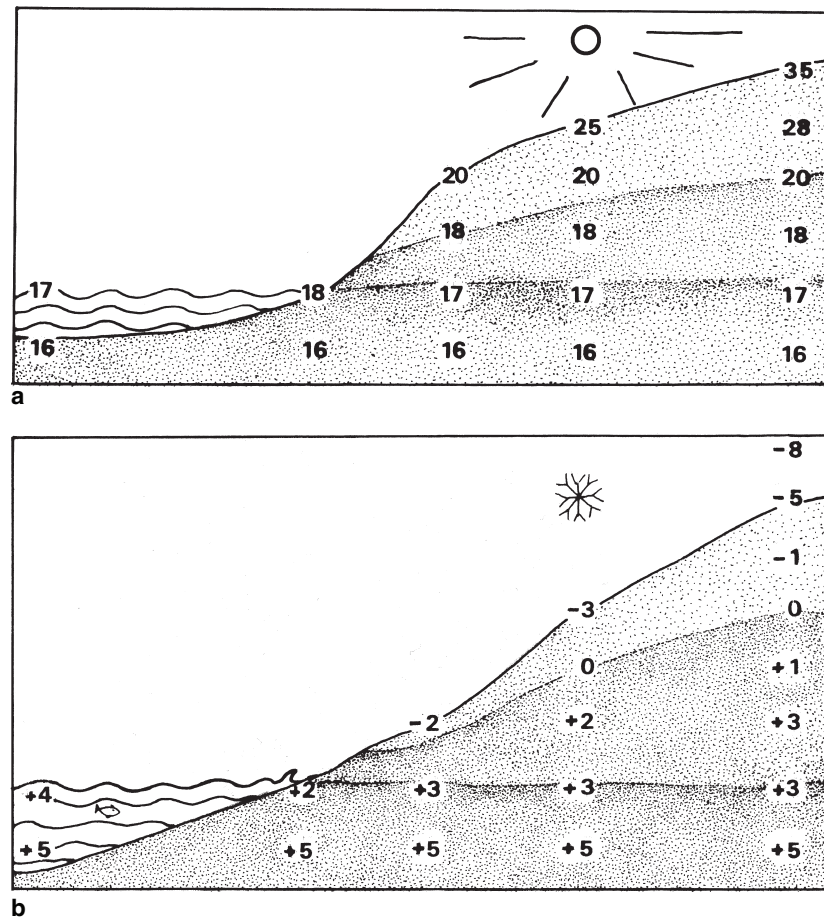


Fig. 2.7a–b A typical temperature distribution in a boreal beach. **a** Summer aspect. **b** Winter aspect. (After Jansson 1966a)

depths are only 10–15 °C because of a strong vertical dampening. In wintertime, even under thick ice cover, the frozen ground at the surface does not extend beyond the uppermost 5 cm (Fig. 2.7). This dampening effect with depth, which is particularly evident when calculating monthly ranges (Table 2.3), is important for the existence of meiofauna in climatically harsh biotopes where sensitive species often perform vertical migrations if other conditions like oxygen supply are favorable. On the other hand, many meiofaunal animals are highly resistant to frost, either by supercooling or protective dehydration. In Lake Taimyr (Siberia) nematodes and oligochaetes have been reported to regularly survive for months frozen in ice at temperatures of –10 °C or less (Timm 1996). The Alaskan ice worm, a black enchytraeid oligochaete, lives permanently in crevices of ice at temperatures of below 0 °C (Goodman and Parrish 1971). The (terrestrial) Antarctic nematode

Table 2.3 Monthly temperature ranges in 1964 at various sediment depths in a Scandinavian beach (Jansson 1967)

Depth	March	April	May	July	October
Air	−9.0	19.9	19.7	18.8	14.5
Surface	−13.0	34.2	38.4	33.5	24.1
2 cm	−8.7	26.0	33.0	24.0	12.8
10 cm	−4.1	9.8	11.2	9.9	4.2
25 cm	−1.0	2.8	3.4	–	–
70 cm	−0.5	0.8	0.5	0.6	1.0

Note: Values represent the differences between the lowest and highest temperatures (minus signs indicate when the sum of the minimum and maximum temperatures had negative values)

Panagrolaimus davidi survives temperatures as low as -80°C and freezing down to $>80\%$ of its water bodies (Smith et al. 2008). Polar sea ice is a permanent habitat for a rich, specialized “sympagic” meiofauna of ecological importance (Gradinger 1999a, Gradinger et al. 2005, see Sect. 8.1.1).

Temperature can be conveniently and routinely measured with a variety of pointed semiconductor probes connected to electronic (field) instruments. Since only the narrow surface of the thin metal probe is temperature-sensitive, in situ measuring is possible even at a considerable penetration depth without much compaction or displacement of the sediment.

2.1.4.2 Salinity

As with temperature, meiofaunal organisms exist under all salinity regimes from freshwater to brine seep areas, from brackish shores to deep-sea bottoms. Because many species are able to adapt to a wide range of salinities, there is often even a diverse meiofauna in those critical brackish water zones where Remane (1934) described a minimum number of species, mainly for macrofauna. Yet, depending much on the frequency of variations, salinity gradients can strongly determine occurrence and species composition of meiofauna (Ingole et al. 1998; Richmond et al. 2007). Habitat-adapted ranges of salinity tolerance or preference have been experimentally found in various meiofaunal species (Giere and Pfannkuche 1978; Ingole 1994; Moens and Vincx 2000b); the physiological capacity for salinity regulation was elegantly recorded for some littoral nematodes by Forster (1998) using an optical method based on the interference pattern of body fluids. Today the international salinity unit is PSU (Practical Salinity Units) which corresponds to ‰ S. In African volcanic lakes high conductivity (often together with extremes of pH, see below) not only structures the occurrence of different meiobenthic assemblages, it locally excludes the existence of meiofauna (Tudorancea and Taylor 2002).

In tidal shores, the steep vertical and horizontal salinity gradients strongly depend, as with temperature, on the water permeability of the sediment. In muds with their water-saturated fine sediments and much reduced vertical water exchange capacity, the surface salinity at ebb tide can rise up to hypersaline conditions due to evaporation.

After heavy rainfalls it can suddenly drop to almost zero. The effects of these fluctuations are greatest in the uppermost centimeter. At a depth of 2–5 cm, the fluctuations in salinity (as well as temperature) are much dampened and often remain amazingly constant. This offers mobile meiofauna a favorable refuge zone, while a drastic decline in meiofaunal abundance after flooding rains or tropical monsoonal rains has been reported for the surface layers (Alongi 1990b). At the highwater line of a North Sea mud flat, salinities of up to 40‰ PSU have been measured on a warm summer day, while immediately below at 5 cm depth, 30‰ PSU was not exceeded. At depths approaching the ground water level, the salinity often drops to brackish water conditions (about 20‰). In contrast, on coarser, well-drained sandy beaches with a high permeability, precipitation can affect salinity to a depth of 30 cm (Reid 1932–33), creating adversely lowered salinity conditions for meiofauna, even in the depths. Consequently, in sandy beaches the drainage system is complicated by the effects of both precipitation and ground water currents. Even in fully marine shores without any direct freshwater influx at the surface, groundwater is often markedly reduced in salinity depending on the local geological, climatic and geographical conditions. In sublittoral bottoms, the salinity fluctuates less and is usually identical to that of the overlying water, and so it is hardly a limiting factor for meiobenthic populations. Only beneath brine seeps (Gulf of Mexico) and in brine basins (Mediterranean Sea) are meiofauna exposed to adversely high (>150 PSU) salinities.

In the high shore, salinity gradients are difficult to record in detail because the amount of water available is often restricted. Two methods, microtitration and electrical conductivity measurements, are often used. Pointed conductivity electrodes measure the electric current between two platinum rings, which is modulated by the conductivity of the pore water. After calibration, this measurement is used to indicate the salinity of the water. In sediment with little moisture, conductivity measurements may be problematic. Here, the salinity of sediment water can be determined refractometrically. Special salinity refractometers are provided with a scale that is converted and calibrated for direct readings of salinity from only one drop of water extracted from the sediment. The precision of these instruments (± 1 ‰ S) is usually sufficient for ecological studies of meiobenthos. As with all methods of salinity measurement, in brackish water the precisions of both the conductive and the refractometer methods suffer because the altered ion composition will cause deviations from the constant relationship that classically defines salinity measurements in pure ocean water.

2.1.4.3 Acidity/Alkalinity (pH Value)

Water acidity, recorded in pH-units, used to play only a minor role for meiobenthos in the marine biome. The slight alkalinity of seawater (pH 7.5–8.5) makes it well buffered against pH fluctuations. Only in anoxic, hydrogen sulfide-containing sediments does the pH drop below 7, and rarely below 6. Hence, pH recordings are essential when sulfide concentrations are calculated (see below). On the other hand, in the surface layers of tidal flats, intensive assimilation of the abundant microalgae can increase the pore water pH to >9. In tropical tidal flats pH values of up to 10

have been measured. Here, high pH in combination with other stress factors such as extreme temperatures and salinity can be detrimental.

However, in the future there is a global risk that the dramatic rise in CO_2 will increase the acidity of seawater, with negative effects on the benthos. pH and pCO_2 are master variables in the formation of carbonate species (Cai and Reimers 1993), the relevance of which has been underlined by Green et al. (1998) based on manipulating the saturation state of carbonate. Hence, particularly calcareous shells and calcifying processes will be impaired by elevated acidity, as has been shown for macrobenthos. In spite of the high resilience of the sedimentary system, undersaturation of calcite (which is typical of many littoral sediments) massively increases mortality and causes shell dissolution in Foraminifera. The authors conclude that dissolution by undersaturation of calcite “likely represents an unrecognized source of mortality for carbonate-bearing meiofaunal-sized organisms.”

Under stable deep-sea conditions, experimental CO_2 deposition caused a decline in sediment pH of up to 0.75 units and significant defaunation among meiofaunal nematodes and protozoans (Thistle et al. 2005, 2006, 2007a). Even mild acidosis with a decrease in pH of only 0.1–0.2 caused mortality among meiobenthos of up to 30% in the affected area (Barry et al. 2005; see Sect. 8.3).

In natural freshwater biotopes, extremes of pH can occur in mires and limestone waters, but also in spring lakes of volcanic origin. Many freshwater bodies are, of course, exposed to anthropogenic pollution, which often causes drastic fluctuations in the pH level. However, the buffering capacity of the sediments dampens the fluctuations in the pore water compared with the overlying water. Subterranean fauna is well adapted to the slightly acidic conditions in continental groundwater aquifers. Thus, a negative impact of acidity or alkalinity on freshwater meiofauna has rarely been demonstrated (Pennak 1988). A reduction in diversity and abundance does however occur in volcanic lakes, where extremely ionic conditions, e.g., alkaline and saline conditions (“soda lakes”), have been found to reduce the diversity or even to limit the occurrence of (nematode) meiofauna (Tudorancea and Zullini 1989; Muschiol and Traunspurger 2008). pH also has a major influence on the balance of many physiological reactions that are not related to calcification, e.g., respiratory processes.

Since the effects of pH changes are often confounded by concomitant parameters (e.g., metabolic processes, oxygen binding) in the field, the specific impact of acidosis or elevated pH should be studied experimentally, separate from other factors. The measurement of pH in situ is not problematic when glass insertion electrodes with the reference electrode combined in the same shaft are used. Usually, the recording is done in parallel with redox potential measurements performed with a mV-meter calibrated for pH. Modern electrode design even prevents clogging of the diaphragm. Correct readings require that the temperature of the electrode’s internal filling equals that of the ambient water or sediment to be measured. Internal and external air pressures must also be equalized. A special pH electrode with a recorder integrated into its shaft has been developed to allow for measurements in a drop of pore water filling a small hollow. This even enables correct measurements of pH to be obtained in water-unsaturated shore sediments. pH electrodes in combination with pCO_2 microelectrodes have been designed for combined recordings (Green et al. 1998).

Box 2.3 Temperature, Salinity, Acidity

In their normal ranges, temperature, salinity and acidity are not limiting to meiofauna. However, in polar or tropical shores, tidal flats or sea ice, and in volcanic waters, extreme values can become limiting for meiofauna and favor resilient communities of relatively low diversity. A global increase in CO₂ will result in the lowering of seawater and sediment pH values and will influence the physiological pH balance and the formation of calcareous structures in sealife. The consequences for shallow-water meiofauna remain to be assessed. Dumping CO₂ into the deep sea as a way of solving the CO₂ problem seems an inappropriate and risky approach for benthic life.

2.1.4.4 An Interacting Complex: Redox Potential, Oxygen, and Hydrogen Sulfide

Increasing temperatures and eutrophication cause a reduced oxygen supply, mostly associated with increases in hydrogen sulfide and ammonia in many areas. This is a particular problem for benthic biotopes, with their rich content of degradable, oxygen-consuming matter (see reviews by Diaz and Rosenberg 1995, Wu 2002).

Redox potential. Before the development of suitable oxygen and sulfide electrodes, platinum electrodes were used to measure the overall reducing or oxidizing capacity of a sediment, the redox potential. The resulting values were simple to record but difficult to interpret. Nevertheless, redox values have become one of the most frequently provided environmental parameters in meiobenthic studies and are sometimes still used. However, redox potential recordings only vaguely reflect the supply of oxygen in the pore water, and the measurement of redox potentials can easily be deceptive: all of the controlling redox couples that occur in the sediment, in addition to those induced by free oxygen, are integrated in a redox potential reading and will influence the measurement.

Moreover, a basic understanding of electrometry and some information about inherent flaws and errors is needed to avoid bias and misinterpretation. The electrical potential between an outer platinum electrode and an internal reference electrode is recorded with a mV-meter, which must be corrected to yield the “Eh value.” The response of the electrode depends to a high degree on the properties of the platinum surface. Eh measurements and their interpretation become even more of a problem because of the low reproducibility of replicate recordings from directly adjacent spots. This problem is largely caused by microchambers of decaying organic matter, entrapped air bubbles or animal tubes encountered by the pin-pointed electrode.

In the field one can encounter values between +550 and –300 mV. In exposed sandy bottoms that are typically yellowish in color, positive values are obtained throughout, while in soft muds with rich organic content, the gray-to-black layers underneath a thin brighter surface layer will yield clearly negative redox values. The transition zone between positive and negative redox values is termed the

“redox potential discontinuity layer” (RPD layer). The RPD layer can periodically move up or down with an increase in the assimilation activity of surficial diatoms or with the incoming tide.

Relation of redox values to sediment color. It is relevant to note (but is often disregarded, even in recent meiofaunal studies) that, for chemical reasons, the RPD threshold does not eo ipso parallel the shift from bright sediment layers to dark ones. Detailed Eh measurements have shown that the change from light (yellowish) to dark instead indicates the transformation of ferric iron to ferrous iron rather than the RPD (the redox potential can still be +125 mV, see Fig. 2.8a, and data in Sikora and Sikora 1982; Jørgensen 1982). Only in those cases where the transition layer is narrow and the change from bright to deeply black is abrupt (in muds) can the color change coincide with the RPD. In other words, a wide and diffuse transition from bright over gray to black just indicates the gradual disappearance of free oxygen to a layer with oxidized compounds, albeit without free oxygen. This is then followed by the fully reduced layers without any traces of free or bound oxygen. The value of an optical sediment indicator for the presence of oxygen is further limited in many calcareous sediments, where the iron-based change of the sediment color (brownish = ferric iron, grayish = iron sulfides) may be absent because of the low iron content in the sediment.

For a long time it was considered a general and practical rule for interpreting Eh values that values of $> +100$ mV would indicate the presence of oxic pore water in the sediment, and < -100 mV its absence. Today, oxygen microelectrodes have shown that free oxygen can be absent in sediments with redox potentials as high as +300 mV. Differentiating between oxic (i.e., with free dissolved oxygen available to animals) and oxidized sediments (with compounds in an oxidized chemical state) is of prime importance for correct ecological interpretations (Sikora and Sikora 1982; Jørgensen 1988). In a coastal sandy sediment, Revsbech and Jørgensen (1986) demonstrated that the oxic zone was only 2 mm thick, while an oxidized sediment layer with a positive redox potential extended down to 3.5 cm. Microelectrode measurements have shown that the oxygen content of the pore water can be “zero” in sediment layers that are still brownish to yellowish, i.e., oxidized (Fig. 2.8a). Likewise, the presence of toxic hydrogen sulfide is not automatically indicated by grayish to dark sediments (see below). Only when oxygen or sulfide ions occur in excess and are not chemically bound will the pore water become oxic or sulfidic, respectively. Today it is preferable in meiobenthic studies to measure the oxygen concentration directly with small oxygen electrodes (see below) rather than using the redox potential as a difficult substitute that cannot demonstrate the microdistribution of oxic/anoxic niches.

Oxygen. Oxygen is the predominant factor among the abiotic parameters determining the habitat conditions and the presence of meiofauna. Meiobenthic organisms have relatively large surface areas and mostly high oxygen demands; only a few specialized forms will prefer hypoxic conditions (see Sect. 8.4). Thus, the distribution of most meiofaunal communities can be correlated to the oxygen supply of the pore water.

Technical progress has largely changed our conception of oxygen supply to the benthos. The classic picture of a vertical oxygen stratification must be abandoned.

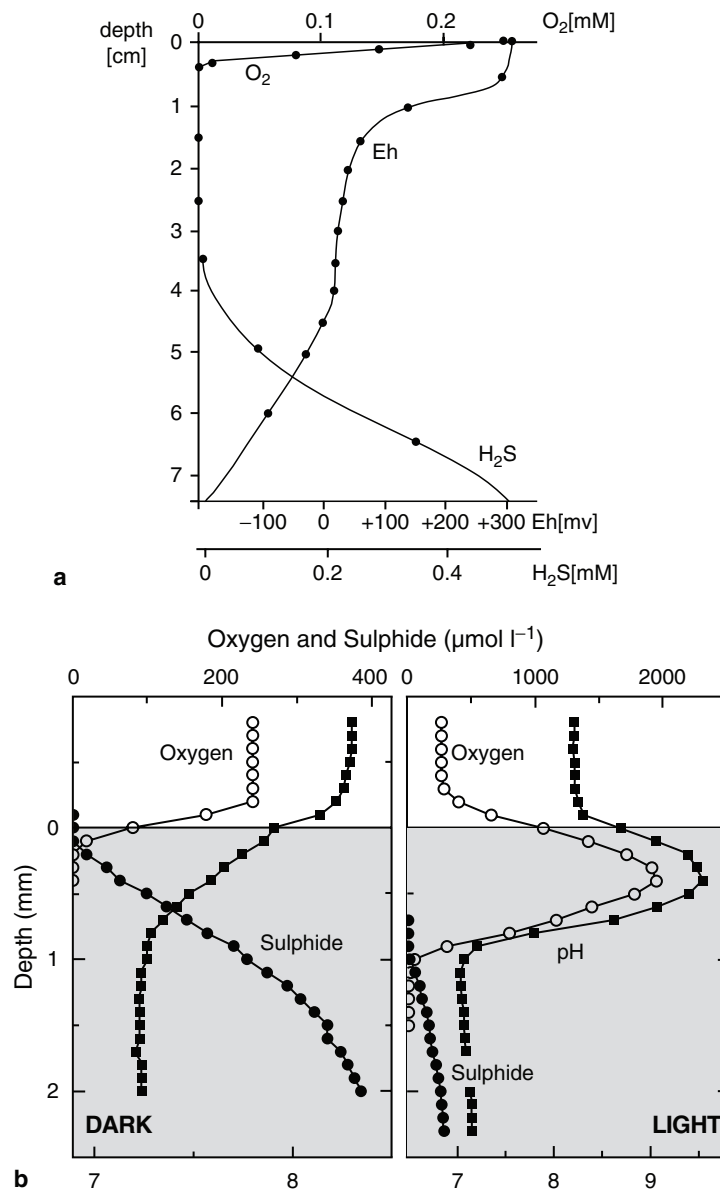


Fig. 2.8a–b Oxygen and hydrogen sulfide gradients in two sediment profiles from tidal flats. **a** Showing relationship with the redox potential (Eh). **b** Showing relationship with the acidity (pH) and assimilation-induced changes. (**a** is after Revsbech and Jørgensen 1986; **b** is own recordings)

New microelectrometric techniques have revealed a much-differentiated pattern of oxic conditions in the sediment. Numerous micro-oxic niches occur within anoxic sediments, creating temporary microenvironments with a potential distributional effect for meiofauna (Forster et al. 1996) in the same vertical layer. Numerous geochemical cycles and microbial processes together with the bioturbative impact of sediment fauna and tidal fluctuations create a complicated three-dimensional net of oxic/anoxic microniches.

Many sands and muds are only oxygenated in the uppermost millimeter-thin layer (Revsbech and Jørgensen 1986; Visscher et al. 1991). In intertidal flats densely populated by meiobenthos, recordings of oxygen and hydrogen sulfide taken with a set of microelectrodes (see below) showed a very strong periodicity in the fluctuations in oxygen and sulfide concentrations (De Beer et al. 2005a; Weber et al. 2007): At ebb tide, the oxygen content declined rapidly and anoxia (plus hydrogen sulfide) often even reached the surface layer. When bioturbation/irrigational fluxes are interrupted, rapid oxygen depletion through bacterial consumption will soon create hypoxic and anoxic conditions in previously oxic burrow walls, the preferred habitat of meiofauna (Wetzel et al. 1995, Fenchel 1996). The incoming tide reoxidizes the interstitial sediment water, even before the flats become inundated again. Even with tidal regularity, these intermittent fluctuations of oxygen and sulfide exert considerable ecological stress on meiofauna that was not realized before. Aside from the tidal fluctuations, the diurnal fluctuations of light exposure cause changing micro-oxic stratifications via the assimilation activity of the phytobenthos (Fig. 2.8b). Similarly variable oxygen conditions have also been reported for other biotopes (e.g., Archer and Devol 1992; Förster and Graf 1992). In seagrass beds, anoxic periods can be particularly destructive and long-lasting (Guerrini et al. 1998). Buried seagrass and algal remains caused black patches on tidal flats devoid of fauna (Neira and Rackemann 1996) and with a delayed recolonization by meiofauna (De Troch et al. 2005).

Other microscale oxygen recordings have revealed that biogenic microtopographic surface structures such as small mounds modify the hydrodynamic and oxidative micropatterns (Ziebis et al. 1996). In a North Sea tidal flat, diffusion of oxygen from *Arenicola* burrows extended only about 1 mm into the surrounding fine sand (Wetzel et al. 1995), results which were also confirmed by Fenchel (1996) for burrows in the mm range (Fig. 2.9). Many microgradients of oxygen available to meiobenthic animals are, in fact, so steep that changes from fully oxic to anoxic conditions can occur within the μm range of microbial mats. The narrow transition zones from oxidized to anoxic layers can imply that aerobic and anaerobic microbial processes can take place at same depths, and that micro-oxic conditions can temporarily persist beside sulfidic ones (Fenchel 1996; Meyers et al. 1988). The view that the micro- and meiobenthos beneath the upper few millimeters live a largely anaerobic life (Revsbech et al. 1980a,b) has to be refined. In fact, these organisms seem to continuously oscillate between (micro)oxic islets, they tolerate short anoxic events which can momentarily cease, and their habitat changes temporarily under the influence of assimilation and tidal influx. Probably, many meiofauna are forced to intermittently gain energy by rapidly switching from aerobic metabolism

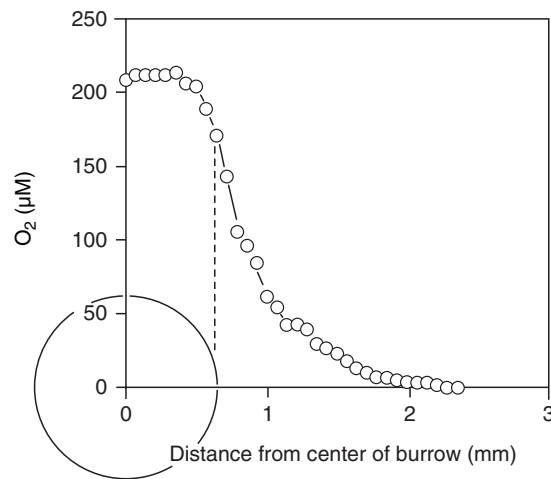


Fig. 2.9 Decrease in oxygen concentration around a thin worm burrow in a muddy bottom. (After Fenchel 1996a)

to phases of passive outlasting or anaerobic metabolism. The oxygen flux is also very limited in deeper shelf and slope sediments. (On the other hand, the deep-sea ooze, with its low content of organic particles, can stay oxidized all the way down to several centimeters in depth.)

The fine-scale assessment of oxygen stratification directly in the pore water system became possible within the last few decades through the use of thin oxygen microelectrodes, which were introduced into experimental ecology mainly by Revsbech and his group (see Revsbech and Ward 1983; Revsbech and Jørgensen 1986). Protected from abrasion by a layer of semipermeable silicon rubber, and provided with a sturdy glass shaft, field versions have been designed (Fig. 2.10; Revsbech and Ward 1983). By ensheathing the electrode in a thin stainless steel shaft (Helder and Bakker 1985; Visscher et al. 1991), the risk of breaking this device during field use is further reduced. In contrast to polarographic oxygen electrodes, microelectrodes do not require any water flow and, if gold-coated, the presence of dissolved sulfide does not tarnish the minute measuring surface.

However, these microelectrodes, with their critical limits of detection (5–10 mmol oxygen), hardly allow for discrimination between truly anoxic and hypoxic conditions—a problem of particular relevance in respiration experiments. Oxygen concentrations in this low range might be still relevant for adapted micro- and meio-benthos with high oxygen affinity (Watling 1991).

The measuring threshold in oxygen recordings was minimized upon the development of novel optical oxygen electrodes (“optodes,” Klimant et al. 1995). These fiber-optic microsensors measure the extremely sensitive luminescence quenching of certain chemical dyes that emit light when oxidized. Their highest sensitivity occurs at an ecologically important low oxygen concentration, and their detection

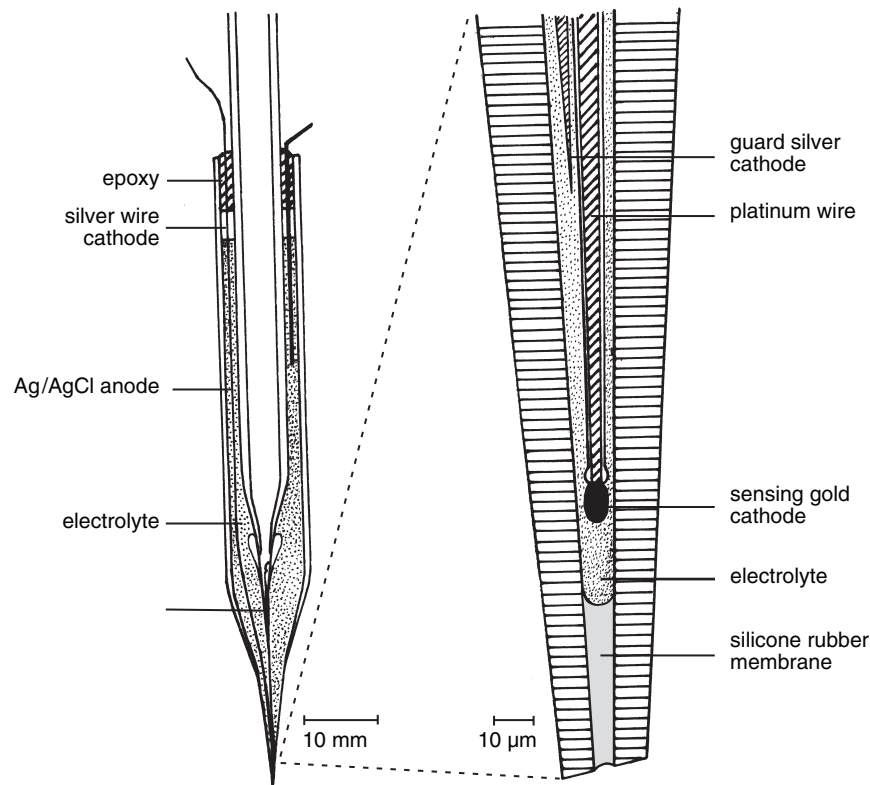


Fig. 2.10 Oxygen microelectrode with a sturdy glass shaft. (After Revsbech and Ward 1983)

limit can be $0.1 \mu\text{M}$ (or 0.5 ppb). The most advanced recording method visualizing oxidative processes online and in situ is the development of 2-D planar opt(r)odes (Glud et al. 1996, 2001; Wenzhöfer and Glud 2004), by which the small-scale dynamics of oxygen distribution, caused by changes in water flow, assimilation or bioturbation, can be continuously and precisely registered on-line (Oguri et al. 2006). The inserted tiny oxygen-quenchable fluorophore creates an on-line, precise and highly stable “oxygen picture” over time. If constructed for field use, these optical sensors can bridge the gap between punctuated microelectrode measurements and the continuous, integrative recordings of chamber incubations. The minimal dimensions and the precision of these microelectrodes allow for the construction of novel microchambers and non-invasive, exact measurements of meio-faunal respiration to be obtained (Moodley et al. 2008; see Sect. 9.3.2). The major disadvantage of this instrumentation is its cost. In recent years microelectrodes and optodes have been adopted and modified by various working groups (Weber et al. 2007), but there is still a need to construct sturdier versions that are suitable for use by nonspecialists in field operations at a reasonable price.

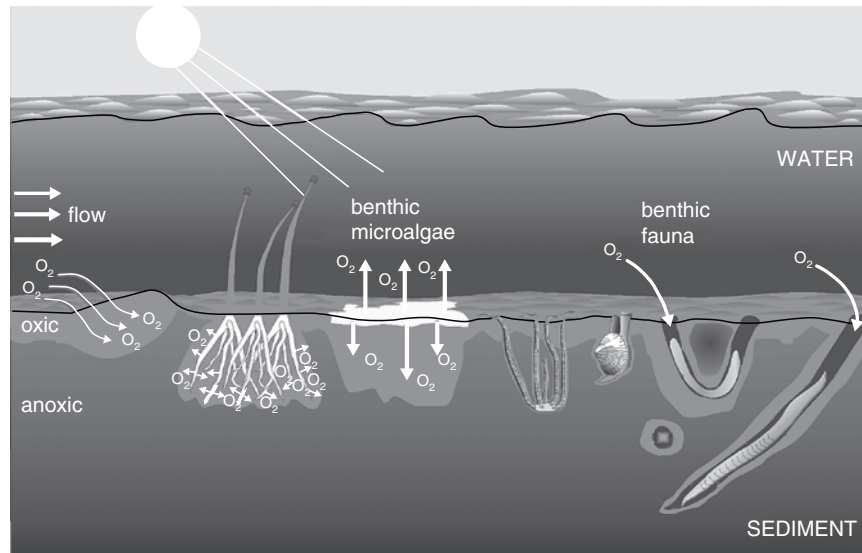


Fig. 2.11 The microdistribution of oxygen in a shallow flat. (Courtesy Wenzhöfer)

The principally new conception of oxygen conditions in the benthic environment is illustrated in Fig. 2.11. The oxygen distribution is extremely patchy and variable, primarily due to the tidal cycle, bioturbation and organismic activities. The overall volume of oxic microniches grossly exceeds that of the “classical” two-dimensional sediment surface. Considering the complexity and dynamics of the “oxygen realm” and its ecophysiological implications for the small benthos, further microscale investigations, especially those performed under natural field conditions, are needed.

It is obvious that oxygen recordings from pore water samples obtained with syringes or by centrifugation (see Sect. 3.3) cannot yield an accurate resolution of the oxygen conditions, whether performed by a micro-Winkler titration (Bryan et al. 1976; Peck and Uglow 1990) or with a polarographic electrode. The fetch area of the pore water is clearly not reproducible. These methods, often still used today, yield a misleading oxygen distribution and should be replaced by direct measurements with microelectrodes. The same holds true for the “oxygen diffusion rate” (ODR, see Jansson 1966a), an historical method that is difficult to interpret and of little relevance today.

Hydrogen sulfide. Hydrogen sulfide (H_2S) is, oxygen aside, perhaps the most relevant environmental parameter in benthic habitats. Under normal marine pH conditions, hydrogen sulfide is predominantly dissolved as HS^- ion. Only in more reducing habitats at slightly acidic pH can the particularly toxic undissociated H_2S molecules prevail. Because it (reversibly) blocks the cytochrome C oxidase of the intracellular respiratory chain, hydrogen sulfide is toxic to animals at just nanomolar to micromolar concentrations and profoundly influences the distribution of the benthos. Especially in marine biotopes, H_2S can develop in high concentrations

through anaerobic microbial reduction of sulfate. Sulfide production can be maintained by sulfate reducers, even under low-oxygen conditions (Jørgensen 1988; Fukui and Takii 1990; Jørgensen and Bak 1991). Plant roots (e.g., *Spartina*) may enhance sulfide oxidation through both oxygen production and catalytic effects (Lee et al. 1999; Lee 2003).

Because of the chemical balance between iron and sulfide ions, in temperate regions a considerable proportion of the generated sulfide will precipitate as iron sulfides, forming a grayish-to-black layer in the depths of the sediment. Particularly in the warm season, the deeper layers of muddy intertidal flats, rich in organic matter, develop high hydrogen sulfide concentrations that sometimes exceed 1 mmol l^{-1} (author's unpublished data; Rey et al. 1992). In polluted sediments, dissolved hydrogen sulfide has an indirect but important impact in fixing toxic heavy metals such as cadmium as solid precipitates. In calcareous sediments of warm-water regions, with their low iron contents, this precipitation process is limited. Here, high concentrations of toxic dissolved hydrogen sulfide can develop without any blackening of the sediment (see above). In freshwater biotopes, periods of anoxia rarely give rise to comparably high concentrations of H_2S . In this environment, sulfate ions are rare and sulfide is derived mostly from the organically bound protein sulfur.

Despite its ecological relevance (see Sect. 8.4), hydrogen sulfide has mostly been ignored in field work and in experiments. In part, this may be due to the widely reported but prejudiced notion that H_2S -smelling sediments are azoic. The difficulty involved in measuring this labile substance quantitatively may also have caused it to be neglected.

Smell is a good criterion for detecting even low concentrations of hydrogen sulfide, because human olfactory organs sense hydrogen sulfide concentrations as low as $0.1 \text{ } \mu\text{m H}_2\text{S}$.

Today, hydrogen sulfide in sediment pore water is usually measured spectrophotometrically after the addition of methylene blue (Cline 1969; Gilboa-Garber 1971). There are some modifications of this method that mostly concern the calibration and the range of concentration. Pore water is obtained by suction corers (see Sect. 3.3) and injected right after extraction into the prepared vials filled with alkaline lead acetate, the precipitate is later dissolved in the laboratory. Although somewhat cumbersome, this "pore water method" with subsequent photometrical analysis remains a versatile and frequently used method of measuring hydrogen sulfide.

As with oxygen, the stratification pattern of hydrogen sulfide in the sediment column is three-dimensional, extremely complex and characterized by sulfidic microniches directly adjacent to oxic spaces and by steep gradients (see Fig. 2.8b). Microelectrodes have been developed in order to obtain a realistic picture. Several companies offer a silver sulfide electrode combined with a reference system of calomel or Ag/AgJ . The recorded voltage (mV) is directly proportional to the logarithm of the S^{2-} partial pressure. Therefore, it is essential to convert all hydrogen sulfide in its various pH-dependent stages of dissociation to S^{2-} and to calibrate the electrode in relation to the ambient pH. In particular,

the micro versions of this electrode, designed originally by Revsbech and Ward (1983), are of interest as insertion electrodes for field use. Early constructions suffered from technical problems (mechanical fragility and abrasion of the silver sulfide coating). Mounting the sulfide microelectrodes in the steel injection needles from medical syringes has made recent versions sturdier and sufficiently protected, even for use in sandy substrates (Van Gemerden et al. 1989). A particularly promising tool for simultaneous recordings of the closely interacting compounds combines an oxygen and a hydrogen sulfide electrode within one thin metal needle (Visscher et al. 1991). The construction of a needle-pointed amperometric sulfide microelectrode combines increased sensitivity with broad applicability (Kühl et al. 1998). Its field use in profiler experiments enabled minute gradients in microprofiles to be recorded. Visman (1996) designed an automatically controlled experimental oxygen/sulfide system with variable pH and temperature conditions that enables complex ecophysiological experiments with sulfide. Although even these new designs do not make measurements of hydrogen sulfide a simple and convenient task, they will hopefully help to ensure that this dominant factor in benthology is no longer neglected in the future.

More detailed reading: Giere (1992); Grieshaber et al. (1994); Grieshaber and Völkel (1998); Wetzel et al. (2001).

Box 2.4 An Interwoven Complex: pH, Redox Potential, Oxygen, and Hydrogen Sulfide

Oxygen availability and exposure to hydrogen sulfide often set the limits on the distribution of benthic animals. In turn, the development and stratification of these chemofactors depend significantly on biotic processes. The microbiological depletion of oxygen to zero restricts most meiobenthic organisms to the surface layer as a suitable habitat in many sediments. However, the boundary to the anoxic strata, which are often dominated by toxic hydrogen sulfide, changes its position because of tidal fluxes and assimilatory oxygen production. This is the preferred biotope for rich microbiota. Bioturbative processes performed by macro- and meiofauna and microtopographic structures (tubes, mounds) locally alter this vertical stratification, creating a complex three-dimensional pattern of oxic and sulfidic microniches. This is often the basis for the notoriously patchy meiofaunal distribution. Measurements with thin microsensors give a more accurate picture of this microscale oxic/sulfidic regime. Their high sensitivity makes it possible to measure even the critical micro-oxic and microsulfidic ranges around the chemocline, which are relevant to many fauna in hypoxic and low-sulfidic sediments. Long-term measurements in benthic chambers have revealed that this micropattern of oxic/sulfidic conditions in the sediment is continuously changing, a scenario that has completely changed the former conception of a two-dimensionally layered system.

(continued)

Box 2.4 (continued)

Because of advances in oxygen microelectrodes and optodes, the use of redox potential as an indicator of oxic/sulfidic conditions is losing importance. Eh measurements in sediments are, at best, inexact and their interpretation is vague. An operational parameter with an integrative character, Eh does not reflect the fine-scaled and dynamic oxic/anoxic/sulfidic system. Commercially available oxygen microsensors remain expensive considering their fragility during field use. Technical attempts to produce robust constructions have been rare.

2.1.4.5 Inorganic Nutrients and Pollutants

Nutrient enrichment and contaminants from anthropogenic pollution are factors that today have an important impact on the meiobenthos in many parts of the world (Nixon 1995). Because of physical adsorption and chemical bonds, nutrients and pollutants in the sediment are enriched by several orders of magnitude compared to the overlying water. Absorption of inorganic and organic nutrients, especially in carbonate sediments, is very high (Rasheed et al. 2003a). Once bound in the sediment, these substances are only slowly released into the water column. Retarded microbial decomposition in the oxygen-deficient deeper layers of many bottoms combined with high absorptive forces can cause long-lasting or chronic negative effects on the benthos. Thus, sediments often represent sinks for pollutants. Here, the intensive transport of oxygen in plant roots can have a phytoremediative effect (Lee 2003). Measurement of nitrogen and total phosphorus are summative indicators and are hardly adequate for assessing the situation. One potentially powerful method indicating the extent by which the meiofauna are aggravated by contaminants might be gene or genome analyses of exposed animals (Staton et al. 2001). In any case, eutrophication and pollution have been linked to patchy distribution patterns of meiofauna (Lambhead and Hodda 1994).

In many coastal areas, while terrigenous eutrophication may have been abated in recent years, fish and mussel farms in formerly often oligotrophic, barely exposed environments (Norwegian fjords, Mediterranean Sea bights) create an ever-increasing source of nutrient input, which has consequences for meiofauna, especially in sheltered coastal sediments. Another widespread man-induced environmental factor in the meiobenthic habitat is sediment pollution by heavy metals, antifouling compounds (TBT), and pesticides. Because they usually have only a local impact, chemical agents are not considered here as general habitat factors. The reaction of meiofauna to chemical pollution will be detailed in the synecological part of this book (Sect. 8.8).

More detailed reading: Kristensen (1988); Watling (1991); Huettel and Gust (1992); Chester (2002).

Box 2.5 The Abiotic Environment of the Meiobenthos

In the natural environment all of the single factors described in the above section interact with counteracting and synergistic effects. Attractive nutrients are enriched by the highly absorptive bonds at the grain surfaces, as are noxious pollutants. Steep oxic gradients favor microbial life, but anoxia and (often co-occurring) hydrogen sulfide are highly toxic. Erosive water currents act negatively on meiofauna, but they also transport solutes and oxygen into the system. These interactions create a three-dimensional pattern of small-scale favorable microniches or adverse patches that represents the abiotic environment of meiobenthic animals. It is a system governed by currents and sediment composition as key factors, which influence a cascading, multifactorial network to which meiofauna respond in varying patterns and sequences. Experiments have revealed some of these reactions (e.g., to temperature or salinity), but the impacts of more complex factors (nutrients, toxicants) and particularly the role of the elusive chemical complexations are far from understood. In addition, in the field the numerous abiotic factors are constantly interacting with the equally complex system of biotic factors (see the following section).

2.2 Biotic Habitat Factors: A Connected Complex

Studies on the impact of biotic factors on meiobenthic communities have increased since about 1975, while work on abiotic factors dominated studies of the 1960s and early 1970s. Today, it is recognized that biotic factors can have a massive influence on the population structure of meiofauna and the benthic habitat in general (Woodin and Jackson, 1979a,b). The array of biotic factors in sediments extends from dead organic matter (detritus) and biogenic structures to mucus aggregates, sedimenting plankton, bacteria, and, of course, living organisms. Detritus—the remains of plants and animals—is the main component of particulate organic matter, but fecal pellets, mucous agglutinations from exudates and excretions, as well as dissolved organic substances also contribute to this complex. In nature, this organic matter is inseparably connected to bacterial growth, colloids, aggregate and biofilm production and remineralization (Jørgensen et al. 1981; Kepkay 1994; Azam 1998). In a wider sense, the activities of other fauna, such as disturbance, competition and predation, also represent biotic habitat factors for meiofauna (Figs. 15, 16). Community aspects of this subject will be discussed in Chap. 9.

Watling (1988, 1991) pointed out that the classical methods of sediment analysis, derived from geology, give a misleading, denatured and biologically rather irrelevant picture of the sedimentary habitat. The world of benthic animals is not characterized by the mineral particles but by the delicate, flocculent organic matter that binds them into a highly adsorptive interwoven fabric. Consideration of the organic material, bacterial colonization, biofilm production, pore-water chemistry and bioirrigation is necessary to achieve a natural conception of the real sediment.

Abiotic factors will predominate in extreme biotopes only, such as in the swash zones of exposed beaches (Hockin 1982b). However, even in the wrack zones of tidal flats, trophic or predator–prey relationships are of significant importance (Giere 1973; Reise 1987; Menn 2002b).

Living organisms (bacteria, microalgae, other animals) also represent important environmental factors that structure the habitats of meiobenthic animals. Among the biotic factors, probably the least known component with a potential influence on the meiobenthos are the microscopic fungi.

Biotic factors interact in complex ways and are difficult to separate and measure. This is probably why they have been investigated far less than abiotic parameters. For better elucidation of this biotic–habitat interaction, the various components are presented separately below. Interpretations of data from such investigations have often been controversial and thus there are few meaningful generalizations. While this has been the case for the better studied macrobenthos (see reviews by Pearson 2001, Wilson 1991), it is even more valid in the case of meiobenthos.

2.2.1 Detritus and Particulate Organic Matter (POM)

Dead organic particles from any trophic level of an ecosystem, as well as organic input from external sources, regardless of its size, are considered to be detritus. Much of the detritus found in sediment samples is derived from dead plankton organisms trapped by the huge filtering systems of shores (Riedl 1971; McLachlan 1989; Berelson et al. 1999; Ólafsson et al. 1999; see Sect. 2.1.3). Decaying phytoplankton blooms can also result in the deposition of a fluffy layer of phytodetritus on the sea floor in coastal, sublittoral and deep-sea areas. These unconsolidated organic deposits, often agglutinated by mucous secretions, enhance the bacterial activity after relatively short time periods (a few days to weeks) and can subsequently cause a significant increase in meiofaunal abundance and diversity (Thiel et al. 1988/89; Fleeger et al. 1989; Lambshead and Gooday 1990; Riemann 1995; Witte et al. 2003; Vanaverbeke et al. 2004). In Kiel Bight (Baltic Sea), the benthic degradation of a phytoplankton bloom was completed after only three weeks (Graf et al. 1982). Especially in surface-feeding meiobenthos, the positive response to these blooms is very direct, while subsurface feeders tend to show a more indirect reaction (onset of reproduction periods, etc.) (Ólafsson and Elmgren 1997).

In shallow, well-illuminated bottoms, benthic macroalgae and seagrass meadows also provide an ample source of detritus known to promote abundant meiofaunal populations (Novak 1989; Blanchard 1991; Urban-Malinga et al. 2008). In return, meiofauna have been shown to stimulate the decomposition of plant litter (Findlay and Tenore 1982; Alkemade et al. 1992). Experimental observations indicate that the detritus is not indiscriminately ingested by meiobenthic animals: debris of brown algae is preferred over red algae (Giere 1975; Rieper-Kirchner 1989), while mangrove litter (with its rich tannin content) is less attractive than other plant debris (Alongi 1987b). The differing origins, the multitude of stimulating and inhibiting substances contained in detritus, and the diversity of the degradation processes led Tenore et al. (1982)

to concentrate on the “available,” attractive detritus in his ecological studies. The organic remains of decaying macrofauna have been shown to be attractants for saprobial meiofauna, especially nematodes (Gerlach 1977; Ólafsson 1992), causing patchy meiofaunal aggregations.

As far back as 1942, Mare stated that the amount of particulate organic matter (POM) had a significant influence on the distribution of meiofauna, a fact which has since been confirmed by many authors (Lee 1980a; Tenore and Rice 1980; Tietjen 1980; Warwick 1989). In silty muds, the dry weight of the organic particles can reach 10% of a sample, while for sandy shores this value is often <1%. However, it has been demonstrated that even the microtopography of the bottom (tubes, ripples) influences the content of organics. Ripples enhance the particle flux by a factor of >2 (Huettel et al. 1996), while organic particles accumulate in the troughs and the depressions around tubes (Hogue and Miller 1981; Hicks 1989).

To obtain a gross measurement of the total organic matter, the ash-free dry weight of the dried sample is generally the parameter most commonly used. This parameter is the mass loss observed upon the combustion of the dried sample at about 400 °C to constant weight, usually for 2 h (for a comparison of methods and a suggested standard procedure for marine sediments see Beyers et al. 1978). Care must be taken to ensure that the combustion temperature does not exceed 580 °C (400 °C according to other authors) in order to avoid the volatilization of sediment carbonates and thus incorrect results. This “loss on ignition” approach yields inaccurate results for sediments with a high content of clay. A more accurate discrimination between the different components of organic matter (e.g., organic carbon, proteins, lipids, carbohydrates) requires high-temperature oxidation (Bale and Kenny 2005). Another method to determine the organic carbon is to measure the reductive potential of the organic matter by titration.

A problem inherent in the assessment of organic content and, consequently, relevant to the analysis of meiofaunal nutrition and distribution is the inclusion of living organisms—microalgae and animals—in the bulk measurement of organic carbon. This is prone to cause a biased conclusion for the microbial and trophic potential of the sediment. Separation of the detritus-linked substances from the live organisms is possible by measuring the ATP content. The procedure for extracting ATP from sediment samples performed by Karl and La Rock (1975) uses the sensitive reaction of the luciferine test for oxidizing substances. However, the ATP contents of organisms vary with their living conditions and ontogenetic events. Consequently, the procedure must be carefully calibrated and the data replicated. The difficulty involved in many of these methods is not so much the technical procedure or the sensitivity of the measurement, but the correct interpretation of the data obtained. For an appropriate conversion of ATP content to weight in (nematode) biomass studies, Goerke and Ernst (1975) report an average ATP concentration of 1.35 mg ATP g⁻¹ wet wt of meiobenthos (nematodes).

Unless the oxygen conditions in the sediment are not adversely diminished, it can be generally assumed that an increase in organic matter will enhance meiofaunal abundance but will also change the community composition and the microdistribution (Ólafsson 1992; Creutzberg et al. 1984). Austen and Widdicombe (2006) were able

to experimentally show that, at intermediate doses, organic enrichment leads to an increase in the number of meiofauna, confirming that Huston's general model (Huston 1979) is also valid for meiofauna.

2.2.2 Dissolved Organic Matter (DOM)

Though often disregarded, dissolved organic matter represents a huge reservoir, 20–30 times greater than that of POM. It originates mainly from bacterial excretion and decomposition (Van Oevelen et al. 2006b), but also from the leaching of decaying plant and animal materials or exudation from bacteria and plants. Therefore, DOM in the mud of *Spartina* salt marshes reaches particularly high concentrations (Gardner and Hanson 1979, see Table 2.4). High DOM values are often due to essential fatty acids derived from plants. Secretion by meiofauna such as nematodes is another source of DOM (Moens et al. 2005). Labile nonhumic substances like sugars (glucose, galactose, sucrose), free amino acids (alanine, glutamic acid, aspartic acid, β -glutamic acid) and the refractory humic acids are the principal organic molecules which become highly enriched in the pore water; their concentrations in pore water are often one or two orders of magnitude higher than those in the overlying water. In freshwater habitats, where the concentration of DOM is even higher than in marine environments, dissolved organic matter plays substantial roles as both food and a possible source of attractants and releasers of developmental signals (Tranvik and Jørgensen 1995; Thomas 1997). The fluvial input into the oceanic pool is considerable. Neritic coastal zones are richer in DOM than the deeper oceanic sediments (Table 2.4). Dissolved free amino acids (DFAA) are

Table 2.4 Dissolved free amino acids (DFAA) and total dissolved organic carbon (DOC)—a comparison of open water and pore water concentrations

Comparison of open water and pore water concentrations			
	DFAA ($\mu\text{mol l}^{-1}$)		Reference
	In the water column	In pore water	
Seawater			
<i>Oceanic regions:</i>	0.5–1.0	12–50	Jørgensen (1979); Jørgensen et al. (1980)
	0.06–6.0	0.5–12.5	Thomas (1997)
<i>Coastal regions:</i>			
Mud	1.0–3.0	15–220	Stephens et al. (1978)
Estuarine regions	1.8–28.5	16.0–56.0	Jørgensen (1979)
<i>Spartina</i> salt marsh	8.9		Gardner and Hanson (1979)
	0.5–12.5	3.9–28.5	Thomas (1997)
Fjord, bight	1.3–2.6	8.7–28.5	Jørgensen et al. (1980)
Fjord, 40 m depth		0.3–3.8	Landén and Hall (1998)
Freshwater			
Lewes Brook, UK	0.6–1.3	30–60	Thomas (1997)
Lake Balaton, Hungary	0.04–0.5	40–90	Thomas (1997)
	DOC (mg l^{-1})		
	In the water column	In pore water	
Coastal regions (silt)	1.7	8.1	Farke and Riemann (1980)

particularly enriched in the upper 0–2 cm and often disappear in sediment strata below 10 cm.

Why is the concentration of DOM in the upper sediment layers so high compared to the overlying water despite these releasing processes? The deposition of degradable detritus is higher on the bottom and in the sediment while degradation is generally lower because of the frequent lack of oxygen. Hence, the sediment particles with their relatively large surface areas and considerable adsorptive forces “retain” DOM in the pore water of the sediment. “New” sand grains with sharp edges have been found to adsorb more glucose than older ones with “smoothed” surfaces (Meyer-Reil et al. 1978). The multitude of substances present in DOM necessitate detailed and complicated chemical analyses (Volk et al. 1997; Burdige 2002).

DOM is actively absorbed by either transepidermal uptake or “drinking” (intestinal uptake). Thus, intensive and permanent contact with the pore water system favors the utilization of DOM by bacteria and meiobenthic organisms (see Tranvik and Jørgensen 1995). This explains why sediments with high DOM concentrations are favored by meiobenthos, primarily by the soft-bodied ciliates, turbellarians and annelids with large relative surface areas (Petersen et al. 1988); but significant uptake also occurs in nematodes. An interesting new aspect of DOM uptake is the capacity of some nematodes to utilize acetate, which they can metabolize into polyunsaturated fatty acids, a pathway usually restricted to algae and bacteria.

Dissolved organic matter (DOM) is released from the sediment into the water column. The slow process of physical diffusion is accelerated by hydrodynamic forces (storms, currents and waves) and by sediment reworking through meio- and macrobenthic animals. This meiofauna-related increase in solute transport seems to be in the range of 1.5–3-fold (Aller and Aller 1992; Rysgaard et al. 2000). Through the concomitant exchange processes, the activities of benthic animals can enhance the physical diffusion of sediment-bound substances by orders of magnitude, thus counteracting the adsorptive and accumulating sedimentary processes mentioned above (see also Hylleberg and Henriksen 1980; Aller and Yingst 1985; Kristensen et al. 1995).

Habitats with high DOM concentrations in the sediment pore water such as flats, deltas and estuaries in the marine realm and eutrophic lakes in freshwater often attract meiobenthos, since DOM is intensively and primarily taken up by bacteria (Moriarty 1980), from which, in turn, the bulk of DOM is recycled (Van Oevelen et al. 2006a). Today, uptake rates of DOM are best indicated by radiotracer methods. Aside from the trophic aspects, the following section will point out that extracellular organic substances have an important structural effect, they cause agglutination of sediment particles, can increase sediment stability, and serve as signal substances that have informative value to aquatic organisms (Thomas 1997; Bale and Kenny 2005).

2.2.3 *Mucus, Exopolymers, and Biofilms*

In both marine and freshwater systems, exopolymer secretions (EPS) and mucous aggregates are considered key structures for the concentration and exchange of nutrients, for the formation of flocculent matter, often termed “snow,” and for the

nutrition and even transport of meiofauna (Yallop et al. 1994; Shanks and Walters 1997; Azam 1998; Wotton 2005). Organic carbon bound in colloids seems to represent a major carbon reservoir in seawater (Farke and Riemann 1980, Kepkay 1994). Microbial activity and coagulation by physical forces transform the colloids into aggregates to which flocculent detrital material adheres, forming nutrient-rich bioreactors. Mucus consists mainly of carbohydrates, especially polysaccharides and glucoproteins; a minor portion consists of loosely bound and labile amino and fatty acids (Meyer-Reil 1994). Passow (2000) regards transparent exopolymer particles as a “distinct group of polysaccharides” formed from dissolved precursor material. They coagulate particularly after phytoplankton blooming periods, but can also be experimentally generated. Condensed as macroaggregates (Logan et al. 1995), they contribute to the “marine snow/lake snow phenomenon” to which bacteria and meiofauna are closely associated (Shanks and Walters 1997; Heissenberger et al. 1996; Simon et al. 2002; Wotton 2005, see Chap. 7). Adhering detritus particles solidify this unconsolidated matrix and accelerate sedimentation.

The mucous biofilm that develops on the bottom is excreted mainly by benthic microorganisms, especially bacteria and diatoms (Meyer-Reil 1994; Smith and Underwood 1998), as well as by benthic meio- and macrofauna. Particularly the mucus trails secreted by nematodes, but also those secreted by harpacticoids, enhance bacterial growth (Moens et al. 2005; De Troch et al. 2005). Decho and Lopez (1993) speak of an “exopolymer microenvironment” of bacteria. Its rich nutrient content (especially polysaccharides) and its capacity to affect the flux of dissolved organics favor colonization with rich bacterial stocks. An EPS coating on sediment particles increases their bioavailability for particle-ingesting meiofauna. The specific composition of the biofilm seems of particular relevance to the growth, reproduction and developmental phases of meiofauna (Brown et al. 2003; Dahms et al. 2007). This underlines the considerable trophic importance of exopolymer secretions for the micro- and meiofauna, from allogromid foraminiferans in tidal flats (Bernhard and Bowser 1992) to harpacticoids copepods and nematodes (Koski et al. 2005; Moens and Vincx 1997a; Riemann and Helmke 2002; Wotton 2005), from freshwater ecosystems to the deep sea. Labile components such as free amino acids are even thought to act as sources of information and communication for the microbenthos (Meyer-Reil 1994; Thomas 1997).

While this superficial mucous biofilm is relevant nutritionally to meiofauna, it also modifies habitat characteristics, enhancing the cohesiveness and reducing the erodibility of the substratum (Yallop et al. 1994; Miller et al. 1996; Black 1997). Through this biostabilization of sediments, dissolved organics bound in mucus derivatives also contribute to the heterogeneous spatial and temporal small-scale occurrence of meiofaunal populations.

Decho (1990) contended that extracellular polysaccharides form “an extensive matrix of amorphous organic material which may provide the bulk of carbon sources for many benthic organisms.” In his seminal article, Azam (1998) states that microorganisms do not experience water as their ambient medium in the sediment, but rather a gel-like matrix of suspended polymers and colloids. He speaks of an “organic matter continuum” connecting DOM via colloids, aggregates and particle-embedded “suprapolymers” to POM. The carbohydrates that represent the

bulk of colloidal exopolymers can be readily measured (Underwood et al. 1995), but the physical structures of these mucoid and gelatinous substances in the void system, which determines the “world” of meiobenthos, are hard to demonstrate. The development of sophisticated methods (often fluorescence dyes) was required in order to visualize, manipulate and study these delicate mucous aggregates (Heissenberger and Herndl 1994; Heissenberger et al. 1996; Schumann and Rentsch 1998; Mari and Dam 2004; Neu et al. 2002).

Today, it is conceivable that the study of mucus secretions and mixed colloidal aggregations and the comprehension of their ecological role will gain importance in future meiobenthological research. It should be promoted more, despite the inherent technical problems (see Murray et al. 2002). Discussing the role of dissolved organics and exopolymers in freshwater, Thomas (1997) stated “The assumption that the energy flow in aquatic ecosystems can be quantified solely by measuring rates of photosynthesis, ingestion of solid food and its digestion by higher organisms, is invalid.” This certainly also holds true for the marine realm (Meyer-Reil 1994).

2.2.4 Bacteria

Bacterial abundance and biomass are several orders of magnitude higher (abundance: 1000×) in the sediment than in the water column. This huge bacterial stock is closely linked to organic debris (detritus) and usually accounts for 4% of the total organic carbon (Jørgensen et al. 1981; Kemp 1990; Schallenberg and Kalff 1993). Experiments have demonstrated that it is the bacterial film, not the detrital substrate, that is preferably utilized by the “detritivorous” meiofauna (Fenchel 1969, 1970; Hargrave 1972; Meyer-Reil and Faubel 1980). Hence, the rich coating of detritus with bacteria may attract high concentrations of meiofauna. As the plant debris ages, the bacterial colonization grows and the protein content increases. This, in turn, makes aged detrital particles more attractive to meiofauna (Warwick 1989). Also, animal remains decomposed by bacterial degradation can attract meiofauna (nematodes) in the sediment so long as oxygen is present (Gerlach 1977a; Ólafsson 1992; Debenham et al. 2004).

Other centers of bacterial growth include gradients, especially at the water/sediment interface and in the sediment at chemical gradients. Many sulfide-oxidizing microbes tend to concentrate in the oxic/anoxic interfaces of decomposing detrital particles, where they are exposed to irrigational fluxes and sediment reworking by infauna (Fenchel and Riedl 1970; Fenchel 1996). Here huge populations of “sulfur bacteria” are of considerable importance to meiofauna (Yingst and Rhoads 1980; Jørgensen and Bak 1991). Sulfur bacteria also thrive in fecal pellets produced by meio- and macrobenthos. Meadows and Tait (1985) found that bacterial numbers in fecal pellets in deep-sea sediments were several orders of magnitude higher than those in the surrounding sediments. In the anaerobic depths of nutrient-rich sediments, sulfate reducers and mat-building cyanobacteria develop rich populations (Jørgensen and Bak 1991; Stal 1991, Ramsing et al. 1993).

Attracted by nutrient aggregations, bacteria often occur in micropatches. These, in turn, are often the basis for the notorious patchy field distributions of bacterivorous meiofauna, even in seemingly homogeneous sediments (Blackburn and Fenchel 1999). In lentic coastal sediments the rich detritus/bacteria complex especially favors nematodes and other taxa linked to the “detritus/bacteria-based food chain.” In contrast, the more “microalgae-based” harpacticoids are less dependent on these factors (Montagna et al. 1989). A warmer climate or season favors bacterial growth. In temperate regions, peak populations occur in summer. In spring and summer, bacteria develop a characteristic extensive mucus coating and provide a rich mucoid nutritive source for deposit feeders (see below).

The capacity of meiofauna to distinguish between various microbes (bacteria, microfungi) and to select certain groups or even strains as food has repeatedly been shown experimentally. This is probably the case for all meiobenthic groups, e.g., ciliates (Fenchel 1969), nematodes (Tietjen and Lee 1977; Tietjen 1980a; Moens et al. 1997, 1999b), harpacticoids (Carman and Thistle 1985), oligochaetes (Chua and Brinkhurst 1973; Dash and Cragg 1972), and polychaetes (Gray 1966a,b, 1971). Montagna (1995) found that meiobenthic rates of feeding on bacteria vary with the developmental stage, in terms of both the amount and the quality of the microbial food. In some cases, the functional correlation between the structures of the mouth parts or buccal armatures and the shapes of the bacteria have been demonstrated in more detail (Wieser 1959, 1960; Jensen 1983, 1987a for nematodes; Marcotte 1984, 1986a; Romeyn and Bouwman 1986 for harpacticoids). Selective bacterivory of meiobenthos is thought to result in a bacterial-induced zonation (mainly nematodes), as demonstrated in laboratory sediment tanks (Boucher and Chamroux 1976), or is a mechanism for microniche segregation (Moens et al. 1999b). Considering the extremely high bacterial productivity (on average $324 \text{ mgC m}^{-2} \text{ d}^{-1}$, Kemp, 1990) the bacterial stock does not seem to be limited under natural conditions by meiofaunal grazing (see Sect. 9.3).

Quantifying the community structure and the abundance of bacterial microorganisms is a difficult task and not without serious methodological flaws. Bacterial number or biomass is typically underestimated and potentially inaccurate by a factor of two (Kemp 1990). The sonification of homogenized sediment in order to count bacteria is only 65–95% efficient. Direct counting of stained (vital dyes, fluorescent dyes) bacterial cells on the particle surface, although tedious, remains one of the more reliable procedures (DeFlaun and Mayer 1983). Even DAPI staining resulted in a considerable underestimate of the bacterial abundance (70%) and biovolume (60%) (Suzuki et al. 1993). Bacterial volume, a neglected parameter of relevance to metabolic processes, can be calculated more reliably through ultrastructural scanning methods (Kaye 1993). According to a detailed working protocol elaborated by Epstein and his group, the combination of careful sonification with tritiated thymidine or CTC labeling will result in particularly efficient enumeration of about 90–95% of the bacteria present (Epstein 1995; Epstein and Rossel, 1995a,b; Epstein et al. 1997). Moriarty (1980) recommends the determination of muramic acid as a good basis for calculations since this substance is a cell wall component of almost all prokaryotes. Another indirect method used to quantify sediment bacteria is the calculation of their biomass by phospholipid or ATP analysis (Findlay et al. 1989, Köster

and Meyer-Reil 2001). Schmidt et al. (1998) showed that scaling bacterial abundance to the fluid volume of pore water within the sediment yields a much greater consistency than traditional relations to dry sediment mass. Molecular screening techniques with general bacteria probes or the incorporation of radiolabeled markers (e.g., tritiated thymidine) are new methods that are increasingly being applied for quantitative recordings (e.g., Ramsing et al. 1993). Homogenization and subsequent Percoll flotation (Sect. 3.2.2) are also valuable improvements.

The numbers of sediment bacteria can vary considerably depending on the evaluation method, on the local microtopography and physiography, and on the sediment quality, water content and climate, but are mostly in the range of 10^8 – 10^9 cells per ml sediment. Hence, the figures in Table 2.5 probably cannot be generalized. Only in the past decade have modern methods yielded more reliable quantitative abundance data. Bacterial biomass, biovolume and productivity are more indicative than abundance data of the importance of bacteria as an eminent ecofactor for meiofauna. In many sediments, bacterial biomass and production is equal to or exceeds that of the macrofauna (Kemp 1990; Bergtold and Traunspurger 2005).

Usually, the bacterial density in sediments corresponds to the amount of degradable organic matter and is reciprocally related to the degree of exposure and the particle size of the sand fraction (Köster and Meyer-Reil 2001). Muddy bottoms and sea grass beds are microbially richer than sand, just as the wrack zone of a beach is richer than its surf zone or its sublittoral bottom. Moriarty (1980) found five times the amount of bacteria in seagrass beds than in the adjacent open sediment. The dependence of bacterial abundance on granulometry is demonstrated by the vertical profile in the North Atlantic (Vanreusel et al. 1995b) from the shelf to the continental slope (70–1,500 m depth). The sandy slope samples contain several orders of magnitude fewer bacteria than the deeper slope (Table 2.5). A rich supply of detritus and oxygen, for most microbes, makes the surface layers of the bottom more attractive than groundwater layers or the anoxic depths. Light-dependent cyanobacteria aggregate in mostly sandy sediments underneath a thin surficial mucus film (Yallop et al. 1994). On the surfaces of seagrass beds, 18% of all organic substances measured were contributed by live bacteria (Moriarty 1980), a significant nutritive amount, even for larger animals. In a sandy tidal flat, almost all of the carbon input was attributed to microbes (Joergensen and Mueller 1995). Typically, bacterial biomass equals about 4% of the total organic carbon (Kemp 1990).

However, the world of meiobenthic animals is determined by a three-dimensional pattern of microniches and particle surfaces. Even at the microscopic scale, sediment particles are colonized by qualitatively and quantitatively different bacteria; this in turn implies differences in the compositions of bacterivorous meiofauna. Colonization of sand grains seems to be proportional to surface area. One mm^2 of grain surface may be populated by up to 260×10^3 bacterial cells (Anderson and Meadows 1969)! This enormous number of bacteria is concentrated on only a very small portion of the huge overall surface (between <1 and 5%). The restriction may be caused by the limited diffusion of oxygen and nutrient molecules through the tortuous and long distances between densely packed particles (Watling 1991), and by micropatches of nutrients, as demonstrated by Blackburn and Fenchel (1999).

Table 2.5 Abundance of bacteria in various marine sediments

Habitat	Bacteria (per g dry sed.)	Reference	Bacteria (per cm ³ wet sed.)	Reference
Beach sand	9.8 × 10 ⁶ 14 × 10 ⁷ to 1.1 × 10 ⁹ 4 × 10 ⁸ to 28 × 10 ⁸ 0.3 × 10 ⁸ to 2.5 × 10 ⁸ 0.5 × 10 ⁹ 1 × 10 ⁹	Westheide (1968) Anderson and Meadow (1969) Meyer-Reil et al. (1978) McLachlan (1985) Moriarti et al. (1985) Epstein et al. (1997)	50 × 10 ³ to 500 × 10 ³ 10 ⁸ to 10 ⁹ 0.5 × 10 ⁸ to 3.9 × 10 ⁸	Boaden (1964) Kemp (1990) McLachlan (1985)
Mud to fine sand				
Tidal flats	2 × 10 ¹⁰ 1 × 10 ⁹	Meyer-Reil et al. (1978) Findlay et al. (1989)	7.5 × 10 ⁸ 2 × 10 ⁹ 1.2 × 10 ⁹ (mud) 1.7 × 10 ⁹ (sand) 3 × 10 ⁹ 2 × 10 ⁹ 4–17 × 10 ⁹ 1.7 × 10 ⁹	Epstein and Shiaris (1992) Kemp (1988) Steward et al. (1992) Steward et al. (1992) Dietrich (1999) Cammen (1982) Schmidt et al. (1998) Kemp (1988)
Salt marsh				
Brackish Estuary				
Mangroves	~10 × 10 ¹⁰	Alongi (1990a)		
Subtidal				
Antarctic			1.5 × 10 ⁵	Dietrich (1999)
Seagrass bed	1–6 × 10 ⁸	Danovaro (1996)		
Mediterranean	0.4–5.2 × 10 ⁹	Koller et al. (2006)		
Coral reef sand	1.6 × 10 ⁹	Alongi (1990a)	1 × 10 ⁸	Uthicke (1998)
Continental shelf slope	1.1–1.5 × 10 ⁹	Schmidt et al. (1998)	1.2–3.0 × 10 ⁶	Vanreusel et al. 1995b
Deep-sea mud	2–5 × 10 ⁸	Schmidt et al. (1998)	2–3 × 10 ⁸	Thiel et al. (1988/89)
Mud			0.1–3 × 10 ⁷	Tietjen (1992)
Lake sediment			6.3 × 10 ⁹ 4–12 × 10 ¹⁰	Schallenberg and Kalff (1993) Starink et al. (1996)

However, mechanical forces also seem to be responsible for the patchy colonization of bacteria. Microscopic inspections of sand grains have revealed the heterogeneous colonization of grain surfaces, with rich microbial clusters in depressions and cracks and barren areas along the edges (Fig. 2.12; see Meadows and Anderson 1966, 1968; Weise and Rheinheimer 1978; DeFlaun and Mayer 1983). On these exposed edges, the destruction of bacteria through the intense agitation of grains by waves or heavy rainfalls is particularly important, while they have more protection in areas of low relief. Thus, exposure and particle size may contribute to the relative scarcity of bacteria in the exposed upper eulittorals of beaches compared to sheltered flats. Large grains ($>300\text{ }\mu\text{m}$ diameter) with fairly smooth surfaces are inhabited by bacterial flora that differ quantitatively and qualitatively from those on smaller particles with many crevices and depressions (Marcotte 1986a) and those of the water column. The relatively small surfaces of silt particles $<10\text{ }\mu\text{m}$ diameter were found to be devoid of bacteria (DeFlaun and Mayer 1983).

According to Azam (1998), many bacteria are found in the transparent gelatinous fabric filling the void system, and are not attached to solid substrates. This would explain why the fresh sediment volume or the fluids contained therein are more appropriate as units to relate to bacterial numbers than the sediment dry mass (Schallenberg and Kalff 1993; Schmidt et al. 1998). The large fluid component may particularly contribute to the rich bacterial populations in fine, silty sediments.

Data on the production and carbon flux of sediment bacteria are given in Sect. 9.4, but in nature only a small proportion represents active cells that contribute to production (Novitzky 1983), which reduces the value of bacterial counts. In the profound experiments by Van Oevelen et al. (2006 a,b) from an intertidal flat, which integrated tracer experiments and modeling, it became evident that most bacterial production (65%) was respired and remineralized back to dissolved organic carbon, while only 3% was consumed by meiobenthos and 24% by macrobenthos. Considering the

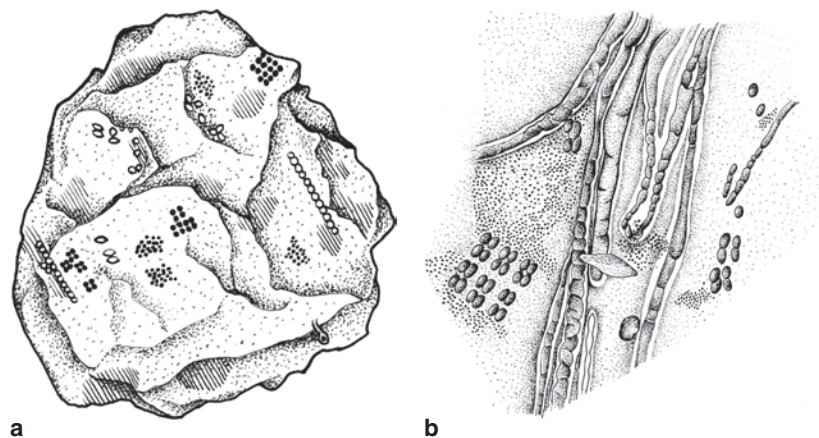


Fig. 2.12a–b Colonization of a sand grain by microorganisms. **a** Overall aspect. **b** Detail. (After Meadows and Anderson 1966)

extremely high bacterial productivity (on average $324 \text{ mg C m}^{-2} \text{ d}^{-1}$, Kemp 1990), the bacterial stock does not seem to be limited under natural conditions by meiofaunal grazing (see Sect. 9.3). In microcosm experiments (Traunspurger et al. 1997), grazing by freshwater nematodes stimulated bacterial activity rather than having a strong grazing impact. In sediments of the North American Great Lakes, bacteria were calculated to contribute about half of the organic matter taken up by metazoa (Schallenberg and Kalff 1993). The numerous relationships between bacteria and meiofauna, reviewed by Coull and Bell (1979), Tietjen (1980a), Kemp (1990, 1994) and Montagna (1995), will be detailed later when dealing with the position of meiofauna in the benthic food web (Sect. 9.4). Here, it is concluded that the significant impact of bacteria on the habitat of meiofaunal organisms makes cooperation between meiobenthologists with sediment microbiologists indispensable to obtaining a profound ecological understanding.

More detailed reading: Detritus: Warwick (1987); dissolved organic matter: Jørgensen (1976); Sepers (1977); Stewart (1979); Aller and Yingst (1980); Ferguson (1982); Stephens (1982); Reichelt (1991); Aller and Aller (1992); Thomas (1997); mucus and exopolymers: Decho (1990); Azam (1998); Simon et al. 2002; Krumbein et al. (1995); Wotton (2005); especially meiobenthos: Tempel and Westheide (1980), Montagna (1984); bacteria: Tenore and Rice (1980); Tietjen (1980); Kemp (1990, 1994); Epstein (1997a, b); reviews: Meyer-Reil (1994); Murray et al. (2002); freshwater: Schallenberg and Kalff (1993).

2.2.5 *Microphytobenthos*

Unicellular microalgae, mainly diatoms and dinoflagellates, act, together with bacteria, as biotic habitat factors for meiofauna through their trophic value and mucus production. In coastal sediments, the microphytobenthos has a central role in carbon flux (MacIntyre et al. 1996, Middelburg et al. 2000). In a study from a Mediterranean seagrass bed, microalgae accounted for 25% of all organic carbon, while bacteria only contributed 5% (Danovaro 1996). Microphytobenthos provided 15–20% of total primary production in brackish muds (Gerbersdorf et al. 1999). Even in the brine network of Arctic sea ice, diatoms have been calculated to represent 26% of the total biomass (Gradinger et al. 1999; see Sect. 8.1.1). Hence, microphytobenthos has been considered a “secret garden” of enormous ecological importance in shallow water habitats (Miller et al. 1996). In recent years relevant papers on benthic diatoms underlined this most important food source for the benthic fauna.

Diatoms prefer the upper, light-exposed layers of sheltered, often silty bottoms (Wiltshire 2000) where they can grow to considerable densities ($20 \times 10^3 \text{ cells cm}^{-3}$ sand or up to $16 \times 10^3 \text{ cells cm}^{-2}$, and sometimes even up to $7 \times 10^7 \text{ cells cm}^{-3}$; Fenchel and Straarup 1971). In flats on the island of Texel, about 5×10^6 diatom cells were counted per cm^2 in mud, and only 2×10^6 cells per cm^2 in sand (Yallop et al. 1994). Other authors found densities in the same range (see Round 1971). From coral reef sand, $1.7\text{--}2.4 \times 10^{-6} \text{ cells cm}^{-3}$ dry sand has been reported (Uthicke 1998). In the polar sea ice, diatoms preferentially grow in the deeper layers. Since the penetration

of light is only 1–2 mm in mud and up to about 2 cm in coarse sand (long-wave red light; for details and modern methods see Lassen et al. 1992, Kühl et al. 1994), in the presence of light, the uppermost 0.2 mm harbored most of the diatoms, while in the dark the distribution was more homogeneous (De Brouwer and Stal 2001).

However, living diatoms and flagellates are repeatedly found down to 5 cm, and have even been recorded at horizons as deep as 20 cm (Taylor and Gebelein 1966; Steele and Baird 1968; Fenchel and Straarup 1971; Wasmund 1989). Correspondingly, at a depth of 5 cm, 20–50% of the surficial chlorophyll concentrations can still be measured. The layer between 0.5 and 2.0 cm depth still provided 40–60% of the diatom biomass (De Jonge and Colijn 1994). Viable diatoms (and other algae) have also been discovered in considerable numbers in the sediment of aphotic subterranean aquifers (Kuehn et al. 1992). For beaches, this unusual distribution for photosynthesis-dependent cells is interpreted as being a result of sediment turbation; however, vertical migrations have also been considered (Janssen et al. 1999). Long-lasting phases of passive resting and intermittent metabolism have also been suggested. There is even supposition that some groups of diatoms can live heterotrophically. Detailed information on the vertical fine-scale distribution of diatoms and associated chemical gradients has been obtained through the use of a “cryolander,” a corer which, in combination with freezing techniques, can retrieve undisturbed mm-samples (Wiltshire et al. 1997).

In tidal flats, the highest population densities of diatoms have been recorded in spring and partly in autumn (Asmus and Bauerfeind 1994). In the Danish Wadden Sea, temperatures correlated with the photosynthetic rate of diatoms, while high salinities and pH values decreased it (Rasmussen et al. 1983). In superficial sediments and depending on the season, microphytobenthos contributed between 3 and almost 17 g C per m² y⁻¹ (De Jonge and Colijn 1994) in estuarine superficial sediments; Round (1971) reported a production of marine diatoms of 100–200 g C m⁻² y⁻¹ in the intertidal. Considerably lower values were reported by Guarini et al. (1998) from a French bay, but even so, about 30–90% of all of the chlorophyll a suspended in the water column was contributed by microphytobenthos. Seasonally varying values of between 90 and 170 g C m⁻² y⁻¹ were recorded as the net production of diatoms in coral reef sand (Uthicke 1998).

Microphytobenthos in tidal flats apparently have a specific spatial microdistribution (Round 1971) which can be associated with various macrobenthic zones (Asmus and Bauerfeind 1994). Saburova et al. (1995) stated that the differentiated spatial structure of diatoms and dinoflagellates in a polar tidal flat was due to the interaction of the biogenic, interspecific effects (small scale) with the granulometry (meso scale) and the emersion period (large scale); see Fig. 2.13.

Many ciliates, harpacticoids, nematodes and oligochaetes often feed exclusively on diatoms. With their specialized mouth structures they can differentiate between various algal species of different shapes (see Fig. 5.20); Brown and Sibert 1977; Pace and Carman 1996; Azovsky et al. 2005; De Troch et al. 2005). The close linkage of many meiofauna, especially the “microalgae-based” harpacticoids (Montagna et al. 1989), to diatoms as a predominant food source was experimentally demonstrated by the rapid and preferred uptake of labeled diatom carbon (Riera et al. 1996; Middelburg et al. 2000), and is evidenced by the numerous test remains in copepod fecal pellets.

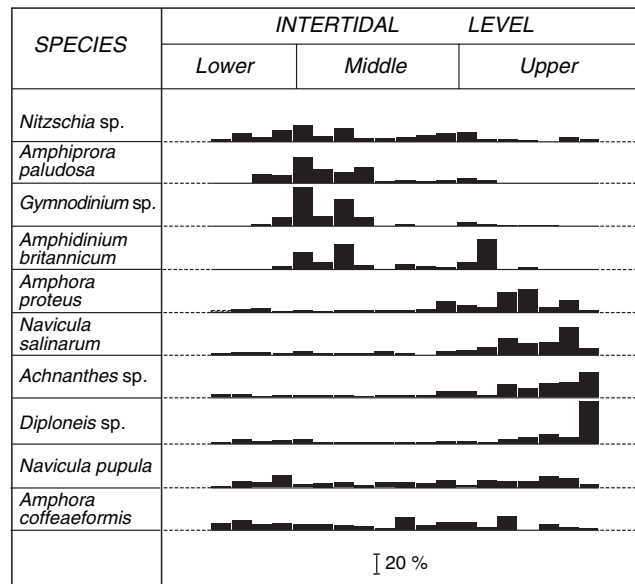


Fig. 2.13 Zonation of benthic diatoms along an intertidal profile in the White Sea. (After Saburova 1995)

In the upper sediment layers numerous spatial and temporal microscale processes tightly link microalgae and meiofauna. The occurrence of diatoms can determine the microdistributions of meiobenthic food specialists (e.g., peaks of naidid oligochaetes in tidal flats coincide with spring blooms of diatoms, Giere and Pfannkuche 1982). Diatom patches were found to correlate directly with aggregations of meiofauna (Montagna et al. 1983; Blanchard 1990). This is understandable considering the intensive utilization rate of microphytobenthos by meiofauna: Escaravage et al. (1989) calculated that 27% of all benthic microalgae were being devoured by meiofauna in a shallow lagoon, 38% in oyster beds, and as much as 89% in seagrass beds. In a Louisiana tidal flat, Pinckney et al. (2003) even found that the meiofaunal grazing rate sometimes exceeded the biomass of benthic microalgae, although, in terms of productivity, the meiobenthos grazed only 17% of the net primary production. The corresponding value in a polar tidal flat was 3–11% (Azovsky et al. 2005), and in a temporarily closed South African estuary 11% (Nozais et al. 2005). In sublittoral sites Montagna et al. (1995) found indications of a diet shift of meiofauna away from the preferred microalgae to bacteria when the algal supply became scarce. This nutritive linkage also explains the decreases in various meiobenthos after experimental inhibition of diatom growth (Hentschel and Jumars 1994). The attractiveness of microalgae as food for meiofauna may be based on their high content of polyunsaturated fatty acids (PUFAs) (Coull 1999, see Sect. 2.2.2). A high proportion of 16:1 ω 7 fatty acids can even be used as a marker indicating that diatoms are a preferred nutritional source.

However, even during periods of high grazing pressure, microalgal productivity was more than sufficient to sustain the meiobenthic consumers. The degree of control meiobenthos exerted on the diatom stock varied greatly. The diatom production in a network of brine channels in Arctic sea ice was in the same range as the ingestion rates of the numerous sympagic (sea-ice-living) meiofauna. Thus, in this special habitat, it was thought to be controlled by the meiofauna (Gradinger et al. 1999). Apparently the meiofaunal impact depends on regional and climatic factors, but also on the specialization for particular food species (Azovsky et al. 2005).

Microphytobenthos is not only of considerable nutritional importance to meiofauna; it also alters the structure and chemistry of the sediment. Through their intense production of mucous substances, the microphytobenthos compact the sediment and enhance its cohesiveness, reduce erosion, and generally modify the activities of the fauna (DeFlaun and Mayer 1983, Madsen et al. 1993, Miller et al. 1996; Black 1997; Widdows et al. 2000). This biostabilization by diatoms has an indirect trophic effect. Mucus can form dense coatings on the sediment which, in turn, promote bacterial growth (see above). On the other hand, massive macrofaunal bioturbation can increase the production of microphytobenthos by enhancing nutrient fluxes (Lohrer et al. 2004). The assimilatory oxygen production of microalgae lowers the oxic/sulfidic threshold diurnally with considerable consequences for the vertical distribution of meiofauna (Fig. 2.8b; page 29).

Studies by Ólafsson et al. (1999) and Josefson and Hansen (2003) drew attention to another group of microalgae in the sediment. In Scandinavian coastal sediments they found that common planktonic species occurred regularly in the upper sediment layers, thus providing an additional trophic source for meiobenthos. Especially for copepods and ostracods, but also for nematodes, settling phytoplankton seems to be an important food source (Modig et al. 2000), either directly or via an increase in bacterial decomposers.

Microphytobenthos is frequently considered to consist solely of benthic diatoms. However, it is becoming increasingly clear that benthic flagellates, mainly heterotrophic Dinoflagellata, are also relevant (Patterson et al. 1989; Hoppenrath 2000; Patterson et al. 1989), and must be considered when dealing with phytobenthos in meiobenthic habitats. In North Sea flats of the Netherlands, there were $50\text{--}300 \times 10^3$ flagellates per ml surface sediment (Bak and Nieuwland (1989), which is somewhat more than the measurements obtained by Epstein and Shiaris (1992) for flagellates on a muddy flat near Boston (10×10^3). Mangrove mud contained about 150 flagellates per cm^2 (Alongi 1986). In brackish bacterial mats, Fenchel (1969) often found a flagellate abundance of 100 to $>100 \times \text{cm}^{-2}$. Voids of sand, especially exposed sand, seem less densely populated: Helsingør beach (Denmark) yielded several $100 \times \text{cm}^{-2}$; sandy flats of the island of Sylt only about 100–200 interstitial flagellates cm^{-3} (Hoppenrath 2000), belonging to about 140 taxa; and a beach at Roscoff (France) exhibited up to 2,000 mesopsammal flagellates cm^{-2} (Dragesco 1965). Sea ice harbors a considerable number and biomass of active flagellates, with a production only somewhat lower than that of diatoms. Freshwater sites also seem to be rich in flagellates, but numbers fluctuate heavily with season: in eutrophic limnic sediments, between $1\text{--}16 \times 10^3$ cells cm^{-3} were retrieved (Gasol 1993; Starink et al. 1996, see

also Kemp 1990). In oligotrophic lake sediments mean densities of about 80×10^3 flagellates were observed (Bergtold and Traunspurger 2004). As with bacteria, quantitative data may vary by orders of magnitude depending on the extraction methods used. Flotation methods yielded efficiencies of between 73 and 100% (Alongi 1986; Starink et al. 1994). Fixation can cause considerable shrinkage of both diatoms and microflagellates and has to be corrected for in order to avoid inaccurate estimates of biovolume and thus carbon biomass (Menden-Deuer et al. 2001).

Closely linked to bacteria, most of the dense populations of flagellates in tidal sediments are heterotrophs grazing intensively on bacteria. However, at least in freshwater, the immense amounts of bacteria produced appear to be only marginally consumed (up to 5%, Kemp 1990; Starink et al. 1996; Hondeveld et al. 1992; Hoppenrath 2000). Using a new fluorescence technique, Starink et al. (1994) calculated that in lake sediments up to 70 bacteria were consumed per protist per hour, while in marine sediments the corresponding consumption was only around five bacterial cells. Microdistribution and abundance patterns also suggest a close trophic correlation between flagellates and ciliates (Santangelo and Lucchesi 1995), a link that had been observed earlier by Fenchel (1969). Kemp (1990) emphasized the preferred occurrence of flagellates in organic-enriched detrital surface layers of the sediment, while ciliates were more linked to the interstices of sand. A differentiating trophic specialization within the microphytobenthos was evident in tidal sand: Epstein et al. (1992) found that ciliates devour 93% of the dinoflagellate production, in contrast with only 6% of the diatom production. Dietrich (1999) contends that in brackish sediments rich in organic matter, about half of the flagellate stock is consumed by meiobenthos.

More detailed reading: Round (1971); Patterson et al. (1989).

Box 2.6 Microphytobenthos: The Garden of Meiofauna

About 20% of all organic carbon is produced by diatoms and flagellates in the uppermost millimeters of shallow sediments. Some 10^3 to 10^4 cells live in each cm^3 of sediment. Combined with their high nutritive value, this emphasizes their central role in the world of meiofauna, where they often mediate between bacteria and meiofauna. Through their oxygen production and light-dependent migrations they provide the sediment layers with oxygen. Many meiofaunal groups have specialized on diatoms as a food source and linked their population dynamics to the annual peaks in their production (spring and autumn in temperate regions). Benthic, mostly heterotrophic flagellates are important bacterivores, however, their nutritional role for meiobenthos is not well known. Particularly in the surface layers, where both microphytobenthic groups co-occur, they can regulate the temporal and microdistributional patterns of meiobenthos. Due to their rich mucus secretion, diatoms produce a nutrient film for bacteria and an effective coagulant that protects sediment particles against erosion.

2.2.6 *Higher Plants*

Sessile macroalgae and seagrasses have a physically structuring effect that influences meiofaunal settlement and distribution (Wieser 1959b). The reduction of sediment agitation and the enhancement of particle suspension under a plant canopy favors meiofaunal abundance. Culms, thalli, mangrove pneumatophores, and holdfasts provide numerous niches and protection for small animals. These plant structures expand the available living space for meiobenthos from the sediment into the water column and into the phytal (see Sect. 8.5). Delicately branched algae or the fuzzy culms of seagrasses are more densely inhabited by meiofauna than the smooth thalli of algae or the blades of seagrass. Conversely, minute epigrowth organisms on plants (e.g., mucous tubes) favor meiofaunal colonization (Peachey and Bell 1997; Gwyther and Fairweather 2002). Plant roots and shoots have a similar structural effect in the sediment. Thus, structural complexity is often positively correlated with meiofaunal abundance and diversity (Remane 1933; Hicks 1985; Hall and Bell 1988; Hull 1997). This has also been experimentally tested using artificial substrates of various complexities (Atilla et al. 2005).

In addition, there are also chemical and nutritional effects by which plants can influence the habitat conditions of meiofaunal biotopes. Enhanced bacterial growth at the frequently damaged and leaching frond ends of plants indirectly promotes the trophic possibilities for meiobenthos. Live plant roots have been found to metabolically create a favorable micro-oxic gradient system in their surrounding sediments (Teal and Kanwisher 1961; Lee et al. 1999), enhancing the density and heterogeneity of (nematode) meiofauna (Osenga and Coull 1983). Algal cover on soft bottoms was found to favor the development of meiofauna in mesocosm experiments (Ólafsson et al 2005). When decaying, the leaves of seagrasses represent an attractive and important source of valuable detritus (see Sect. 2.2.1).

An aggravating impact on the meiobenthos by mechanical disturbances has been shown by Hicks (1989). His field experiments indicated that (artificial) seagrass not only promotes meiofaunal populations, but can also disturb mainly epibenthic meiofauna assemblages, probably through the sweeping action of the blades and alteration of the microtopography (depressions, ripples). Lower numbers of meiofauna on mangrove pneumatophores as compared to mimics may result from the secretion of anti-fouling substances produced by the plants (Gwyther and Fairweather 2005). A discussion of other effects of plants relevant to meiofaunal habitat will be presented in Sect. 8.5, which deals with the phytal.

2.2.7 *Animals Structuring the Ecosystem*

The effects of macrobenthos on the habitat conditions of meiobenthos are extremely variable, species-dependent and are often not clearly delimited (Ólafsson 2003). They comprise both negative interactions and positive, facilitative effects.

Among the negative interactions, we can differentiate: (a) mechanical disturbance; (b) reduction by sediment ingestion; and (c) alterations of the chemical milieu.

- (a) Mechanical disturbances can be produced in areas with water currents by protruding macrofaunal tubes, which, enhance the boundary friction of the sediment and thus can exert an erosive force that negatively affects meiofauna (Eckman 1979; Gamenick and Giere 1994; Widdows et al. 2000; Ólafsson 2003). The spacing, the density and radius of the tubes largely govern whether the network of animal tubes will impair or promote meiofaunal life (see below). Those meiofaunal groups with a more passive, strictly sediment-bound lifestyle (nematodes, annelids) will be less affected, while the more epibenthic and temporarily suspended harpacticoids are more strongly affected (McCall and Fleeger 1995).

Mechanical disturbance is caused also by disruption and reworking of the sediment, due to the digging of horse shoe crabs, rays, crabs, molluscs and sea urchins, the pipetting of *Tellina* (Bivalvia) siphons, and reworking by anthozoans, polychaetes, priapulids, amphipods, echinoids, fish and birds (Creed and Coull 1984; Reise 1987; Warwick et al. 1990 b; Hall et al. 1991; Ólafsson and Moore 1992; Ólafsson and Ndaro 1997; Aarnio et al. 1998). Meiofauna is usually considered relatively insensitive to disturbance and less persistently affected than macrofauna (Alongi 1985; Austen et al. 1989; Hall et al. 1991). Nevertheless, in open tidal flats, lugworm activity (*Arenicola*) led to a decrease of about 20% in meiofaunal density, as shown by exclusion experiments (Reise 1987, 2002). Physical disturbance (experimental raking) had a clearly negative effect on intertidal meiofauna (Austen and Widdicombe 2006). A study performed by Warwick et al. (1990b) enabled a discrimination of mechanical disturbance that reduced the stability of the sediment from pollution stress. The impact of shore crabs (*Carcinus*) on nematodes seems to be sediment-related (Schratzberger and Warwick 1999b): disturbance dominated in muddy bottoms, while predation prevailed in sands. Usually, disturbance-induced losses of meiofauna in tidal flats soon recover (see Sect. 9.1 on recolonization; Sherman and Coull 1980; Ólafsson and Moore 1990; Warwick et al. 1990b; Hall et al. 1991). The recovery potential of meiofauna in the deep sea is unknown, but disturbance-induced negative impacts of large epifauna on meiofauna have been documented (Thistle et al. 2008).

- (b) Sediment ingestion, the second impact type, occurs wherever deposit-feeding macrobenthos prevails: the feeding galleries of *Arenicola marina* contain lower numbers of nematodes (Jensen 1987a; Reise 1987); a negative impact of intensive digging was also noted for the priapulid *Halicryptus* (Aarnio et al. 1998). However, the reduction apparently depends on the intensity of the reworking and was not noted for other sediment feeders. The negative effects of disturbance by sediment ingestion can gradually merge into predator–prey relationships, particularly when meiofauna and macrofauna interact (meiofauna vs. burrowing polychaetes, crustaceans or fish, see Sect. 9.4.2). Disturbance (and predation) will mainly affect the meiofauna at the sediment surface and the upper sediment layers (Bell 1980). Some groups may react by performing

downward migration, which creates surface layers with reduced meiofaunal abundance. Effects of direct predation on meiofauna by macrofauna will be considered elsewhere (see Sect. 9.4.2).

- (c) Alterations in the chemical milieu, the third type of impact of macrobenthos on meiobenthos, affect meiofauna in mussel and oyster beds where thick layers of organic debris, fecal pellets and decaying algal mats accumulate. Here, oxygen soon limits the meiofauna in the layers beneath (Dittmann 1987; Diné et al. 1990; Neira and Rackemann 1996; Reise 2002). Brominated compounds excreted by some echinurids and enteropneusts into their tube-wall linings have been suggested to exert a toxic impact on bacteria and meiobenthos (King 1986; Jensen et al. 1992b). In deep-sea bottoms, manganese diagenesis may be affected by meiofaunal oxygen consumption (Shirayama and Swinbanks 1986).

Among meiobenthic animals, the competition (mostly) caused by identical nutritional resources can structure the ecosystem. Trophic competition can cause spatial niche segregation and can ultimately lead to amensalism or mutual exclusion (e.g., Fenchel 1968a for ciliates; Joint et al. 1982 for nematodes). This exclusion has been documented as a within-group effect among meiobenthic species (nematodes, Ott 1972a; Alongi and Tietjen 1980, Santos et al. 2008a; harpacticoids, Chandler and Fleeger 1987). However, competitive exclusion has even been described between taxonomically distant meiofaunal groups (foraminiferans vs. harpacticoids, Chandler 1989; oligochaetes vs. turbellarians, Dörjes 1968; capitellid polychaetes vs. nematodes, Alongi and Tenore 1985; ciliates vs. nematodes, Bergtold et al. 2005). Competition can also result in a shift in life history characteristics (Heip 1980a, Marcotte 1983). A good example is the mutual exclusion of two species of the ciliate genus *Condyllostoma*, *C. arenarium* and *C. remanei*, which have contrasting population dynamics, with maximum numbers occurring in June and November, respectively (Hartwig 1973b).

Many negative interactions among certain meiofaunal taxa are difficult to analyze. Is the mutual exclusion of enchytraeid oligochaetes and turbellarians in the upper sandy beach, reported by Dörjes (1968), a result of trophic competition or merely an unknown, animal-mediated factor? Why is there a negative interrelation between the naidid *Amphichaeta sannio* and the nematode *Tobrilus* in the freshwater flats of the River Elbe (Schmidt 1989)? What causes the negative correlation between ciliates and freshwater nematodes (Bergtold et al. 2005), or that between the two bacterial symbiotic nematodes *Catanema* and *Astomonema* in mangrove muds (Bezerra et al. 2007). These questions remain largely unanswered. The causative factors of the inverse relationship between the harpacticoid *Tisbe furcata* and nematodes (Warwick 1987) and the contrasting population fluctuations of the gastrotrich *Turbanella hyalina* and its annelid counterpart *Protodrilus symbioticus* (Boaden and Erwin 1971) are also unknown. Similarly, the negative interaction between the foraminiferan *Ammonia beccari* and the harpacticoid *Amphiascoides limicola* in muds from tidal flats (Chandler 1989) has not been conclusively explained.

Of particular relevance and widespread occurrence is the mutual regulation between permanent and temporary meiofauna (Elmgren 1978; Warwick 1989), which is in fact a series of effects ranging from predation to sediment reworking.

Permanent meiofauna, through their more effective and intensive feeding activities, initially attenuate the population development of newly settled polychaetes, bivalves, and very young amphipods. Subsequently, the growing macrofaunal species, through their intensive sediment reworking and their direct predatory impact, have an aggravated negative influence on permanent meiofauna (Bell and Coull 1980; Watzin 1986). The extent to which large beds of suspension-feeding bivalves reduce suspended meiofaunal populations in tidal flats needs to be experimentally verified. First studies do not suggest a density reduction (Boeckner, Recife: O 10).

Examples of positive mutual effects between species arose from experiments by Reise (1983), where the bioturbation of lugworms enhanced solute fluxes and acted positively on the development of bacteria and meiofauna. Facilitative effects among nematode species were also reported by Santos et al. (2008a,b). Other effects are of a more indirect nature, yet their impact on the structure of the habitat, increasing habitat heterogeneity, can be considerable. Levin et al. (1997) considered the rapid subduction of plant material into the sediment by nonselective macrobenthic deposit feeders (some polychaetes or sipunculids) to be a “keystone resource modification” which massively influences the structure of the bottom and the fate of settling organic matter (see also Sect. 2.2.1 and 9.4).

This example shows that besides the animals themselves, animal-produced structures can also positively influence meiofauna (Murray et al. 2002; Ólafsson 2003). Tubes and burrows and mounds piled up by benthic animals can have a massive impact on the habitat conditions of meiofauna. Around the tubes of macrobenthic polychaetes, nematode numbers were up to five times higher than in the unstructured controls. The small mounds around the openings created by many crustaceans in soft sediments have been documented to massively influence the hydrodynamics of the water on a microscale and thus to modify the influx of oxic surface water and the drainage of pore water (Hüttel et al. 1996; Ziebis et al. 1996). Nematode numbers were doubled along the tubes of thalassinid decapods in sublittoral Mediterranean sand, and foraminiferans increased as much as a hundredfold in number (Koller et al. 2006). In the deep sea, where animal-created structures tend to persist for long periods, distinct habitat patches of polychaetes fostered the abundance of harpacticoid copepods (Thistle et al. 1993). Intensive promotion of meiobenthos colonization by macrofaunal burrows and tubes was found to be responsible (among other factors) for meiofaunal spatial patchiness. This close interdependence has been simulated by mathematical models that show a good agreement between the model and sample situations (Pfeifer et al. 1996). Such modeling needs to be used more commonly in meiofaunal research.

One important stimulus is the enhanced bacterial growth resulting from tube flushing effects, which profoundly influence the porewater circulation and the geochemistry of the bottom (Alkemade et al. 1992; Webster 1992; De Beer et al. 2005a; Weber et al. 2007). Burrows of decapod crustaceans, especially those of thalassinids, can be termed “hot spots” for bacteria and meiofauna (Förster and Graf 1992 in the North Sea; Koller et al. 2006 in the Mediterranean; Dittmann 1996 in Australia). However, meiofaunal populations also more than doubled the transport

rates of solutes (Aller and Aller 1992; Rysgaard et al. 2000), an increase that is particularly important for the transport of oxygen in the deeper layers (Zühlke et al. 1998). In freshwaters, the bottom is often densely covered by protruding tubes and mounds of tubificid oligochaetes, which exert a corresponding positive role on the geochemistry at the sediment/water interface.

Another stimulus with a positive effect on meiofaunal populations is the secretion of exopolymers and the enrichment with fine organic particles. This will solidify the texture and enhance organic content and bacterial stocks (Eckman et al. 1981, Dobbs and Guckert 1988; Meadows and Tait 1989; Meadows et al. 1990; Decho 1990; Nehring et al. 1990; Jensen 1996).

Macrofaunal tubes can also provide protection for meiofauna from predators and thus have a positive effect (Bell and Coen 1982). As a result of biogenic structures in/at the bottom, meiofaunal species richness increased (Ólafsson 2003). A network of more or less permanent tubes can also be produced by some meiofauna, preferably in silty sediments, but also in mucous biofilms (harpacticoids, Chandler and Fleeger 1984; Williams-Howze and Fleeger 1987; nematodes, Cullen 1973; Riemann and Schrage 1978; Platt and Warwick 1980; Nehring et al. 1990; Jensen 1996; Fenchel 1996a; Mathieu et al. 2007). As a result of biogenic structures in/at the bottom meiofaunal species richness increased (Ólafsson 2003).

Considering this array of factors that are beneficial to meiofauna, it is understandable that the positive effects of biogenic structures have been suggested to yield 10–50% of the meiofaunal colonization of tidal flats (Fig. 2.14), with even higher figures for harpacticoids and gnathostomulids (Reise 1981a). In exclusion experiments, the presence of lugworms was estimated to promote the abundance of >90% of meiofauna (Reise 1983).

In recent years, various large-scale, man-made physical disturbances have affected the biotopes of meiofauna with increasing intensity and frequency, including maintenance dredging and habitat (beach) enhancement. Climatic extremes, intense fishing with bottom trawls and dikes and other constructions along the shores and waterways have escalated erosive forces in the last few years. Maintenance dredging and habitat (beach) enhancement have become regular counteractions by which huge masses of unconsolidated sediment are mechanically distorted. Amazingly, the meiofauna appear to recover much more quickly from these maximal disturbances than macrofauna, as micro/mesocosm experiments and large-scale field surveys have shown (Schratzberger et al. 2006; Bolam et al. 2006). Supported by meticulous statistical analyses, they disclosed that the impact of this mechanical sediment distortion was mitigated by the concomitant intensive transport of meiofauna with slush water and intensive migration activities. The meiofaunal species richness recovered from an initial reduction after relatively short periods (weeks), while density reductions remained for longer periods (>1 year) than in the reference areas. In sandy habitats recovery was quicker than in mud, and nematodes were less affected than harpacticoids. The recolonization processes of meiofauna in the freshly consolidated sediments must be differentiated. They not only follow passive settling, but also depend on the water transport capabilities of the taxa and their reproductive potentials (see Sect. 7.3).

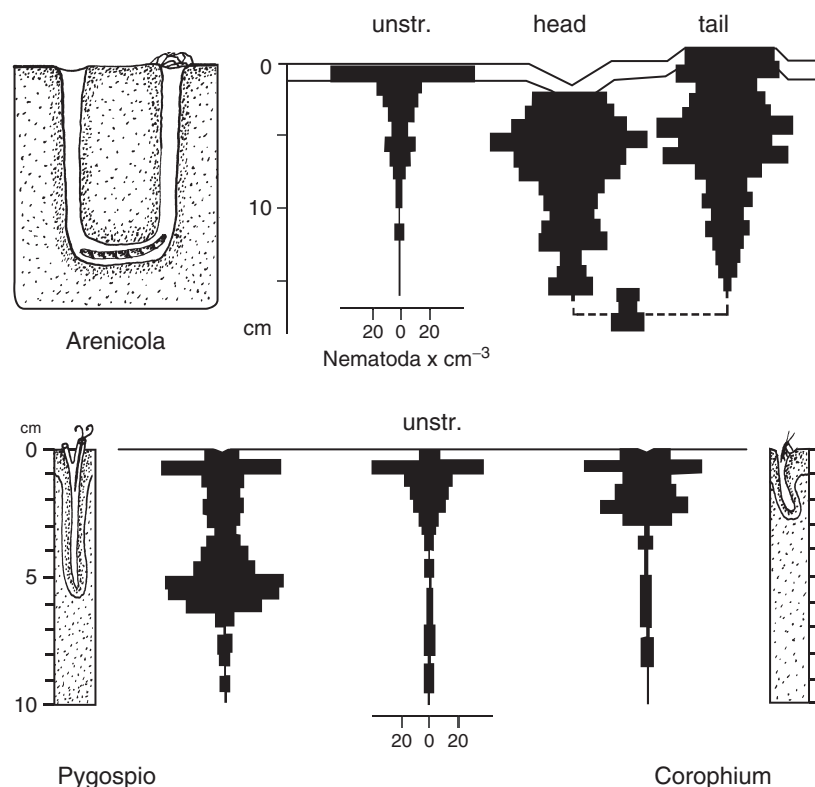


Fig. 2.14 Impact of biogenic structures on meiofaunal density. Nematodes around burrows of various tidal flat macrofauna in comparison with unstructured (*unstr.*) reference sites. (After Reise 1981a)

Box 2.7 Animals as Habitat Factors

Direct interactions between meiobenthic animal groups often result in competition, niche partitioning or even mutual exclusion. Structuring effects through food competition are hard to delineate from predator–prey relations, especially when dealing with macrofauna–meiofauna interactions, but have even been documented between unrelated meiofaunal groups. Disturbance (the other animal-mediated structuring source), on the other hand, is due not only to predation but also to bioturbative effects. Mechanical disturbance of meiobenthos is mostly the result of sediment reworking by digging or bulldozing macrofauna, and has mostly adverse effects on meiofauna. However, only extreme and long-lasting disturbing effects tend to degrade the meiofauna for a long time. Short disturbance events are quickly compensated for, making meiobenthos fairly resistant to environmental stress. Burrows of benthos usually have a benign effect on meiobenthic populations; they diversify the habitat structure and ameliorate the mechanical and nutritional properties of the sediment by compaction. This positive structuring is enhanced by the greater influx rates of oxic water and attractive mucus secretions. Beyond that, protruding macrofaunal tubes provide shelter and foster the settling of organic particles, modulating the hydrodynamics at the surface.

2.3 Conclusion: The Microtexture of Natural Sediments

Natural sediments are characterized by a net of intricately interacting abiotic and biotic (biogenic) factors rather than just the grain size, porosity or sorting of the particles. The interactive and multiple nature of numerous determinants in the field, illustrated in Fig. 2.15 and schematically in Fig. 2.16 was nicely demonstrated in a small study performed by Warwick et al. (1986b), who investigated the impact of the macrobenthic, tube-dwelling polychaete *Streblosoma* on the meiofaunal assemblage. Around the tubes that extend slightly above the surface there is an area with rich meiofauna, probably because of the improved flux conditions caused by the tube and also because of the worm's mucus secretion and concomitant microbial activities. Slightly further away, in the grazing range of the polychaete, the meiofauna was impoverished through mechanical disturbance and perhaps uptake by *Streblosoma*.

Mainly through the activation of geochemical fluxes and microbial activity, an inhomogeneous small-scale topography is created (Fig. 2.15) which supports the aggregation and a patchy distribution of meiofauna, even in superficially uniform sediments (Sun and Fleeger 1991). The mucus film secreted by bacteria, phyto-benthos and many burrowing animals like nematodes and annelids decreases the amount of erosion and meiofaunal suspension from currents. This entire web of biotic ecofactors which influence the occurrence of meiofauna is intricately combined with and influenced by the multitude of abiotic parameters described in Sect. 2.1. Any schematic attempt to illustrate the complexity of the "meiobenthic habitat" (Fig. 2.16) is too static to adequately reflect the dynamic interactions of the components.

In addition to the more regular factorial system, depicted in Fig. 2.16, the meiobenthic ecosystem is, of course, subject to stochastic or "accidental" factors, such as local irregular and temporary disturbances (e.g., storms, pollution events) and benefits (e.g., food input through the settling of larval forms or decaying macrofauna). These erratic alterations, even those of a small-scale nature, may influence the system unpredictably. They certainly contribute to the notoriously patchy distribution pattern of meiofauna and support their high diversity, two characteristics of meiobenthic communities that make generalization very difficult. A high diversity is also maintained by the well-developed nutritional selectivity of meiofauna, which seems to exceed that of macrofauna. The resulting differentiated resource partitioning of the available food stock renders biotic (trophic) factors more relevant than physiographic parameters: the occurrence and distribution of meiofauna appear to be controlled by a multifactorial dynamic network in which the biotic factors in particular must be considered.

More detailed reading: Round (1971); Coull (1973, 1986), Coull and Bell (1979); Rhoads et al. (1977), Eckmann (1985), Warwick (1989), Decho (1990); Watling (1988, 1991); Reichelt (1991); Krumbein et al. (1995); Meyer-Reil (1994); Snelgrove and Butman (1994); Fenchel (1996a); Reise (2002); Murray et al. (2002); Ólafsson (2003); Meysman et al. (2006a).

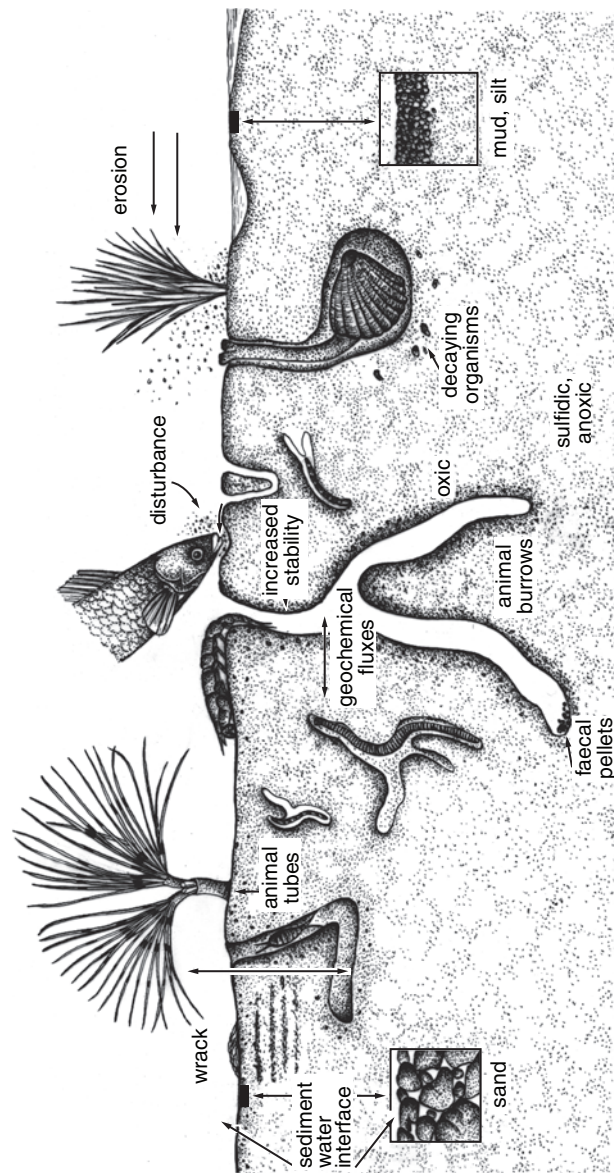


Fig. 2.15 An illustration of the biotic factors structuring the occurrence of meiofauna in a tidal flat sediment. (Compiled from Meadows 1986; Anderson and Meadows 1978, and other authors)

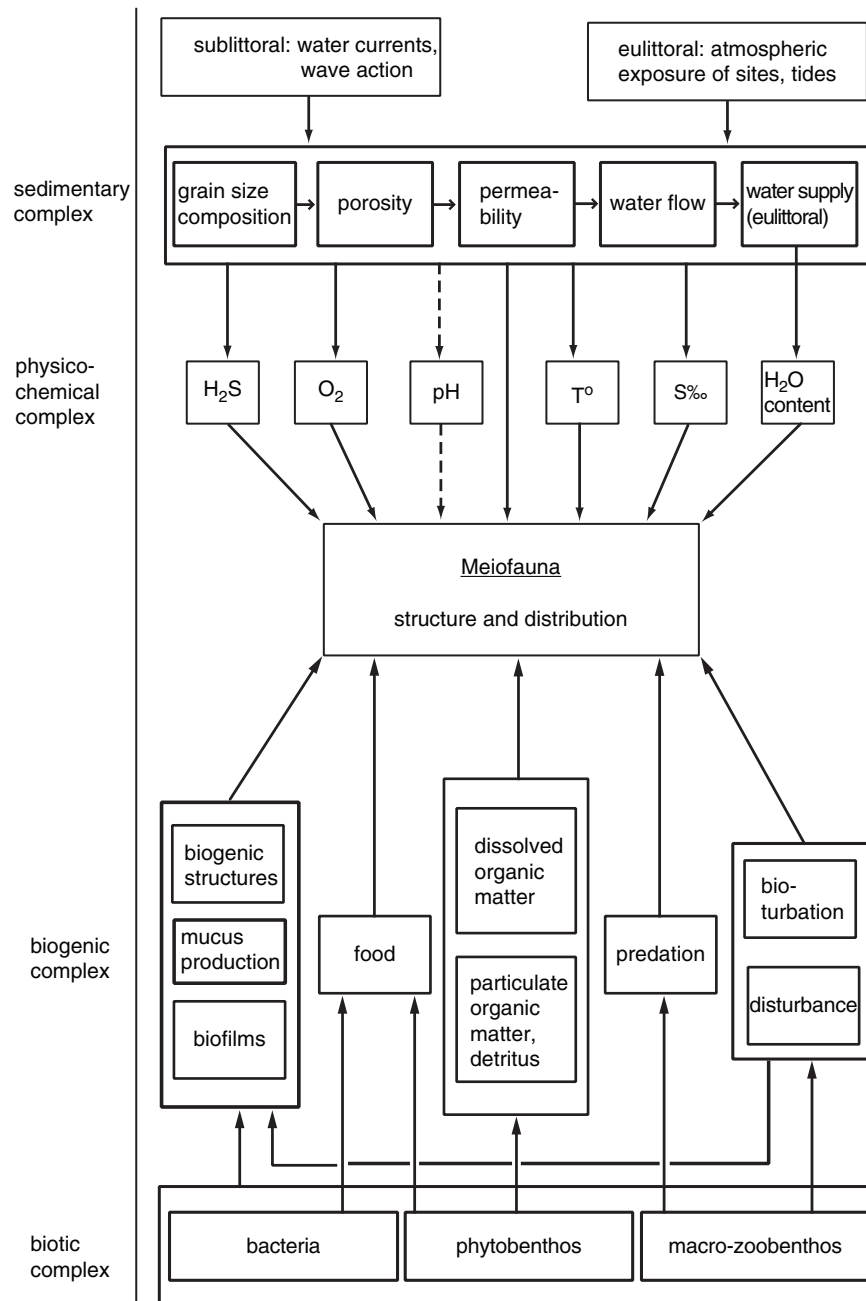


Fig. 2.16 A schematic factorial web structuring the habitat of meiobenthos

Box 2.8 Sediments: The Real Picture

The natural sedimentary fabric is an interacting, living system of organic components, mucous excretions, detrital agglutinations and microbial films interwoven with the inorganic particles. Thus, the real habitat of meiobenthos cannot be defined by grain size and sorting or characterized by sieving. Particulate organic matter (POM) and debris represent major components that are inseparably linked to bacterial coatings and biofilms produced by bacteria, diatoms and fauna. When oxygen is present, this organic complex is highly attractive to many meiofauna and is often the basis for their patchy microdistribution. Dissolved organic matter (DOM), which consists mainly of carbohydrates and amino acids and is released by many microorganisms, is mostly bound to colloidal complexes and mucous layers. It represents valuable nutrition for meiofauna. All of these components influence geochemical fluxes, microbial activities, the degree of biological reworking (bioturbation), and fauna-mediated bioirrigation and pelletization (Watling 1988, 1991; Meysman et al. 2006b). The huge surfaces of this nutrient-rich sedimentary web are ideal substrates for rich microbial colonization. Bacterial stocks that are orders of magnitude richer in the sediment than in the open water represent a dominant nutritive source for meiobenthos. The metabolic waste products of the meiofauna, in turn, attract bacteria. The spatially and temporally variable interactions between fauna, plants, bacteria and detritus become further complicated by the release of substances which exert specific stimulatory or inhibitory effects on all components of the system (Tenore and Rice 1980, Meadows 1986). Meiofaunal colonization is further controlled by biogenic microstructures such as animal burrows and tubes, mucus tracks, and fecal pellets. These are not only the nutritional basis for many meiofauna, but also act as mechanically important biostabilizers, reducing erosion. The complexity of this network renders the measurement of single parameters difficult. Recent advances in simulating and measuring have been accomplished using microelectrodes and on-line experiments. These innovative approaches will contribute to understanding the dynamics of the living sediment.

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