Chapter 8
Meiofauna from Selected Biotopes and Regions

The ongoing rapid global decline in species number tells us that assessments of natural diversity ("species richness" or "biodiversity" are necessary not only for scientific reasons, but also to aid in conservation or sustainable regulation. Thus, studies have been initiated to file our knowledge of meiofauna diversity in numerous marine and freshwater biotopes (see international programmes and projects such as the Global Biodiversity Assessment, UNEP 1995; Convention of Biological Diversity, UNEP 2001–2005; BIOMARE, MarBEF, CenSeam; overview in Costello et al. 2006). Due to methodological problems, estimates of marine biodiversity lag behind the numerous terrestrial census studies, and meiofauna were initially not included in comparisons of marine and terrestrial species richness. Between 10 and 100 million meiobenthic species and 10 million macrobenthic marine species are assumed to exist (Lambshead, pers. comm.). The recent book by Queirago et al. (2006) provides general information about marine biodiversity, the compilation by Segers and Martens (2005) provides corresponding information for freshwater habitats.

In terms of investigations into the biodiversity of (marine) meiobenthos (both species richness = alpha diversity, and assemblage richness between habitats = beta diversity), many previously neglected regions have been studied in greater detail over the last decade. These have increased our knowledge of areas such as the polar seas, tropical beaches and deep-sea bottoms. Some of these sites have turned out to be “hot spots” of meiofaunal diversity. The following chapters will characterize the ecological conditions and diversity of meiofauna in some relevant biotopes from different latitudes. The resulting questions regarding the latitudinal gradient concept (Pianka 1989) and its validity for marine meiofauna will be discussed in Box 8.1.

More detailed reading: Lambshead (1993); Gaston (2000); Gray (2000); McCann (2000); Warwick and Clarke (2001)

8.1 Polar Regions

Since the 1990s research activity in the polar regions has greatly increased and ecologically oriented long-term studies have been performed in Antarctica (compiled in Vanhove et al. 1998, 2003), and in the Arctic (mainly by Szymelfenig et al. 1995).
There are also numerous Russian papers on polar meiofauna of the White Sea shores based on long-term collections, but these papers are not readily available. The more accessible arctic coasts of Svalbard (Spitsbergen) are relatively well studied (see below). Interestingly, the deeper sediments are often better covered by sampling campaigns than the eulittoral (e.g., Hoste et al. 2007; Fonseca and Soltwedel 2007). The increase in the number of taxonomic papers is demonstrated by the monograph of Scott and Marchant (2005) on Antarctic protists, and by numerous descriptions of nematodes provided by Tchesunov (e.g., Tchesunov and Portnova 2005). Therefore, a more detailed picture of the meiofauna in these remote areas can now be provided.

The polar and subpolar meiobenthos do not seem, in both abundance and composition, to be very different from those found at boreal latitudes at corresponding depths and sediments. Kendall et al. (1997) ascribe the low endemism of (shallow) Arctic meiobenthos to the fact that they originated at lower latitudes. The similarities of the vertical temperature ranges of Arctic shallow and deep-sea sites may explain the fairly similar abundances of polar meiofauna found at different depths.

The eulittoral is characterized by strong seasonal oscillations of two rigid factors to which the meiofauna is apparently well adapted: (1) temperature (an ice cover is present for many months, which is aggravated by destructive ice scouring), and (2) food input (there is a rich microphytobenthos in spring and summer and short pulses of phytodetritus from dense plankton blooms). Due to the strong impact of physical factors, eulittoral meiofaunal populations are relatively scarce, and show high seasonal and inter-annual fluctuations (Table 8.1). In less exposed or deeper muddy bottoms with their rich organic matter, the density of meiofauna is one or two orders of magnitude higher. The sediments under marginal ice zones harbor especially rich meiofauna communities, which feed on the highly enriched phytodetritus of marginal sea ice (Fonseca and Soltwedel 2007; Hoste et al. 2007), indicating a close benthopelagic coupling (see below). Even the polar deep-sea beneath the ice margins is governed by a rich amount of surficial phytodetritus which provides the basis for a diverse and rich meiofauna. The transition is smooth from this ice margin towards the typical deep-sea basins (Sect. 8.3). Towards the deep sea and in sediments containing less organic matter, the meiofauna decreases in abundance, despite a physiographically less aggravating milieu. A general difference between the meiofauna densities of Arctic and Antarctic sites does not seem to exist; however, the considerable local variations only permit gross generalizations.

Regarding community composition, the polar and subpolar meiofauna correspond to those from boreal latitudes, with nematodes clearly dominating (>60%, often 80–90%), followed by harpacticoids, ostracods and/or turbellarians (Chen et al. 1999; Hoste et al. 2007). In sand samples this meiofauna is supplemented by a typical interstitial fauna with turbellarians, gastrotrichs and polychaetes (Arctic: Rysgaard et al. 2000; Antarctic: Skowronski and Corbisier 2002). In (Arctic) eulittoral sediments, enchytraeid oligochaetes were surprisingly numerous and, aside from nematodes and turbellarians, were the dominant taxa (Szymelfenig et al. 1995; Urban-Malinga et al. 2005), while harpacticoids attained only low densities. In muddy sediments of the sublittoral Arctic, rich diatom populations allowed
<table>
<thead>
<tr>
<th>Location</th>
<th>Prevailing sediment</th>
<th>Abundance (per 10 cm²)</th>
<th>Main taxon</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Eulittoral</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mid-tidal</td>
<td>Medium-to-fine sand</td>
<td>0–10,000; mostly &lt;1,000</td>
<td>Nematodes</td>
<td>Szymellénig et al. (1995)</td>
</tr>
<tr>
<td>Low-tidal</td>
<td>Fine sand</td>
<td>100–900</td>
<td>Oligochaetes</td>
<td>Urban-Malinga et al. (2005)</td>
</tr>
<tr>
<td>Bear Island</td>
<td>Coarse sand</td>
<td>&lt;50 to &gt;600</td>
<td>Nematodes</td>
<td></td>
</tr>
<tr>
<td>Exposed beach sand</td>
<td>Muddy sand flat</td>
<td>10–270</td>
<td>Turbellarians</td>
<td></td>
</tr>
<tr>
<td><strong>Shallow sublittoral</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>South Orkney Islands</td>
<td>Fine sand</td>
<td>6,200</td>
<td>Nematodes</td>
<td>Vanhove et al. (2000)</td>
</tr>
<tr>
<td>Magellan Strait, Beagle Channel</td>
<td>Mud with some sand</td>
<td>&gt;3,000</td>
<td>Nematodes</td>
<td>Chen et al. (1999)</td>
</tr>
<tr>
<td>Antarctica</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brazilian Station, Martel Inlet, Sand</td>
<td>Mud, org. enriched</td>
<td>10,000–15,000</td>
<td>Nematodes</td>
<td>Gheller and Corbisier (2007)</td>
</tr>
<tr>
<td>King-George Island</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Deep shelf, cont. margin</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arctic Laptev Sea</td>
<td>Mud</td>
<td>500–1,000</td>
<td>Nematodes</td>
<td>Vanaverbeke et al. (1997)</td>
</tr>
<tr>
<td><strong>Deep sea</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Central Arctic Ocean</td>
<td>Mud</td>
<td>70–250*</td>
<td>Nematodes**</td>
<td>Schewe and Solwedel (2000)</td>
</tr>
<tr>
<td>Central Arctic Ocean</td>
<td>Mud</td>
<td>150–3,400</td>
<td>Nematodes</td>
<td>Hoste et al. (2007)</td>
</tr>
</tbody>
</table>

*Includes Foraminiferaug *without Foraminifera
harpacticoid copepods to dominate during the summer season, while in the deeper sediment layers nematodes prevailed (Rysgaard et al. 2000). Towards greater depths, foraminiferans, if included in the evaluation, often surpass nematodes in abundance (Schewe and Soltwedel 2000).

The community structure of the littoral meiofauna in polar and subpolar regions follows the typical rules for extreme biotopes: strong variations related to season, substrate and food supply (Vanhove et al. 2000), and occasional mass populations of a reduced number of opportunistic species (Ólafsson 1991). Diversity was also low in the eulittoral of Svalbard: for example, only three taxa (Szymelfenig et al. 1995) or six nematode genera comprised 97% of the overall nematode abundance (Vanhove et al. 2000). On the other hand, between 15 and 80 nematode genera were found per station by Vanhove (pers. commun.) along the Antarctic continental margin, representing a high genus diversity. The deep-sea areas of the Antarctic and Arctic regions embody a much higher meiofaunal diversity with a high degree of endemism, at least at the species level. However, it seems that in the polar regions this increase with depth does not unequivocally follow the typical exponential curve. Often the intermediate, bathyal depths have a higher diversity than the more oligotrophic abyssal, resulting in a hyperbolic diversity curve (Lambshead 1993). In other studies, the diversity (of nematode genera) decreased with depth (Vanaverbeke et al. 1997) or fluctuated irregularly, apparently caused by changes in sediment composition. The application of different methods may also influence calculations of diversity (see Sect. 8.8). The reduced abundance reported by Hartmann (1990) for Antarctic ostracods does not generally apply to meiofauna judging from the rich stocks of nematodes found in deep water sediments of both the Arctic (Vanaverbeke et al. 1997) and the Antarctic (Vanhove et al. 1995).

8.1.1 Sea Ice

Sea ice with its exotic, highly structured channel system, has gained increasing attention as a habitat for a rich "sympagic" meiofauna, in conjunction with augmented studies of polar, mostly Arctic regions. Sea ice covers, depending on the season, about 35 million km² of the ocean surface with ice floes that are meters thick. The porous summer sea ice contains an especially huge and complex internal channel system: 1 kg of sea ice has an internal surface area of 0.6–4 m² (Krembs et al. 2000). The channels of varying widths and structures (Weissenberger et al. 1992) originate from the underside of the ice and extend deep into the median and upper parts of the ice floe. This interstitial, lacunar system is filled with brine of that undergoes extreme changes in salinity depending on freezing and melting processes. The texture of sea ice varies greatly depending on how it was formed, its location and its fate. Ice floes formed on the open sea differ from shallow-water pack ice or landfast ice; first-year ice differs in compactness from many-year ice or ephemeral ice due to daily melting and freezing processes. From seasonal Arctic “melt ponds” have been described (Spindler 1994), which form on the surfaces of
the ice floes, often beneath a layer of snow, and provide a habitat for mostly microorganisms. Since they are provided with permanent light during the summer season and ample amounts of particulate or dissolved nutrients, pennate diatoms and flagellates densely cover the narrow channel walls. With some 200–300 species, diatoms are the most prominent form of microalgae in terms of both species richness and biomass (some 100 × 10^3 cells cm^{-3} ice). They can grow under the very low light and temperature conditions encountered in winter and at brine salinities of up to 95 PSU. Almost one-third of the total southern primary production is provided by algae associated with sea ice (Spindler and Dieckmann 1994). These microalgae are the nutritional basis for a rich sympagic meiofauna consisting of a peculiar blend of (1) autochthonous, mostly endemic species that remain exclusively in the ice throughout their life cycles, (2) allochthonous taxa from the ice-adjacent benthos, or even (3) the plankton beneath the ice cover (calanoid copepods and their nauplii). Temporary meiofauna are represented by numerous polychaete and mollusc larvae. Compared to benthic substrates, high proportions of turbellarians seem to be characteristic of both the Arctic and the Antarctic sea ice and of ecological relevance (Gradinger et al. 1993; see below), since they often dominate in terms of biomass (e.g. 45%; Schnack-Schiel et al. 2001). Interestingly, the turbellarian species in Arctic areas are closely related, if not identical, to those in boreal latitudes. The presence of foraminiferans and ciliates varies widely, depending on the extraction methods used, on the nature of the sea ice, and on the region. In the Weddell Sea (Antarctic), foraminiferans numerically dominated (75%) the sympagic meiofauna, while ciliates dominated in Arctic sea ice by 53% (Gradinger 1999). Nematodes, mainly Monhysterida, are characteristic of Arctic sea ice, especially in coastal fast ice (Nozais et al. 2001). Here, they develop populations of many thousands per m^2 (Riemann and Sime-Ngando 1997). Nematodes from Antarctic sites have not yet been found in sea ice, although they are dominant in eulittoral sediments. Also, rotifers, which are frequently a major taxon in Arctic sea ice (see Table 8.2), have not been reported from Antarctic ice samples. In the sea ice, foraminiferans, ciliates and harpacticoids—typical grazers of diatoms and flagellates—are at the base of the heterotrophic food web, and many of the unusually frequent acocel turbellarians feed on diatoms too (Gradinger et al. 1993). The food spectrum of the monhysterid nematodes most likely probably includes microalgae, bacteria and dissolved organic matter, which is fairly rich in the brine (Gradinger et al. 1992). Cyclopoid copepods, together with predatory turbellarian species, live on other meiofauna, while the network of narrow brine channels prevents access by most (larger) predators, so that in the inner narrow channel system meiofauna are protected from macrofaunal predators. Hence, the utilization of meiofauna by macrofauna (scavenging amphipods, shrimps) is limited but seems to occur at the lateral or lower edges of the sea ice floes, where meiofauna are especially abundant. The most aggravating ecofactor for the sympagic meiofauna are the drastic changes in interstitial salinity caused by the freezing and melting of the seawater. Salinity in the channels can range from 0 to >200 PSU, with steep gradients in the
### Table 8.2 Abundance and main composition of “sympagic” meiofauna in sea ice from various locations (ciliates and foraminiferans are not considered)

<table>
<thead>
<tr>
<th>Area</th>
<th>Abundance (ind. 10^3 m^-2)</th>
<th>Composition (% ranked)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Arctic regions</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Baffin Bay (both Apr–May 98):</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pack ice</td>
<td>1.5</td>
<td>90 cop + naup/8 nem/1,1 pol</td>
<td>Nozais et al. (2001)</td>
</tr>
<tr>
<td>Land-fast ice</td>
<td>18.0</td>
<td>97 nem/3.3 cop + naup/0.1 pol</td>
<td></td>
</tr>
<tr>
<td>Greenland Sea, pack ice, summer 94, 95</td>
<td>31.7</td>
<td>68.1 nem/5.5 turb/2.4 cop/6.9 rot</td>
<td>Gradinger et al. (1999)</td>
</tr>
<tr>
<td>Frobisher Bay: Feb 81</td>
<td>17.3–110.3</td>
<td>88.9 cop + naup/10.1 nem/0.4 pol</td>
<td>Grainger et al. (1985)</td>
</tr>
<tr>
<td>May 81</td>
<td>110.3</td>
<td>98.6 nem/1 cop + naup/4 nem/1.2 rot</td>
<td></td>
</tr>
<tr>
<td>June 81</td>
<td>17.4</td>
<td>92.3 nem/4.7 cop + naup/2.7 rot</td>
<td></td>
</tr>
<tr>
<td>Beaufort Sea: Apr 80</td>
<td>11.1</td>
<td>45.9 pol/45.7 cop/3.2 nem</td>
<td>Kern and Carey (1983)</td>
</tr>
<tr>
<td>June 80</td>
<td>48.2</td>
<td>51.9 nem/31.4 turb/14.5 cop</td>
<td></td>
</tr>
<tr>
<td>Stefansson Sound:</td>
<td>4.5–8.0</td>
<td>67.3 pol/32.2 cop. + naup/0.7 nem</td>
<td>Carey and Montagna (1982)</td>
</tr>
<tr>
<td>Mar 79</td>
<td>8.0</td>
<td>76.9 nem/23.1 cop + naup/0 pol</td>
<td></td>
</tr>
<tr>
<td>May 79</td>
<td>4.5</td>
<td>46.9 nem/28.5 rot/15.4 cop. + naup/15.4 turb</td>
<td>Recalculated from Gradinger (1999)</td>
</tr>
<tr>
<td>Central Arctic Ocean:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aug–Sept 91</td>
<td>ca. 15</td>
<td>45% cop/33% rot/16 nem/3 turb</td>
<td>Schünemann and Werner (2005)</td>
</tr>
<tr>
<td>Northern Fram Strait:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Summer)</td>
<td>0.6–34.1</td>
<td>45% cop/33% rot/16 nem/3 turb</td>
<td></td>
</tr>
<tr>
<td>(Winter)</td>
<td>3.7–24.8</td>
<td>93% naup/4 rot/2 nem/0.5 turb/0.1 nema</td>
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<tr>
<td><strong>Antarctic regions</strong></td>
<td></td>
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<tr>
<td>Weddell Sea:</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Sept 89</td>
<td>1.5</td>
<td>34.4 cop + naup/31.2 turb/7.3 others</td>
<td>Recalculated from Gradinger (1999)</td>
</tr>
<tr>
<td>Apr–May 92</td>
<td>78.1</td>
<td>51.8 cop + naup/48.3 turb/5 others</td>
<td></td>
</tr>
</tbody>
</table>
mm range. The authochthonous ice species *Drescheriella glacialis* (Harpacticoida) and *Cyclopina gracilis* (Cyclopoida) tolerate salinities of up to 80 PSU. For the fauna in the brine of the deeper channel system the constraints must be intense, while the peripheral ice portions, which have temperatures and salinities similar to the open water, offer more benign conditions. Is the relatively high proportion of rotifers in Arctic sea ice (22%, Gradinger et al. 1993), normally a group that is common in brackish and freshwaters, related to the occasionally low brackish salinity? Rotifers also have a physical advantage here: their flexible bodies favor life in the narrow ice channels, and they can squeeze through passages 50% smaller than the diameters of their bodies. Turbellarians also match their body dimensions to the varying channel width by adjusting their osmotic pressures (Krembs et al. 2000). Further physiological and experimental studies that analyze the living conditions in the intricate web of ice channels are needed.

Within a single ice core the meiofauna are mostly concentrated in the bottom layers, but even the upper layers harbor a few meiofauna (Dahms et al. 1990; Schnack-Schiel et al. 2001). Terrestrial meiofauna have also found access to polar ice: rich numbers of the enchytraeid *Mesenchytraeus solifugus* (Oligochaeta) live as “ice worms” or “glacier worms” in the fissures of glacier ice, mainly on the Alaskan coast. They feed on microalgae and pollen, and their strikingly blackish coloration can stain the ice dark (Shain et al. 2001).

The changes in the abundance and production of sympagic meiofauna are as irregular as the changes in composition. Table 8.2 demonstrates these variations by region, season, and even in replicate samples. When appropriately processed (salinity-buffered melting of the sample), one core of 1,000 cm$^3$ sea ice can contain 9,000 specimens. Densities from a few thousand up to several hundred thousand per m$^2$ have been recorded (Carey Jr. 1992; Gradinger 2001); nematodes alone accounted for 24,000/m$^2$ (Canadian sea ice, Riemann and Sime-Ngando 1997). However, comparisons are problematic: sympagic fauna in land ice are completely different from those in adjacent pack ice. Drastic changes in meiofaunal abundance and composition may occur at the same station from month to month, with abrupt quantitative fluctuations ranging from more than 100 × 10$^3$ m$^{-2}$ to less than 20 × 10$^3$ m$^{-2}$. Rotifer, usually a rare group, can locally dominate; acocel turbellarians can comprise >60% of the total sea ice fauna (Gradinger et al. 1993), and sometimes even temporary meiofauna can form the bulk of the sea ice fauna. Arctic sea-ice fauna differs profoundly from its Antarctic equivalent.

Compared to the biomass of flagellates and diatoms (100 mg C m$^{-2}$), meiofauna (5–7 mg C m$^{-2}$ sea ice) represent only a few percent (Friedrich et al. 1996), while the ciliate contribution is 20% (macrofaunal amphipods represent less than 1 mg C). In terms of biomass, the intensive primary production performed by microalgae (although varying with season, region and texture of the ice) exceeds that of the sea ice meiofauna more than tenfold. This is higher than required by the meiofauna, so rates of diatom ingestion by the sympagic meiofauna are only between 3–4% (Arctic) and 16% (Antarctic) (Gradinger et al. 1999; Schnack-Schiel et al. 2001), even during the dark winter season. For Arctic sea ice in Baffin Bay, Nozais et al. (2001) noted a similar rate of consumption of the primary
production (6%). These low values correspond to daily grazing rates of only 1% of the algal production. These calculations suggest unlimited feeding conditions for the sympagic meiofauna in most areas (Gradinger 1999; Nozais et al. 2001; Gradinger et al. 2005). Within meiofauna, turbellarians, which are often the dominant taxon by biomass, are the main predators and have considerable grazing rates (Gradinger et al. 1993).

Sea ice meiofauna is not an isolated or stable biota. It closely interacts with the benthic and pelagic environments depending on the water depth, its proximity to land and its age (Werner 2005). Shallow water ice (water less than 10 m deep) predominantly contains a selection of meiofauna from the underlying benthos, whose populations are much larger than those in the overlying ice (Carey 1992). The frequently suspended harpacticoids and cyclopoid copepods and turbellarians (see Sect. 7.2.1) easily colonize the ice habitats. The contact of an ice floe, of which 80% is below the surface, with the bottom provides benthic meiofauna with the chance to access the ice interstitial. With each melting or freezing period, seasonal ice floes release and take up meiofauna and thus contribute not only to the coupling of bottom fauna and ice fauna, but also to the distribution of the meiobenthos via long drift passages (Carey 1992; Schnack-Schiel et al. 2001). During ice-free periods, land ice represents a retention habitat and provides a “stepping stone” that enables recolonization when new ice is formed in winter. Figure 8.1 illustrates some seasonal processes in sea-ice colonization. Additionally, during freezing periods ice platelets are formed and lifted from the bottom, with some sediment underneath. This may contain meiofauna which are then incorporated into the ice system, and this would explain why coastal fast ice usually harbors more meiofauna than remote sea ice (Gradinger et al. 2005). The “benthic-oriented” Arctic sea ice in particular permits an intensive interaction between the benthic and sympagic meiofauna (Carey 1992).

However, only about one-third of all sympagic meiofauna seem to be of benthic origin. Oceanic sea ice contains a blend of autochthonous meiofauna, meroplanktonic larvae and true plankton organisms. It is not clear whether they are enclosed while the floe is freezing or they actively colonize the channel system. In any case, freezing and melting processes contribute to their uptake and their release to and from the ambient sub-ice plankton (Fig. 8.1). During seasonal ice-free periods in the open water, the remaining areas of fast ice in coastal areas serve as refugia for ice fauna and as seeding grounds for the colonization of newly formed ice floes. The origin and fate of meiofauna in old ice floes drifting across the open polar seas and their pathways of colonization are often unclear. The various endemic species (e.g., the harpacticoid Dreschierella glacialis, the cyclopoid copepod Cyclopina gracilis, perhaps also the nematodes Cryonema and Hieminema) must have had long evolutionary lines with authochthonous, ice-bound life histories. Chunks of ice generated by multi-year ice floes may have provided appropriate rafts for (long-distance?) transport and further distribution. In all polar regions, sea ice acts as an important retention substrate and transport vehicle that contributes to meiofaunal redistribution. The extent to which polar meiofauna are interlinked between the three large compartments (benthic, sub-ice and sympagic fauna) may vary with the texture of
the ice, and with region, season and climate; quantitative data remain to be assessed. However, the ecological role of meiofauna in/on sea ice is certainly important. A universal ice melt resulting from global warming would point to a bleak future for polar ecosystems and their fauna, including their meiofauna.

More detailed reading: Carey (1985); Spindler (1994); Gradinger et al. (1999); Gradinger (2001); Nozais et al. (2001).

Box 8.1 Life Under Icy Conditions: Meiofauna in Polar Regions

Despite the harsh conditions, meiofauna seem to thrive in Arctic and Antarctic regions. Their abundance and diversity are often no lower than those in temperate climates, and many boreal species also populate polar bottoms. Polar meiobenthic life depends on pulses of phytodetritus from the strong blooms of microalgae during the polar light season and is characterized, as in other extreme biotopes, by strong seasonal, interannual and local fluctuations. In the shallow bottoms mechanical disturbance by ice scouring adds to the physical stress, but under more favorable conditions densities of several 1,000 meiofaunal individuals per 10 cm² are common. Nematodes and harpacticoids are normally the dominant taxa. In eulittoral sediments oligochaetes are common, while towards greater depths foraminifers become increasingly dominant. Here diversity is often highest and many endemic species are found.

Fig. 8.1 Seasonal pattern of sea ice colonization by meiofauna, emphasizing the intensive cryopelagic coupling (After Werner 2005)
A particular compartment of polar meiofauna lives in the channel system of sea ice. On the walls of this interstitial web filled with water of changing salinity thrive masses of microalgae, the food basis of a rich “sympagic” meiofauna, dominated by ciliates, foraminiferans and copepods. Turbellarians and rotifers are surprisingly frequent. Nematodes are common in the Arctic ice but they, as well as rotifers, have not yet been found in Antarctic sea ice. Sea ice meiofauna are patchily distributed and show strong temporal fluctuations. This depends, apparently, on the processes forming the channel system, on the position and size of the ice floe, its distance from land, and on changing light conditions. Donor populations are from the bottom or from suspended meiofauna. A few autochthonous species live their whole life cycles in the ice. They are often endemic and highly adapted to the special conditions in this exotic biotope, e.g., extreme salinities and temperatures.

The meiofauna of sea ice is a food-unlimited community of specialists with reduced predation pressure. Only the rich meiofauna populations on the underside of sea ice are accessible and grazed upon by various macrofauna (particularly amphipods). Sea ice is a nutritious sheltered biotope for many meiofauna and a nursery ground for macrofauna. Linking the benthic and planktonic polar food webs, sea ice is of considerable ecological relevance. The consequences of its accelerated melting in the global warming process for oceanic life are by no means understood.

8.2 Marine Subtropical and Tropical Regions

In the last decade, studies of the meiofauna from subtropical and tropical regions have greatly increased following the pioneering studies on Indian beaches (McIntyre 1968), various Pacific islands (French researchers around Salvat and Renaud-Mornant) and the Bermuda Platform (Coull 1970). In a review of tropical meiofauna, Alongi (1990a) outlined a picture with large geographical, biotopical and seasonal variations. The tropics have a great range of habitat types for meiofauna, with carbonate sands on beaches and shelves, terrigenous estuarine muds, mangrove thickets, and enclosed lagoons. The present account will first focus on some general data and then present the meiofauna of some characteristics tropical biotopes.

Despite the usually oligotrophic tropical seas, the abundance of littoral meiofauna in the tropics is very similar to that in temperate coastal areas: from several hundred to several thousand specimens per 10 cm² (McIntyre 1968; Gourbault and Renaud-Mornant 1990; Alongi 1990b; Vanhove 1993). Dense populations beyond this range (e.g., >10,000 per 10 cm² on the Malaysian coast; 17,000 nematodes per 10 cm² in an Indian salt marsh) represent probably local aggregations and should
perhaps not be generalized. In samples from the subtidal and the continental shelf, mean densities gradually decrease. Even the large local variations correspond to conditions in temperate regions and do not allow generalization.

Unexpectedly, under tropical conditions the density fluctuations often also exhibit a seasonal pattern (Bermuda: Coull 1970; Galápagos: Westheide 1981; Philippines: Faubel 1984; Red Sea: Arlt 1993). However, in contrast to temperate climates, the richest populations often develop in the cooler parts of the year (at least in habitats in the “dry tropics,” see Alongi 1990b). Breeding and reproduction are also mostly seasonal, and are often adjusted to climatic extremes such as torrential rains in the monsoon season. Monsoonal floods, with their high mud loads of river run-off, hurricanes (typhoons) and cyclones, which are characteristic of the tropical girdle, can cause a sudden and sometimes complete turmoil of the ecosystem, with severe destruction of meiofaunal assemblages, especially in the eulittoral (Suresh et al. 1992). A similarly negative effect has been recorded in South Africa after the seasonal flooding of estuaries (Nozais et al. 2005). However, these are natural disturbances to which meiofauna seem adapted, since the populations normally recover fairly rapidly, albeit often with an altered community composition (Alongi 1990a; Ansari and Parulekar 1993).

Typical of certain tropical areas are oscillations such as “El Nino” or seasonal upwellings. These hydrographic events also have a marked impact on coastal meiofauna. By enriching the nutrient supply they augment meiofauna populations. Where river inputs provide a rich supply of organic matter, meiofauna will develop into particularly dense populations, so long as the load of fine sediment does not lead to anoxic events. In estuaries and coastal lagoons the great salinity and temperature stress reduce meiofauna to densities of around or less than 100 ind 10 cm⁻² (Alongi 1990b); this is lower than observed in corresponding temperate or boreal brackish waters. During their reproductive phases, even those meiofaunal species adapted to tropical conditions are limited in their tolerance to changing physical conditions (see Sect. 8.6).

As seen in nontropical meiofauna, grain size composition, the indicator of complex abiotic factors, seems to be related to meiofauna composition: the meiofauna in tropical sediments mostly correspond to the typical community structure, with nematodes the most abundant and diverse group, while in coarse sands with a low silt content harpacticoids may prevail. This relation to grain size and silt content has been found in both tropical quartz and biogenic coralline sands. In contrast with most studies from temperate regions, polychaetes and oligochaetes play a substantial role in the tropics and can represent important taxa (Ansari and Ingole 1983; Faubel 1984; Ingole et al. 1997; Westheide 1991; Sasekumar 1994; Villora-Moreno 1997; Netto et al 1999). A local scarcity of annelids may suggest the presence of turbellarians, their main predators, which occasionally exhibit considerable abundance in tropical studies.

8.2.1 Tropical Sands

The littoral fringes of many tropical seas, atolls and islets consist of calcareous biogenic sands. These splinterly biogenic sediments are structurally complex, relatively
unsorted and of high porosity. Due to the “open” grain surface, the adhesive forces are strong and permeability (at least in experimental sediment columns) is often markedly higher than in corresponding siliceous sands. This results in high contents of nutrients, organic matter and rich stocks of microorganisms (Suess 1973; Rasheed et al. 2003a,b; Wild et al. 2005). This means a rich food supply for meiofauna with an unusually high biodiversity. This richness contrasts with the often low number of individuals per taxon (Renaud-Mornant & Serène 1967; Coull 1970; Gúzman et al. 1987). Gourbault et al. (1998) identified in their study on the beaches of Guadeloupe 122 spp of nematodes belonging to 112 genera, while the 42 spp of harpacticoids found by Villiers and Bodiou (1996) in Polynesia belonged to 21 genera! In somewhat coarser sediments (unprotected beaches and reef slopes), the dominant group is often the harpacticoid copepods; the nematodes here are relatively large, epigrowth-feeding or predacious types. Many other, often rare, taxa (foraminifera, interstitial ostracods, polychaetes, molluscs, priapulids, and tardigrades) also occur. Overall, in the coarse, exposed sites meiofauna densities are relatively low (<500 ind. 10 cm−2; see Guzmán et al. 1987).

Many calcareous tropical sediments harbor a typical thiobiotic and sulfide-dependent meiofauna at depths below 10 cm (Ott et al. 2003; Bright and Giere 2005; Van Gaever et al. 2004; see Sect. 8.4.2). How can anoxia/sulfide develop beneath the upper few oxic centimeters in sediments of high porosity and in hydrodynamically exposed areas? As evidenced by the mostly low degree of sorting, between the calcareous fragments of shells and skeletons, a large amount of fine, powdery abrasion accumulates which tends to clog the pores, causing low permeability in the deeper strata. In addition, mucilage sheaths, which are not present to such a large extent on silicate grains, coat the particles (Suess 1969, 1973; Rasheed 2003a,b). These biogenic films and the rich organic content of the sediments may cause the rapid oxygen depletion in the deeper layers.

In contrast, the finer sands and muds of more sheltered sites (lagoons, pools) harbor a more monotonous meiofauna (Coull 1970; Vanhove 1993; but see contrasting conditions in Gourbault and Renaud-Mornant 1990), with numerous small, deposit-feeding nematodes dominating (e.g., 30–540 × 10 cm−2; Grelet et al. 1987 (80–90% nematodes); about 1000 inds × 10 cm−2; Netto et al. 1999; several thousand × 10 cm−2; Guzmán et al. 1987); the turbellarian fauna is also rich here. Biomass at the surface was almost 4 g m−2 (wet, 0–5 cm), twice that of corresponding records from North Sea sands (Grelet 1985).

This increase in meiofaunal abundance with the reduction in the permeability of the interstitial system occurs mostly at the expense of taxonomic diversity. The switch from copepod to nematode dominance can occur within short periods of time (<1 year), depending on the fluctuations in currents. Thus, in biogenic sediments the rule that the numerical density of the meiobenthos increases with the proportion of detritus and silt (up to certain limits) remains valid. The high taxonomic diversity in more exposed habitats is often also reflected by a high statistical diversity (H'), especially in the surficial layers. H' values (for nematodes) of >5 in the Great Barrier Reef or even up to 11 for the Red Sea coast have been reported. More sheltered lagoonal ecosystems in the Pacific had a lower diversity of >3
On the other hand, Coull (1970) reported that the highest species diversity of Bermudian copepods occurred in the muddy, not the sandy, substrates. Hence, a simple relationship between granulometry and species richness does not seem to exist (Boucher 1990). In any case, the meiofaunal community structure in calcareous sands differs from that in comparable silicate sands with a similar granulometry. In a direct comparison between the meiofauna of calcareous and siliceous sites from Italian shallow sites (Giere et al. 2004), indices of similarity and dominance differed profoundly, while the abundance, taxonomic richness and H’diversity remained comparable (Fig. 8.2). The differences in community composition become most evident at the species level, not when higher taxa were compared.

The zonation of meiofauna on tropical shores corresponds to that in temperate climates: the highest diversity but not necessarily abundance occurs near the low-water mark, a low diversity occurs in the higher shore. The intermediate zone often harbors fairly high meiofauna abundances. In the shelter of tropical algal assemblages, rich in habitat structure and food supply, a particularly abundant and taxonomically diverse epiphytic meiofauna is commonly observed (Faubel 1984; Arlt 1993; De Troch et al. 2001). Microhabitat complexity, exposure and sediment transport are major determinants of meiofauna abundance and composition in these phytal communities (Muralikrishnamurty 1993).

**Box 8.2** Calcareous Sands: A Bonanza of Fascinating Meiofauna

The rubble among tropical and cold-water coral reefs, the sediments in many marine caves, the tops of many sea mounts, the beaches of atolls, the shoals along limestone shores: these all are of biogenic origin, and their sands have fascinating structural complexity. A look through a microscope shows a

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(Fig. 8.2 Comparison of similarity (Jaccard index) and dominance (Renkonen index) in meiofaunal samples from calcareous and siliceous sands in two adjacent Mediterranean sites. Low Jaccard values indicate marked differences between the species at the sites, while Renkonen percentages indicate the degree of similar dominance relations in the compared sediments (Giere et al., unpubl.).)
8.2.2 Mangroves

One of the most characteristic, biologically rich and ecologically important habitats of the tropics, the mangrove girdle, has also attracted studies on its meiofauna. As in other tidal shores, differences in exposure generate various zones. The high shore with the most rigid fluctuations is usually the least populated, while the mid-tide or low shore harbor the densest populations of mangrove meiofauna. Although the sediment compositions in these zones vary slightly (the low shore has somewhat coarser particle fractions), in general mangrove sediment consists of fine mud that is rich in organic matter. With its low porosity and water percolation, mostly brackish and fluctuating salinities and limited oxygen supply, mangrove sediments are comparable to the tidal flats of temperate regions. Additionally, the various zones are characterized by different highly adapted and partly submerged mangrove trees. Their dense prop roots, the pneumatophores and the leaf litter create a much higher structural diversity than seen in temperate tidal flats. The horizontal distribution of meiofauna is determined by tidal changes in inundation, salinity and temperature. Tropical seasonal monsoons cause extremes in salinity fluctuations and, along river mouths, flooding by riverine silt loads. Intense microbial degradation restricts the oxygen supply in the sediment to the uppermost millimeters, aggravating meiobenthic life. In addition, the tidal currents and torrential rainfalls can erode the silt,
creating patches of somewhat coarser sediment, at least in the lower reaches. This habitat variability plus seasonal fluctuations (pre-monsoon vs. post-monsoon) may contribute to the extreme differences in population density and depth of vertical zonation found in many studies (Alongi and Sasekumar 1992; Castel 1992). A specific chemical factor for mangroves seems to be the high tannin content in the mangrove litter and pore water (Alongi 1987a,b). Thus, the mangrove meiofauna, like that found in silty tidal mud flats, must not only be adapted to temporary oxygen depletion and changing salinities, but it must also tolerate the adverse effects of tannin. It is thought that the low ability of meiofauna to break up mangrove litter may reduce meiofauna abundance (Coull 1999).

Records on the vertical distributions of meiofauna in mangrove sediments are contrasting. Some authors have encountered meiofauna, mainly nematodes, way beyond the oxic/anoxic interface in the reducing layers, down to 15 or even 20 cm depth (Nicholas et al. 1991; Vanhove et al. 1992; Ansari et al. 1993); others claim that the presence of meiofauna at depths below a few centimetres is negligible (Sasekumar 1994). For an account of the problems associated with meiobenthic life under conditions of low/no oxygen, see Sect. 8.4 on thiobios.

In almost all mangrove studies, nematodes, especially *Daptonema* and *Microlaimus*, represent 80–90% of the meiofauna. However, they do not form a biologically uniform group. In the different mangrove zones the variations in the silt content of the sediment relate to the nematode feeding type (Schrijvers and Vincx 1997). In the coarser sediments of the low shore and on roots and leaf litter, epistrate feeders (e.g., *Spilophorella, Ptycholaimellus* in a Kenyan mangrove) are more common in African, Indian and Australian mangroves (Nicholas et al. 1991; Ólafsson 1995; Chinnadurai and Fernando 2007). Their occurrence coincides with the increase in benthic microalgae and phytodetritus (Alongi 1990b). In Australian mangroves, the mid-level, particularly the silty zone, harbored numerous deposit-feeding nematodes, while omnivores/predators prevailed in the high water zone (Alongi 1987a; Nicholas et al. 1991), resulting in proportions of 50, 28 and 22%, respectively. In the deeper layers, the classical “sulfide nematodes” (*Metalinhomoeus, Astomonema or Catanea*) can prevail by feeding on their symbiotic chemosynthetic bacteria (see Sect. 8.4.2). However, the proportions of feeding guilds are not static. They can change rapidly depending on the seasonal input of microalgae and phytodetritus and on the silt loads that are often flushed in by monsoonal rains.

A clearer relation to sediments was evident in harpacticoid copepods. Low species numbers are typical of muds, and much higher ones of sand. Harpacticoids are usually second in abundance (around 5–10%) after the nematodes. The lower, more sandy mangrove girdle not only harbors richer populations of these copepods than the higher shore, but it has also the highest taxonomic diversity (Alongi and Sasekumar 1992; Ólafsson 1995). In very soft mangrove mud, members of the Canuellidae, Ectinosomatidae and the genus *Stenhelia* were the dominant harpacticoids in Queensland, Australia (Coull et al. 1995). Favoring detritus-rich silty bottoms and often brackish water, burrowing macro- and meiobenthic tubificid and naidid oligochaetes are common in mangroves (5–19% in African mangroves). Although not often included in studies of meiofauna, ciliates can be quite common
among mangrove meiofauna. In a South African mangrove they were the second most abundant (6.4%) after nematodes (80%) but before oligochaetes (4.5%, Dye 1983). In the more seaward Avicennia muds, kinorhynchs also attained considerable densities (up to 5%).

Although both northern tidal flats and mangroves are detritus-based decompositional ecosystems, in mangroves the overall densities and diversities of meiofauna are often lower than those found in corresponding intertidal mud flats of temperate/boreal shores. In mangroves, with their higher structural complexity (vegetation), only the epibenthic meiofauna is more abundant (and more diverse) than in northern tidal flats. On the other hand, salt marshes (which have high structural diversity but lack extreme climatic and chemical aggravations) can reach significantly higher meiofaunal densities (Wieser and Kanwisher 1961; Teal and Wieser 1966; Bell 1979). About 1,000–7,000 individuals (mostly nematodes) per 10 cm² have been documented in mangrove samples from different areas and continents (Dye 1983; Nicholas et al. 1991; Castel 1992; Vanhove et al. 1992; Vanhove 1993; Ólafsson 1995), but there are also records of much lower densities from nonestuarine and unpolluted mangrove forests (Alongi 1987a; Alongi and Sasekumar 1992; Chinnadurai and Fernando 2007), reflecting the high variability of local conditions and climates. The seasonal impact varies depending on the geographical location (the distance from the equator). In the dry tropics, the hot temperatures in spring and summer seem to decrease meiofauna, while in subtropical areas, (late) summer produces the highest densities. In general, the torrential rainfalls of monsoons have a negative impact on meiofauna, so that lowest densities were found in the post flood period (India). Biomass values from mangrove meiofauna are rare. Varying seasonally and locally, they may range (mean biomass) between 0.2 and 2.3 g m⁻², which, on the basis of an assumed turnover rate of 8 or 9, would give an annual production of as high as 1.5–8.4 g C m⁻² (Dye 1983; Vanhove 1993).

Similar to temperate tidal flats, in mangroves the dynamics of bacteria/microalgae communities and protozoan/meiobenthos assemblages are tightly linked (Schrijvers et al. 1995; Schrijvers and Vincx 1997): In the African mangroves, exclusion experiments on epibenthic grazers (gastropods) increased the stock of microalgae (chlorophyll a concentration) as well as the prevalence of epistrate-feeding nematodes. Exclusion of macro-epibenthic detritivores resulted in an increase in silty debris as well as a parallel increase in the population of detritivorous meiofauna (deposit-feeding nematodes and oligochaetes). Hence, a link between two different decompositional chains was revealed in the meiobenthos, one based on microalgae, the other based on (non-mangrove-derived) detritus. Stable isotope analyses (¹³C) showed that allochthonous, phytoplankton-derived seston was also an important food source in the upper centimeters of the sediment, which calls into question the prevailing trophic role of autochthonous mangrove litter.

The rich epibiota in the thickets of prop roots and trees is another assemblage in mangrove shores that influences the mangrove meiobenthos due to their structural diversity. Areas densely overgrown with mangrove vegetation often embody higher meiofauna densities. On the other hand, areas with many burrowing crabs have been
found to be less densely populated (Dye and Lasiak 1986). This decline was interpreted as being more to disturbance and competition than to predation. Conversely, dense populations of epibenthic gastropods in a tropical mud flat led to the destabilization of the sediment surface and increased meiofaunal fluctuations (Carlén and Ölafsson 2002). Whether this negative effect was caused by competition for food or by physical disturbance is hard to discriminate in the field. However, in mangroves, with their abundant natural food supplies, why would competition among deposit-feeding snails and the much smaller nematodes exist at all? In all probability, the continuous fluctuations that characterize this habitat would rapidly reduce any long phases of resource limitation. However, before we can generalize about interactive contact between meiofaunons with other live compartments (Alongi and Sasekumar 1992; Schrijvers et al. 1995; Schrijvers and Vincx 1997), further scrutiny is needed to gain a better understanding of the unique ecosystem of mangroves.


Box 8.3 Tropical Plethora vs. Polar Purity: A Latitudinal Diversity Gradient in the Meiobenthos?
The latitudinal gradient, derived from terrestrial studies, is one of the best-known large-scale biodiversity patterns. The mechanisms governing this pattern, which have been disputed since the review of Pianka (1966), remain a challenge for the marine realm. But is the “classical” decline in species diversity from the tropics to the polar seas globally valid, and does it also apply to meiofauna? Has it only developed in the deep sea or in shallow sites too? Many questions, but they have different answers. Recent (and fossilized) Foraminifera seem to globally decline in species richness from the Equator to the North (Culver and Buzas 2000). However, nematodes in various deep-sea areas show a converse decline with increasing numbers of species towards the Arctic. This pattern was found to be linked to increased surface productivity and supply of organic matter (“food-driven gradient”), and is not related to a latitude gradient per se (Lambshead et al. 2000, 2002). In the southern oceans and the Antarctic deep sea, the highly diverse assemblages of meiofauna challenge the contention of a depressed diversity at higher latitudes (Brandt et al. 2007). Other studies and taxa also failed to detect a latitudinal gradient, whether in nematodes or in harpacticoids. At shallow sites, meiobenthic species richness and diversity were as high as or even higher in temperate and boreal habitats than in the tropics (see Kotwicki et al. 2005b). An absence of any gradient between shallow tropical and temperate sites was also experimentally confirmed for nematodes (the main representative of meiofauna) using artificial collectors (Gobin and Warwick 2006). Also, in studies of freshwater meiofauna, a relationship between species number (mainly harpacticoid copepods) and latitude could not be discerned (Reid 1994; Rundle et al. 2000).

(continued)
8.3 The Deep Sea

Deep-sea research is largely instrument-limited. Since the first study of the deep-sea meiofaunas (Wigley and McIntyre 1964), the development of suitable corers (e.g., the multiple Aberdeen corer, Barnett et al. 1984) has enabled quantitative evaluations. Today, scientists on numerous research cruises are equipped with sophisticated remotely controlled instrumentation, and can even perform experiments on the deep-sea bottom, deploy and retrieve automatic devices such as “bottom landers,” and record environmental variables on-line. The application of new analytical methods (e.g., analysis of proteins, chloroplastic pigments, adenosine nucleotide content, and electron transport system activity) has refined our knowledge of the deep-sea meiofauna. These biochemical parameters that are related to biomass often render more reliable results than those obtained by direct counting and weighing.

8.3.1 The Habitat

Compared to the shallow benthic zones, the bathyal and abyssal bottoms are rather static and monotonous; wide regions of the muddy bathyal and abyssal plains represent a fairly uniform “desert environment.” However, interspersed with the widely prevailing mud plains are hydrodynamically complex areas where water currents are strong enough (5–10 cm s⁻¹) to suspend the silty deep-sea sediment and form sandy patches (Thistle 1988). Upwelling regions can create oxygen minimum zones (OMZ), while mountainous ridges cause complex and little-explored small-scale near-bottom currents. We know of big river outflows, steep canyons and disastrous turbidites that influence the assemblages of deep-sea fauna. In addition to these hydrodynamic and geological patterns, manganese nodule fields, cold-water reefs and aggregations of sessile macrofauna result in a benthic structural heterogeneity that is greater than previously assumed and is important for the diversity and distribution of meiofauna. However, perhaps the most biologically important and unexpected factor is the seasonality of deep-sea processes (Gooday 2002), because
this vast depth is coupled to the phototrophic surface, inferring that the ocean is one interactive biome that is continuously changing.

While the temperature of the deep bottom is usually 1–2 °C, it is considerably elevated in the Red Sea (21 °C), the Mediterranean (about 10–14 °C), and in sediments associated with volcanic and hydrothermal activity (5–35 °C). Oxygen content is one of the most important abiotic factors in shallow sites, but wide areas of the deep-sea bottom are well oxygenated, often down to 10 cm depth. This results from the small amount of degradable organic carbon present in most deep-sea sediments. Conversely, in upwelling areas, which have a rich input of sedimenting debris after plankton blooms, oxygen can become limiting for many meiofauna, at least in the subsurface layers. Low oxygen contents also occur in warm deep-sea regions (Red Sea, Sulu Sea in the Pacific Ocean) and remind us that complete anoxia prevailed in the deeper oceans for millions of years (e.g., during the oxygen crisis at the Permo-Triassic transition or the Mid-Cretaceous).

Decaying plankton blooms cause seasonal pulses of organic matter that largely sustain the deep-sea ecosystems. Fluffy masses of phytodetritus reach the bottom after weeks and settle there as a greenish (from chloroplastic pigments) unconsolidated surface layer of high nutritive value (Pfannkuche and Thiel 1987). Since most meiofauna prefer this layer, if reliable results are to be obtained it is imperative to prevent the “green fluff” from being flushed away by inadequate sampling (Bett et al. 1994). Thus, variable deep-sea meiofauna recordings do not necessarily reflect merely local and seasonal fluctuations in sediment structure; it may be that they are attributable to inadequacies in sampling methods.

There are three main factors that control the structure of meiofauna assemblages in the deep sea.

1. Sediment characteristics (mud vs. sand). Changes from muddy to sandy areas caused by hydrographical properties and different sedimentation rates are paralleled by a change in community structure. In sediments with a high content of fine particles (silt), the meiofaunal abundance is usually relatively high and dominated by the large community of nematodes that live in deeper, often anoxic layers. Especially in cores with calcareous ooze, meiofauna can attain high densities (Shirayama 1984). In sandy areas a relatively diverse meiofauna is dominated by harpacticoids in the upper few centimeters. These typical changes in community composition can be best compared on neighboring flanks of ridges with different exposures and sedimentation rates (Jensen et al. 1992a).

2. The supply of organic matter (measured as chloroplastic pigments or adenylates), which is usually reflected by the silt content of the sediment, regulates the abundance of meiofauna in all oceans. Every degradable organic substance added, whether it comes from seasonal phytodetritus or from horizontal advection by currents, influences the composition and abundance of the deep-sea meiobenthos in this precarious nutritive environment (Thiel et al. 1988/89; Gooday and Turley 1990). However, the effect largely depends on the quality of the settling particles (larger, fast-sinking, fresh aggregates compared to lighter, more degraded ones that drift for longer; see Soltwedel 1997). Despite its
biological degradation as it drops down the water column (at a speed of about 100 m per day), about 3% (in other estimates 5–10%) of the surficial primary production reaches the deep-sea bottom. The response to phytodetritus is most obvious in the temperate and northern oceans, especially underneath the ice margin, but the reasons for these regional differences are not always clear (Pfannkuche and Thiel 1987; Lambshead and Gooday 1990; Tietjen 1992; Vincx et al. 1994; Gooday 2002; Witte et al. 2003). A lesser food source is terrigenous detritus, which often accumulates near big river mouths and at the feet of continental slopes. Remains of dead large animals and plants (“food falls”) provide large food packages that contribute about 10% of the energy inputted into the deep sea. These are particularly used by nematodes, which aggregate despite the high oxygen deficiencies around sunken carcasses (Debenham et al. 2004). The last food source to be mentioned here are the bacterial films that colonize the mucus strands and excretions of the ubiquitous benthic foraminifera. Bacteria and protozoa, which react rapidly to periodic pulses of phytodetritus and fecal pellets, can increase bacterial production by an order of magnitude. In contrast, the metazoan meiofauna exhibit a delayed reaction (with a delay of up to eight weeks).

3. Habitat heterogeneity on a small scale plays an important role in both species richness and diversity. Sessile macrofauna protruding from the surface (sponges, coelenterates), worm tubes, agglutinated foraminifera shells, komokiacean “mud balls” and “manganese nodules” (see Bussau et al. 1995) represent small-scale structures that increase the habitat complexity and also the species richness and functional diversity of meiofauna. These favorable conditions prevail for long periods since they persist in the quiescent deep-sea conditions (Thistle et al. 1993). A structuring effect is also ascribed to the bioturbative activities of megafauna (e.g., holothurians and enteropneusts; see Meadows and Meadows 1994) or to fragments of cold-water corals and sponges that accumulate on the deep-sea bottom (Raes and Vanreusel 2006). Increases in sediment complexity attract a community of specialized epistrate feeders, which contribute to local variations. The ameliorating effect of protruding tubes can be attributed to a complex interaction of favorable factors, such as enhanced growth of bacterial stocks, increased vertical transport of solutes, better protection from predators and the establishment of hydrodynamically favorable sheltered zones with the accumulation of debris (Thistle and Eckmann 1990, Eckman and Thistle 1991). Cage experiments preventing bioturbation by macrofauna showed enhanced concentrations of chloroplastic pigments with successively enhanced meiofaunal density. On the other hand, experimental protection from bioturbation produced a negative interaction of large, motile epifauna with the meiofaun, particularly with harpacticoid copepods (Thistle et al. 2008).

Increased structural heterogeneity with strong hydrodynamic variability and the downward transport of large amounts of food material are also thought to be the reason why steep submarine canyons that cut into the continental margin represent “hot spots” of diversity (Ingels and Vanreusel 2006). The geological heterogeneity of the bottom (sheltered and exposed sides of submarine mountains, slopes and
faults) may also contribute to variations and increased diversity in the pattern of meiobenthos colonization (Alongi 1990b; Grove et al. 2006).

Recently, another geological phenomenon has received particular attention in meiofauna studies: hydrothermal vent areas. Here, an enhanced abundance of the meiobenthos—compared to the non-vent surroundings—results more or less directly from the enormous biomass and production of “sulfur and methane bacteria” (van Harten 1992). On the other hand, the species spectrum is restricted to the few forms that can tolerate the temporarily hostile sulfidic conditions (see Sect. 8.4). On the negative side, collapsing sediments of turbidites represent huge physical disturbances that have long-lasting and highly adverse effects on natural communities (Lambshead et al. 2001).

### 8.3.2 The Meiofauna

The typical deep-sea meiobenthic organism is highly adapted in terms of its biology and ecology to the scarcity of food. favored by the prevailing low temperatures, it grows slowly and has a long life span with low maintenance expenditure. Its metabolically costly reproduction is also affected by the need for energy conservation, resulting in a low number of eggs, often combined with brooding and asexual multiplication (protozoans). Hermaphroditism is frequent and reduces the energetic costs of finding a partner. Sometimes, especially at lower latitudes, reproductive activity in the depths changes seasonally, due to the seasonal supply of surface-derived organic matter. Additionally, the predominant mode of nutrition in the deep sea, passive deposit feeding, is energetically more favorable than the more active selection of food particles. All of these features characterize deep-sea meiofauna as specialized K-strategists, with a remarkable degree of trophic partitioning and evolutionary diversification.

The structuring influence of a scarce food supply is also evident in analyses of size spectra, which have been best studied in the dominant deep-sea taxon, the nematodes. Thiel’s (1975) general rule for deep-sea fauna is valid for various deep-sea regions: with decreasing food supply (chlorophyll content) and mostly parallel with increasing depth, the average body size of nematodes decreases (Soetaert and Heip 1989; Tietjen 1992; Schewe and Soltwedel 2000; Kaariainen and Bett 2006; Rex et al. 2006). The same concept also seems to hold for harpacticoids: in a deep-sea area of the South Pacific, more than 50% of the copepod specimens were less than 200 µm in length (Schriever, personal communication). Only in the nematode fauna inhabiting the deeper sediment layers with hypoxic or sulfidic conditions has another trend evolved. Here, a long, filiform body size seems to be more favored, perhaps because it is better adapted to the uptake of dissolved organics or to higher mobility in the semi-liquid mud (Jensen et al. 1992a; Soetaert et al. 2002). Gigantism relative to the average representatives of a taxon also occurs in the deep sea among meiofauna, e.g., in Loricifera, but it is probably ecologically irrelevant.
High specialization and slow biological processes in the deep sea make meio- 
fauna, especially the rarer species, sensitive to disturbances and much more vul- 
nerable than their relatives in shallow sediments. Processes of recovery from a major 
disturbance have been found to last for years, a fact that should be considered when 
planning the economic exploitation of deep-sea bottoms (Ingole et al. 2005), e.g., 
the mining of manganese nodules (Radziejewska 2002) or the deposition of CO₂ 
(Carman et al. 2004).

In this context, the possible role of meiobenthos in the formation of polymetallic 
(manganese) nodules in the Pacific Ocean should be mentioned briefly. Although 
the chemical processes involved in the massive accretion of valuable heavy metals 
are not yet understood, each nodule is densely covered with and colonized in its 
internal interstices by a diverse meiobenthic community of deep-sea protozoans 
and also metazoans. It may be of relevance that Foraminifera are known to selec- 
tively excrete manganese, iron and other metals as xenobiotic particles (xanthoso- 
mes). Perhaps these excretions serve as the initial granules for the formation of new 
nodules, since mineral centers have been found in all of them (Riemann 1985)? 
Thus, it is conceivable that meiobenthic organisms influence the growth of these 
structures of high economic potential in one way or another (Shirayama and 
Swinbanks 1986). However, the expected large-scale exploitation of polymetallic 
nodules by deep-sea mining would certainly massively threaten the slow-growing 

deep-sea meiobenthos.

Meiofauna community composition. The ubiquitous Foraminifera (Protozoa) 
play the dominant ecological role in the shelves, the slopes and the plains of abyssal 
deep-sea bottoms (Fig. 8.3). Usually 50% of all individuals (maximally 90%) and 
about 30% of the meiofaunal biomass consists of foraminifers (Shirayama and 
Horikoshi 1989; Moodley et al. 2002). This group alone is a match for all remain- 
ing metazoan meiofauna in terms of abundance. Aside from the foraminiferans, 
other rhizopods such as Amoebina and the large Xenophyophoria have also been 
found to richly populate the deep-sea bottoms (Levin 1991). It seems that there is 
no square centimeter of the deep-sea bottom that is not interwoven with rhizopod 
pseudopodia. While many predator species among foraminiferans directly affect 
the metazoan populations, Foraminifera also have a considerable indirect impact on the 
metazoan meiofauna, consuming about 50% of the incoming phytodetritus. 
Increasing sediment heterogeneity, e.g., through the seasonal input of phytodetritus, 
may temporarily alter the species composition of deep-sea meiobenthos (Lambshead 
and Gooday 1990).

Among the metazoans, nematodes dominate in almost all studies, with a share 
of between 80 and 90%—an even higher value than in shallow reaches. In the 
muddy abyssal plains and often in the deeper layers below the sediment surface, the 
meiobenthos is essentially a nematode community consisting primarily of 
Desmodoridae and Microlaimidae. In a Mediterranean deep-sea canyon, 
Comesomatidae (with Sabattieria) were the prevailing (up to 40%) nematode family 
(De Bovée and Labat 1993). Typical deep-sea genera are Acantholaimus, 
Molgolaimus, Microlaimus, Thalassomonhystera and Halalaimus. Bacterivorous 
deposit feeders seem to prevail, followed by predators and omnivores, e.g.,
Sphaerolaimidae, while epistrate feeders usually only represent a low percentage. A 7% share was assigned to gutless nematodes by De Bovée and Labat (1993).

Occurring in much lower numbers and particularly in the surficial layers of somewhat coarser sediments are harpacticoids (e.g., *Pseudomesocra*, *Zosime*, *Malacopsyllus*) and polychaetes. Juvenile bivalves and some kinorhynchs are encountered in muddy samples. In studies from the northern Atlantic, polychaetes...
ranked second after nematodes. The meiofauna of sea mount sediments differs from that of general deep sea bottoms (see below). Meiofauna (e.g., harpacticoids) even exists in the hadal troughs at depths of below 10,000 m, although in reduced abundance. Interestingly enough, even representatives of oligochaetes, a group purportedly of limnogenous/terrigenous descent and lacking propagatory stages, have been found at >7,000 m depth. Nemertines, reported by Ingole et al. (2005) to rank second after nematodes, certainly represent a local exception.

Diversity. The deep sea is renowned as a “hot spot of biodiversity.” Based on high patch dynamics, meiofauna confirm this general rule. The alpha-diversity, “weighted” or “expected species richness” or “Shannon diversity” are unexpectedly high, especially in the bathyal and abyssal depths and around Antarctica. Foraminifera alone can exist at an abundance of 40 different species per cm². On average 25–50 distinct species of nematodes or harpacticoids can be discriminated per 100 individuals of meiofauna found; the equatorial and southern Pacific seems to have a particularly speciose nematode community (Snelgrove and Smith 2002). Based on nematode data, the average taxonomic diversity increases with water depth, although the number of genera may decline approaching deep-water sediments. In samples from the deep-sea bottom under the Arctic ice margin, 300 species of nematodes were discriminated, most of them new to science (Hoste et al. 2007). In a manganese nodule field, an assemblage of 2,022 nematodes consisted of 250 distinct species belonging to 110 genera (Miljutina et al. 2006). Also, Arctic deep-sea bottoms structured by a rich sponge assemblage exhibited a correspondingly high alpha-diversity (Hasemann and Soltwedel 2006). On a small scale, the diversity of species is extremely high in the deep sea while comparisons of diversity between large biogeographic regions (gamma-diversity), especially at the genus level, often yield low values.

Compared to abundance, biodiversity (alpha-diversity) seems to be more intricately influenced by food supply and habitat heterogeneity. Whereas in some studies both diversity and abundance decreased with the depth-related decrease in particulate organic matter (POM), many other reports, especially those from bathyal and abyssal sites, measured an inverse relation between POM flux and diversity, i.e., diversity was higher in bathyal and abyssal depths than along the shelf slopes (Rex et al. 1993; Boucher and Lambshead 1995). A comprehensive literature evaluation (Mokievskiy et al. 2007) confirmed, regardless of the methodology applied, an increasing dominance of nematodes, with a maximum at depths of below 1,000 m. Again, this pattern appeared to be controlled by the habitat heterogeneity and the food supply. Only in the hadal regions did the extreme food scarcity cause both parameters to decline in parallel. Here it appears that a rich meiobenthic life cannot be sustained. The resulting hyperbolic (“hump-shaped”) bathymetric gradient of biodiversity from shallow reaches to the deepest parts of the ocean, with a maximum occurring around 2,000 m, has been corroborated for (nematode) meiofauna in the North Atlantic (Lambshead 1993). A multiple regression re-analysis of numerous nematode data sets using latitude, areas scale, sampling effort and depth as independent parameters (Mokievskiy and Azovsky 2002) also resulted in a hyperbolic diversity curve for depths >100 m,
with the highest values obtained at latitudes of between 30 and 60°N. However, the evaluation of another comprehensive data set of nematode genera from numerous sites at depths of between 200 and >8,000 m from a wide spectrum of regions did not show the expected hyperbolic curve of species richness (Gambi et al. 2007). The critical point when looking at diversity patterns seems to be the choice of an appropriate scale that separates local from regional data sets. This would perhaps explain the problematic and partly contradictory results (Lamshead et al. 2000).

Why is the deep-sea meiofauna (and macrofauna) so diverse? Depth is probably not the causative factor involved per se. The limited food supply promotes niche partitioning, which results in strong functional and morphological specialization and spurs the process of evolutionary diversification. Additionally, structural complexity influences the trophic interrelationships and contributes to biodiversity. This is demonstrated in studies of meiofauna from submarine canyons and from sea mounts. Both of these regions are increasingly recognized as being “hot spots” of meiofaunal diversity. Their variable and complex hydrodynamic patterns create sediment heterogeneity, sometimes combined with a favorably rich flux of organic particles, which differ considerably from the uniform deep-sea plains and enhances meiobenthic diversity. While the origin and fate of this genuine “sea mount fauna” remain disputed, they are clearly hot spots of meiofaunal biodiversity when compared with the surrounding plains. Also, in cold-water coral reefs, coral and sponge rubble enhance habitat complexity and create islets of high diversity in the deep-sea bottom (Raes and Vanreusel 2006). These are preferred by robust nematode taxa that mostly act as epistrate feeders on microbial films (Epsilonematidae, Draconematidae). *Epsilonema multispiralum* is particularly common in North Atlantic deep coral sediments.

**Box 8.4 Meiofauna in the Deep Sea: Diversity in Scarcity**

Scarcity of food and low temperatures are the key factors that determine the life of meiobenthos in the deep sea. The most distinctive aspect is the high biodiversity, which exceeds that at shallow sites. Hydrodynamic patterns and macrofaunal activities structure the bottom and provide heterogeneity; sufficient oxygen and pulses of phytodetritus as food are usually available. This combination results in a deep-sea ecosystem that is far from monotonous, containing a meiofauna with a particular composition, low abundance and biomass, but high diversity. Foraminiferan protists dominate the meiofauna, and the sediment is interwoven with their pseudopodia. The other main component is nematodes, while harpacticoids remain relatively rare. The number of specimens per species/taxon is extremely low: any random selection of 100 meiofaunal individuals would usually include 25–50 distinct species of nematodes and harpacticoids. What causes such a high diversity? Scarc and patchy food pulses support energy-efficient K-selection in most deep-sea (continued)
8 Meiofauna from Selected Biotopes and Regions

Distribution pattern. At a large geographic scale, the horizontal distribution pattern of deep-sea meiofaunans is rather monotonous (see Box 8.1 for an essay of the “latitudinal diversity gradient”). In areas of little sedimentation, the ubiquitous muds harbor a rather evenly distributed association of deposit feeders of high conformity at the genus level. However, changes in sediment structure, e.g., local accumulations of phytodetrivous, seem to correspond with a nonrandom meiofaunal distribution and differing compositions. The Northeast Atlantic, with its high primary production, harbors a particularly rich deep-sea meiofaunal compared to other large ocean basins and the Mediterranean. In the more hydrodynamically complex sandy areas of the deep sea, suspension feeders with mucus filtration become more frequent.

Vertical cores profiles also demonstrate that deep-sea meiofauna is mainly controlled by the restricted food supply. About 90% of all meiofauna are concentrated in the upper 2–5 cm, where the nutritive detritus accumulates. In contrast to shallow sediments, this concentration at the surface does not result from decreasing oxygen levels at greater depths. As a result of the extremely low input of organic matter, the biological oxygen demand is reduced so much that the upper 5–10 cm of the deep-sea bottom remain oxic. Especially foraminiferans, harpacticoids and polychaetes aggregate near the surface, while the deeper strata are the domain of nematodes. Only areas with richer organic input—where food does not limit the occurrence of meiofauna—suffer from low oxygenation, which then becomes an additional key factor. In regions intensively bioturbated by macrobenthos, meiofauna (mainly nematodes) also occur in deeper layers beyond the usual 5–10 cm threshold, since the oxygen penetration is enhanced in this case and the detritus is buried deep down. In the deep sea of the Indian Ocean, Ingole et al. (2005) reported that only 16% of the meiofauna was present in the upper 2 cm, while meiofauna was recorded down to a sediment depth of 35 cm.

The density of deep-sea meiofauna is largely determined by three sediment factors (Shirayama 1984): calcium carbonate content; heterogeneity of the substrate (low sorting coefficient); and organic matter, indicating food availability. Abundances of 100–1,000 meiobenthic organisms per 10 cm² (without foraminiferans) are quite...
typical of the deep sea (Table 8.3; Tietjen 1992). At great depths, meiofaunal density often declines to 10–100 per cm² (Shimanaga et al. 2007). Sediments with a high abundance of shell remains (calcareous ooze) harbored up to 1,300 ind. ml⁻¹ of metazoan meiofauna (Shirayama 1984). Even Protozoa (Foraminifera) do not markedly exceed this range (maximally 2,000 ind 10cm⁻² or 150–200 ind. ml⁻¹ sediment). Compared to surface values, these figures document the often limiting effect of the organic particle flux on the existence of a deep-sea meiobenthos (Tietjen 1989). Since the amount and the nutritive value of this flux decrease with increasing depth, the meiofauna in most deep-sea regions follow a negative hyperbolic abundance/depth relation (Fig. 8.4; Pfannkuche and Thiel 1987; Tietjen 1992). When adverse hydrodynamic patterns prevail, even shallow bottoms can support low meiobenthic stocks. This can cause an exceptional increase in abun-

Table 8.3 Meiofaunal composition (%) and abundance in samples from increasingly deep marine sites (Coull et al. 1977)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>400 m</th>
<th>800 m</th>
<th>4000 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foraminifera</td>
<td>30.8</td>
<td>33.1</td>
<td>65.2</td>
</tr>
<tr>
<td>Nematoda</td>
<td>45.1</td>
<td>59.7</td>
<td>30.2</td>
</tr>
<tr>
<td>Harpacticoida</td>
<td>10.7</td>
<td>2.4</td>
<td>2.0</td>
</tr>
<tr>
<td>Unidentified</td>
<td>5.1</td>
<td>1.5</td>
<td>1.1</td>
</tr>
<tr>
<td>Polychaeta</td>
<td>2.8</td>
<td>1.6</td>
<td>0.5</td>
</tr>
<tr>
<td>Organisms per 10cm² (average values)</td>
<td>442</td>
<td>892</td>
<td>74</td>
</tr>
</tbody>
</table>

Fig. 8.4 The decrease in meiofaunal abundance with ocean depth. (Tietjen 1992)
dance (and diversity, see above) at greater depths of between 3,000 and 6,000 m. Even deeper down, the usual decrease towards hadal depths begins, so that the resulting abundance/depth curve here is parabolic (Rex et al. 2006).

Population densities of more than 1,000 ind. 10 cm⁻² have been recorded in deep-sea areas with a high input of food particles. In polar regions, especially beneath the ice margins with their rich supply of phytodetritus, meiofaunal abundance can even exceed these values (up to 5,000 ind. 10 cm⁻² have been sampled) (Pfannkuche 1992; Soltwedel et al. 2003; Vanhove et al. 1995). Also, in upwelling areas, along the foot of the continental slope or in sites where currents accumulate debris, the richer nutrient supply gives rise to a generally higher meiofauna density (Alongi 1990b). Whereas in temperate and boreal waters phytodetritus from plankton blooms drives seasonal variations in deep-sea meiofauna, in some tropical areas, monsoon-driven fluxes in surface production seem to cause seasonal variations in the deep sea. In Indian Ocean samples, the deep-sea meiofaunal density at 5,000 m depth was unusually high, about 45 × 10³ m⁻² (Ingole et al. 2005). Compared with the macrobenthos, the deep-sea micro- and meiofauna are more responsive to nutritional changes arising from the surface (Vincx et al. 1994; Gooday 2002). The close correlation between food supply (measured as chloroplastic pigments) and meiofaunal abundance was not found in the warm deep sea of the Sulu Sea, where (corresponding to the conditions at the bottom of the Red Sea) low rates of degradable organic matter and low-oxygen conditions act as stressors (Shimanaga et al. 2007). Biomass and production. Towards the deep sea, all animal groups experience significant exponential decreases in both abundance and biomass. Smaller size classes replace larger size classes. Since the general decline with depth is particularly rapid for larger animals, their fraction of the total community biomass compared to the fraction represented by the meiofauna shows a steeper decline towards the deep sea and favors the meiofauna. This can result in a biomass ratio between the macro- and meiofauna of 1:1 (Tietjen 1992). With the benthic protozoans included, the preponderance of the macrobenthos is even more attenuated (see Sect. 9.3.3). The strong relationship between the meiofaunal abundance and biomass and the supply of organic matter, which in turn depends on depth, allowed De Bovée and Labat (1993) to suggest a linear regression with sample depth as the main variable.

Meiofaunal biomass from the abyssal plains is often only 50–100 mg fresh wt m⁻² (corresponding to approximately 4–8 mg C m⁻²). Canyons and the feet of continental slopes, with their larger influxes of organic matter from the shelf, are usually more productive. 37 mg C m⁻² was measured for the meiofauna of a Mediterranean canyon (De Bovée and Labat 1993). The meiobenthic biomass in Arctic regions was 3–10 times lower than that in richer East Atlantic bottoms (Pfannkuche and Thiel 1987). These low values underline the oligotrophic character of wide abyssal regions, although in the areas that receive a high flux of organic matter, values of around 1 g wwt × m⁻² or more have been recorded. Monsoon-driven high flux rates of particulate matter (Arabian Sea) increased nematode biomass. At various Pacific stations, Shirayama (1984) found unusually high biomasses (calculated from ash-free dry weight): metazoan meiofauna was between 103 and 4,120 mg fwt m⁻²,
depending on depth and sediment type (corresponding values for foraminifers were 130 and 3,414 mg fwt m\(^{-2}\)). The few biomass data from the Indian Ocean are not sufficient to provide a consistent picture.

In general, productivity rates in deep-sea bottoms are 2–3 orders of magnitude lower than in shallow-water sediments. Shirayama (1995) calculated that a generalized deep-sea meiofauna specimen will ingest about 10 ng C per day, while the same value can be ingested per hour in shallow sediments (Tietjen 1980a). If we consider production rates, the relevance of the meiobenthos becomes even more impressive than just comparing biomass values (see above): 80% of all metabolic processes in the deep sea refer to meiobenthic organisms (Shirayama and Horikoshi 1989). An annual mean consumption rate for the meiobenthos of about 10 g C m\(^{-2}\) has been calculated (De Bovée and Labat 1993). Locally (e.g., in the Mediterranean) this rate can be lower (about 2.9 g C m\(^{-2}\)). This demand is largely supplied by seasonal pulses of organic matter from the surface and by horizontal advective currents, sometimes influenced by the tides. The specific role of the meiobenthos in the biological productivity of the deep sea is still rather difficult to assess, since the problems involved in measuring production (see Sect. 9.3.2) are aggravated in the deep sea. The following promising methods have been suggested:

- Recording community respiration in a limited sediment area under a bell jar (Pfannkuche and Lochte 1990).
- Quantitative analysis of the most important nutrient input, the chloroplastic pigments. This parameter, which depends directly on the production of phytoplankton in the euphotic zone, couples the meiobenthos in the deep sea with the ocean surface (Thiel et al. 1988/89; Fig. 8.5). However, there may be disadvantages to this approach, since the nutritive value (palatability) of phytodetritus can vary (fresh vs. aged detritus: Soltwedel 1997; Witte 2005).
- Measuring the ATP content as well as the activity of the electron transport system (ETS), both of which reflect the (meio)benthic metabolic rate.

The deep sea is the largest biotope but the one that is least explored biologically. We do not yet have a reliable picture of the composition, diversity, distribution and ecological role of the deep-sea meiobenthos. Why were the composition and the abundance of the deep-sea meiobenthos, with its dominance of protozoans, not recognized earlier? Apart from problems with accessibility and inadequate equipment, the dominant taxon—the benthic foraminifera with their irregular shells that are covered by agglutinated detritus—has often been overlooked. Considering the global extent of the deep sea, a representative exploration seems impractical. Large parts of the southern oceans in particular must still be considered “terra incognita” in terms of their meiobenthos.

More detailed reading: Thiel et al. (1988/89); Tietjen (1992); Vincx et al. (1994); Gooday (2002a); manganese nodules, Mullineaux 1987; Foraminifera, Gooday et al. 1992; Snellgrove and Smith (2002); latitudinal gradient, Clarke (1992); Rohde (1992); Rosenzweig (1995); Gaston (2000); Lambshead et al. (2000); monograph on the deep sea, Gage and Tyler (1991)
Life began in an anoxic and sulfidic world. Even in today’s oxic world there are a variety of environments where suboxic (dysoxic) or even anoxic conditions prevail. They originate under the influence of bacterial degradation wherever low oxygen supply meets high organic enrichment. The bacterial consumption of oxygen is often accompanied by the formation of toxic hydrogen sulfide. Hence, hypoxic/anoxic sediments develop naturally around the world, although human activities also continuously increase the number and persistence of anoxic/sulfidic sites. Eutrophication and deposition of organic matter accompanied by rising temperatures often create anoxic and sulfidic conditions, as evidenced by the frequent appearance of (black) sediment patches in the summer months. The organically enriched sediments in sheltered hydrographic conditions will be most affected, while the oxygen depletion will be less severe in places where plant roots release oxygen or bioturbation provides access to it.

As general interest in ecology has increased, the fauna adapted to sulfidic conditions have also attracted more attention. This sulfide community was named the

![Fig. 8.5a–b](image-url) The correlation between phytodetritus (chloroplastic pigments) and meiofaunal abundance (a) and biomass (b) in the deep sea. (Pfannkuche 1985)
“thiobios” by Boaden and Platt (1971), who described a “living system of the sulfide biome” (Fenchel and Riedl 1970). This fauna consisted mostly of ciliate protozoans along with some meio-benthic metazoans. Among these taxa, the “most conservative” bilaterian phyla—Plathyhelminthes and Aschelminthes—predominated, while crustaceans were absent. Boaden and Platt were not the first to find animals under low-oxygen and high-sulfide conditions. For many years, specialized animals were known to thrive under hypoxic or completely anoxic conditions, and even when exposed to free sulfide, conditions that were thought intolerable for free-living fauna. Fenchel and Riedl (1970) realized that there is a distinct, definable community of eukaryotic life that is specifically adapted to reducing conditions. Referring to nematodes, Ott (1972) emphasized that “the sulfide system has a homogeneous and stable … fauna of its own right” (compare Fig. 8.6). Since complete

Fig. 8.6 The vertical distributions of various nematodes in sediments of the Kattegat (Baltic Sea). Separate oxibiotic and thiobiotic faunal assemblages are apparent. (After Jensen 1987b)
anoxia had not been considered a prerequisite for the existence of a thiobios, it was an unfortunate and ecologically unrealistic approach to link the existence of a thiobios to the absence of oxygen. Reise and Ax (1979) questioned the term “thiobios,” since they could not find “a specific meiofauna confined to oxygen-deficient horizons of the sediment,” regrettably without measuring the microgradients of oxygen or hydrogen sulfide. In the modern understanding of “thiobios,” it seems adequate to base the definition on an etymological root (ϑιος, theion, Greek for “sulfur”), emphasizing hydrogen sulfide (and/or other reduced substances) as the controlling factor:

“Thiobios represents a diverse community of organisms characteristic for biotopes where hydrogen sulfide and other reduced substances are regularly dominating ecofactors. The thiobios is directly or indirectly linked to sulfidic habitats.”

The existence of a meiobenthic thiobios is neither questionable nor ecologically irrelevant considering the trend towards more hypoxic/sulfidic environments. Among the thiobios, soft-bottom meiobenthic forms play a substantial role.

8.4.1 Reducing Habitats of the Thiobios

Oxygen depletion is often connected with the development of hydrogen sulfide. The distribution of this important ecofactor is mostly antagonistic to that of oxygen (see Fig. 2.11), and part of a complicated and changing system with intermingled processes and differentiated gradients of \( \text{O}_2 \) and \( \text{H}_2\text{S} \). The few general features that exist in this dynamic web are (a) ubiquitous transitions between oxic/anoxic and anoxic/sulfidic microenvironments, often in the range of micrometers or even just cell diameters (see Fig. 2.8; Revsbech et al. 1980; Bock et al. 1988; Fenchel 199), and (b) their continuously changing dynamics based on microbial metabolism (Reichardt 1989).

Since these transitions are often suboxic (also termed “dysoxic”), from an ecological perspective they belong to the reducing habitats, and so will be considered here too.

Areas where sulfidic biotopes can be encountered are as numerous as the processes associated with them, and include deep-sea hydrothermal vents, gas and oil seeps, and silled marine basins such as the Baltic and the Black Sea. Large suboxic to anoxic and highly sulfidic areas also prevail in upwelling zones off the coasts of Peru and Chile, where organically rich muds are blocking from taking up oxygen by upwelling currents. Oxygen minimum zones (OMZ) are widespread at the continental margins of the oceans (Levin 2003). Basins filled with anoxic brine that has elevated levels of hydrogen sulfide and methane occur in the Mediterranean and in seep areas in the Gulf of Mexico. The subsurface layers of tidal mudflats and mangroves and coastal sites polluted by sewage represent large sulfidic habitats. Stratified deep lakes develop completely anoxic, often sulfidic, layers in their profoundal depths. In stratified deep lakes the profundal muddy sediments are often separated from the oxic surface layers and become anoxic/sulfidic.

Reduced sediments develop dissolved hydrogen sulfide in two general ways:

(a) The deeper layers of organically rich marine shore sediments (tidal flats, mangroves, estuaries, enclosed seas) become oxygen-depleted. Then, through the
microbial reduction of oxidized sulfur species (mainly sulfates), sulfide develops. If produced in excess, not all sulfide becomes bound chemically, so that free sulfide will accumulate as toxic hydrogen sulfide. Because of the rich concentrations of sulfate in seawater, marine habitats reach higher (up to millimolar) concentrations of dissolved hydrogen sulfide than limnetic ones, where the sulfide mainly originates from the degradation of the proteins contained in organic matter.

(b) Tectonic activities often lead to the venting of anoxic, volcanic, geothermal waters and gases rich in hydrogen sulfide, often combined with rich amounts of methane and ammonium (geothermal reduction). Particularly frequent in the deep sea, hot smokers or diffuse venting sites characterize these hydrothermal activities (see Sect. 8.4.7).

The structures of the ubiquitous reducing/sulfidic areas and their relevance as biotopes for animals can only be understood by considering microbiological and geochemical aspects, which, in turn, leads to a more dynamic understanding of their biota (e.g., Jørgensen and Bak 1991; Watling 1991; Diaz and Rosenberg 1995; Levin 2003). Some important aspects to be considered in this scenario are:

- Microbial sulfate reduction, which produces sulfide, is possible under both anoxic and low-oxic conditions (see Jørgensen 1977a; Jørgensen and Bak 1991).
- In natural marine sediments, thiosulfate is the predominant sulfur species, and it breaks down to a large extent into sulfide and sulfate (Jørgensen 1990; Fossing and Jørgensen 1990).
- Microchambers (often only 50–200 µm ø) with reduced conditions amid oxic sediment can form a three-dimensional network of oxic and sulfidic microgradients (Jørgensen 1977a; Wilson 1978; Gowing and Silver 1983; Ramsing et al. 1993; Fenchel 1996; Förster 1996). Bioturbation and plant growth complicate their continuous dynamics and alteration (Fenchel 1996; Wetzel et al. 1995; Lee 2003).
- The narrow light-colored haloes around tube structures in the sulfidic depths contain oxygen that is mostly in a chemically fixed form; free oxygen is available only temporarily (Jørgensen and Revsbech 1985; Watling 1991; Wetzel et al. 1995; De Beer et al. 2005a).
- Oxidized sediment layers can lack free oxygen, but they can still have positive redox values, see Sect. 2.1.4). Oxygen respiration by most animals requires dissolved free oxygen (Sikora and Sikora 1982; Jørgensen and Revsbech 1985; Watling 1991).

The following chapter will show that all of these diverse sulfidic biotopes are, at least temporarily, habitats for a characteristic, specialized meiofauna, and it will challenge their alleged azoic nature.

### 8.4.2 Thiobiotic Meiobenthos

The following chapter describes the organismic world of anoxia and sulfide, the thiobiota. What is the composition of the typical meiofauna thiobios? Which groups are regularly encountered in the sulfide biome?
Foraminifera: In temporarily oxygen-depleted and sulfidic sediments, Foraminifera prevail in abundance. Numerous species have been found in dysoxic or even completely anoxic sediments (Bernhard 1996; Bernhard et al. 2000; Moodley et al. 1997). Their quantitative prevalence under temporarily anoxic conditions has been tested experimentally and is not restricted to the deep sea (see Sergeeva and Gulin 2007). Especially under conditions of high organic enrichment, they can form high-abundance but low-diversity communities.

Ciliata: In many beaches, most of the ciliates are probably migrating between anoxic and oxic strata (Fig. 5.6; see Berninger and Epstein 1995). A rich ciliate fauna can be found mainly around the RPD layer (e.g., *Kentrophoros*), and many of these thiobiotic ciliates maintain a veritable "kitchen garden" of prokaryotic symbionts (Fenchel and Finlay 1989). Other ciliate species (*Metopus, Plagiopyla*) harboring methanogenic bacteria as symbionts live as true anoxybionts deep in the black layers (Fenchel et al. 1977; Fenchel and Finlay 1991). They lack normal mitochondria but possess hydrogenosomes (Hackstein et al. 1999). The hydrogen excreted by the ciliates is coupled to the reduction of CO₂ by the methanogens and the resulting methane is released.

Platyhelminthes: Among the turbellarians, numerous representatives of the Acoela (e.g., *Solenofilomorpha, Oligofilomorpha, Parahaploposthia*) and Catenulida (Retronectidae, *Paracatenula*) are found in the deeper horizons around or underneath the oxic/sulfidic interface (see Figs. 8.7, 8.8; Sterrer and Rieger 1974; Boaden 1975; Crezée 1976; Powell 1989). Their preference for hypoxia has been known for quite a while, and has been experimentally documented by Meyers et al. (1987, 1988). Scherer (1985) found most thiobiotic turbellarians in the close vicinity of macrofauna burrows, where they probably take advantage of an enriched food supply (Fig. 8.6).

Gnathostomulida: While in most meiobenthic groups the thiobiotic species are exceptional specialists, it seems that all of the gnathostomulids prefer low oxic to anoxic or mildly sulfidic biotopes (Müller and Ax 1971). They are regularly encountered along the tube walls of endobenthic burrowers and they have been found confined (although present with considerable diversity) to the reduced fine sand underneath cyanobacterial mats or the roots of surf grass (Westphalen 1993). They even dominate all other meiofauna in the permanently anoxic sediments underneath deep-sea brine seeps (Powell and Bright 1981; Powell et al. 1983). This phylum of primitive Bilateria is a typical component of thiobiotic meiofauna.

Gastrotricha: The close relation of some gastrotrich genera to the reduced milieu of the thiobiota is documented by their scientific names: *Thiodaysys, Turbanella thiophila, T. reducta* (Boaden 1974, 1975). Frequently, these and other gastrotrichs can be found in the black layers of sand underneath the chemocline. *Urodaysys* is represented by several species in the anoxic Santa Barbara Basin (Balsamo et al. 2007).

Kinorhynchs (indet.) have been reported from the anoxic bottom of the Black Sea (Sergeeva 2003).

Nematoda: The most abundant animals in suboxic and reduced sediments are particular groups of nematodes (Moodley et al. 1997; Gooday et al. 2000; see Fig. 8.7).
Most of them are unusually slender or threadlike (Jensen 1987b), and belong to Siphonolaimidae and Linhomoeidae (Monhysterida), but typical inhabitants of sulfidic biotopes also occur in the enoplid family Oncholaimidae (Pontonema), the chromadorid families Comesomatidae (Sabatiera), Xyalidae (Daptonema), the Desmodoridae (subfamily Stilbonematinae: Leptonemella, Eubostrichus, Miljutin et al. 2006); accumulation of large globular granules in the intestinal cells (Siphonolaimus, Sphaerolaimus, Sabatiera, Terschellingia); inclusion of crystals in the muscle cells (Tobrilus, Sabatiera). In Tobrilus, the
formation of crystals could also be observed in species that did not occur beneath the chemocline. Therefore, it is unclear whether they function as sulfide-precipitating structures (Thiermann et al. 2000). It has been assumed by various authors that the furry covers exhibited by the Stilbonematinae, which consist of symbiotic sulfur-oxidizing epibacteria, are related to a thiobiotic lifestyle (Ott et al. 1991, 2004). Oncholaimus campylocercoides from shallow hydrothermal vents has been experimentally found to accumulate globules of polysulfur underneath the cuticle if exposed to hydrogen sulfide. This metabolic capacity is considered rare among aposymbiotic metazoans (Thiermann et al. 2000). Chemoautotrophic bacterial mats on the surface of a freshwater pool in Movile Cave (Romania) are inhabited by several nematode genera, among them the endemic Chronogaster troglodytes. This species has been experimentally shown to

Fig. 8.8 The occurrence of various oxibiotic and thiobiotic turbellarians in a depth profile of a tidal flat and around a worm burrow. (After Powell 1989)
be well adapted to the methanic and sulfidic water and the extremely low oxygen concentrations in the mats (Muschiol et al. submitted)

Oligochaeta: Various isolated macrobenthic species, mainly tubificids, are tolerant of hydrogen sulfide (particularly *Euliodrilus heuscheri* and *Tubificoides benedii*), but in the meiobenthos there are two marine genera, *Inanidrilus* and *Olavius* (Tubificidae), with numerous species that all are typically thiobiotic (Giere 1981; Giere and Langheli 1987; Erséus 1984, 1990b). Occurring mostly in calcareous sands of warm water regions, all of these species (about 90 described so far) are gutless and lack nephridia, and those studied so far have incorporated subcuticular bacteria (see below).

Polychaeta: A few adapted species occur in anoxic bottoms of the Black Sea (*Nerilla*, *Protodrilus*, *Victorniella*). In some nerillids, endo- and ectosymbioses with bacteria of unknown function are established (Tzetlin and Saphonov 1995; Bernhard et al. 2000).

Crustacea: A few specialists among the normally oxygen-demanding ostracods (e.g., *Cyprideis torosa*) and harpacticoid copepods (e.g., *Cletocamptus confluens*) were experimentally found to not only tolerate low oxygen concentrations but also unusually high rates of hydrogen sulfide. Among copepods, the Dirivultidae (Siphonostomatoida) dominate around hydrothermal vents (see Sect. 8.4.7). The harpacticoids *Ectinosoma melaniceps*, *Parastenhelia spinosa* and some others are regularly encountered in anoxic muds of the Black Sea; here copepod resting eggs were also quite common (Sergeeva 2003). The same study also reports that malacostracan crustaceans, widely held to be sensitive to any oxygen deprivation, occur under complete anoxia in the depths of the Black Sea (tanaids, amphipods). Various crustaceans such as the cephalocarid *Lightiella* live regularly under low-oxic conditions in marine caves (Schiemer and Ott 2001).

### 8.4.3 Persistence and Mechanisms Enabling the Survival of Thiobios Under Anoxic and Sulfidic Conditions

Survival and even persistence for months and years under anoxic/sulfidic conditions have been recorded in various meiofauna, but are yet to elucidate the underlying physiological pathways that enable them to do this. In protozoans, a broad spectrum of Foraminifera are tolerant to complete anoxia, even in combination with the presence of hydrogen sulfide (Bernhard 1996; Bernhard et al. 2000; Bernhard and Sen Gupta 2002; Moodley et al. 1998a,b; 1997; Moodley et al. 2008). A subset of hard-shelled foraminifers was viable for three months under anoxic conditions, surviving even longer than the nematodes species in the same sample, which lived for up to two months in complete anoxia (Moodley et al. 1997). The authors therefore suggested a foraminiferan/nematode ratio as a bioindicator of prolonged anoxia. The capacity of many ciliate species to live under suboxic to anoxic conditions formed the basis of Fenchel’s conception of a sulfide biome (see above, Fenchel et al. 1977).
Among the metazoa, nematodes almost always dominate in suboxic to sulfidic biotopes (Cook et al. 2000). Some sampling sites in Kenyan mangrove muds were dominated by the bacterial symbiotic Astomonema sp. The nematode Eudorylaimus andrassyi and the tubificid Euilyodrilus heuscheri were retrieved from the permanently anoxic Lake Tiberias (Por and Masry 1968) and subsequently kept for several months in a sealed jar under complete anoxia. Even the symbiotic oligochaete Inanidrilus leukodermatus could survive in a sealed jar with its original sediment and in the strong presence of H₂S (notable for its smell) for five months despite the need for bacterial oxidation of reduced sulfur species. Gnathostomulids and nematodes occurred in reduced sediments cut off from oxic seawater by a thick-layered seep of brine (Powell and Bright 1981; Jensen 1986a). Various other species of nematodes, turbellarians and gastrotrichs have been reported from the black depths of various tidal flats. In the oxygen minimum zone (OMZ) off the coast of Peru and Chile the anoxic/suboxic sediment interface is covered with large bacterial mats (mainly Thioploca) and harbors, besides the dominating nematodes, considerable numbers of rotifers, annelids and nemertines (Aramayo et al. 2007).

Compared to these rather isolated reports of perhaps periodic survival under anoxia, the meiofauna found in the world’s largest anoxic basin, the bottom layer of the Black Sea, undoubtedly proves the existence of a fairly diverse and rich benthos that lives under anoxia and in relatively high methane/sulfide concentrations. Nematodes of the genera Desmoscoleax, Tricoma and Cobbionema and some tubificid oligochaetes ("Tubificoides" sp.) have been reported from the permanently anoxic depths (>300 m) of the Black Sea (Zajcev et al. 1987). Confirming these reports, Luth et al. (1999), Sergeeva (2003), and Sergeeva and Gulin (2007) found a meiofauna with an abundance of 50–75 ind 10 cm⁻² (dominated by nematodes and foraminiferans) living below the oxycline in permanently anoxic and highly methanic/sulfidic conditions. They also found crustaceans (harpacticoids, tanaids and ampipods), kinorhynchs, and acarids. Even polychaetes (Nerilla, Protodrilus, Victorniella), mites, and juvenile molluscs were encountered. In addition, the muddy sediment contained numerous (>200 10 cm⁻²) dormant eggs of copepods and cladocerans. A considerable portion of this peculiar anoxic fauna was not attributable to known taxa, even to phylum (Sergeeva 2003).

The sea floor beneath brine basins in the Gulf of Mexico harbored an aberrant meiofauna dominated by gnathostomulids (Powell and Bright 1981; Powell et al. 1983); also, anoxic and sulfidic brine basins of the Mediterranean played host to a remarkable meiofauna that was not dominated by nematodes (Lampadariou et al. 2003).

As yet, we cannot directly determine the physiological pathways that lead to this survival capacity, since most physiological methods are still inappropriate for animals of such minute size. In contrast to macrofauna, in animals below 1–2 mm body diameter (i.e., meiofauna), the oxygen supply can be maintained even under low oxygen concentrations by diffusive gradients alone (Powell 1989; Fenchel and Finlay 1995; Fortey et al. 1996). Theoretical considerations and recorded oxygen consumption rates of different meiobenthic groups led Powell (1989) to infer that meiofauna can use an aerobic metabolism at oxygen concentrations as low as
0.1 μmol l⁻¹, which is below the detection levels of many oxygen electrodes. Even when physiologically adapted to low-oxygen conditions, meiofauna must still nevertheless be protected from toxic and highly permeable hydrogen sulfide in order to exploit the ecological potential of sulfide-exposed habitats (Giere and Langheld 1987; Ott and Novak 1989; Powell 1989; Schiemer et al. 1990; Vopel et al. 1996; Grieshaber and Völkel 1998; Bernhard et al. 2000). The underlying physiological pathways that allow this remain largely unexplored. Extreme metabolic specialization of whole communities was demonstrated by studies in the oxygen minimum zone (OMZ) off Chile. Here, higher meiofaunal abundances were found under oxygen concentrations as low as 0.8 ml l⁻¹ than in the more oxygenated sediments (Veit-Köhler et al. 2008).

The toxicity of H₂S is believed to be the main factor that controls the occurrence of thiobiotic meiofauna, since it (reversibly) blocks cytochrome c oxidase and thus the oxygen uptake required for “normal” ATP production. However, the physiology of the lugworm (Arenicola) demonstrates that organisms can develop other energy production pathways, e.g., gaining energy from the oxidation of sulfide using sulfide-insensitive cytochrome complexes (Grieshaber and Völkel 1998). However, in meiofauna, the physiological pathways that enable their existence under anoxia remain unclear. “An ecological compromise between the food requirements of these organisms and their adaptations to the toxic influence of HS” (Sergeeva and Gulin 2007) describes the situation in the Black Sea, but does not reveal the underlying cellular physiology.

Ecophysiological experiments by Wieser et al. (1974) not only confirmed the long-term survival of nematodes in anoxic sediment; for Paramonhystera wieseri, they documented that the presence of oxygen impaired the ecophysiological capacity and viability of this nematode, which exists solely in deep, black sediments. The long persistence and even growth of nematodes under anoxia remains enigmatic, since the formation of cuticular and collagenous material requires oxygen. Long-term survival under anoxic conditions was also reported for the turbellarian Parahaploposthia, which was found to be CN- and H₂S-insensitive (Fox and Powell 1986, 1987). Also, Jensen (1995) reported that juvenile Theristus anoxybioticus (Nematoda) from sublittoral muds died in oxic water while adults survived well, which corresponds to their field behavior where the long-lived juveniles preferred the deep, anoxic sediments. Schiemer and Duncan (1974) showed experimentally that the nematode Tobrilus gracilis stayed, metabolically, largely anaerobic, even in the presence of oxygen. In experiments performed under anoxia and slightly sulfidic conditions, Metachromadora vivipara even increased in abundance (Steyaert et al. 2007), while other nematode species in these experiments decreased in number and showed reduced activity. Many animals with a high tolerance for anoxia still try to maintain an oxic metabolism at extremely low residual oxygen concentrations (Powell 1989; Gnaiger 1991; Giere et al. 1999).

Thiobiotic animals are usually sluggish animals of low activity. They can considerably reduce their oxygen uptake rates compared to typical aerobic species (Fox and Powell 1987; Schiemer et al. 1990). Many nematodes and gnathostomulids living below the chemocline can regulate their metabolic levels down to low
rates (Schiemer and Ott 2001), often falling into quiescence when exposed to pro-
longed anoxia and sulfide concentrations (Vopel et al. 1996). In many species the
role of mitochondria seems to be important. Such adaptations are enabled by either
including a relatively high number of these organelles in the tissues, or by signifi-
cantly modifying the structures of the mitochondria compared to their normal
appearance (Duffy and Tyler 1984; Giere et al. 1988a; Jennings and Hick 1990).
Balsamo et al. (2007) speculated that the absence of mitochondria in the sperm of
some gastrotrichs might be related to the occurrence of suboxic/anoxic muds in the
Santa Barbara Basin.

In macrobenthic species, the mitochondria have been identified as the site of
sulfide oxidation (Powell and Somero 1986; Vökel and Grieshaber 1996). Parallel
to conditions in the macrobenthos (Powell and Arp 1989), in some specialized
meiobenthos the properties of hemoglobin also seem to have been adapted to ena-
ble it to scavenge the slightest traces of oxygen (e.g., Colacino and Kraus 1984 for
the gastrotrich *Neodasys*). Boaden (1975, 1977) discussed the role of heme proteins
as efficient oxygen scavengers in various red-colored species of Gnathostomulida
and Turbellaria; without further explanation Tsurumi et al. (2003) related the pres-
ence of hemoglobin in dirivultid copepods of hydrothermal vents to their tolerance
of reduced oxygen levels. Unusual organelles possessing sulfide-oxidizing activity
(“sulfide-oxidizing bodies”) have also been suggested for meiofauna, but have
never been documented.

Anoxia in nature is mostly accompanied by hydrogen sulfide, one of the most
toxic natural agents. However, there are almost no studies that examine the com-
bined effects of these often co-occurring ecofactors. This may be due to the
complex instrumentation required to reliably work with defined concentrations of
volatile solutions (Visman 1996). Despite some inconsistencies, there is usually a
negative synergism for hydrogen sulfide and anoxia. The presence of sulfide trig-
ners a switch to a fermentative metabolism at an earlier phase than for anoxic but
nonsulfidic conditions (Cyprideis torosa, Ostracoda: Jahn et al. 1996; Cletocamptus
confluens, Harpacticoida: Vopel et al. 1996). In some typical thiobiotic meiob-
enthos the activities of oxygen-metabolizing, sulfide-insensitive enzymes were
found to be higher than in oxybiotic and macrobenthic fauna, indicating a speciali-
zation to cope with the toxicity of oxygen radicals (Morill et al. 1988). It is conceivable
that in an environment free of dissolved oxygen, oxidized substances such as nitrate
or thiophosphate can become enzymatically activated to serve as oxygen donors.
This pathway is known from prokaryotes, from the ciliate Loxodes (Finlay et al.
1983), from representatives of the bacterial symbiotic Stilbonematinae (Nematoda),
and gutless interstitial oligochaetes (Hentschel et al 1999; Woyke et al. 2006).

An increasing number of meiobenthic species from dysoxic or sulfidic habitats
have been found to rely on the symbiotic association with sulfide- or methane-oxi-
dizing bacteria (for reviews see Giere 1996; Ott et al. 2003). A large group of gut-
less interstitial oligochaetes completely depend on their subcuticular extracellular
symbionts and rely on the integrated cooperation of a bacterial consortium, each
with a complicated and highly adapted metabolism (for an overview see Bright and
Giere 2005; Dubilier et al. 2006). All of these oligochaete species have incorporated
beneath their cuticles a thick layer of sulfide- or methane-oxidizing bacteria which continuously remove the toxic sulfide as they metabolize. This active protection enables the hosts to live in the subsurface layers of shallow sands. Obligate endosymbiosis with bacteria, combined with a reduction of the functional gut, has also developed in nematodes such as *Astononema* that occur in sulfide-enriched sediments (Musat et al. 2007), and in *Rhaptothyreus* (Miljutin et al. 2006). The symbiosis of numerous stilbonematine nematodes (*Leptonemella*, *Catanema*) with sulfur-oxidizing ectobacteria, which decoratively ornament their cuticles, enables these worms to live in deeper layers of sand beneath the chemocline (Ott et al. 2003). There are several other individual meiofaunal species within the turbellarians or the polychaetes that live in symbiosis with bacteria, but details about their symbionts' nature and function are lacking. While further analysis of symbiotic bacteria is required, it should be noted that many thiobiotic animals can survive in extreme sulfidic environments without “bacterial metabolic help.” Beyond certain specific threshold values, they will switch over to an anaerobic metabolism that can sustain them for long periods of time. Severely sulfidic habitats are avoided, a reaction that corresponds to those of numerous macrobenthic animals (for reviews see Somero et al. 1989; Fisher 1990; Vismann 1991; Bagarinao 1992; Grieshaber and Völkel 1998).

The production of sulfur-containing granules or crystals and protection from sulfide by external precipitation (Giere et al. 1988b for *Tubificoides benedii*) is probably of limited importance, although the quantitative roles of these processes are still to be assessed. Iron has been found in various tissues of sulfide nematodes, and it is suggested that it binds reduced sulfur (Nuß and Trimkowski 1984; Nicholas et al. 1987; Giere 1992). However, the exportation of the resulting precipitates needs to be demonstrated before this pathway can be verified as a means of detoxification. A more efficient option is the oxidation of sulfides into long-chained polysulfur, which can be stored as an inert but easily activated product in the tissues. This pathway is known from “sulfur bacteria,” but apparently also occurs in a thiobiotic nematode (Thiermann et al. 1994, 2000). However, considering the high diffusion rate of hydrogen sulfide through the minute bodies of meiothobenthos, the efficiency of any protective method remains doubtful (Powell 1989). A pathway using accumulated carotenoids, common accessory pigments in photosynthesis, as energy-rich substances and oxygen reserves, as suggested by Zajcev et al. (1987), has not been demonstrated in physiological detail for invertebrates. Nonetheless, the multiple ecophysiological approaches that have evolved in meiobenthic animals to cope with life under anoxic and sulfidic conditions indicate the complexity of the ecological and physiological processes involved.

The sulfidic ecosystem, which is dominated by the presence of reduced substances such as dissolved sulfide, methane and ammonium, is much too complex to allow for simple right or wrong opinions that arose in the early debate about the existence of a thionios. It is the regular exposure to hydrogen sulfide in a spatially and temporally changing combination of micro-oxic and microsulfidic niches that characterizes the world of the thionios, and not an either/or situation. With today’s deeper knowledge, we have a better understanding of “sulfide habitats,” their ecological
conditions, and their physiological demands on the “sulfide fauna.” Future discussions about the possibility of animal life under anoxic conditions would be enhanced if studies were always accompanied by careful microelectrometric oxygen and sulfide measurements (see Sect. 2.1.4), and where possible combined with physiological analyses.

### 8.4.4 Food Spectrum of the Thiobios

Two thirds of all carbon reduction is performed by anaerobic sulfate-reducing bacteria, and only one third is achieved by aerobic reduction. Thus, oxic/anoxic and sulfidic chemoclines are trophically favorable for meiofauna, especially since they offer an environment with reduced competition and predation (Giere et al. 1991), provided the problem of sulfide toxicity (see above) is solved. Areas of steep gradients between anoxic/oxic and sulfidic layers are the preferred habitats of rich bacterial stocks with densities of $10^9$–$10^{10}$ cells cm$^{-3}$ (Jørgensen 1977b; Aller and Yingst 1978; Ramsing et al. 1993). The sea bottom beneath the upwelling area off Peru and Chile is covered so densely with mats of the sulfur bacterium *Thioploca* that the sediment has been termed “Thioploca mud.” It has frequently been pointed out that thiobiotic meiofauna utilize the rich stock of sulfur bacteria (Fenchel 1969; Fenchel et al. 1977; Yingst and Rhoads 1980; Grossmann and Reichardt 1991). This attractivity influences the microdistributions of not only the rich ciliate fauna but also of many nematodes and other metazoan meiofauna that graze on the thick bacterial mats. Bacterial mats are the sole food source for freshwater nematodes from the isolated thermomineral Movile Cave (Romania) (Muschiol and Traunspurger 2007).

The development of bacterial symbioses is another means of utilizing the thiobiotic environment (see above). Many symbiotic animals take advantage of the ability of microbes to metabolize reduced substances such as sulfide, thiosulfate and possibly methane. Studies on the gutless *Inanidrilus* and *Olavius* (Oligochaeta), on *Kentrophoros* (Ciliata) and on Stilbonematinae (Nematoda) indicate that these forms use their microbes as a convenient food source. The most complicated symbiosis that has been functionally examined so far is a complex syntrophic web of five different bacterial taxa that cooperate in their host, the oligochaetes *Olavius algarvensis* from the Mediterranean (Woyke et al. 2006). The bacteria not only provide the host with bacterial food, but they also remove its wastes by reducing nitrate. Within the gutless oligochaetes and ciliates, at least some species derive their food directly from their internal symbionts by digesting their subcuticular bacteria via phagocytosis (Giere and Langheld 1987; Fenchel and Finlay 1989). The stilbonematine nematodes feed by grazing on their symbiotic epibacterial fur (Ott and Novak 1989; Ott et al. 1991). The food spectra of the thiobiotic turbellarians Solenofilomorphidae and Kalyptorhyncha as well as those of the specialists among the crustaceans and polychaetes have not yet been ascertained.

**Dissolved organic matter.** Dissolved organics are present in considerable amounts in anoxic sediment horizons (Liebezeit et al. 1983; Sect. 2.2.2). Acetate,
an important substrate for sulfate-reducing bacteria (Jørgensen 1977a; Gibson et al. 1989; Michelson et al. 1989), is utilized by nematodes (Riemann et al. 1990) and is probably an important organic food source for the thiobios. Boaden (1977) even postulated that absorptive feeding on dissolved organics was a general feature of the (primeval) thiobios. The length/width ratios of the bodies of members of the meiobenthic thiobios are characteristically extremely high (Boaden and Platt 1971; Giere 1981; Jensen 1986b; Wetzel et al. 1995). This significant feature is believed to favor transepidermal uptake of dissolved organic substances by the thread-like animals. Combined with endosymbiosis, this nutritional pathway favors the repeated reduction or transformation of the intestinal tract in the thiobiotic (meio)benthos. The degeneration of mouth and anus has generated names like Astomonema (Nematoda), Inanidrilus (Oligochaeta) and Astomus (Polychaeta).

8.4.5 Distribution and Succession of the Thiobios

Thiobiotic species have a vertical distribution that is different from the usual, characteristic concentrations of oxybiotic meiofauna (Boaden 1977; Giere et al. 1982; Ott and Novak 1989). They aggregate in the deeper hypoxic and sulfidic layers where rich bacterial stocks are found. Benthic foraminiferans were found at or below the oxic/anoxic chemocline (Bernhard 1996), and ciliates from Scandinavian sites occurred over a wide range of depths (Fenchel 1969; see Fig. 5.6). Berninger and Epstein (1995) even contended that most typical beach ciliates live under anoxic conditions, probably migrating up and down. An analysis of the nematode vertical distribution in the Kattegatt (Baltic Sea) revealed an assemblage of oxybiotic species that was clearly separated from the thiobiotic species (Jensen 1987b; Fig. 8.7). Jensen (1981) also demonstrated the presence of a very species-specific vertical pattern within the genus Sabatieria. S. pulchra, a typical thiobiotic species, lives deep in the anoxic sediment, while S. ornata occurs close to the surface.

Among limnic nematodes, a similarly differentiated pattern occurs in the genus Tobrilus (Traunspurger 1997a). Powell (1989) summarized experimental studies on various turbellarians with different preference reactions to oxic and sulfidic layers (Fig. 8.8).

In normal oxybionts, decreasing the oxygen content and increasing the sulfide content cause avoidance reactions in almost all meiobenthos, first through upward migrations and even emergence from the sediment into the bottom water layers. This avoidance behavior is barely developed in typical thiobios. However, even well-adapted thiobiotic species such as Pontonema vulgare or Sabatieria pulchra (Nematoda) are often found on the sediment surface during periods of oxygen depletion (see Hendelberg and Jensen 1993; Wetzel et al. 2001). A preference for layers around the oxic/sulfidic chemocline has been experimentally demonstrated in thiobiotic ciliates, turbellarians, gutless oligochaetes and stilbonematine nematodes (Fig. 8.9). However, this preference is combined with a dynamic positioning: thiobiotic animals typically migrate between oxic and sulfidic horizons, traversing the chemocline each
time. They do not maintain a stable position at the chemocline. For the bacterial symbiotic thiobios it appears that the bacteria recharge their energetically valuable reduced sulfur store while the host stays in the sulfidic layers and subsequently gains energy from the oxidation of reduced sulfur when the host migrates into the oxic layers (Schiemer et al. 1990; Giere et al. 1991; Ott et al. 1991).

As a whole, meiofauna is less severely affected by these conditions than macrofauna (Josefson and Widbom 1988; Austen and Widbom 1991; Thiermann et al. 1997). The reaction to a hypoxic/sulfidic event differs depending on the meiofaunal taxon. Soon after the onset of dysoxic conditions, most harpacticoids, ostracods and other crustaceans as well as meiobenthic polychaetes will drop out. Specialized species of turbellarians and gastrotrichs belonging to classical “thiobios taxa” will persist longer. However, if extremes of summer temperatures and low pH act as synergistic stressors, the tolerance range is usually heavily reduced. Only after an increase of hydrogen sulfide to millimolar concentrations will most nematode and foraminiferan species disappear (Moodley et al. 1997). Some specialized thiobios can withstand up to millimolar levels of H$_2$S in complete anoxia (Jahn et al. 1996; Vopel et al. 1996). Concentrations of H$_2$S above 5 mM are usually lethal, even to the most tolerant thiobionts (but see Sommer et al. 2003).

With the return of oxic conditions, the recolonization of the sediment by meiofauna proceeds rather rapidly, normally within a few weeks depending on the distance and status of the oxic donor assemblage. It is mainly the hydrographic regime that determines processes of recolonization, since drift through the water column is
the main pathway for harpacticoids and also for nematodes. Usually the fauna is recruited by colonizers of the ambient oxic fauna, and in its first phases it is characterized by low diversity and high dominance indices (Wetzel et al. 2002).

### 8.4.6 Diversity and Evolution of the Thiobios

Compared to its oxic counterparts, the thiobiotic meiojentos seems impoverished, at least in diversity, while abundance and biomass can be rather high. This is particularly evident in shallow sulfidic areas (Neira and Rackemann 1996). In the polluted Baltic Sea basins and bights, during anoxic and sulfidic periods the meiojentos is mainly represented by dense masses of the nematode *Pontonema vulgare*, which feeds on dead macrofauna (Lorenzen et al. 1987). Under similar circumstances, the nematode *Terschellingia communis* can also develop huge populations. Deep-sea sediments beneath a brine stream, which were continuously exposed to sulfide and frequent anoxia, harbored a specialized fauna of mainly meiojentos forms (Powell and Bright 1981; Powell et al. 1983), dominated by gnathostomulids, turbellarians and nematodes. In meiofaunal samples from the oxygen minimum zone off Peru, Neira et al. (2001a,b) found the proportion of nematodes to be extremely high (99%), with a remarkable dominance of one epsilonematid species (*Glochinema bathyperuvensis*). Below the OMZ, the oxygen content was restored; here the abundance of nematodes decreased and that of harpacticoids increased. The authors related the nematode maximum in the OMZ to the high and barely degraded organic content of the sediment. A prevalence of just a few specialized nematode species that exhibited considerable abundance was also noted by Soetaert et al. (2002) for sediments on the shelf and in canyons with frequently anoxic conditions. The rich amount of food in the OMZ supported a selected protistan and metazoan meiofauna, which can reach high abundances (Levin 2003). A 10-ml sample of *Thioploca* sediment from the Peru upwelling area contained about 400 nematodes belonging to more than 20 species of numerous genera (Riemann, pers. comm.). A change in relative dominance from nematodes to harpacticoids was also recorded by Levin et al. (1991) when sampling a seamount from the summit in the OMZ down to the flanks which were better oxygenated.

This example confirms the generally higher sensitivities of harpacticoids compared to nematodes. In oxygen-depleted and sulfidic biotopes a decreasing diversity is observed along with an increasing dominance of single species, and the relative abundances of major taxa change markedly from oxic to suboxic/sulfidic depths (Gooday et al. 2000; Cook et al. 2000).

Anoxic/sulfidic events exert a considerable selective pressure. Does this pressure become significant from an evolutionary perspective? Is it possible to characterize thiobios by particular anatomical features (bacterial symbioses, malformations or degenerative trends, see above)? The phylogenetic relevance of the thiobios is debated (see Fenchel and Finlay 1995). A fauna that has existed since archaic times
should have considerable evolutionary relevance and should represent primitive life forms. However, suggestions “that the sulfide biome would contain at least some primary (faunal) elements... of the oldest biosystem on Earth” (Fenchel and Riedl 1970) were vehemently refused (Reise and Ax 1979).

Today it is widely accepted that the extant thiobios is derived from oxybiotic predecessors. Even the evolution of complex bacterial symbioses in some meiofauna must be considered a relatively recent development, despite the profound anatomical reorganizations involved. This does not refute that the earliest metazoan fauna did indeed evolve under anoxic/sulfidic conditions. The various hypotheses about the environment of archaic metazoa center around the question of whether primitive, meiobenthic metazoan life had already evolved in the Proterozoic. The appearance of oxygen at the lowest concentrations probably predates the Ediacaran period (Jenkins 1991; Mangum 1991; Runnegar 1991; Thomas, 1997). During the late Proterozoic the water above the bottom may have contained low concentrations of free oxygen. However, at the sediment/water interface, with its rich organic matter, degradation will have caused intense oxygen consumption. Hence, according to modern insights into sedimentary ecology (see Sect. 2.1.4), during that geological period the sediment strata (the habitat of meiofauna) were probably largely anoxic (Revsbech et al. 1980a,b; Watling 1991; Giere 1992).

If subsurface sediment layers in the late Proterozoic world were devoid of oxygen, but the water above the surface was poorly oxic, why should animals prefer the hostile conditions below the surface and live an endobenthic life? Unlike recent geological periods, the employment of organic matter for nutrition was rare in the Proterozoic. It would have accumulated at the surface and in the upper sediment layer, probably leading to a richer microbial life compared with the water column. These microbial aggregations plus the shelter from erosion and the elevated UV radiation would have favored the existence of small metazoans at the semisolid, fluffy sediment/water interface. Selective pressure to reduce predation might have been a later incentive to stay below the surface in the upper sediment layers. Only with the advent of bioturbation (early Cambrian) were oxic microhabitats formed, and additional migrations might have sustained a microaerophilic life. It is probably the parallel existence of oxic and sulfidic microinches in the sediment, especially in the fluffy surface layers, that enabled mobile microscopic animals to adapt to oxic environments. The small dimensions of the most primitive metazoa (see Fortey et al. 1996), today classified as meiofauna, were an important prerequisite for their utilization of the traces of oxygen present, via diffusion gradients (Powell 1989; Fenchel and Finlay 1995).

Fenchel and Riedl (1970), in their initial paper on the thiobios, did not postulate the restriction of thiobiotic animals to complete anoxia. They included in their reasoning for an archaic thiobiotic fauna “the necessary assumption of a low-oxygen atmosphere in the Precambrian age.” Boaden (1977) also considered low oxygen concentrations to be important for the thiobios when he described a “metabolism adapted to very low levels of dissolved oxygen.” However, Boaden (1975, 1989b) also hypothesized an anaerobic, interstitial and holobenthic primitive “thiozoon.” Today, the possibility of the continuous existence of some “lower animal groups”
belonging to the meiobenthic thiobios in a “plesiomorphic biotope” (Boaden 1975) is rejected by most authors (cf. Mangum 1991; Fenchel and Finlay 1995). Some of the animal clades that dominate among the thiobiotic fauna are considered primitive (Plathelminthes). Others (e.g., Gastrotricha and Nematoda) have attained a derived phylogenetic position and are not primitive descendants of an archaic low-oxic or anoxic biotope. Their thiobiotic representatives are instead metabolic specialists among the “normal,” oxic fauna. Hence, it remains speculative to link thiobios with an anaerobic metabolism and an evolutionary origin in the Proterozoic.

As demonstrated above, there are many meiofauna that remain viable under anoxic/sulfidic conditions for extended periods of time or even permanently. The fact that aerobic respiration is much more frequent today than anaerobic fermentation reflects the dominance of present-day oxic environments. Among free-living benthos, one could consider strictly anaerobic life and completely aerobic life as extremes in the wide continuum of varying oxygen supply. Further research will discover many more highly interesting meiobenthic thiobios; perhaps more free-living metazoans from different biotopes (not only from the Black Sea and the OMZ sediments). The ability of free-ranging animals to thrive permanently in anoxia provides a relevance far beyond the meiobenthic scope. However, based on the aforementioned definitions and considering the necessary differentiations, this does not really affect the discussion about the existence of a meiobenthic thiobios.


Box 8.5 Thiobios: An Old Debate and Modern Data

“Does a thiobios exist?” The debate about this question arose from several discrepancies: ecological field observations vs. geochemical microscale measurements, physiological understanding vs. palaeoclimatic reconstructions, classical taxonomic ordination vs. molecular positioning. Meiofauna of (sheltered) sediments have been known to harbor species typically encountered in the black, H2S-smelling mud layers which traditional methods record as being anoxic. So these species live under sulfide and anoxia; they are “living systems of a sulfide biome,” or “thiobios” (Fenchel and Riedl 1970). Provocatively, it was claimed that some thiobios were primitive representatives of a Proterozoic anoxic fauna. In the light of modern molecular methods this contention cannot be upheld. On the other hand, our traditional ecological picture was also erroneous. Detailed geochemical microrecordings (continued)
8.4.7 Chemoautotrophy-Based Ecosystems: Vents, Seeps, and Other Exotic Habitats

The globally famous hot vents or seeps are based on chemoautotrophic processes and not on photoautotrophy; thus, they are unique ecosystems inhabited by a spectacular macrofauna. What about their meiofauna? Mud volcanoes, oil seeps or decaying organic masses (large carcasses, wood) also belong, from an ecological perspective, to these biotopes. However, in contrast to the spectacular macrofauna observed at chemoautotrophic sites, their meiofauna are less exceptional and striking. Therefore, meiofauna have only recently been included in studies of chemoautotrophic ecosystems and detailed knowledge about them is still rare. However, the “Meiovent” initiative (Bright and collaborators, Vienna) characterizes how awareness of such meiofauna is increasing.

Meiofauna occur either in the thickets of mussel and tube worm colonies (*Alvinella, Riftia, Bathymodiolus*) or at the few sites where soft sediments accumulate. The higher the structural complexity of the epifauna thickets, the richer the meiobenthic life (Tsurumi and Tunnicliffe 2003): tightly interwoven tubes are more densely populated than bush-like structures; in mussel beds with young *Bathymodiolus* (small shells), copepods were more abundant than nematodes, which prevailed in the older beds (Copley et al. 2007). Vents are characterized by irregular pulses of sulfide- and often methane-rich water alternating with influxes.
of ambient oxygen-rich seawater. Hence, the ecophysiological potential of the vent meiofauna is comparable to that of the typical thiobios in oxygen-deficient environments as outlined above.

Because of the accumulated detritus, meiofaunal abundances near vents can be elevated when compared to neighboring sediments. In the methane-dominated center of the Håkon Mosby mud-volcano, a density of 500 copepods per 10 cm$^2$ is indicative of a rich but monotonous meiofauna (Van Gaever et al. 2006); cold seeps in Japanese waters harbored a total of around 400 meiobenthic individuals per 10 cm$^2$ (Shirayama and Ohta 1990). Sediments from methane seeps off the Oregon coast (USA) often contained 1,000 or more individuals per 10 cm$^2$ (Sommer et al. 2007). However, densities of up to 11,000 nematodes per 10 cm$^2$ belonging to only a few species (Sommer et al. 2003; Van Gaever et al. 2006) may be exceptional. These figures make these sites deep-sea “chemosynthetic oases” for meiofauna (Soltwedel et al. 2005).

However, at hot-vent effluent in the South Atlantic, some samples (coarse sand) contained no meiofauna whatsoever (unpublished data)—a unique experience, without a readily apparent explanation (toxic composition of the effluents?). Surprisingly low densities and species richness (10–200 individuals per 10 cm$^2$ belonging to 30 copepod species and 4 nematode species) were also recorded in evaluations of the hot-vent meiofauna among macrobenthic epigrowth from thickets of the tube worm Riftia in the East Pacific Rise (EPR), as well as from cold (oil) seeps in the Gulf of Mexico (Zekely et al. 2006a,b; Gollner et al. 2006, 2007). At one sampling site in the EPR up to 950 ind. 10 cm$^{-2}$ were counted. Also, the first compilation of hydrothermal meiofauna by Dinet et al. (1988) from the Guaymas mud seeps and West Pacific vents has reported relatively low mean densities.

What are the compositions of vent and seep meiofauna assemblages? Worldwide, more than 80 meiobenthic species have been identified at vents so far: Pacific samples average 24 species; Atlantic samples 15 species. Nematodes usually represent the bulk of the meiofauna in chemoautotrophy-driven habitats, around deep-sea and shallow hot vents or in seeps (Kamenev et al. 1993; Buck and Barry 1998; Debenham et al. 2004; Flint et al. 2006; Sergeeva and Gulin 2007; Copley et al. 2007). Since many species belong to separate genera, often in a 1:1 ratio (Vanreusel et al. 1997; Zekely et al. 2006a), the generic diversity is rather high. In Mid-Atlantic Ridge sites nematodes prevailed (63%), and in various macrofauna substrates of the East Pacific Rise (EPR) the nematode Thalassomonhystera dominated, accompanied by other monhysterids and a few other families (Draconematidae, Cythalaimidae, Leptolaimidae, Microlaimidae, and Desmodoridae) (Flint et al. 2006; Zekely et al. 2006a,b). The monhysterid nematode Geomonhystera disjuncta was the only abundant species around a deep-sea mud volcano (Van Gaever et al. 2006). Shallow vent sites mainly harbored the species of Oncholaimus campylocercoides, Sabatieria and Chromadorina (Thiermann et al. 1997; Zepilli and Danovaro 2007). The bacterial symbiotic stilbonematines, common around shallow gaseohydrothermal vents (Kamenev et al. 1993), seem to be lacking at deep-sea vents.

The second most common taxon among many hydrothermal meiofauna is copepods. Their diverse taxa represent about 15% of the total vent fauna, with most of
them belonging to the siphonostomatoid families Dirivultidae and Ecbathyriontidae, while harpacticoids are of a subordinate rank. A good example of the dominance of dirivultid copepods are the meiofauna in hydrothermally active areas on the East Pacific Rise, with Aphotopontius and Stygiopontius being the most typical genera endemic to hydrothermal vents (Heptner and Ivanenko 2002a,b; Martinez Arbizu et al. 2006; Gollner et al. 2006; Zekely et al. 2006a).

Among the subdominant or rare meiofauna taxa are polychaetes (often dorvilleids), turbellarians, halacarid mites, ostracods, solenogastres, and recently kinorhynchs and gastrotrichs (Van Harten 1992; Scheltema 2000; Flint et al. 2006; Katz et al. 2006; Sergeeva and Gulin 2007; Copley et al. 2007). The roles of hydrothermal foraminiferans and ciliates, which are certainly of relevance to the chemosynthetic biota, have not yet been duly assessed. At Japanese vents, 13% of the hydrothermal fauna consisted of Foraminifera (Shirayama and Ohta 1990). In methane seeps of the Black Sea, other taxa, including polychaetes, hydroid polyps and turbellarians, have also been found under anoxic conditions. At oil seeps, few specialized harpacticoids with widespread occurrence were encountered.

Large food falls in the ocean or thermomineral freshwater caves with high concentrations of methane and sulfide represent special cases of chemosynthetic habitats. Specialized nematodes also prevail in these unusual biotopes (Debenham et al. 2004). The isolated thermomineral Movile Cave (Romania) contains a simple meiofaunal food web. The bacterial mats are grazed upon by various ciliates and five nematode species, among them the endemic Chronogaster troglostyles. At least in experiments, the populations of Chronogaster are devoured and controlled by the copepod Eucyclops subterraneus (Muschiol et al. 2008). Different meiofauna taxa have been found in other chemosynthetic habitats: sediments around methane hydrates with sulfide concentrations of up to 17 mmol harbored, besides the usual nematodes, two species of Lecane (Rotifera). As sulfide concentrations increase their populations become richer, such that they form the dominant taxon (Sommer et al. 2003; Sommer et al. 2007).

The adaptations that enable these specialists to survive under the toxic conditions of chemosynthetic sites are not understood. They have this in common with the typical thiobiotic meiofauna (see above). Ovoviviparous reproduction, as found in Geomonhystera (Nematoda), might help to ensure the survival of the offspring (Van Gaever et al. 2006). Detoxification of hydrogen sulfide by oxidation into inert polysulfur might be another pathway that is realized in the dominant nematode around shallow gaseothermal fields in the Mediterranean Sea (Thiermann et al. 1994, 2000). Elemental sulfur was also shown to exist in thiobiotic turbellarians (Powell et al. 1980). Symbiosis with sulfide- or methane-oxidizing bacteria as a means of detoxification (as often found in other reducing environments) is rarely documented for meiofauna at vents and seeps. The significance of the biased sex ratios (clearly more females than males) found for both vent nematodes and copepods (Tsurumi et al. 2003; Gollner et al. 2006; Zekely et al. 2006a) is unclear; it is a phenomenon that is also common in “normal” deep-sea environments. A prevalence of slender filiform nematode species, interpreted as an adaptation enabling the effective uptake of dissolved organics in thiobiotic biotopes (see above), is not
always seen at vent sites (Buck and Barry 1998). The significance of numerous dormant benthic eggs of copepods and cladocerans and also copepod nauplii in the permanently anoxic Black Sea mud remains unexplained. The absence of adults suggests long migrations (Sergeeva and Gulin 2007).

The food web structure in hydrothermal and seep sites is relatively simple—another indication that this is an extreme habitat. Most of the dense meiofauna associated with chemoautotrophic sites are primary consumers that depend on the copious food supply from bacterial deposits condensed as mats or biofilms, resulting in a positive correlation between the abundances of the vent meiofauna and the (bacterial) debris. Hence, nematodes with weakly cuticularized buccal cavities, typical of deposit feeders (see Sect. 5.6.1), prevail (Dinet et al. 1988). Also, stable carbon isotope analyses suggest that bacteria provide a chemosynthetically derived food source (Van Gaever et al. 2006). Moreover, the considerably larger body sizes of hydrothermal nematodes (Vanreusel et al. 1997) may reflect an abundance of food in the normally food-depleted ambient deep-sea bottom. Because this trend is not a general one for all sites (Buck and Barry 1998) its significance remains uncertain. The dirivultid copepods, frequent among mussel beds, crawl over the substrate and mostly graze on the rich bacterial films. They are also found associated with the tubes of polychaetes; some species of *Ceuthocetes* may exist as parasites (Gollner et al. 2006), while some occur in the gill chambers of shrimp (Dinet et al. 1988; Heptner and Ivanenko 2002).

Chemoautotrophic biotopes show highly variable fluctuations that are often associated with extreme environmental parameters. Judging from the macrobenthos, this should favor specific adaptations, resulting in an independent vent or seep community that is different from the neighboring “normal” fauna and rather isolated in its distribution. The completely benthic larval stages of dirivultid copepods found by Gollner et al. (2006) would suggest distributional restriction (but in other studies vent nauplii were caught in the plankton above the vent; Ivanenko 1998). Comparisons of the meiofaunists in different regions emphasize its high endemism and independence from the ambient fauna. If analyzed at the species level, we find a patchy community controlled by local conditions with low correspondence to neighboring sites (Fricke et al. 1989; Shirayama and Ohta 1990). In a comparison of Pacific and Atlantic deep-sea mussel beds, the overlap between meiofaunal species was zero (Zekely et al. 2006a), which emphasizes the local and patchy characters of most vent meiofauna at the species rank. This would also explain why comparisons of hydrothermal vent and seep fauna with other sulfide/suboxic habitats display a low affinity. However, this isolation only refers to the species level (Shirayama and Ohta 1990; Vanreusel et al. 1997, Flint et al. 2006; Zekely et al. 2006b). The genus composition is often similar to that of the surrounding normoxic environment rather than to those of other disjunct chemoautotrophic sites. The reported absence of predatory meiofauna in hydrothermal vent sites would be surprising in habitats that are rich in deposit feeders, and so needs further assessment. We know that a variety of carnivorous species are present in corresponding photoautotrophic ecosystems with rich bacterial stocks and organic deposits.
Summarizing, hydrothermal vents and seeps with their copious supply of bacterial food can be perceived as extreme habitats harboring a specialized thiotrophic meiofauna with typically local characteristics. A high density with a low species richness would characterize the extreme nature of these biotopes. The low density and diversity of meiofauna at Pacific hydrothermal vents and seeps, as found in some reports, is perhaps not a general feature. Occasional aggregations of almost 1,000 ind. $10\text{cm}^{-2}$ (Sommer et al. 2003; Zekely et al. 2006b) suggest a population patchiness that is typical of extreme habitats. The meiofaunal results from hot vents in the eastern Pacific published so far seem to support a gradient pattern from the hot and toxic smoker walls (*Alvinella* community) with hardly any sediment to the diffuse venting sites (*Bathymodiolus* community), where detritus accumulates on the shells and in the crevices. Meiofauna among the tubes of alvinellids represent a highly specialized association of low abundance and high dominance of some dirivultid copepods. Towards more diffuse venting fields with “milder” conditions and more available sediment, nematodes gain in importance and the community becomes more diverse and speciose. While it appears that the meiofauna at vents along the East Pacific Rise is poorer in terms of both biodiversity and abundance compared to the “non-vent” deep-sea surroundings; the abundance of meiofauna from other vent regions seems to support vents as favorable habitats for meiofauna. However, for meiofauna, vents cannot be considered “oases in the depth” (Dinet et al. 1988; Shirayama and Ohta 1990; van Gaever 2006; Vanreusel et al. 1997; Olu et al. 1997; Soltwedel et al. 2005).

*More detailed reading*: Mokievsky and Kamenskaya (2002); Levin (2005); Van Gaever et al. (2006b); Zekely et al. (2006a).

### 8.5 Phytal Habitats and Hard Substrates

Remane (1933, 1940) characterized the phytal as a habitat populated by an abundant and diverse faunal community, which he termed the “phyton.” Wieser (1959b), in his comprehensive study of the phytal meiofauna from various shores, noted a relationship between the size, body structure and locomotion type of the inhabitants, the shape of the algae and the biotopical differentiation of the phytal. For example, on foliose, shrub-like algae of exposed sites, >50% of the often flattened harpacticoids have clawed clinging legs adapted for climbing (see below), while in tufted, fine-filamentous algae only 10% of the harpacticoids are armed with claws.

The main reason why algal belts on hard bottoms attain a significant role for vagile benthic animals is their structural complexity. This is modified by a complex of (often local) abiotic and biotic conditions, such as water depth or exposure. This general conclusion about the phytal meiofauna emerged as early as the fundamental studies by Remane (1940) and Wieser (1959).

In exposed phytal zones, the usual dominance of nematodes in terms of abundance and production is depleted. Hence, unlike other meiobenthic habitats, the phytal is characterized by a high percentage of harpacticoid copepods and ostra-
cods. Compared with their low abundance in soft sediments (usually less than 10%), harpacticoids in phytal habitats regularly comprise more than 30% and often more than half of the total meiofaunal abundance and production (e.g. Danovaro et al. 2002; Hopper and Davenport 2006). The high percentage of copepods is also notably high on the blades of seagrass meadows, in strata under dense algal cover, and specifically on the fronds of algal thalli. In both tropical and boreal phytal, copepods are the prevalent meiofaunal inhabitants (Wieser 1959; Jarvis and Seed 1996; Danovaro 1996; Danovaro and Fraschetti 2002), primarily represented by Tegastidae, Tisbiidae (*Tisbe, Scutellidium*), Peltidiidae and Porcelliidae.

Only in the deeper, hardly exposed phytal are the climbing meiofauna replaced by wriggling meiofauna (nematodes). The closer the phytal is to soft sediments and detritus, the higher the percentage of nematodes (very often oncholaimids). In addition to copepods and selected species of nematodes, other widespread members of the phytal meiofauna are regularly encountered, e.g., ostracods, especially *Xestoleberis* spp., *Paradoxostoma* sp. and *Loxoconcha* sp. (Hull 1997; Frame et al. 2008) and halacarid mites, especially the plant suctorial Rhombognathinae (Pugh and King 1985b). These taxa are adapted to climbing in the thickets of densely branching algae. Other commonly encountered taxa include turbellarians, syllid polychaetes and tanaidaceans (peracarid crustaceans) (Arroyo et al. 2004).

Which adaptive features characterize members of the phytal meiofauna? As we saw above, the fact that the plants are exposed to waves and tidal currents necessitates that the animals have highly developed attachment capabilities (Fig. 8.10): flattening of the body, development of “haptic” organs such as sucker-like structures, adhesion by mucus secretion. Most of the inhabitants of the upper strata are climbers. For this locomotory type, long, prehensile grasping legs and hairy spines are of high adaptive value (e.g., *Porcellidium*, *Ectinosoma* and *Thalestris* in harpacticoids, *Paradoxostomatidae*, *Xestoleberidae*, *Bairdiidae* in ostracods, *Rombognatidae* in Halacaroidea).

Exposure and tidal stress are the main factors influencing the composition and microdistribution of the littoral phytal meiofauna (Hopper and Davenport 2006). Turbellarians were found most commonly on the less exposed underside and inner parts of the thalli (Boaden 1996), where retained water better prevents desiccation. The harpacticoid *Porcellidium* (see Fig. 8.10a) avoids tidal stress by migrating into eulittoral algae (Gibbons 1991).

Algal branches and thalli and seagrass plants offer numerous microhabitats, mitigate harsh hydrodynamic forces, and provide shelter from predators (Coulf and Wells 1983; Webb and Parsons 1991; Muralikrishnamurti 1993). The thalli/blades also accumulate sediment and detritus, which adhere to the exudations and the biofilms on the plants. These sediments seem to increase the overall structural complexity and favor meiofauna colonization. Some colonizers have been found in both the organic layer covering the surrounding rocky substrate and in the detrital film on the surfaces of the fronds. Hence, in densely branching, turf-forming, tufted or fine filamentous algae meiofaunal abundance and diversity is enhanced; these microhabitats become more rapidly colonized than the foliose, blade-like thalli (Gibbons 1991; Frame et al. 2008). On the other hand, if accumulations of fine
deposits become too rich, the habitable area and structural complexity are reduced, yielding a parallel decrease in phytal meiofaunal abundance and diversity. Less complex, shrub-like algae that do not retain much sediment and often grow in more exposed areas are populated by a less abundant and less diverse meiofauna. The epigrowth of small, often ephemeral, filamentous algae on the thalli or well-developed biofilms is especially important in terms of enhancing the species richness and the density of the meiofauna (Hall and Bell 1993; Peachey and Bell 1997).  

Along boreal shores, there are three general macroalgal types, which are distinguished by their decreasing structural complexity: the Laminaria–Delesseria zone, the Fucus zone, and the Zostera zone (Remane 1940). The corresponding algae in warm-water areas (Hall and Bell 1988), Cladophora, Corallina and Delesseria, harbored a much richer “meiophyton” than Laminaria, Fucus and seagrass blades. The complex pelagic Sargassum rafts are also regularly inhabited by a rich meiobenthic fauna. Even the smooth laminose thalli of the green alga Caulerpa taxifolia, an invasive neophyte in the Mediterranean, are colonized by a rich and diverse community of meiofauna. Here, epiphytic macrofauna are yet to be found (Travizi and Zavodnik 2004).  

Macroalgae (e.g., kelp) provide three subhabitats for meiofauna (Hicks 1985): the surfaces of the thallus fronds, the interstices of holdfasts (rhizoids), and the deposited
sediment and detritus that accumulates at the bases of the stems. Many phytal meiofauna differentiate between these microhabitats. Algal fronds are dominated by harpacticoid copepods, especially by rarer taxa, while the holdfasts harbor the highest abundance of more eurytopic meiofauna, primarily nematodes (Arroyo et al. 2004, 2007). The meiofauna of the algal holdfasts and the stems of seagrasses (see below), which are often rich in sediment and detritus, are frequently recruited from local soft-bottom sediments and are not tightly linked to the phytal fauna proper. This lowest phytal stratum seems to represent an ecotone that combines the structural complexity of the phytal with the rich food supply of the sediment below, which would explain the high meiofaunal densities and the similarity to the bottom fauna.

Experiments with artificial substrates (standardized bottle brushes, blade mimics) confirmed the positive relation between structural complexity and meiofaunal density and between reduced water flow and meiofaunal colonization (Gibbons 1991, Attila et al. 2005; Mirto and Danovaro 2004). These authors conclude that structural density controls the species richness of copepods and nematodes, whereas the surface area of the plants controls the abundance of copepods. Apparently, the "realizable niche" of the phytal, which structures meiofaunal colonization and modifies its "value," depends on multiple factors: the natures and positions of elements of the phytal, their protective potentials, hydrodynamic exposures, surface areas and the amount of their surfaces covered with (Attila et al. 2005; Hopper and Davenport 2006). The structural complexity can be numerically described and compared by plotting outlines of the phytal fronds and calculating the fractal dimensions. Multiple fractal scaling seems an appropriate approach to describe the complex physical environment of phytal meiofauna (Gee and Warwick 1994).

Aside from spatial differentiation into various strata, meiofauna also display a structured temporal occurrence. A number of phytal meiofaunal species are known to periodically leave their substrate for (nightly) excursions into the overlying water column and can subsequently be caught in suspension traps (Kurdziel and Bell 1992). In the Black Sea phytal, Kolesnikova et al. (1995) found a differentiated diurnal behavior that varied depending on the meiofaunal taxon. While during the daytime harpacticoid copepods and nematodes both settled on macrophyte thalli, they separated at night, with harpacticoids ascending into the water column and nematodes heading for the bottom sediment. The authors interpret these migrations as avoidance reactions to fish predation. Because of the close structural and trophic ties of phytal meiofauna to the plants and their surface films, there is often a marked seasonal variation in the population dynamics of phytal meiofauna that depends on the cycles of growth and decay of the algal stocks. Even in the tropics, marked temporal variations were noted (Arlt 1993, Faubel 1984; Jarvis and Seed 1996).

This seasonality becomes particularly apparent in seagrass beds with their decaying external blades in the winter (Novak 1992; Danovaro 1996). Growing in soft bottoms rich in detritus, seagrass beds usually develop in little-exposed subtidal zones with fairly stable conditions. The rich availability of detrital food makes phytal habitats of high ecological importance. They differ in their structural characteristics from algae-covered hard bottoms, i.e., the shape and the surface of the smooth blades is structurally rather simple. Here, the relevance of the biofilms,
adhering detrital particles, and tiny algal epibionts on the blades becomes apparent. This epigrowth provides a microstructure of high protective and nutritive value, and has been found to control the density and diversity of phytal meiofauna (Hall and Bell 1993; Peachey and Bell 1997). Moreover, the fairly tall and rugged seagrass stems offer a wealth of microhabitats, especially when growing in dense stands. It is this density of plant patches per area that has been found to influence the meiofaunal density. In general, seagrass meiofauna has a high share of nematodes (often monhysterids and oncholaimids) and is more similar to the inhabitants of the ambient soft bottom than to those of algal belts. In Mediterranean *Posidonia* beds, the structurally complex and meiofaunally rich “stem stratum” has been distinguished from the more monotonous “upper leaf stratum” and “lower leaf stratum” (Novak 1989). The ease with which seagrass can be mimicked by artefacts allowed numerous manipulative studies of the impacts of structural complexity, biological aging of surfaces, protective effects and colonization potential on phytal meiofauna (Bell and Hicks 1991; Edgar 1999).

In many cases the physical components are modified by the (micro)biological coating and the sedimentation of natural debris on the pristine artefacts. These components affect the rate, density and variety of meiofaunal colonization. Newly settled meiofauna came from the ambient sediment as well as from surrounding plants, thus demonstrating the high vagility of the phytal meiofauna (Bell and Hicks 1991). Comparable results have been reported for the meiofaunal colonization of artificial mangrove pneumatophors (see below; Gwyther and Fairweather 2002, 2005).

One biotope typical of American tidal flats are the extensive *Spartina* salt marshes. The root system, the culms and the leaves of the plants provide the basis for a richly structured, well-protected habitat (Bell et al. 1978; Osenga and Coull 1983). With its abundant supply of organic matter, *Spartina* marshes harbor rich and genuinely adapted meiofaunal populations of ecological importance (Wieser and Kanwisher 1961; Rutledge and Fleeger 1993). In a complex, mutually regulating system, rich stocks of insect larvae, juvenile fish and shrimp seem to exert a severe predation pressure, acting as a top-down control for copepods in particular, but also for nematodes (Feller and Coull 1995). A peculiar subhabitat in salt marshes of the southern United States is the rich system of “gas passages” (aerenchyma) in the stems of *Spartina alterniflora* (Healy 1994; Walters et al. 1996). These are regularly inhabited by an amazingly rich and diverse meiofauna characterized mostly by specialized oligochaetes (Enchytraeidae) and epsilonematid nematodes. Together with the meiofauna found under the *Spartina* leaf sheaths, the inclusion of this stem biotope increased the overall abundance of salt marsh meiofauna by an order of magnitude!

Another richly structured habitat of a particular character is provided by mangroves (see Sect. 8.2.1). The branched roots and the numerous pneumatophores, with their high degree of complexity, allow for comparisons with classical phytal habitats. Experiments with artificial mimics have demonstrated the relevance of natural surfaces, with their specific biofilms and mature epigrowth, for meiofaunal colonization, so that the degree of convergence and intrinsic patchiness remained rather low (Gwyther and Fairweather 2002, 2005).
In terms of their “taxo-ecological” structure, phytal habitats from tropical and south temperate sites correspond to those from temperate shores (Hicks 1985; Arlt 1993; Muralikrishnamurty 1993; De Troch et al. 2001). This underlines, despite climatic divergences, that comparable algal complexity and structural impact create meiobenthic “isocommunities” in geographically disjunct zones. An example of this is the dominance of enoploid nematodes in both the North Sea and Chilean phytal habitats. Also, many oncholaimid nematodes are trans-regional, characteristically inhabiting the phytal, and epsilonematids populate the stems of seagrasses in many areas. A similar trans-regional parallelism can be found in families of harpacticoids, ostracods and halacarid mites. The existence of isocommunities separated by continental distances with far-reaching similarities in their fauna (compare Wieser 1959; Arroyo et al. 2004) probably relates to the close adaptive links between the fauna and the phytal structure. This may also explain the similarity in phytal fauna between areas of varying exposure and water depth.

Only a few members of the phytal meiofauna feed directly on their substratum, the plant’s tissue, by piercing the cells and sucking their cytoplasm. Some nematodes (Halenchus), tardigrades (Echiniscus), halacarids (Rhombognathidae), siphonostomatid cyclopoids and ostracods (some Xestoleberidae, Paradoxostomatidae) have adopted this specialized mode of living. Some phytal nematodes, harpacticoids and ostracods grasp and crack diatoms on the plants with specialized mouth parts. Other specialized phytal meiofauna may take up exudates secreted by the plants. However, the bulk of the meiofauna encountered in the phytal live on detritus, diatoms and microorganisms that have accumulated on the plants. This organic film, and not the plant itself, is the grazing ground for the meiofauna and the basis of the phytal food chain. An example is decaying frond ends, which are densely populated by bacteria, and so attract a meiofaunal assemblage that grazes on the microbes. In seagrass beds, nematodes have been found to specialize on the brown, decaying parts of the blades (Moens and Vincx 2000a).

The other trophic line in the phytal is, in fact, detritus-based. Lower current velocity within algal thickets causes an accumulation of plant debris and fine sediment. Experimental work with artificial substrates has shown a better correlation of meiofaunal colonization with debris accumulation on the plants rather than with an enhancement of the structural complexity (Edgar 1999). In seagrass beds, experimental results have also suggested a close relationship between meiofaunal settlement (harpacticoids) and the deposited detritus layer (Meyer and Bell 1989). It is largely the detrital food accumulating on the surface that controls the meiofauna and correlates with their density and diversity (Hall and Bell 1993). Dense, tufted filamentous algae retain more detritus particles and thereby harbor mostly detritus-feeding meiofauna, while epistrate feeders prevail in coarse, branching algal bushes (Wieser 1959). Conversely, the mobilization and reduction of the detrital layers on the blades and thalli by feeding meiofauna may also be advantageous for the plants and enhance their growth. More sessile members of the phytal meiofauna regularly utilize the outer parts of plants as prominent substrates for filter feeding (e.g., rotifers, cladocerans). Rotifers are particularly frequent in the phytal fringes of brackish waters. Some harpacticoids (Diarthrodes sp., Amphiascoides sp.) live on macroalgae, where they mine the fronds and ingest the medullary tissues, producing
algal galls (Hicks and Coull 1983). In relation to the successive alteration of the surface coating, Gwyther and Fairweather (2002) noted a succession in nematodes from epi-growth-feeders to deposit-feeders, while omnivores and predators followed later.

The abundance of meiofauna exploiting the complex habitats in rocky algal belts has been repeatedly emphasized (Crisp and Mwaiseje 1989; Danovaro and Fraschetti 2002; Frame et al. 2008). Seagrass beds also harbor twice as many meiofaunal species as the adjacent sediments (Hicks 1986), and are considered “hot spots of meiofaunal production,” producing around 10 g C m⁻² y⁻¹; a value equivalent to the world’s most productive sediment sites (Danovaro et al. 2002). A phytal meiofauna of 10⁶ individuals per m² of macroalgae is not uncommon and, in terms of biomass, may correspond to 10% of the macrofauna. In addition, hard substrate communities comprising crusts of mussel beds, barnacle, bryozoan and hydrozoan colonies, or thickets of worm tubes represent habitats with a rich yet poorly studied meiofauna (Somerfield and Jeal 1995). They provide shelter even under exposed littoral conditions, and are, in many respects, comparable to the belts of crustose, twisted or upright algae.

The phytal biotopes, with their highly productive meiofauna, represent an important food source for higher trophic levels. While meiofauna are usually scarce on bare rocky shores, valuable meiofaunal food is available in algal belts and among seagrass beds, mainly for small fish and shrimps. However, experiments demonstrated that the accessibility to this food source is reduced by the vegetation and stems. In experiments with grass shrimps (*Palaemonetes*), this shelter function of the phytal resulted in a 40% decline in the consumption rate compared to unvegetated cages (Gregg and Fleeger 1998). In a New Zealand rocky intertidal Coull and Wells (1983) demonstrated that more complex algal habitats exhibited less predation on meiofauna by tide pool fish. However, there appeared to be a complexity threshold above which the prey removal rate was reduced. In many phytal ecosystems meiofauna provide an important link to higher trophic levels (see Sect. 9.4).

Studying phytal meiofauna poses some problems in terms of quantitative sampling. The plants have to be carefully placed in sampling bags underwater so that any loss of fauna is avoided. An open cylindrical jar with a thick and softly attached rim of flexible silicone sealant has proven to be a simple and useful tool (Gibbons and Griffiths 1988), but in contrast with bags with planktonic gauze, solid enclosures easily cause currents which may displace some of the meiofauna. After the injection of some formalin in order to release the attached meiofauna, the water volume of the sample is siphoned off. For better reproducibility this procedure should be repeated several times.

Since a good proportion of the phytal meiofauna are linked to not only the plants themselves but to the ambient sedimentary meiofauna and the overlying water column, the meiofauna of phytal habitats have an important function as a link between benthic and pelagic fauna. Regarding the often small sizes of the vegetated areas, the phytal meiofauna exhibits high diversity and species richness, which it achieves by exploiting the structural complexity of the phytal, with its numerous microhabitats and ecological niches. A recent study (Bracken et al. 2007) shows that there is also a “reversed” mutualistic link between meiofauna and the algal community.
The excretions of meiofauna (ammonium) easily provide the nitrogen needed by the algae (Cladophora).

More detailed reading: Posidonia meadows, Novak (1989); production, Danovaro et al. (2002); reviews, Hicks (1985a), Gibbons (1991); monographs, Remane (1940); Wieser (1959).

**Box 8.6 The Phytal Meiofauna: A Haven Depending on Structural Complexity**

The meiophyton, which lives preferably on and among plants (algae on hard substrates; seagrass on sand or mud), wonderfully exemplifies the influences of habitat structure and heterogeneity on faunal diversity and abundance. On foliose thalli or blades lives a meiofauna that is different in composition and abundance from tufted or crustose algae. The colonizers of the fronds and blades, with their frequent excursions into the demersal water layer, differ from the inhabitants of lower stems and holdfasts that merge with the sediment fauna. Regularly migrating meiofauna further blur the limits of the ambient biotopes—yet, the phyton is understood to be a meiofaunal unit with specific adaptations and with a faunal composition of its own. Harpacticoid copepods often dominate, while nematodes often rank second. Ostracods and halacarids are other frequent members of the fauna. Climbing among the plant thickets is supported by a flat body surface and clinging legs. The phytal habitat with its numerous retreats provides shelter against strong currents and larger predators such as small fish and shrimps, while the microbial biofilm on the surfaces and a well-developed layer of debris provides an ample food supply. There are many parallels to the meiofauna populating clumps of barnacles, mussels, bryozoans, or dense patches of hydrozoans or annelid tubes. This suggests an ecological incorporation of substrates formed by animal epigrowth into a wider definition of the phytal. Favorable ecological conditions are the basis for one of the highest production rates in benthic habitats and afford the meiophyton a considerable ecological role.

**8.6 Brackish Water Sites**

Marine and limnetic sediments are connected by a brackish zone that is primarily characterized by its variable salinity. This is influenced by the tides, climatic, hydrodynamic and/or geographical factors. Coastal lagoons and tidal estuaries are typical brackish sites, as are large, semi-enclosed water bodies such as the Baltic Sea or the Black Sea. The salinity range of between about 30 and 3 PSU can physiologically stress many fauna and can often limit their distributions. Another huge brackish water habitat, particularly for the meiobenthos, is the coastal subsurface zone where the marine and continental groundwater systems merge. The brackish coastal groundwater extends well above the supralittoral fringe of the seashore into
the limnetic biome. Hence, it has always been pivotal for colonization and migration. Perhaps it was more shelter and less competition in this coastal groundwater system (see Sect. 8.7.2) that allowed meiofauna to adapt to brackish salinities. This long-term process, facilitated by biotopical stability, then led to a gradual transition from marine to limnetic conditions. Thus, this brackish zone has considerable relevance as an evolutionary pathway for the immigration of marine meiofauna into the continental groundwater system (see Chap. 7). This would also explain the relatively high percentage of genuine brackish water species among the meiobenthos (Fenchel 1978) and the high diversification of meiobenthic species adapted to all haline regimes.

As a consequence, in contrast to the macrobenthos and the plankton, the meiobenthos is less constrained by a “brackish water species minimum” around salinities of 8–10% PSU (Remane 1940). Of course, in the most stressful intermediate range, between 5 and 10% PSU, even the number of meiobenthic species will decrease. However, the depletion of meiofaunal species in this critical range is relatively indistinct (Riemann 1966; Dauer et al. 1993; Yamamuro 2000; see Gerlach 1954 for nematodes). The weak separation of macrobenthic from meiobenthic biomass size spectra under brackish water conditions (see Sect. 9.2) may reflect this wide occurrence of meiofauna in various salinity zones (Drgas et al. 1998; Duplisea and Drgas 1999). A significant size reduction, known to be exhibited by macrofauna in brackish areas, has also been found in marine nematodes from brackish lagoons compared to marine sites (Yamamuro 2000). Morphological aberrations, e.g., in the number, structure and position of amphids in populations of some Black Sea nematodes (e.g., *Terschellingia longicaudata*, *Axonolaimus setosus*, *Sabatteria abyssalis*), have also been interpreted as an indicator of extreme water conditions in combination with anthropogenic stress (Sergeeva 1999).

In contrast with macrofauna, surprisingly many marine and freshwater meiofaunal species have developed a high tolerance capacity, usually to not only an unstable salinity but also combined variations in temperature and oxygen supply. As a result, the distributional ranges of many marine and freshwater meiofauna in estuaries or in the Baltic Sea characteristically extend more widely into critical brackish zones than those of macrobenthos. A comparison of various mesohaline regions in the Baltic Sea disclosed the influence of sediment characteristics as a controlling mechanism. Riga Bight, with its rich supply of organic matter, is populated mainly by deposit feeders, in contrast with sediments with a low organic load around the Swedish east coast, where epistrate feeders dominated (Pallo et al. 1998). Estuarine sediments harbor many euryhaline marine species of nematodes and turbellarians, which co-occur with freshwater and brackish water forms (Riemann 1966; Heip et al. 1985a; Sopott-Ehlers 1989; Alongi 1990a; Ax 2008). Euhaline meiofauna even populate oligohaline reaches with considerable densities. On the other hand, the meiobenthic rotifer species that colonize the brackish region are limnogenic, while the percentage of marine species is very low. Therefore, under brackish water conditions a relatively diverse and rich meiofauna gains in importance when compared with the less resistant macrobenthos.
Despite this high tolerance, experiments have demonstrated that meiofauna displays the characteristic discrepancy between survival and reproductive range in salinity gradients known from macrobenthos. Meiobenthic animals survived over a fairly wide salinity range, but they only reproduced over a rather narrow range (Ingole and Parulekar 1998). In nature this means that in a gradient of salinities, e.g., along an estuary, the area of successful reproduction will be distinctly smaller than the area of a mere persistence (see Ekman 1953).

In recent years the meiofauna in the brackish Black Sea and Sea of Azov have been examined in more detail by the teams of Sergeeva (1996) and Vorobyova (1999). The pertinent publications deal not only with the meiofauna of anoxic and sulfidic depths in the Black Sea (see Sect. 8.4.1) but also with the littoral sediments, mussel beds and algal epigrowth of this strongly stratified brackish water body. Some of these studies also cover the adjacent Sea of Azov (Vorobyova 1999; Sergeeva and Burkatsky 2002). Meiobenthic communities of high abundance but low species richness characterize the shallow sites of these brackish habitats (5–13% PSU in the Sea of Azov) as extreme habitats. In muddy sediments foraminiferans and nematodes (plus some kinorhynchs) prevailed, while sandy areas harbored relatively numerous harpacticoid copepods. Other important groups were ostracods; polychaetes, and oligochaetes. Meiobuna accounts for about 38% of the total invertebrate species identified so far in the Black Sea. With average densities of almost 300 ind. 10 cm\(^{-2}\) in the Black Sea and about 500 ind. 10 cm\(^{-2}\) in the Sea of Azov (corresponding biomass (wet weight) of >10 mg) (Vorobyova 1999; Sergeeva and Burkatsky 2002), meiofauna are important for the overall productivity of these brackish sites. The growth in the meiofaunal density upon increasing anthropogenic impact suggests that the meiobenthos is compensating for the decreasing macrobenthos.

In estuaries, the astatic tidal regime, the salinity and the sediment characteristics are the main determinants of the meiofaunal distribution (Soetaert et al. 1995; Coull 1999). Fine estuarine sediments support a less species-rich meiofauna than coarser ones (Dye and Furstenberg 1981). Because of the typically rich content of organic matter, food is rarely a limiting factor that facilitates meiobenthic life in the harsh oligo- to mesohaline zone (Austen and Warwick 1995; Heip et al. 1995; Ingole and Parulekar 1998). In a South African temporarily open estuary, the meiofauna was likely not food-limited, because the main food source, the microphytobenthos, was abundant despite intensive grazing rates (Nozais et al. (2005). Salinity gradients seem to exert control over various estuarine regions. In Dutch North Sea estuaries, the outer polyhaline regions harbored a meiofaunal community rich in deposit-feeding nematodes (annual average 3,200 ind. 10 cm\(^{-2}\)), while in the mesohaline region the meiofauna were less numerous (average 2,300 ind. 10 cm\(^{-2}\)) and more linked to a detritus food chain (Li and Vincx 1993). From South African estuaries, an average meiofaunal population density of 1,000 ind. 10 cm\(^{-2}\) was compiled (Dye and Furstenberg 1981), but locally up to 6,000 ind. 10 cm\(^{-2}\) was recorded. A seasonally varying meiofaunal abundance was noted by Coull (1999) in subtidal estuarine sites on the North Carolina coast of the US: during the first half of the year higher meiofaunal densities (max. 1,800 ind. 10 cm\(^{-2}\)) were encountered in mud sites, and during the second half higher densities occurred in sand sites (max. 1,400 ind. 1,400 ind.
10 cm$^{-2}$) (average values for a 22-year data set). A marked seasonality especially among harpacticoid populations was also observed in Belgian estuaries (Smol et al. 1994). Williams (2003) emphasized the aggravating role of a vertically increasing salinity gradient in the sediment of estuarine river mouths. Here, salinity and sediment characteristics appeared to be major influences on the distribution pattern, with a clearly negative relation to silt content observed.

Like their marine counterparts, the highly productive freshwater tidal flats, with their rich meiofauna, are ecologically important feeding grounds for juvenile fish. Here, the meiofauna appears to be an important trophic link (Yozzo and Smith 1995; Coull 1999). Since estuaries are often important traffic routes and are massively impacted by anthropogenic activities, Smol et al. (1994) calculated the influence of man-made hydrodynamic changes on the meiofauna. They predicted that increasing the tidal amplitude and current velocity due to shoreline regulations would decrease meiofaunal diversity but increase overall meiofaunal biomass. Since epibenthic species will replace interstitial species, the meiobenthos will be a more readily available and important food for the macrobenthos.

The species composition of meiofaunal communities in brackish sites usually follows the general rule that nematodes are the main representatives. However, there are deviations from this rule that reflect locally varying conditions. In the Baltic Sea, the numerous nematode species, despite their high diversification, show a steady decline in species richness from the western Belt Sea to the eastern Bothnian Gulf (Arlt et al. 1982). Regarding taxon abundance, nematodes are not always followed by harpacticoids. In the rich meiofauna of an Indian estuary (average density 387 ind. 10 cm$^{-2}$) turbellarians ranked second in abundance after nematodes (which contributed 60% of the total meiofaunal abundance); oligochaetes were third and harpacticoids fourth (Inglee and Parulekar 1998); ostracods are also fairly common inhabitants of estuaries. In some semi-enclosed brackish lagoons, the percentages were 50–85% nematodes, 8–33% turbellarians and only 7–25% harpacticoids (Escaravage et al. 1989).

In the muds of Australian mangroves, turbellarians were the dominant taxon, followed by nematodes (Alongi 1987a; see Sect. 8.2.1). The high reproductive potential of many opportunistic turbellarians may explain this unusual prevalence. Among the Baltic Sea turbellarians, no endemic fauna were reported. All of the species also occurred in the supralittoral of the adjacent North Sea, where they represent a genuine brackish water fauna (Armonies 1988d). The surprising degree of faunal identity between Alaskan, Canadian and European coastal turbellarians has been ascribed to the well-developed brackish water tolerance capacity of meiofauna and the uniformity of brackish water biotopes. This results in a community of Platyhelminthes with a circumpolar distribution (Ax and Armonies 1990; Ax 2008). A lack of indigenous Baltic Sea representatives is also known for halacarids (Bartsch 1974), which are regular and frequent members of the brackish meiofauna. In a South African temporarily closed estuary, astigmatid mites (Tyrophagus) play a considerable role after nematodes (Nozais et al. 2005). Here, the extreme abundance varies between almost 0 and 888 ind. 10 cm$^{-2}$, indicating the high temporal and spatial variations that occur in estuaries.
Lagoons appear to be brackish water bodies that are particularly favorable to meiobenthos, although here the salinity extremes seem to limit species richness and abundance of meiofauna (Castel 1992; Yamamuro 2000). In his review paper on the meiofauna of brackish lagoons, Castel (1992) emphasized the role of the nutrient-rich sediments in the abundance of meiobenthos. Since high abundances (often ranging from 3,000 to >5,000 ind. 10 cm\(^{-2}\)) are often linked to a low species richness, he categorized lagoons as extreme biotopes. Meiob fauna other than the usual nematodes and harpacticoids can make up the relevant population stock in lagoons; high proportions of turbellarian (see above), ostracod and oligochaete species, well adapted to brackish conditions, are often found. In these shallow brackish systems, meiofauna can represent a particularly importan t nutritional resource for higher trophic levels, especially for juvenile fish. With their open accessibilities and limited species richness, coastal lagoons appear highly suited to population studies and experimental work on meiofauna.

More detailed reading: Dye and Furstenberg (1981); Heip et al. (1995); Coull (1999); Ax 2008.

**Box 8.7 Brackish Sites: Instability as a Criterion**
Salinity gradients of high temporal and local variability are the prominent character of brackish sea basins, estuaries and coastal lagoons. Interactions with other unstable factors such as changing temperature, oxygen depletion and solute composition in this stressful physiological milieu control the viability and restrict the distribution of species. Whereas in the critical mesohaline “minimum zone” macrofaunal assemblages are typically reduced in diversity, meiofaunal species often have a higher tolerance. Thus, in this critical salinity range the meiobenthos become more important in species number and abundance compared to macrobenthos. Even so, the extreme nature of many brackish biotopes is often exemplified by huge populations comprising just a few adapted and widespread species. Yet, even in the hardy nematodes, species richness declines in the intermediate haline ranges. The resistant nature of many brackish water species is demonstrated by the rich meiofauna in enclosed seas such as the Baltic or the Black Sea. Numerous meiofauna are found even in the anoxic sediments of the Black Sea. Brackish shallow lagoons with their rich nutrient supply and often intense primary production are particularly favorable sites for rich stocks of meiofauna with an important role in the trophic web. The more stable brackish groundwater horizons probably acted as important invasion routes for some marine meiofauna that gradually adapted to brackish and ultimately freshwater conditions. Hence, many subterranean continental aquifers and cave waters are populated by meiobenthic species of marine origin.
8.7 Freshwater Biotopes

When the first edition of this book was published, research on the small invertebrates of freshwater habitats was rarely considered in the context of “meiobenthology.” Links to the marine realm were rare and the terminology was different. The scattered literature was published in specialized journals not regularly read by the marine researcher. An early exception was the compendium *Stygofauna Mundi* (ed. Botosaneanu 1986a), a faunistic and zoogeographic compilation of the subterranean fauna: the stygofauna. Beside freshwater fauna, this volume also considered some marine taxa. Several comprehensive and competent reviews on the various freshwater biotopes have since appeared (Gibert et al. 1994; Palmer et al. 2006; Hakenkamp and Palmer 2000; Robertson et al. 2000a; Wilkens et al. 2000), and improved methods have been developed in order to overcome sampling problems, especially in groundwater research (Mathieu et al. 1991; Malard et al. 1994). Detailed accounts of the various meiobenthic groups in sediments of running freshwater sites are given in the treatise on *Freshwater Meiofauna* edited by Rundle et al. (2002). The compiled knowledge of important taxa (e.g., nematodes: Traunspurger 2002; Eyualem-Abebe et al. 2006; ostracods: Horne and Martens 1994; turbellarians: Kolasa 2000; protists: Patterson 1996) now serves as a solid platform for further detailed studies. In groundwater research, the comprehensive publication by Hancock et al. (2005) and volumes on groundwater ecology (ed. Gibert et al. 1994; Wilkens et al. 2000) provided major progress. Supplementing the chapter on meiofauna in the second edition of *Methods in Stream Ecology* (Palmer et al. 2006), there is an electronic key to freshwater meiofauna (Strayer 2006) that can be downloaded to help the beginner in the field.

Previously, various independent limnetic research lines had developed a diverging, specialized nomenclature and used different methods, originally with astonishingly little interconnection. Now, many of the new studies use a terminology that is similar to that applied to marine analogs, which had previously only been applied in the pioneering papers of Palmer (1990a,b). Bridging this traditional nomenclature gap indicates just how many aspects and trends freshwater and marine meiobenthos have in common, and fruitfully deepens our understanding of the structures and functions shared by both fields (e.g., Palmer et al. 1996). The field of groundwater research in particular demonstrates the numerous parallels and transitions between freshwater and marine meiobenthology. The recent emphasis on freshwater meiobenthology necessitates a section on this topic in this second edition. This section outlines the more general or summarized results without claiming complete coverage. For more on the relevant results, the reader should consult the literature cited above.

This increase in literature indicates that freshwater meiobenthology has gained considerable momentum. It is now apparent that: (a) much of the biodiversity in freshwaters is contributed by meiofauna (Robertson et al. 2000b,c); (b) they are many times more abundant than the macrofauna, and; (c) its biomass could potentially be half that of the macrofauna, or may even exceed it (Poff et al. 1993; Stead et al. 2003). The biotopes of freshwater meiofauna are perhaps more heterogeneous.
than their marine counterparts, each harboring a specialized meiofauna. Groundwater aquifers, river shores, cave pools and lake bottoms all are inhabited by a particular meiofaun. Research on running waters was initially neglected, but recent research momentum (see above) has filled many ecological gaps and compensated for some of the previous lag in this field. The influential and early freshwater research on subterranean, mostly karstic fauna by Karaman and his school (e.g., Karaman 1935) as well as Chappuis (1942) and Rouch (1968) may have contributed to the notion that interstitial animals represented most of the freshwater meiofauna. Easier access and an apparent relevance also prompted early studies on the small bottom fauna of standing water bodies such as lakes and ponds (Wiszniewski 1934; Pennak 1940).

Ecologically, the freshwater meiofauna often attains considerable importance, since together with bacteria and protozoa, meiobenthic animals are involved in the remediation of wastewater and the natural regeneration of our groundwater. The ecological constraints and the typical faunistic composition of the freshwater meiofauna differ much from those of its counterpart in the marine domain, although nematodes frequently dominate in abundance and biomass, just as in marine habitats. However, in many freshwater biotopes, rotifers are of equal importance, followed by copepods (cyclopoids and harpacticoids), tardigrades, “cladocerans” (Chydoridae), hydrachnid mites and oligochaetes. Insect larvae (mainly chironomids) are a specific component of temporary freshwater meiofauna that lack a counterpart in the marine world, but are of considerable relevance in the limnetic food web (Pennak, 1940; Williams 1984; Schmid and Schmid-Araya 1997). However, variations from this generalized picture of freshwater meiofauna are often found when studying the different biotopes (Schwoerbel 1961a, 1967; Pennak 1988; Hakenkamp and Palmer 2000; Hakenkamp et al. 2002), and so they each require separate discussion. An artist’s view of the biotopes can help to illustrate the low concordance between marine and freshwater meiobenthic taxa (Figs. 8.11 and 8.12).

### 8.7.1 Running Waters: Stream and River Beds

*The habitat.* Although much of the biodiversity of the fauna populating stream beds is due to meiofauna, this faunal compartment is often neglected by freshwater ecologists (Stead et al. 2003). The first ecological studies on freshwater meiofaunths were performed in river beds, but this “hyporheic” and “phreatic” (deeper) meiofaunths is less well known than the meiofaunths in lakes (see Hakenkamp and Palmer 2000; Robertson et al. 2000b; Sect. 8.7.3). In many headwater habitats with coarse sand or gravel bottoms, this is probably due to problems with accessibility and sampling, making quantitative data scarce. The hyporheic habitat of the riverbed is mainly characterized by water flow, while the phreatic sediments continuously merge to the groundwater horizon (Fig. 8.13; Pennak and Ward 1986). In the groundwater aquifers underlying phreatic habitats, the fauna becomes more homogeneous with little or no altitudinal differentiation. Regarding the intense interac-
Fig. 8.11 Artist’s impression of the freshwater interstitial environment and its fauna

Fig. 8.12 Artist’s impression of the marine interstitial environment and its fauna
tions between the epigean, hyporheic and groundwater zones of a river, Brunke and Gonser (1997) termed the hyporheic zone a “connecting ecotone”—a corridor used and inhabited by rich, diverse and interacting meiofaunal communities. These physiographic connections, which result in exchange rates that were higher than previously purported, make any strict delineation of the biotopical subunits (Fig. 8.13) rather arbitrary (Danielopol 1989, 1991; Lafont and Durbec 1990; Lafont et al. 1992; Dole-Olivier and Marmonier 1992).

The dominant ecological factor in freshwater habitats is water flow. Water flow separates the torrential headwater streams with their beds of pebbles and barren cobbles from the slower lentic lowland rivers, with their fine sediments and rich macrophytes. The other characteristic of all hyporheic habitats is astatic and seasonal fluctuations. Hence, hyporheic meiofaunal assemblages differ in the various parts of a running water system. Seasonal changes in temperature and water level together with a variable chemical milieu add to this instability. Especially at low water levels, the hyporheic fauna can become threatened by river pollution. Characteristic abiotic features of the hyporheic pore water system compared to the overlying river water are an increased CO₂ content, which is reflected by a decrease in pH by 1–2 units. Strong adsorptive forces in the sediment often also cause an increase in the concentrations of silica, iron and manganese. In the coarser sediments of the riverine headwater region, the strong water currents maintain an open interstitial system with a good permeability, which compensates for the oxygen depletion caused by the supply of organic matter. In particular, crystalline sediments based on primary rocks maintain an open pore system, acting as a filter system for detritus particles. Detritus will accumulate in the more lentic lower river bed, clogging the interstices of the sand. Silt and mud particles compact the river bed in sheltered riverine side-arms and coves. Combined with intense bacterial growth, this accounts for typical decreases in oxygen and pH (Fig. 8.14) as well as nitrate and sulfate concentrations, while reduced substances and free hydrogen sulfide may develop locally and can act as major controls over hyporheic communities (Strayer et al. 1997).

Fig. 8.13 The habitat zonation of a riverbed. (After Pennak and Ward 1986)
Generally, the hydrological and geomorphological regimes seem to override all other factors in running water ecosystems and determine the interactions and roles of meiofauna (De Bovée et al. 1995; Strayer et al. 1997; Hakenkamp and Palmer 2000): at high flow rates the macrobenthos dominates and the meiobenthos attains a subordinate role despite its often considerable diversity. At intermediate flow rates the meiofauna gains importance, filtering detrital particles and breaking down organic matter. This intensifies bacterial processes and contributes greatly to total secondary production. At low flow rates patches of accumulating detritus develop, where the depletion of oxygen can cause upward migration of the hyporheic meiofauna and can increase losses by drift. These discontinuities in the interstitial water flow and local biotic factors may modify the general hydrological and geomorphological scenario and thus the hyporheic fauna (Dole-Olivier and Marmonier 1992, Ward and Palmer 1994). Overall, and in contrast to the aquatic epibenthos, the hyporheic fauna of running waters is structured by the site-specific physiography rather than the elevation (mountain vs. lowland river).

Among the biogenic factors, organic matter is the key component that attracts hyporheic meiofauna and controls their patchy distribution. The load of detritus, with its rich epigrowth of bacteria and microalgae, serves as the main food source. Sites in headwater streams with open access to both detritus and oxygen will support a diverse and quantitatively important meiofauna (Ward and Voelz 1990). Suboxic reaches often develop in low-flow riverbeds. Here, the composition of the

![Fig. 8.14](image-url) Gradients of chemical characteristics in a vertical profile of a typical lakeshore. Note the decrease in oxygen values (in ppm) and the increase in carbon dioxide values (in ppm). (After Pennak 1939)
meiofauna changes; the diversity and abundance will decrease. As an adaptation, many of the hyporheic animals seem fairly tolerant of a reduction in oxygen content in the pore water. However, water velocity, sediment composition, oxygen and detritus supply may vary on small scales—around one boulder, within a stand of vegetation, or in a sand riffle. Depending on the bottom microstructure, downwelling and upwelling sites can form. For meiofauna, these local properties are often the real controls over the distribution pattern and community composition. For instance, cyclopoid copepods and cladocerans prefer areas with reduced flow, while harpacticoids are more common in coarser sediments with a high water flow and shear stress (Robertson 2002).

Water flow also enhances the rate of faunal suspension. Although surface films of bacteria and diatoms tend to stabilize the sediment, sudden floods with subsequent heavy erosion and faunal suspension are common phenomena, and not only in montane rivers. Passive drift accounts for a repeated redistribution of meiofauna and is important for the dispersal and regeneration of communities after severe disturbances by flash floods (Palmer 1992; Palmer et al. 1996). The degree of community destruction apparently depends on the duration of the flood, but is usually redressed within a few weeks and only occasionally within several months (Hancock 2006). This swift recovery is largely made possible through transport from regions higher up the river. Turbulence will increase the probability of hitting the bottom and resettling (McNair et al. 1997). Although only a small proportion of the fauna has been found to immigrate from the hyporheic strata (Palmer et al. 1992), the (deeper) hyporheic biotope can be considered a refuge area for fauna, allowing them to avoid currents and drift. With its transitional position between the exposed riverbed and the stygobiotic groundwater sediments, the hyporheos attains considerable importance as a sheltered recruitment zone, especially for insect larvae. Nematodes were encountered down to 50 cm depth in running water sediments. While the deep hyporheic zone as well as lentic “pockets” along the shore may be important as havens that are well supplied with accumulating debris, their role as centers of recolonization, supporting the “hyporheic refuge hypothesis,” is limited (Robertson 2000; Palmer et al. 1992; Olsen and Townsend 2005). Thus, dispersal by flooding, regeneration by incoming drift, a high potential for rapid colonization, as well as frequent redistribution of communities are regular features of running water biotopes. Combined with a high degree of resilience, the consequences of flood events are limited (Palmer et al. 1995, 1996; Robertson 2000). At reduced interstitial flow rates micropatches with favorable or unfavorable combinations of factors can develop and create a high spatial heterogeneity that changes temporarily whenever flow conditions change. The previously fairly homogeneous spatial distribution of meiofauna in the hyporheic zone starts to become patchy.

Hydrodynamics apparently also structure the temporal development and composition of riverine meiofauna. Seasonality in hyporheic abundance patterns is well developed, with minima in the spring following high waters in springtime. Under low-water conditions (which often occur during the summer months), the epibenthic fauna is confined to a thin surface horizon while the endobenthic fauna dominate throughout all the deeper layers. This situation reverses at times of high water
discharge. In the summer, during phases of low stream velocities, the fauna of deeper horizons often suffer from stagnant pore water conditions that favor the development of hydrogen sulfide. In the cold season, nematodes, copepods and oligochaetes were found deeper down in the sediment (Palmer 1990a). In cold winters, the surface layers are easily exposed to frost and ice scraping, with its concomitant noxious impact on the inhabitants of these layers. They may survive frost by evading deeper down into the hyporheic interstitial (Schwoerbel 1967).

Species composition. In the hyporheos, in great contrast to the marine meiofauna, rotifers, microcrustaceans (cyclopoids, harpacticoids, cladocerans, ostracods), microdrilinel oligochaetes and insect larvae often attain numerical dominance over nematodes. Usually, nematodes are favored in physically severe sites and can occur in densities of $10^6$ per m$^2$, while other groups may prevail under less severe conditions. The headwaters of a river, with its bed of pebbles and gravel, its huge internal surface and its high structural complexity, harbors a more diverse hyporheic meiofauna than the sandy-to-muddy lower reaches. Cyclopoid and harpacticoid copepods, small isopods, tardigrades and smaller insect larvae prevail in the headwaters. With finer sediment and often increasing organic load, the riverine meiobenthos becomes dominated by oligochaetes and chironomid larvae, while the soft sediments of lowland streams are the domain of nematodes, chironomids and rotifers (Hakenkamp and Palmer 2000). In the bed of a low-gradient stream, Palmer (1990a) found 35–85% rotifers, followed by 20% juvenile oligochaetes, then chironomid larvae, and, to a lesser degree, nematodes and copepods. Nematodes preferred the experimental tubes filled with the finest sand (0.25 mm), while harpacticoids were most frequently found in tubes filled with gravel of size 4–6 mm; the third group of importance, chironomid larvae, dominated in sand of 1–4 mm grain size (Schwoerbel 1967). Some rotifer genera (Notholca, Lecane) were found to be numerically dominant in alpine streams (Schmid-Araya 1995, 1998). In another stream, Ward and Voelz (1990) found that small ostracods and chironomid larvace accounted for 65% of all meiofauna. Another group characteristic of the hyporheos are chydorid cladocerans. Small isopods, which are rather frequent in European riverbeds, seem to be absent in North America (Williams 1989). In northern latitudes, springs were dominated by oligochaetes and ostracods (Särkkä et al. 1997). A relatively rich taxonomic diversity (nematodes, oligochaetes, microcrustaceans, flatworms, tardigrades and midge larvae) along with high abundances can be attained mostly at intermediate ($\sim 30$ cm s$^{-1}$) water velocities (Whitman and Clark 1984).

In many lotic habitats the meiobenthos contribute far more than half of the total species richness (Robertson et al. 2000; Stead et al. 2003). Complete inventories often yield 150 species and can even exceed 300 species, of which nematodes contribute 30–50 spp (Hodda 2006). The sheer variety of microhabitats in lowland streams supports species richness. This is especially true for microcrustaceans, some of which are restricted to running waters (Rundle and Ramsay 1997). Still, our knowledge of the quantitative composition of hyporheic meiofauna is limited. Problems with quantitative sampling and detailed determination make calculations of species richness and population density per area or volume difficult (see below).
Abundance, biomass, and production. In general, sediments of streams are not particularly densely populated by fauna. Coarse sand bottoms in the riverbed (less so in the shore sediments) harbor meiofauna with abundances of 20–30 ind. 10 cm$^{-2}$. In an acidic stream the number of meiobenthic individuals was even less, although at >10 ind. 10 cm$^{-2}$ (maximum 84 ind $\times$ 10 cm$^{-2}$) it exceeded that of the macrofauna (Stead et al. 2003). Schwoerbel (1967) found a relatively high abundance of hyporheic meiofauna, 60–100 ind. 10 cm$^{-2}$, in the sand of an alpine mountain stream; a range that is often similar to that of nematode communities (see compilation by Hodda 2006). Extremes of several thousands per 10 cm$^2$ may represent patches, e.g., up to 6,000 meiobenthic organisms per 10 cm$^2$ in the bed of a North American low-gradient stream with mostly rotifers (Palmer 1990a) or 4,100 nematodes 10 cm$^{-2}$ in a small sandy river in Germany (see Hodda 2006). However, these figures do underline the taxonomic and numerical relevance of the hyporheic community of streams. Interestingly, Pennak and Ward (1986) found substantially more interstitial crustaceans in a mountain river than plankton in a nearby lake.

Estimates of biomass and production rates for lotic meiofauna are rare. Depending on the substratum, between almost zero and 22% of the biomass (in sand) has been attributed to hyporheic meiofauna (Hakenkamp et al. 2002), with a higher contribution of small-sized organisms to the overall biomass in lentic than in lotic environments. Stead et al. (2003, 2005) published even higher meiobenthic biomass values: between 10 and 100 mg m$^{-2}$ (dry wt), values close to the macrofaunal biomass. According to Kowarc (1990), the meiofaunal production in the gravel of mountain streams is rather low, with a P/B ratio of 3–6, which is probably caused by the low temperatures and generally oligotrophic conditions. A low-to-moderate (often less than 5%) contribution of meiofauna to the metazoan production has been adopted for lotic ecosystem productivity (Robertson et al. 2000; Hakenkamp and Morin 2000, Bergtold and Traunspurger 2006), but Hakenkamp et al. (2002) also report values of up to 50% in streams. Only exceptionally, especially in creeks with sandy bottoms, does this value increase considerably (Poff et al. 1993). However, regarding the rapid meiobenthic turnover, low biomass values can sustain a sizeable production (see Sects. 9.3.2 and 9.4). Stead et al. (2005) assessed the complete faunal spectrum of the benthos (retained in sieves down to 42 $\mu$m mesh size), evaluated over a period of more than a year, in an acidic English stream. They found that 15% of the total production (5.2 g dry wt. m$^{-2}$ y$^{-1}$) was due to the activity of permanent meiofauna, and together with the temporary meiofaunal taxa (oligochaetes, chironomids, plecopterans) more than half the production was contributed by meiobenthos. The authors argue that this result points to a “substantial underestimation” of meiobenthic productivity, arising from problems with appropriate assessment.

Food relations. The predominance of bacterivores and detritivores among the meiofauna highlights the role these trophic components play, even in lotic freshwater habitats. Many chironomids, rotifers, ciliates and (to a lesser degree) nematodes graze extensively on bacteria. Particularly at times of high meiofaunal densities, the grazing pressure on bacteria and diatoms is significantly high (Borchardt and Bott 1955). Thus, meiofauna gain importance as a link between microbial grazing, reworking of the sediment and food for macrofauna. Numerous studies of various
running-water habitats and experimental data conclude that the balance between macro- and meiofauna in terms of biomass and production as well as functional relevance will favor meiofauna in fine-grained sediments and a low interstitial flow regime (see also Hakenkamp and Morin 2000). At the predatory level of the food web, considerable activity from mites and the larvae of tanypodid chironomids and plecopterans has been reported (Schmid and Schmid-Araya 1997). Caging experiments demonstrated that predation on meiofauna is significant, particularly among young fish. Also, the biomass size spectra of meiofauna can be used to gauge the importance of differently sized organisms, indicating predator–prey interactions. However, for lotic freshwater habitats this approach is controversial: the results of some studies indicate well-separated biomass peaks for meio- and macrofauna (Poff et al. 1993), while in others the biomass distribution is more even and macrofauna only slightly prevail (see Sect. 9.2; Robertson et al. 2000c).

When generalizing the data on the meiobenthos in running water systems, the following aspects should be emphasized:

- Much more information beyond local studies is required to provide a general, zoogeographically reliable overview.
- While streams are relatively better understood ecologically, the meiofaunal ecology of large rivers requires urgent investigation, especially since the meiofauna here are purportedly of higher ecological importance, but are being placed under much anthropogenic stress.
- Life history data, estimates of turnover and the productions of key species are urgently needed.
- The impacts of ecological parameters such as bioturbation or water drift still need to be assessed.
- An appropriate methodology that catches epibenthic as well as interstitial fauna is a prerequisite for a total-component analysis.

Methods. The scarcity of generalizable data on the hyporheic meiobenthos is often due to inherent technical and methodological problems. Only in the sandy bottoms is quantitative work with regular station profiles possible. Here, the standpipe corer (Williams and Hynes 1974) allows quantitative sampling into deeper strata too, enabling intact samples to be collected from defined depths. Battery-powered suction corers, constructed for quantitative sampling in marine bottoms (Taylor et al. 1995), might be applicable, as might the use of Scuba divers. In the pebbles and gravel of most riverbeds, sample holes can only be driven with massive corers, and the pore water that enters is pumped up for faunal analysis. The typical method used for lotic freshwater habitats as well as for groundwater research (see below) is pumping with the Bou–Rouch pump (Bou 1974; Fig. 8.15). A small pump is mounted on a perforated metal tube that has been hammered into the riverbed and remains in position for the repeated sampling of interstitial water. This pore water and its inhabitants can enter the tube through perforating holes. It is arguable whether this method will yield reliable reproducibility or area-related quantification, since most of the methods based on pumping do not allow exact references to a distinct depth or area. These arguments also apply to trapping methods (Hahn 2003),
which have yielded comparatively satisfying results in test series. The corers designed by Danielopol and Niederreiter (1987) and Tabacchi (1990) provide more quantitative access. They allow for fractionated vertical subsampling of interstitial water and fauna by subdivision of the coring tube into small chambers, which are evaluated separately (Fig. 8.15). Quantitative results can be obtained with a more sophisticated but expensive method. A sediment core obtained in a metal tube is shock-frozen in situ by liquid nitrogen and then retrieved undisturbed after previous anesthetization of the fauna by electropositioning (Bretschko and Klemens 1986). Limitations on quantitative sampling could perhaps be mitigated by increasing experimental work (Palmer 1993).

More detailed reading: general and ecology, Schwoerbel (1961a); Pennak and Ward (1986); Palmer (1990b, 1992); Ward and Palmer (1992); Brunke and Gonser (1997); Hakenkamp and Palmer (2000); Robertson et al. (2000c); Rundle et al. (2002); methods, Bretschko and Klemens (1986); Palmer et al. (2006).

8.7.2 The Groundwater System

Groundwater represents a freshwater reservoir of eminent importance. About 40% of all freshwater, ice included, is stored in the continental groundwater system (Danielopol 1989); the water masses in all lakes and rivers account for only about 4% of the global groundwater reservoir. An account of groundwater ecology (not specifically meiofauna) has been edited by Gibert et al. (1994). An even wider topic is covered by *Subterranean Ecosystems* (ed. Wilkens et al. 2000). The importance of groundwater aquifers is based on the fact that they supply us with drinking water, an indispensable human resource.

The contact with the surface waters, mediated by the hydraulic conductivity and the texture of the sediment, determines the typical abiotic characteristics of this biotope. With increasing depth, the homogeneity of its sediments, the constancy of its physiographic conditions and homeostasis over long geological periods are the main biotopical features of the groundwater system. Its abiotic milieu is characterized by fairly constant, low temperatures, a somewhat lowered pH, a slightly undersaturated oxygen content, a high amount of free CO₂, and oligotrophic conditions (Fig. 8.14). However, groundwater systems are not separated from surface waters. They are progressively more “open” the closer they are to the surface and the coarser the sediment pores.

The “stygobiotic” meiofauna of the groundwater aquifers and the “troglobitic” cave meiofauna are specifically adapted to the above ecofactors. They exhibit slow locomotion and thus migratory ability, low metabolic activity and growth, long generation times and lifetimes, late maturity and low fecundity (a few, large eggs), and hardly any diurnal rhythms. Progenesis seems to be a relevant evolutionary factor (e.g., in syncarid crustaceans, in some amphipods and isopods). All of these attributes characterize them as K-selected specialists with a high rate of specialization. Adaptations of the interstitial fauna to groundwater life are detailed in Coineau...
Fig. 8.15 A coring tube for fractionated sampling of groundwater fauna. For details see the text. (After Danielopol and Niederreiter 1987)

(2000). Typical stygobiotic species are mostly cold stenothermal but they are well adapted to the low oxic conditions of many groundwater habitats (see Fig. 8.16). A relatively well-developed tolerance to (low) salinity points to the evolutionary origin of many stygobionts from the coastal groundwater (see below). Energetic
sources in the groundwater realm are scarce; the food web is rather simple with few
trophic links (Gibert et al. 1994). The absence of primary producers and the scarcity
of predators (cyclopoids) in the groundwater community are why Gibert and
Deharveng (2002) considered subterranean ecosystems “functionally truncated.”
Depending entirely on heterotrophy and living on detritus entrained from the
surface, the groundwater community shows ecological and sometimes even taxo-
nomic parallels to that of the deep sea (see below and Sect. 8.3).

Altogether, the underground biocenoses are less densely populated than the
hyporheic riverbeds. In the ecotone layer, where hyporheic and groundwater meio-
fauna mix, biodiversity and density are concentrated. The groundwater meiofauna
can be considered almost unknown at the global scale; our knowledge is mainly

![Diagram](image.png)

**Fig. 8.16** a–b Occurrence of stygobiont specimens in groundwater habitats of Caribbean islands. a Abundance of stygobionts vs. “normal” marine specimens in relation to oxygen saturation. b Occurrence related to depth in the substratum and oxygen saturation. (After Stock 1994)
limited to a few areas in North America and Europe. They are characterized by a wealth of crustacean species (in Europe about 40% of all crustacean fauna are stygobites!) and an absence of the insect larvae that usually dominate in the riverine and lacustrine meiofauna (Danielopol et al. 2000). Figure 8.17 attempts to depict some characteristic inhabitants, the stygobites, of this "unseen ocean beneath our feet," which extends worldwide and to a depth of several hundred meters. Stygobites are often continentally distributed and their compositions are consistent enough to form characteristic biocoenoses (e.g., the Bathynella–Parastenocaris community).

In many ways these biocoenoses are related to the fauna of caves and springs, as exemplified by the freshwater polychaete Troglochaetus beranecki or the amphipod genera Niphargus and Bogidiella.

Typical representatives of the groundwater fauna are minute malacostracan crustaceans: amphipods and isopods that are tiny enough to live in the interstices of the mostly karstic sediments (amphipods Niphargus spp, Salentinella spp., Stygobromus, so far only found in North America; isopods: Microcerberidae, Cirolanidae, Microcharon, Prousellus, Microparasellus). The other characteristic group is the copepods; often cyclopoids (Dacyclops, Acanthocyclops) but also some harpacticoids (e.g., Nitocrella; Phyllognathopus spp.; Chappuisius spp.). In addition, stygobitic ostracods are well represented, especially members of the family Candonidae. A few representatives of the rare crustacean orders Thermosbaenacea (Pancarida) and Syncarida (Bathynellidae) supplement the suite of crustacean groundwater inhabitants. The microdriline oligochaetes frequently encountered in groundwater

Fig. 8.17 The interstitial habitat of subterranean meiofauna in an Austrian aquifer. (After Danielopol et al. 1994a)
belong to the haplotaxids, rhyacodrilids, and tubificids. Some of them are descendants of marine lineages such as *Phallodrilus* *sp.* or *Troglochaetus*, while other annelids represent temporary meiofauna. Even minute gastropod molluscs are encountered in the subterranean aquifers (e.g., *Paladilhia*, *Arganiella*).

Groundwater aquifers and caves have attracted the attention of zoologists, initially for evolutionary reasons, and later (and especially in the karstic regions of Europe and North America) as reservoirs of new species, “hot spots” of biodiversity. The abundance of species decreases sharply with increasing depth and isolation from the surface waters. Here, the number of endemics and relicts without a connection to surface fauna is enhanced. This is especially evident among small crustaceans, such as thermosbanaceans, which are found in groundwater biotopes in seemingly complete isolation. There are both geological and ecological reasons for this interesting evolutionary diversity. A scarcity of predators and reduced competition have permitted the persistence of taxa with low mobility and little competitive strength in a biotope with numerous microhabitats characterized by ecological isolation.

What were the paths by which the groundwater was colonized with meiofauna? Here there are two main scientific schools of thought, the dispersionists and the persisters, who are not always clearly separated. Both suggest that the seashore, with its river mouths, brackish lagoons and marine caves, was the most probable source for the colonization of the continental subterranean sediments. A connection to recent or ancient seashores could explain the distribution of some taxa in present-day continental groundwater habitats. According to the “persisters” hypothesis, meiofaunal taxa with their poor dispersal abilities populated wide areas of ancient seashores (e.g., the Tethys Sea). From here they were forced by changes in the sea level to adapt to the new conditions in their originally littoral marine habitat.

Rising or falling sea levels since the Tertiary period can explain the often vicariant, e.g., amphi-Tethyan or amphi-Atlantic, distributions of many a karst stygobite (for details see Stock 1994). The driving force for a “stygobization” may have been large desiccation events during warm geological periods (e.g., the Mediterranean in the “Messinian crisis”). This is based on the contention that the numerous endemic and archaic animal groups presently found in the groundwater systems passively persisted close to their places of origin in the fairly static refuges of an environment which maintained many of the living conditions of their former epigean presence (“relict refuge model”; Botosaneanu and Holsinger 1991). This dynamic geological history of repeated marine transgressions and regressions created new local environments and allowed those animals of adequate evolutionary plasticity to adapt over time. Preadapted by their frequent exposure to brackish water conditions (see Sect. 8.6), they could slowly adjust to freshwater conditions provided that they were exempted in their new localities from the stresses present in surficial habitats. It was not just small size that adapted them to become competent colonizers of the groundwater system and caves, but also their euryoxic nature. This enabled their evolution in caves and groundwater systems, which are often dysoxic (Fig. 8.16; Stock 1986, 1994).

This process resulted in the separation of the originally large, connected littoral populations into small, isolated hypogean “founder” populations that favored subsequent
intense radiation/speciation. Along this marine–groundwater route of meiobenthic dispersal and evolutionary change, anchihaline caves may be regarded as interconnecting pathways (see Chap. 7). The often isolated locations of the evolutionary “ports” into the groundwater system may have contributed to the high allopatric speciation in the stygobios. This would explain their rich number of zoological peculiarities. The stable nature of their refuges, with little competition present, would favor slow speciation or structural stasis and lead to the often relict characters of stygobiotic species. Morphologically primitive and often neotenic crustacean groups like Bathynellacea and Pancarida (see Fig. 5.36) are good examples of this. As a result, many stygobiotic animals from the continental groundwater are endemics and considered relics of a primitive marine fauna that reflects their old “plesiotope.” This “geological scenario,” mainly developed by Stock (1994; see also Strayer 1994) would explain the rich and isolated insular groundwater fauna of the Caribbean and Middle American shores, where anchihaline caves are particularly frequent. Numerous fascinating meio- and macrobenthic animals have been retrieved from their shelter and stability. Present-day islands, often previously seamounts, also play a dominant role as stepping stones and centers of speciation (see Chap. 7).

The “dispersionist school” of groundwater researchers is inclined to consider hypogean fauna as being mainly represented by animals that keep actively invading the stygobiotic freshwater milieu from other, often marine biotopes (Danielopol and Rouch 1991). Studying subterranean ostracods, Danielopol et al. (1994) state that dispersal by drift and active migration enable hypogean meiofauna to constantly proliferate into the surrounding habitats. The ostracod distribution is better explained by an ecological, dispersive scenario than a scenario of geological events. It is again mainly the degree of ecological flexibility and the capacity for tolerance that control the distribution of the species into the subterranean and epigean aquatic system.

Another source of groundwater colonization may be the riverine meiofauna. There are, indeed, numerous connections between the groundwater and the hyporheic and epigean fauna of running waters. In downwelling areas of gravel bars, the epigean fauna from the surface becomes infiltrated into the interstitial of hypogean sediments. Contrastingly, in areas with prevailing upwelling groundwater, the contribution of stygofauna from the deeper layers progressively increases in the interstitial system (from 8 to 47%, see Ward and Palmer 1994). A correspondingly varying influx of stygofauna into the riverbed was observed in studies of the floodplain of the River Rhone at sites with differing hydrological regimes (Dole-Olivier and Marmonier 1992). These studies emphasize the close connections of the groundwater assemblages to those of the surface waters.

Boutin and Coineau (1991) point out that the colonization process represents a combination of dispersion and persistence. Their “two-phase model” is characterized by several successive steps. Initially there is active dispersion and vertical transition from surface waters to the interstitial. This is followed by passive persistence combined with gradual adaptations that further separate the interstitial fauna of the continental groundwater from that of the original marine habitats.

Whichever mechanism, per se or in combination, was the driving evolutionary force, a confusing mosaic of archaic and derived characters is typical of the stygobios.
Ecological stability and reduced competition in the simplified subterranean ecosystem would explain the high biodiversity combined with the low abundance of the stygofauna. As examples, the karst regions in Europe and North America, and to a lesser extent the interstitial of alluvial aquifers, represent rich species reservoirs for some crustacean groups such as ostracods, harpacticoids, amphipods, and isopods. For these taxa and biotopes, the species richness can be equal or can even exceed those of surface freshwater habitats (Rouch and Danielopol 1997; Danielopol et al. 2000).

In North America, the glacial boundary of the last ice age seems to represent an important distributional barrier for the hypogean fauna. A typical groundwater fauna that is speciose and rich in K-selected endemics, e.g., Bathynellacea, has only been found in formerly unglaciated areas. Both the upland plains (influenced by the ice cover) and the coastal plains (under the impact of the marine regime) are poorer in groundwater fauna (Strayer et al. 1995). Characteristic groundwater cyclopoids on the North American continent seem to follow the same distributional constraints. Once adapted to the physiological constraints of freshwater, stygobiotic species do not seem able to bridge the oceans (Schwoerbel 1967). Their continental distribution is linked to the large aquifers, for instance those of the Rhine and the Danube in Central Europe. Considering the limitations described above, the surprisingly frequent circummundane distributions of stygobiotic species cannot be conclusively explained. With the ongoing discovery of huge subterranean systems, it is likely that many more zoological “preciosa” will be discovered and that the distribution patterns of stygobiotic animals will become better understood.

The ecological knowledge of groundwater meiofauna clearly lags behind that of rivers and lakes. This is especially true if we consider the scarcity of quantitative data on biomass (allowing for calculations of productivity), which is mostly due to methodological problems. Direct sampling of defined volumes in the aquifers deep beneath the surface is restricted. Even elaborate fractionated samplers (see Fig. 8.15), traps (Hahn 2003), and pumping systems that allow access through narrow drill holes (Malard et al. 1994) do not allow us to draw quantitative conclusions about the sample volume collected.

Notable exceptions are water accumulations in caves. If sufficiently isolated from the outside, the ponds and streams of caves harbor a “cavernicolous” (troglobiotic) meiofauna, which usually represents a typical groundwater fauna that shares the restrictive characters of stygobitic life but allows for quantitative evaluation. Ecological studies performed under these cave conditions, preferably experimental work, might allow conclusions on the biomass and production of the ambient groundwater fauna to be made.

Usually, aquatic cave habitats are oligotrophic and carry little meiofauna. Exceptions include some thermomineral caves with effluents of methanic and sulfidic water, e.g., Movile Cave in a karstic area of Romania. Here the ponds are populated by an ecosystem completely based on a rich bacterial production which, in turn, supports a meiobenthic community dominated by bacterivores (mainly nematodes) and predators (cyclopoids). The rich supply of bacterial organic matter (and the high temperatures) enables high population growth and consumption rates (Muschiol and Traunspurger 2007; Muschiol et al. in press).
The groundwater fauna inhabits a very delicate biotope that is of great importance to mankind’s water resources. Their high sensitivity to pollutants makes stygobiotic species valuable indicators of declining water quality. Changes in their populations should be used as early signals of the potential contamination of drinking water and the need for bioremediation. Contamination by anthropogenic chemicals requires a sustainable water management concept for groundwater habitats. Considering the slow speed of hypogean regenerative processes, implementing such a concept is imperative in order to secure our future, considering the decrease in and long-term deterioration of our groundwater reservoirs globally. Areas with a diverse or unique meiofauna possess a particularly high value beyond just the scope of scientific exploration: they demand protection (Hancock et al. 2005; Marmonier et al. 1993; Danielopol 1989, 2000b).

More detailed reading: Delamare Deboutteville (1960); Danielopol (1990b, 2000a, b), Botosaneanu and Holsinger (1991); Gibert et al. (1994); Stock (1994); Brunke and Gonser (1997).

8.7.3 Standing Waters, Lakes

The habitat. Lake sediments are more easily sampled quantitatively and thus have been more thoroughly investigated than other freshwater biotopes. However, only the meiofauna from a few lakes have been reported, in contrast to the numerous papers on the littoral parts of the sea. In particular, quantitative data on lake meiofauna (abundance, turnover and production) acquired over longer periods of time are scarce, although the ecological role of such meiobenthos is becoming increasingly apparent (see below). Modern lacustrine meiobenthic research is based on the classic book by Strayer (1985) on Lake Mirror, USA. In Europe, thorough investigations of northern lakes have increased our knowledge of the contribution of the meiobenthos to benthic biomass and productivity (Kurashov 2002; Sarvala 1998, focusing on copepods). Some oligotrophic lakes in Germany have been studied in quantitative detail by Traunspurger (2000) and his team (Bergtold and Traunspurger 2005). A chain of volcanic lakes in Ethiopia was the focus of an international project coordinated by Tudorancea and Taylor (2002). The latter study connects calculations on the production of bacteria and protozoa to meiobenthic production (mainly nematodes) and discusses their role in the total benthos, underlining the need for a holistic ecosystem approach. The need for comprehensive, interdisciplinary projects in lacustrine (meio) benthology was also the basis for the Cytherissa Project in the Austrian Mondsee (Danielopol 1990a).

The permanently submerged sediments of most lowland lakes and ponds (the “hydropsammal” according to Wiszniewski 1934) usually consist of fine sand rich in organic particles and silt, often covered with plants. The concentration of dissolved inorganic and organic substances in this sediment is often 40–50% higher than in the overlying lake water. During estival warm-water conditions, there oxygen deficiency and the formation of hydrogen sulfide in the subsurface layers...
frequently occur. Here, burrowing macrofauna and epifauna largely prevail; the meiofauna is restricted to the uppermost centimeters. Nematodes usually dominate, followed by crustaceans (cyclopoid copepods, ostracods), often rotifers, (juvenile) oligochaetes, and chironomid larvae. Tardigrades occur irregularly, but can locally reach a high abundance (Neel 1948; Holopainen and Paasivirta 1977). All other taxa are considered insignificant.

In deeper oligotrophic lakes in both the mountains and lowlands the ecological situation is different. The amounts of organic matter in the profundal bottom sediments of these lakes are much less; oxygen is present even in the warm season while temperatures remain low. Further comparisons indicate that the ecosystems of very large and deep lakes (sensu Beeton 1984) often differ from those of smaller ones (Särkkä 1996b; Kurashov 2002). While in ponds and small lakes adverse factors such as pollution and/or oxygen deficiency can easily and rapidly affect the whole benthic ecosystem, in large lakes these remain local problems that are often compensated for due to mixing with other water bodies.

The moist shore sediments above the water level (“hygropsammal,” Wiszniewski 1934) usually comprise a sandy belt of 1–3 m width with a grain size composition that depends on the exposure and the slope of the shore, with the more exposed sites having medium sand (Md > 250 µm). This zone, which is well supplied with oxygen and rich in detrital food because of the debris washed ashore, is richly populated by meiofauna. Pennak (1940) found that rotifers sometimes dominated the psammosfauna with extreme densities (>10,000 ind. 10 cm⁻³). Next in abundance were a few species of harpacticoids (e.g., Parastenocaris; Phyllognathopus), represented by numerous individuals. In addition, nematodes, oligochaetes (including aeolosomatid annelids) and tardigrades belonged to the ecologically dominant groups of these lacustrine shores; all others were considered less important.

Meiofaunal compositions in lakes vary considerably, mostly depending on the trophic status, the profundal oxygen content, and the size and depth of the lake. Water depth and eutrophic conditions are negatively correlated with species richness and trophic group diversity. About 50 nematode species (but sometimes >100) can be expected in an oligo- or mesotrophic lake. Strayer (1985) reported from the shore sediments of Lake Mirror (USA) that 70% of all meiobenthic animals were nematodes, accompanied by turbellarians (often found only occasionally), gastrotrichs, cladocerans, copepods, just a few rotifers and tardigrades, and hardly any harpacticoids. A similar composition with a dominance of nematodes (between 70 and 189 10 cm⁻² = 77%) but a relatively high share of rotifers (up to 21 10 cm⁻²) was recorded from oligotrophic lakes in Southern Germany (Bergtold and Traunspurger 2004, 2005; Peters et al. 2007). In a seasonal study of a lake receiving thermal effluents from a nuclear plant in South Carolina, USA, Oden (1979) recorded 400–3,047 nematodes and 88–740 rotifers 10 cm⁻² in the control (cold) section; these densities were reduced in the effluent-affected (warm) areas of the lake. Oden found that rotifers, with 372 species from 19 families, were second in abundance to nematodes. In a eutrophic Chinese lake (total meiofaunal abundance between 15 and 400 ind. 10 cm⁻²) nematodes prevailed, followed by crustaceans and occasionally also rotifers or oligochaetes (Wu et al. 2004). Other eutrophic lakes contained
40–6,000 nematodes 10 cm$^{-2}$. Upon compiling the various data on the predominance of nematodes in different lakes it would appear that, in sediments with a high organic load, nematodes can reach densities comparable to marine sites and can dominate as long as the sediment is oxidized.

Copepoda, mainly Harpacticoida, are numerically and ecologically second in abundance in many lakes (around 50 ind. 10 cm$^{-2}$ in Lake Brunnsee). In oligotrophic lakes at northern latitudes with a good oxygen supply and moderate organic input, their share, was relatively high compared to nematodes (max. 250 ind. 10 cm$^{-2}$; Sarvala 1998). Together with cyclopoids (20 ind. 10 cm$^{-2}$) they were especially common in the periphyton and in shallow sediments. Towards the deeper profundal, harpacticoids decreased in abundance, meaning that nematodes gained in importance. The total abundance of the meiobenthos in the meso/eutrophic Upper Lake Constance (Germany/ Switzerland), which has a typical, nematode-dominated meiofauna composition, was 550 ind. 10 cm$^{-2}$ as a mean value, while the Lower Lake Constance contained 800 ind. 10 cm$^{-2}$. Maximal meiofauna density in this large lake was almost 2,000 ind. 10 cm$^{-2}$ (Kurashov, unpubl.). The rich ciliate fauna is not usually taken into account in assessments of meiofaunal abundance. Pennak (1939) counted about 10,000 protozoans compared to only about 500 metazoans per 10 cm$^{2}$!

Strayer (1985) quantified the whole spectrum of lacustrine meiofauna and related it to macrofauna. He found the lake bottom was on average inhabited by 1,200 ind. 10 cm$^{-2}$, 60 times the number and one-third the biomass of the corresponding macrobenthos. Nutritionally, most of this fauna fed on diatoms, including the food-selective species like some rotifers. Diapausing resting eggs of planktonic copepods ("zooplankton egg banks") have also been assumed to be a food source for meiobenthos, an interesting aspect of benthopelagic coupling (Hairston and Kearns 2002). The large majority (80%) of the meiobenthos was grazed down by the predaceous larvae of Tanypodida (Diptera) and other insects. In the oligotrophic Lake Brunnsee (Bergtold and Traunspurger 2005), meiofauna contributed only 0.1 g C m$^{-2}$ or about 4% of the total biomass (for comparison, the proportion of macrobenthos was 40%). In Finnish oligotrophic lakes this biomass value was surpassed by the biomass of benthic littoral copepods alone (15–30%), and with increasing depth and diminishing macrofauna, the copepod biomass increased to up to 40% of the total meiofauna biomass (Sarvala 2002). This shift is in line with the general trend that meiofaunal biomass in food-limited freshwater environments may exceed that of macrobenthos (Strayer 1991; Kurashov 2002). On a general scale, this wide range is reflected in a biomass contribution from the meiofauna of 7–61% to the total zoobenthos biomass (Morgan et al. 1980). Compared to streams, the meiofaunal biomass in lakes is on average 25% higher, and in certain favorable lacustrine sites it is >50% (Hakenkamp et al. 2002).

Since calculations of annual production and biomass/production (B/P) ratio are strongly dependent on fluctuating factors (individual body mass, temperature, nutrient supply; see Plante and Downing 1989), the production values for lake meiobenthos in relation to macrobenthos and total zoobenthos vary widely in the literature. While production figures will be given in Sect. 9.3.2, the contribution of
the meiobenthos to the overall production of the lake and its comparison with the value for the macrobenthos are of interest here. In many oligotrophic lakes the meiobenthic production is 2–4× lower than the production of macrobenthos. If microorganisms are included in this calculation (total benthic production), the value exceeds 12× the production of meiofauna (Bergtold and Traunspurger 2005). Again, under food limitation, the relative importance of meiobenthos may increase considerably (Sarvala 1998). According to Kurashov (2002), in large lakes the ratio of meiobenthic to macrobenthic production is on average 50–60%, while in the profundal of smaller lakes with scarce macrobenthos the meiobenthic production increases considerably and can surpass that of macrobenthos by a factor of >10 (small lakes in Latvia). However, under the impact of eutrophication, the macrobenthos gains in abundance while the meiofauna loses its productive relevance, becoming negligible. Compiling data from various lakes, Hakenkamp et al. (2002) concluded that the biomass and production of lake meiofauna will be highest in fine sand containing a limited amount of detritus where the meiofauna is exposed to a limited predation pressure and relatively frequent disturbances.

Considering the divergence in generation time and metabolic needs between meio- and macrobenthos, the productive turnover, measured as the mean P/B ratio, perhaps better underlines the ecological role of lake meiofauna. P/B ratios > 10 are reported in Bergtold and Traunspurger (2005) for the oligotrophic Lake Brunsee; in other lakes P/B ratios of up to 37 (Bergtold and Traunspurger 2006) suggest a high importance of meiofaunites in the ecosystem. However, in numerous less productive northern lakes with slower growth, the P/B ratios did not exceed five regardless of their trophic classifications (Kurashov 2002). Sarvala (1998) computed a ratio of only 1–7 for harpacticoids. These values are in the same range as those for marine meiofauna (see Sect. 9.3.2).

Using biomass as a basis, Strayer (1986) analyzed the size spectra of benthos from various limnetic biotopes, comparing it with corresponding figures by Schwinghamer (1981a) for the marine benthos. Regardless of biotope (lakes and streams) or sediment character, he could not group the limnobenthos into separate units of micro-, meio- and macrobenthos. This remarkable difference between marine and freshwater benthos was also confirmed by lotic freshwater studies (Traunspurger and Bergtold 2006; see Sect. 9.2 for explanations). Calculation of size spectra is now an accepted way of describing the holistical functioning of ecosystems and assessing the ecological relations of benthic groups and their metabolic roles (Hakenkamp et al. 2002). But, as Strayer (1991) cautioned, many factors other than grain size also have a potential influence on the size structure of the benthos, such as the degree of physical refuge or the predation pressure. These multifactor relations will cause considerable ambiguities in interpretation.

Regarding nematode feeding groups, it seems that deposit feeders (mainly bacteria) dominate the littoral in all lake types. In oligo/mesotrophic lakes, the range of chewers (predators and omnivores) increases considerably, especially at profundal depths. Suction feeders living mainly on plants and fungi are of (limited) importance and occur mostly in the littoral region (Traunspurger 2002; Moens et al. 2006). This corroborates the findings of Wu et al. (2002) that the greatest variety of
feeding groups and nematode species (20) were found in the least nutrient-rich area of an otherwise eutrophic Chinese lake. As for copepods, oligotrophic northern lakes were inhabited by some 20 harpacticoid species and 30 cyclopoid species (Sarvala 1998).

Data on lacustrine meiofauna are difficult to generalize, because each lake is a restricted biotope with its own environment. Its meiofaunal composition and ecological role in relation to other faunal compartments will differ, being subject to a variety of controlling influences. The conditions, and therefore meiofaunal functioning itself, depend much on seasonal fluctuations, which are influenced by the geographical location and the climatic situation of the body of water studied. In contrast to many marine habitats, the relatively small water bodies of lakes are directly subject to these factors. Thus, performing quantitative comparisons of different lakes and sampling periods, beyond considering different sampling methodologies, is a problem.


**Box 8.8 Freshwater Meiofauna—A Parallel World: Similarities, Dissimilarities and Transitions to the Marine Realm**

Hydrodynamics, hydrochemistry (particularly oxygen), disturbances, food supply, and competition: many of the same factors control both freshwater and marine meiofauna. And yet there are far-reaching dissimilarities—differing methods, distributional pathways and research histories. Studies of community dynamics and functional structure suffer from impediments to adequate sampling, especially in streams and groundwater aquifers. The unique and barely accessible world of groundwater animals is sometimes visible in cave waters, where “troglobites” closely correspond to the “stygobites,” the groundwater fauna. Groundwater studies offer unique opportunities to reconstruct zoogeographical connections and evolutionary pathways. How can we explain the meiofaunal paradox: a wide distribution of animals with almost no dispersive capacity? For an adaptive fauna (oxygen, salinity), the coastal groundwater, river mouths or marine caves are believed to be ports to the continental groundwater aquifers. The reduced competitive pressure in the groundwater or cave habitats enables the survival of relict and often primitive taxa. Thus, groundwater studies can help us to understand evolutionary trends linking marine and freshwater meiofauna. The composition of the freshwater meiofauna is quite different from the marine world. Nematodes often lose their dominance while harpacticoids take the lead; insect larvae are important temporary meiofauna, both as detritivores and predators; and the predacious cyclopoid copepods have no equivalent in marine environments.

(continued)
8.8 Polluted Habitats

8.8.1 General Aspects and Method Survey

The assessment of ecosystem health using meiofauna was an innovative approach when the first edition of this book was written. This changed with the review by Coull and Chandler (1992). This major compilation of the field still provides an important foundation and will most likely serve this function in the future. Success in pollution research means convincing laymen and critical opponents, as well as obtaining research investment, for the sake of the health of the environment. Impact studies using meiofauna have now been accepted by international governmental agencies because the advantage of using (inconspicuous) meiofauna is obvious. Today, the use of meiofaunal data is a widely acknowledged method of assessing the environmental status of a biotope. What is the basis for this paradigm change? Monitoring programmes and case studies performed after both natural and man-made disturbances have shown that the resolution can be improved by studying the meiobenthos because of its commonly higher sensitivity and turnover compared to those of the macrobenthos. Meiofauna are speciose, abundant and ubiquitous; meiofauna are even represented in extreme areas where macrofauna become scarce; and meiofauna are relatively cost-effective to handle.

The multitude of anthropogenic impacts and ecotoxicological agents and the diversity of meiofaunal investigations from polluted habitats is overwhelming and, in a treatise like this, forces reductive concentration. Hence, we will first discuss general aspects and problems. This will be followed by sections on the impact of petroleum hydrocarbons, metals and pesticides: three priority categories, as the almost 300 marine meiofaunal studies on the impact of pollution demonstrate (see Coull and Chandler 1992, plus more recent compilations). Oil obviously has a strong impact, but recovery is often surprisingly fast. Metals are persistent and recovery by metabolic degradation is limited, so long-term

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Box 8.8 (continued)

Running freshwaters (streams, creeks, rivers) are favorable sites for (experimental) studies on meiofaunal drift, emergence, and recolonization. Parallels can be drawn from their unidirectional flow regimes to the more complex multidirectional hydrodynamic patterns in the sea. In lakes, the composition and ecology of the meiobenthos vary strongly with the physiography and chemistry. Aside from the nematodes that usually dominate, other groups such as rotifers, chironomid larvae or oligochaetes can locally and temporarily become abundant. Copepods may prevail in the oligotrophic profundal of deep lakes. The lacustrine meiobenthos, despite its low relative biomass compared to the macrobenthos, can be a highly important producer.
effects and subtle changes to community composition are common. Pesticides share both features: some are highly toxic but biodegradable and the meiofauna exposed have a substantial recovery potential. The more persistent and/or adsorptive ones cause long-lasting community effects that require special attention. Impact studies on freshwater meiofauna have been compiled by Traunspurger and Drews (1996), Särkkä (1996a) and Höss et al. (2006). The comprehensive body of information in these papers and their bibliographies allow one to focus here mainly on the marine realm. A well-structured survey of the advantages and problems associated with using meiobenthos in pollution studies is presented by Kennedy and Jacoby (1999). The underlying mathematical principles and details of calculation will not be covered here. The reader is referred to the competent accounts by Underwood and Chapman (2005) and to references cited below.

The effects of pollution by anthropogenic organic enrichment on meiofauna will not be detailed here, although they do occur universally, especially in coastal sites and freshwater bodies. The compilations mentioned above should be consulted here. The general effects in this field are rather uniform and well investigated: an initial enrichment in meiofaunal numbers in the eutrophicated area is linked to a decrease in diversity and an increase in the dominance of a few species, mainly r-strategists. Most harpacticoids disappear before nematodes. As oxygen concentrations decrease, all of the physiologically demanding species will drop out. Development of hydrogen sulfide will exterminate all but the thiobiotic species, which can persist by feeding on the rich supply of bacteria and decaying animals and plants (see Sect. 8.4).

While pollution by organic anthropogenic wastes is today of minor relevance for most marine sites, it still devastates many freshwater habitats. An increasing threat to the marine coastal benthos, however, is the rapidly growing aquaculture industry. Especially in its initial phase, an aquaculture plant in a sheltered bight can often caused heavy depletion of (meio)benthic assemblages. With better knowledge and sophisticated, controlled feeding methods, it was shown that the deterioration can be greatly reduced and localized to small areas that are recolonized relatively quickly (see Sutherland et al. 2007).

As Heip (1980b), Hicks (1991) and Warwick (1993) point out, there are a suite of indisputable advantages to using meiofauna rather than macrofauna in pollution studies:

- Widespread occurrence, high availability
- Permanent and intimate contact with contaminated sediment
- Superior sensitivity and rapid reactions allow for short research periods
- High abundance, even in small sites or usually macrofauna-impoverished biotopes (estuaries, exposed beaches, high organic loads), allows for reliable statistical evaluation (e.g., Josefson and Widbom 1988, Austen and Widbom 1991)
- High species richness allows evaluations of changes in community structure
- Indicator species are widespread and present in various taxa
- Short generation cycles allow for tests of sensitive reproductive stages
- Cost-effective experimental and field work
- Low sensitivity to mechanical disturbance of the sediment enhances the possibility separating mechanically induced and pollutant-induced impairment (Austen et al. 1989, Warwick et al. 1990a).

These advantages of using meiofaunas for impact studies stand against some inherently “weak” arguments that seem to suggest the superiority of the macrobenthos as a pollution indicator:

- *Little previous information*: Baseline studies and time-series observations on meiofauna prior to the pollution event are rare (e.g., Herman et al. 1985; Bodin 1988). Extrapolating from “similar” biotopes is a deceptive approach because of the inherent patchiness and variability of meiofauna. Long-term sampling and monitoring is needed.
- *Unimpressive size of the affected fauna*: Pollution studies with inconspicuous microscopic animals pose a problem to the public (see Box 9.3)—they cannot see them! The choice of the relevant indicator species is crucial.
- *High sampling frequency*: The high temporal and spatial heterogeneity of meiofauna requires detailed spatial and temporal coverage.
- *Difficult identification*: Only instructive, easy-to-use and computer-based pictorial keys can help in the identification of fauna as diverse and small as meiofauna.

Recently, some additional achievements have further promoted the use of meiofauna in impact studies. Standardized bioassays acknowledged by national and international agencies as being generally applicable have been designed (Chandler 2004; ASTM 2004; Bejarano et al. 2006a); electronic identification keys exist for major meiobenthic groups (Diederich et al. 2000; Wells 2007); pollution-specific manuals facilitate evaluation (Somerfield and Warwick, 1996); computation is supported by reviews (e.g., Neher and Darby 2006) and software programs. New indices using meiofauna have refined pollution analyses in both freshwater and marine habitats (Särkkä 1996a; Neher and Darby 2006; Vassalo et al. 2006). Genetic-based ecotoxicological studies of meiofauna material have become a priority research field (Staton et al. 2001; Kammenga et al. 2007).

Thorough research on the impact of pollutants should generally evaluate several aspects: the intrinsic toxicity, as evidenced by the immediate responses, and the recovery potential of the community. This requires a combination of (1) chemical analyses, (2) field studies, and (3) laboratory experiments. This “triad” in pollution research (Long and Chapman 1985; Chapman 1986) obviously also applies to impact studies performed with meiofauna. In general, the main strategies (all of which require evaluation by careful statistical analyses) are:

1. Chemical analyses of the pollutant and its concentration
2. Field studies of the meiofaunal assemblage with time-series observations (case studies after incidents, large field experiments)
3. In-vitro laboratory assays of toxicity thresholds in the aqueous phase (unifactorial, multifactorial) using test animals (acute toxicity with representative species, long-term impact through generations with culturable test organisms)
4. Mesocosm studies in containers with sediment, agar (nematodes) or artificial substrates, either applied with a toxicant or transplanted into the polluted environment

In addition to the traditional surveys performed after pollution incidents, large-scale field experiments have recently been performed (Schratzberger and Warwick (1998 a,b)). Furthermore, standardized experimental field approaches have been designed (Mirto and Danovaro 2004). Despite their complex interpretation, the results from these studies in the natural marine environment are probably more generalizable than single-factor tests performed in the laboratory. Many aquatic pollutants are sorbed to the sediment particles and so there are typically higher concentrations in the sediment than in the overlying water. This would suggest that sediment-associated tests yield more realistic information for meiofauna, considering their intimate contact with the sediment (Kovatch et al. 1999; Schratzberger et al. 2000; Chandler and Green 2001). However, toxicants in sediments have typically proven to be less toxic than their counterparts under “in-water conditions” (e.g., Austen and McEvoy 1997b; Green et al. 1993 for metals). In the “sediment situation,” many toxicants may not be bioavailable to meiofauna, their toxicities having been reduced by chelation or complexation, or by binding to organic ligands and colloidal aggregations on the sediment surface. Hence it is the bioavailability, not the absolute concentration of pollutants measured in water, that determines the noxious effects on the benthic environment.

In nature, where single factors often act synergistically, the multifactorial impact of pollutants interacting with natural stressors (salinity, temperature, perturbation, high organic load) is usually more detrimental than the effect of adding the impacts of each individual toxicant (but there have been exceptions where the combined effect was less severe than the additive one). Hence, multiple stress experiments (e.g., low salinity plus elevated metal concentrations) will achieve more representative results. Another facet that illustrates the complexity of toxic interactions is that the pollutant toxicity can be modified by the addition of dissolved organic matter (DOM) (Höss et al. 2001; Bejanaro et al. 2005).

One specific advantage of using meiofauna in pollution studies is their short generation times, since multigeneration tests are often needed to obtain reliable results on long-term community effects, which are cryptic at first sight. Sometimes, shortly after a pollution event, the overall abundance of meiofauna may increase (depending on the species, the nature and concentration of the pollutant, etc.), superficially suggesting a negligible impact. This could easily lead to erroneous rash conclusions about a nondetrimental effect. Often it is long-term parameters, such as lowered reproductive rates, decreased taxonomic diversity and a reduced ecological diversity, that provide the most severe consequences for the community. It is generally more informative to concentrate on the highly sensitive reproductive output parameters (clutch size, larval stages) than to focus on adult abundance and biomass (Giere and Hauschildt 1979; Bejarano et al. 2006a,b, for oil pollution; Chandler 1990; Bejarano et al. 2004, for pesticide contamination).

Toxicity tests with developmental stages for pollution assessment require laboratory cultures, experiments and standardized bioassays with sensitive and preferably widespread and common “indicator species.” But are there any easy-to-recognize species? And can we perform life cycle bioassays with them? Experiments with
about 50 continuously lab-cultured meiobenthic species (among them about 15 harpacticoid copepods and some 30 nematodes) have been performed. The harpacticoids in particular combine sensitivity with frequency (mainly *Amphiascus tenuiremis, Microarthridion littorale, Nitokra* sp. and *Robertsonia* sp.). The culture of marine harpacticoid species as pollution indicators is most advanced in the USA (Chandler 1986; Chandler and Green 2001; Bejarano et al. 2006a,b). *Tisbe* sp. and *Tigriopus japonicus* are often used in Europe or in the Pacific area and new representatives are added regularly. Chandler’s working group succeeded in getting standardized bioassays officially licensed by the American Society for Testing and Materials (ASTM 2004), and (more recently) globally licensed by the OECD. Among the marine nematodes, *Chromadora* spp., *Chromadorita tenuis, Pellioditis marina* and *Diplolaimella* spp. are classical targets for culture (Tietjen and Lee 1984; Jensen 1983; see compilation by Moens and Vincx 1998); nematodes cultured for bioassays often belong to Monhysteridae. Meiobenthologists have also elaborated culture methods for freshwater nematode species (*Panagrellus redivivus, Caenorhabditis elegans*; see Traunspurger and Drews 1996; Heininger et al. 2006; Höss et al. 2006). Bioassays that permit the environmental impacts of noxious events on communities and the re-establishment of assemblages integrated into the natural multifactorial network to be monitored require standardized substrate conditions (e.g., bottle brushes, plastic sheets) (Mirto and Danovaro 2004).

With the progress in technology, modern analytical procedures do not require large amounts of biomass, which was an obstacle that often disadvantaged meiofauna with respect to macrofauna (see below). Bioaccumulation studies can be performed by analyzing tissue extracts in the microgram range (Wirth et al. 1994; Haitzer et al. 1998); changes in the genetic backgrounds of populations exposed to chemicals can be detected by “ecotoxicogenomic” screening (Watanabe and Iguchi 2006); the DNA barcoding of whole populations on a few slides (Bhadury et al. 2006a) offers the chance to exploit their biodiversity, which is often reduced as a response to pollution and environmental depletion (Warwick 1988b). Rapid in vivo effects of toxicants on meiofauna and their offspring can be documented and evaluated semiquantitatively under a confocal laser scanning microscope, thus linking the huge potential of fluorescence labeling to bioassay techniques (Chandler and Volz 2004). Ecophysiological parameters such as microrespiration measurements can be used to derive the status of physiological resistance (Moens et al. 1996).

Studies on meiofauna from many regions suggest that stress caused by disturbances, organic wastes or toxicant contamination causes a decrease in the various types of diversity (Warwick 1988b; see Sect. 9.1) and an increase in dissimilarity compared to reference communities. This deviation from “normal” is indicated by similarity indices that compare differences in the species compositions of two sites (Sørensen Index, Jaccard Index, Hill’s Index). Dominance indices (e.g., Simpson’s Index) relate the total abundance of species in samples (communities) to single species abundances. The Shannon diversity relates the observed species number to the (expected) species number, while the evenness considers aspects of how the individuals are apportioned among species (distribution/aggregation). Biodiversity (taxonomic diversity in its various forms, such as weighted diversity) measures the number of taxa (species) per habitat/sample. All of these “classical” indices have a
distinct information value and are used in pollution studies (see the good overview in Neher and Darby 2006). We do not detail how they are calculated here, since such explanations can be found in numerous ecology textbooks and software programs; for comments and restrictions see Heip et al. (1988). Recent enhancements of these indices also allow (using a probabilistic approach) those species present at the sites but unseen in samples to be considered (“expected number of species index” or “improved Shannon index”), and they reduce the considerable bias in many indices. Thus, they allow for more refined results than do the routine procedures (Chao and Shen 2003; Chao et al. 2006). Most meiofaunal studies have demonstrated that pollution results in marked changes in diversity (Fig. 8.18).

Lambshead et al. (1983) introduced into ecology a method of assessing stress through pollution, the “k-dominance method.” An updated method, the “ABC method” (Warwick, 1986; Warwick et al. 1990a) relates abundance to biomass in two comparative curves. Both calculations are based on the assumption that in undisturbed biotopes the more K-selected specialist species (persisters) account for high individual biomass, even though they have low population densities and thus only a low numerical rank. In contrast, communities of r-selected generalists (colonizers), which dominate in disturbed areas, are typically characterized by just a few species that exhibit low individual biomass but large population density, thus attaining a high numerical rank (Fig. 8.19). (The general meanings of the character complexes of r- and K-strategists are reviewed in Parry 1981.) Now, if the species are plotted on a log-scale on the abscissa according to their rank, and their corresponding cumulative percentage dominances are plotted on the ordinate, the result can be highly indicative when comparing the curves for abundance and biomass. A disturbance

![Graph showing decrease in harpacticoid copepod diversity related to distance from a polluted site.](image-url)
(e.g., due to pollution) can be postulated if the abundance curve is elevated above that the biomass curve. If the biomass curve exceeds that of the abundance, the site can be considered undisturbed (Fig. 8.19). Essentially, this method is a graphical comparison of the two components of diversity, species richness and evenness (Platt et al. 1984). Although this convenient graphical method only allows a rather coarse discrimination of a few levels of pollution, it does not require control samples: the two curves represent an “internal control.” Warwick et al. (1990b) demonstrated that the k-dominance method can also be applied to meiofauna as a valuable indicator of disturbances despite the minute divergences in biomass between meiobenthic r- and K-strategists. On the other hand, this study also revealed the inherent problem of interpretation: depending on the taxon, each kind of disturbance has a different impact and causes a curve shape; e.g., nematodes are clearly affected by sediment disturbance (bioturbation), harpacticoids less so.

Many of the characters listed above should make meiofauna an ideal tool for studying changes in benthic ecosystems. However, there is one major impediment: for optimal information value, many of the above indices require identification to a low and uniform taxonomic rank (species, genus). Even with the necessary instrumentation and literature, this thorough identification requires manpower, time and experience. To circumvent this problem, approaches based on “taxonomic minimalism” have been developed, which require bulk recognition to higher taxa only, and can be performed (with some guidance) by untrained personnel too. However, is too much informational value lost if we simply compare characteristic groups? Does the high ecological differentiation in meiofauna allow for a summative identification of higher meiobenthic taxa? Large-scale and comparative meiofaunal studies have shown that data based on taxonomic ranks as high as families still allow a

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Fig. 8.19 Hypothetical k-dominance curves for areas polluted to varying degrees. (Warwick 1993)
fairly clear separation of stations according to their degree of disturbance/pollution (Heip et al. 1988; Herman and Heip 1988; Warwick 1988a; Heininger et al. 2007). Especially in nematodes, data aggregated to higher taxonomic ranks yielded a fairly consistent discrimination between sites.

The frequently used “maturity indices” (Bongers 1990; Bongers et al. 1991) characterize the relation between the “quality” and the stress situation of an environment. Based on species, genera or even families, they rank the taxa according to their life history characteristics into various degrees of “persisters” or “colonizers.” These are known to be differently sensitive to stress or pollution. In disturbed sites the index is low; in areas with little or no disturbance the values are high. Upon applying this maturity index to various areas stressed by an oil spill, an overload of organic matter, heavy metal contamination, etc., it was shown that the index is widely applicable for the discrimination of stressed from unstressed biotopes in terrestrial, freshwater, marine, deep sea and tidal flat habitats (see Essink and Romeyn 1994). With the increasing reliability of the allocation of taxa to stress classes, this method could provide a relatively simple means of assessing biotope disturbance. However, it can currently give results that conflict with the chemical assessment (see Heininger et al. 2007). Modifications of the classical maturity index incorporate feeding groups, which, again, reflect environmental variables (see Neher and Darby 2006).

Another approach that attempts to simplify working with meiofauna when investigating the effects of pollution is to focus on characteristics of the two most abundant taxa, nematodes and harpacticoids. In cases of organic enrichment, and often also chemical pollution, nematodes are on average more tolerant of the effects than harpacticoid copepods. This often observed ecological discrepancy is the basis for the “nematode/copepod ratio” (N/C index; Raffaeli and Mason 1981), proposed as easily applicable means of measuring the impact of pollution. The authors contended that this trend would be generally valid for sandy eulittoral coasts. However, the N/C ratio also turned out to be sensitive to environmental variables (grain size, water content), which brought its general reliability into question (Coull et al. 1981; Lee et al. 2001). Nevertheless, the ease of calculation made this ratio one of the most applied but also debated pollution indices in the field of marine meiofaunology. Raffaeli (1987) partly corrected his earlier oversimplified contention.

What is the basis for the different ecological reactions of the two dominant meiofaunal taxa, and in which cases did the N/C ratio yield questionable results and thus require refinement? Harpacticoids comprise two major groups with different substrate-related life histories. The mesobenthic (interstitial) species live in sand, while their epibenthic or endobenthic counterparts instead prefer water-saturated fine sand and mud. Nematodes seem less dependent on sediment structure. This substrate difference is enhanced by the differences in the trophic niches of the two groups. Most nematodes are linked to a short, detritus/bacteria-based food chain. Hence, with organic enrichment of the site (generally typical of finer sediments), their abundance will usually increase even if the oxygen levels sometimes decrease (Fig. 8.20, compare Essink and Romeyn 1994). In contrast, harpacticoids are mainly microalgae-based and oxygen-sensitive members of the food web. The
interstitial subgroup of copepods will react negatively to an increase in the organic load (compare Rudnick 1989; Vincx et al. 1990) with concomitant depletion in oxygen and clogging of the void system by debris. This scenario would explain the divergent N/C reactions of the taxa in many cases of organic pollution. Various studies (e.g., Sandulli and De Nicola 1991) that performed experimental work alluded to the different reactions of the two meiofaunal groups.

However, there are still interpretations that are not easily explained and that reduce the general applicability of the N/C ratio: the endo/epibenthic subgroup of harpacticoids is not greatly impaired by enrichment of organic matter. It may even initially increase in abundance with the increased food supply. This questions the indicative value of a generalized N/C index. Therefore, Shiells and Anderson (1985) suggested restricting the calculation of a refined N/C ratio to just the interstitial (mesobenthic) harpacticoids. Moreover, in cases of chemical pollution, the

Fig. 8.20 The divergent response of nematodes and copepods (harpacticoids) to a pollution gradient. For further explanation see text. (After Raffaeli 1987)
nematode populations can also decrease, so that the curves for both groups are similar and are not indicative. It appears that a refined version of N/C ratio is useful in cases where the effects of a pollution incident in a restricted area and the recovery phase are monitored over time without detailed identification (Raffaeli 1987).

When not over-interpreted and not universally applied, the community indices outlined above, regardless of some criticism related to their insufficient consideration of ecosystem interactions, still appear to be useful and indicative tools for investigating many manmade changes in (meiofauna) community structure.

The taxonomic distinctness of a community—the degree of relatedness of the taxa sampled—has been transformed into an index, the TDI index (Warwick and Clarke 1995, 2001; Clarke and Warwick 1998). This index incorporates biological and ecological aspects as well as the distribution pattern. With increasing stress and decreasing habitat heterogeneity, the community will become more monotonous and the taxonomic distinctness will tend to decrease (Barbuto and Zullini 2005). For practical work it is important that the TDI is independent of the sampling success during data collection, while the other indices are strongly influenced by the number of sampled taxa.

While many of the procedures outlined above also are applicable to freshwater field studies that are performed to assess anthropogenic impacts, some specific and simple indices may help to avoid the need to evaluate all fauna. For northern lakes, Särkkä (1996a) contends that characteristics of the meiofauna such as easy access, large diversity and abundance, as well as its reduced seasonality, would support the use of meiofauna compared to macrofauna in assessing pollution. As easily recognizable indices, he proposed the numerical relation of permanent to total meiofauna, the ratio of aeolosomatid annelids to oligochaetes, and the percentage of oligochaetes that were naidid oligochaetes. For riverbeds, Zullini (1976) focused on nematodes and showed that the relation of the more tolerant Secernentea to Adenophorea might be a good pollution indicator. A valuable overview of the methods used in freshwater environmental science is given by Höss et al. (2006).

Perhaps the most biologically meaningful methods of linking community data to an environmental impact such as pollution are multivariate statistics. In many independent papers on meiofauna it has been shown that multivariate analyses (e.g., classification using the Bray–Curtis dissimilarity and multidimensional scaling ordination) are more sensitive and superior to disturbances and impact events than univariate indices (Gray et al. 1990; Austen and Somerfield 1997; Schratzberger and Warwick 1999b; Wetzel et al. 2002; Saunders and Moore 2004; Heiniger et al. 2007 for freshwater). Although the computational basis of multivariate statistics is fairly complex, especially in the case of the multidimensional scaling method (MDS) (Field et al. 1982), the yields are an easy-to-understand graphical document: a “map” of sample similarities influenced by environmental variables, e.g., pollution (Fig. 8.21).

The superior sensitivity and the general applicability of MDS methods have proven valuable in numerous examples related to the macro- and meio-benthos, and for both abundance and biomass values (Warwick et al. 1993a; Somerfield et al. 1994). Moreover, MDS ordinations allow for a “taxonomic minimalism.”
Calculations based on ranks above the species level (genera: Somerfield and Clarke 1995; families: Herman and Heip 1988; Warwick 1988a; Christie and Berge 1995) result in essentially similar patterns (Fig. 8.22), although a loss of discrimination/information with coarser resolution is evident (Quijon and Snelgrove 2006; but see Carman and Todaro 1996). Nematodes seem especially robust to the grouping in higher taxa. Hence the MDS method, often combined with additional analyses, represents a valuable tool for revealing the impact of an environmental variable (e.g., pollution), even in cases where mere diversity assessment could not give a significant answer (Warwick 1988a).

Today the statistics in meiofaunal studies on disturbance and pollution are usually analyzed using convenient software programs (e.g., PRIMER in its various versions; Plymouth Marine Laboratory; http://www.pml.ac.uk/primer/index.htm). This classic in the field of ecological impact studies is available as a comprehensive package containing, among other methods similarity profiles, Bray–Curtis dissimilarity calculations, cluster analyses in illustrative graphics, and various univariate indices. Training courses for the application of PRIMER are being offered.

By using factorial correspondence analyses, interconnections between environmental parameters and meiofaunal community structure can be revealed (e.g., Villiers and Bodiou 1966). Their interpretation, though, requires a good biological understanding and is not as easy as deriving them using a computer. An easier
graphical interpretation is offered by the principal response calculation (PRC), a multivariate method that illustrates the relation between the sampling period and the first principal component responsible for the variance. In canonical correspondence analyses (CCA), the taxon data are compared with various environmental variables depicted as vectors on a biplot. The relative importance of the vector (variable) is then indicated by its length, and its correlation to other, neighboring variables by its angle. Canonical correspondence methods are embodied in the PRIMER package mentioned above, which facilitates their use considerably.

Recent methods emphasizing the functional diversity and complexity of communities sometimes offer a useful option for indicating disturbance/pollution-induced changes in ecosystem structure. In nematode studies especially, alterations of feeding group abundances are examples of such changes. However, the interdependence of trophic structure and substrate granulometry, which is especially well known for nematodes (see Figs. 5.21, 5.22; Kennedy et al. 1994; Schratzberger et al. 2007b), may confuse a simple interpretation (Höss et al. 2004).

Regarding the rapid advance of simple-to-use and graphically attractive mathematical/statistical software, one caveat is appropriate: as easy as it may become to apply statistical programs, the user’s understanding of the underlying principles is also required. The use of sophisticated statistics/factor analyses/correlations often
gives the impression of an erratic trial and error procedure without too much comprehension of the underlying biological processes. Easy application of statistical tests cannot substitute for a lack of understanding, an unclear conception, insufficient background knowledge and a thorough literature inquiry.

The various methods used to assess changes in community structure (and community stress), as summarized by Warwick and Clarke (1991), Clarke (1993) and Warwick (1993), are:

1. **Univariate methods**, where the relative abundances of the various species are reduced to a single index. The appropriate statistical test is the classical ANOVA; the most frequently used univariate method is the Shannon Wiener diversity index \( H' \) (Shannon and Weaver 1949), usually combined with calculations of evenness (equality of distribution).

2. **Graphical/distributional methods**, where the relative abundance (or biomass) of a species is plotted as a curve. The typical example is the k-dominance curve. This group of methods provides more information about the distribution of the fauna than a diversity index.

3. **Multivariate methods** of classification and ordination, where faunal communities are compared in terms of their specific identities and (relative) quantitative importance. These methods are exemplified by techniques such as multidimensional scaling ordination (MDS).

The two first types of methods have a disadvantage: they can yield identical results from communities with completely different taxonomic compositions. They are also less sensitive to detecting community changes than the multivariate methods. However, they can give a fairly clear assessment of the presence of detrimental (e.g., pollution) effects. On the other hand, the third group of analyses, multivariate statistics, document faunal changes with precision and are widely applicable, but they give few indications of the possible reasons. One option that can be applied to compensate for the shortcomings of the different types of methods and to optimize their specific advantages is the combined use of several methods (Clarke 1993; Dauer et al. 1993).

### 8.8.1.1 Selected Cases of Pollution and Meiofauna

#### Oil Pollution

Oil spills frequently devastate the environment, especially in coastal regions. Since environmental oil spills are dreadfully spectacular, the effects of petroleum hydrocarbons on marine sites are frequently studied. Surprisingly, benthic fauna, including meiofauna, often appear only mildly affected. A long-lasting depletion of the fauna is only rarely reported, even after a major oil spill. But has the fauna really recovered? After a dramatic decline in abundance and diversity immediately after the impact, the return of the fauna is quite rapid (weeks, some months). Pioneered by some of the more robust species, this return may misleadingly indicate an environmental
recovery. The complex and sometimes controversial impact of hydrocarbon compounds on the environment can only be comprehended by detailed investigations involving field and experimental work, long-term monitoring and acute toxicity tests. Below I attempt to provide a clear picture of the multifactorial effects of oil pollution in the environment.

Crude oil, consisting of thousands of chemical compounds with various toxicities, reactivities and behaviors, is a natural product to which many meiofaunal species can partially adapt. During the “aging of oil,” the most toxic substances—the short-chained aromatics—evaporate and dissolve very quickly, so the oil remaining in the sediment is more persistent. Natural oil seeps in the sea are equivalent to organic enrichment (Montagna et al. 1989, 1995; Lee and Page 1997), and the stocks of nematodes are particularly rich here. Even negative impacts of oil platforms appear to be restricted to the direct vicinity of the outlet (Carr et al. 1996). Some of the negative results recorded from areas contaminated with oil were probably caused by the oxygen depletion induced by the degradation of excess organic matter rather than the toxicity of the oil itself (Bodin 1988).

For the benthos in subtidal sediments, dissolution of many toxic substances in the water column further reduces the toxicity of natural crude oil; only a small part of spilled oil reaches the bottom (1–13% according to Lee and Page 1997). Boucher (1980) could not find a significant reduction in subtidal meiofauna, even after the huge Amoco Cadiz oil spill (see below). For shallow subtidal diatoms, Suderman and Thistle (2004) confirmed a lack of significantly noxious effects of fuel oil. In subtidal samples from the Ligurian Sea (Mediterranean), meiofaunal populations after oil contamination returned to normal after only one month (Danovaro et al. 1995).

The effects of oil spill accidents on shore life, specifically on meiobenthic communities, are divergent and difficult to summarize because of the nature of the oil and the local physiographic and climatic conditions, e.g., wave exposure, sediment structure, season and temperature. This complexity makes reliable general predictions about the impact of oil spills almost impossible. In the large oil spill off La Coruña (Northern Spain) in 1976, all of the eulittoral meiofauna on beaches adjacent to the oil outflow were exterminated, and only a few opportunistic species were recorded one year after the spill (Fig. 8.23). A similar massive destruction of meiofauna was reported from oil spills off Hong Kong and in brackish water of the Baltic Sea (Wormald 1976; Elmgren et al. 1983). Since spilled fuel oil can drastically destroy the meiofauna (Ansari and Ingle 2002), the risk of massive destruction does not apply solely to oil tanker wreckages.

In less destructive cases, the immediate meiofaunal response to oil spills is usually a strong reduction in harpacticoids, ostracods and turbellarians, and a less severe impact on annelids. The decrease in nematode populations is often only subordinate and difficult to separate from natural fluctuations. Correspondingly, nematodes are usually first to begin to recover. Experiments have also demonstrated that nematodes have a greater ability to survive oil compared to copepods (Christie and Berge 1995). Subtle sublethal effects resulting from oil contamination and bioremediation are often characterized by shifts in the dominance pattern and altered diversity and evenness (Warwick et al. 1988; Schratzberger et al. 2003). In
microcosm experiments with differentially oiled salt marsh sediments and impact periods, Carman et al. (1997) found changes in trophic patterns. Here, grazing rates of most copepod species were reduced with increased exposure to and concentration of oil (see also Christie and Berge 1995).

The Amoco Cadiz spill in 1978 represented a rare case in which the meiofauna (nematodes) had been monitored for years prior to the oil spill. However, at least for nematodes, univariate statistics did not reveal a significant negative impact that was discernible from the disequilibria caused by natural environmental variables. The complexity of the field conditions did not allow for a straightforward interpretation (Bodin and Boucher, 1983; Bodin 1988). Only the sensitive harpacticoids reacted with a decline in abundance and diversity right after the spill. Specifically, the more susceptible juvenile stages of harpacticoids were severely reduced and reproduction was delayed, which caused changes in the population dynamics due to depleted copepodite stages. Only MDS and ABC methods were sensitive enough to demonstrate the impact of the oil spill (Warwick and Clarke 1993). After two or three years, the “degradation phase” ended, but according to long-term studies it took almost six years for the meiofauna to recover and re-establish their status prior to the spill (Boucher 1985; Bodin 1988, 1991).

Recovery after a spillage starts often with an unbalanced blooming of microalgae within a few months. This first sign is followed by rapid population outbursts of some robust nematodes (e.g., *Sabatieria pulchra*) and harpacticoids (e.g., *Cletocamptus deitersi*) accompanied by erratic fluctuations in the dominance pattern. Strong population growth in some species/groups is accompanied by the destruction of more sensitive competitors and predators and supported by a rich supply of microalgae (Fleeger and Chandler 1983; Montagna et al. 1995). These outbursts are
often followed by sudden population breakdowns. Especially in exposed, sandy shores, complete recovery of meiofaunal assemblages (measured in terms of diversity and evenness) may be achieved relatively rapidly, sometimes in less than one or two years (Rodríguez et al. 2007). The speed of recolonization depends much on the presence of neighboring donor assemblages (Gourbault 1987). However, in sheltered muddy bights and estuaries, depletion will last much longer due to the long persistence of toxic substances in the absence of oxygen in deeper layers. In the Amoco Cadiz spill, the depression of the meiofauna in the ecologically delicate muddy Bay de Morlaix was so pronounced that (based on abundance-related species-rank calculations) it took six years before the meiofauna recovered from the spill (Gourbault 1987). After a smaller oil spill in the Ligurian Sea, Danovaro et al. (1995) could not determine any impact on the nematode populations using the N/C ratio (see also Carman and Todaro 1996; Ansari and Ingole 2002). However, a decreasing diversity is apparently a better indicator: as shown after the oil spill at the Hebridean shores (Moore and Stephenson 1997). Refined multivariate statistics may reveal that these seemingly mild cases of oil pollution might also have a clearly negative effect on meiofaunal communities (Warwick and Clarke 1993).

What about cleaning up oil-polluted sites with dispersants? Does bioremediation with fertilizers help? While earlier oil dispersants often acted as additional stressors that enhanced the toxicity of the oil/dispersant mixture (Giere and Hauschildt 1979), modern products are fairly neutral if appropriately applied. Bioremediative additives might stimulate the growth of oil-degrading bacteria but they do not seem to enhance recolonization rates of meiofauna (Schratzberger et al. 2003).

Experimental work on the impact of oil on meiofauna can be problematic considering the labile chemical processes and the multifactorial situation in the field. Small-scale laboratory experiments often result in extremely rapid recoveries, in the range of weeks or a month (Alongi et al. 1983; Fleeger et al. 1996). On the other hand, larger mesocosm experiments have produced drastic declines in meiofaunal populations, especially of harpacticoids, and recovery times of about two months (Grassle et al. 1980–81). In field experiments three months were needed until the depressed diversity and increased evenness of meiofauna in artificially oiled sediments returned to the values of the corresponding reference samples (Schratzberger et al. 2003). Also, from a beach site treated with different dosages of crude oil, McLachlan and Harty (1982) recorded a recovery period (especially of the more robust nematodes) of a few months after an initial general decline.

In order to discover sensitive reactions that are not concealed by the survival of robust species, laboratory work often focuses on life cycle-based assessments of oil toxicity. Standardized and normative experiments on the impact of oil bioassays have been developed by Chandler and his team (see Bejarano et al. 2006 a,b), with the harpacticoid Amphiascus tenuiremis used as test species. As already shown with oligochaete offspring (Giere and Hauschildt 1979), reproduction and development of these copepods is a sensitive indicator of pollution damages at concentrations that are harmless to adults: for example, maturation time gets delayed, fertility is reduced, and larval stages (especially nauplii) become impaired or halted in their development.
Palmer et al. (1988) summarized three main reactions of meiofauna after oil spills. (1) A “dramatic decline” in the abundance and diversity of the meiobenthos occurring in direct contact with the oil. (2) “No change,” probably only found in subtidal sites not immediately exposed to the most toxic, highly volatile/soluble oil compounds. (3) “Enhanced abundances” after contamination represent momentary phases of the unbalanced, erratic fluctuations of some robust species. Typical of stressed communities (Warwick and Clarke 1993b), they indicate a severe disturbance in the early contamination phase.

Twenty years after the summary by Palmer et al. (1988), additional compiled experiences on the reaction of meiofauna to oil impact allow a differentiation of the variable and partly controversial meiofauna reactions:

(a) Depending on the extension of the spill and the nature of the oil, the initial losses in meiofaunal abundance and diversity will (at least in “high energy” sites) only persist for a relatively short time (months to a year) compared to more sheltered areas. Here the recovery will be retarded and take much longer (on the order of several years). Since the statuses of the neighboring sites are crucial to recolonization, small-scale contaminations, especially in exposed areas, will return to normal in the range of several weeks.

(b) Juveniles are more sensitive to oil pollution than eggs or adults. Hence, bio-assays analyzing reproductive success (fertility rates) and survival of first larval instars will reveal sublethal damage even after light contamination (Bejarano et al. 2006a,b).

(c) Only the most recent formulations of oil dispersants or bacterial fertilizers do not enhance the toxicity of the oil. In most cases, natural chemical and biological degradation processes and the natural supply of oil-degrading bacteria, with their high multiplication rates, will be appropriate for effective oil-cleanup.

Of course, these natural but “invisible” clean-up activities are often not exciting enough for the media. Rash conclusions based on the behavior of some robust species only embody a potentially high political and societal risk that there are few effects of oil spills and recoveries from them occur quickly.

8.8.1.2 Effects of Pollution by Metal Compounds

Invisible, highly persistent and ubiquitous, metal compounds are probably a greater threat to the environment than the spectacular but transient and local oil spills. Reflecting this notion is the increasing number of meiofaunal studies on the impact of (heavy) metals and their derived compounds, such as antifouling agents. However, the majority of these studies are laboratory in vitro tests (Coull and Chandler 1992). In situ, metal compounds, like other pollutants, are less toxic when sediment-bound rather than in the aqueous phase. This is especially true in organic-rich muds (Austen and McEvoy 1997b; Austen et al. 1994). Modifying processes include chemical, physical and biological processes: chelation, binding preferences depending on the redox situation and pH, bioturbation, adhesion to biofilms and
mucous secretions, metabolic uptake or selective storage. The synergism or even antagonism of several metals acting simultaneously in polluted areas confounds dosage effects of single metals (Mahmoudi et al. 2007). Hence, the toxicities of metals depend greatly on their bioavailability and barely relate to “total concentrations.” Therefore, the specification of actual threshold concentrations is probably not helpful, since interactions with ecological factors and different community patterns render them of local significance only.

Metals vary in toxicity; according to the impact scale, mercury and copper seem to be particularly toxic, more so than zinc, cadmium or tin (see Van Damme et al. 1984; Austen et al. 1994, Austen and McEvoy 1997a,b; Austen and Somerfield 1997). This explains why many meiofaunal studies have been performed with this metal. Moreover, copper compounds are particularly relevant since they are present in numerous antifouling paints and are thus widespread in the aquatic world. Experiments by Alsterberg et al. (2007) found that total meiofauna biomass decreased significantly with exposure to copper pyrithione. Freshwater harpacticoids with a high content of the food-derived carotinoid astaxanthin were better protected against toxic oxidants such as copper (Caramujo et al. 2008).

Mixtures of several metals can act differently to the individual metals (Fig. 8.24). In solutions containing copper with mercury or with zinc, paired (synergistic) exposure was less toxic to the common marine nematode Monhystera disjuncta than exposure to each metal individually (Vranken et al. 1988a). However, in corre-

![Fig. 8.24](image_url)  
**Fig. 8.24** Impact of heavy metals on the nematode Monhystera disjuncta. Higher mortality results from exposure to single metal compounds than from paired exposure to two metals. (After Vranken et al. 1988a)
sponding experiments with the harpacticoid *Nitokra spinipes* the combined effect of mercury and copper increased the mortality (antagonistic effect) (Barnes and Stanbury 1948). Newly developed organometal compounds such as copper pyrithione are effective antifouling biocides that are added to paints. They seem to have little negative impact on meiofauna (nematodes) and tend to affect prokaryotes and fungi more (Larson et al. 2007). On the other hand, exposure to metals in combination with the organic pesticide phenanthrene (see below) proved more toxic to meiofauna than any of the pollutants alone (Fleeger et al. 2007). The physiological mechanisms behind these different combined or singular effects on the different meiofaunal groups are unclear. Toxicity even differs with the chemical form of the metal administered to the meiofauna; for example, methylmercury is more toxic than other mercury compounds.

In contrast to the contention of Somerfield et al. (1994), the overall data suggest that harpacticoids are on average more sensitive than nematodes, just as they are to other pollutants. Females seem more severely affected than males, a conclusion derived from several studies and related to the better solubility of metal compounds in the richer lipid deposits of the (mature) female body. The overall flux of metals through the food web from meiofauna to macrofauna varies depending on the transfer rate, which is, apparently, greater in nematodes than in harpacticoids (Fichet et al. 1999).

Ecological group parameters might suggest changes in community structure where single-species analyses fail. Parallel to increased levels of metal concentrations, the diversity, dominance pattern and evenness of meiofaunal nematodes decreased in the heavily polluted New York Bight (Tietjen 1980b). Conversely, an increasing species richness and abundance paralleled decreasing contamination in a North Sea estuary (Somerfield et al. 1994). In this study, the superiority of multivariate statistics again demonstrated concealed changes and suggested “that nematode community structure changes in a smooth and ordered fashion with increasing sediment metal concentration.”

Among both harpacticoid copepods and nematodes, there are even adapted species (or local intraspecific strains?) with a high tolerance to heavy metal compounds (e.g., *Tachidius discipes*, *Microarthridion fallax*, *Pseudobradya* sp., *Tisbe* sp. among harpacticoids and *Molgolaimus demani*, *Sabatieria pulchra*, *Axonolaimus paraspinosus* among nematodes, see Warwick et al. 1988; Somerfield et al. 1994). Species of the harpacticoid genera *Cletodes*, *Laophonte* and *Stenhelia* are also considered robust (Saunders and Moore 2004). Additionally, adaptive effects may expand the tolerance range within the same species: *Enoplus brevis* (Nematoda) from a polluted site was more tolerant than specimens from unpolluted sites (Somerfield et al. 1994).

A certain selection for communities with tolerant species only seems to influence the composition after longer periods of exposure: along a copper-enriched estuary the number of Cu-tolerant nematode species increased when compared to uncontaminated reference sites (Millward and Grant 1995). The drastically depressed abundance of harpacticoids in the Westerschelde estuary (North Sea) was considered by Van Damme et al. (1984) to be due to the increased levels of heavy
metals, especially of copper. In Chilean beaches exposed for years to copper mine tailings, meiofauna was restricted to certain tolerant nematode species, while the number of harpacticoids, correlating with the copper concentration in the pore water, was negligible at many stations (Lee et al. 2001b). These results suggest that harpacticoids, especially their larval stages, are sensitive indicator organisms for ecosystem deterioration due to exposure to metal pollution.

A bizarre and hopefully unique experience regarding meiofauna and metal contamination is the report by Pogrebov et al. (1997) on the severe plutonium pollution in the bottom sediments of an Arctic inlet after several nuclear test explosions. While changes in the macro- and meiobenthic communities were not reported to be severe, in some areas the ciliate fauna was found to be massively impoverished or “eliminated,” while flagellates seemed unaffected. Moreover, the genus *Euplotes* showed clear morphological, anatomical and behavioral aberrances.

There are a few publications on freshwater meiobenthos exposed to metal pollution. Most results correspond to those outlined for the marine realm (Burton et al. 2001), with copper being most directly correlated to reductions in the species richness of meiofauna. Again harpacticoid copepods seemed notably sensitive (exception: *Bryocamptus* spp.). Cyclopoid copepods (especially *Diacyclops* spp.) and semibenthic cladocerans (*Chydorus* sp.) as well as water mites (especially the halacarid *Porohalacarus*) were more tolerant. The authors ascribe the small changes in species richness between contaminated and uncontaminated sites not to a mild impact of heavy metals, but to a replacement of susceptible species by robust ones. Hence, metal contamination in freshwater (streams) also seems to massively alter the community composition of meiofauna. In sediments from various polluted and unpolluted German rivers, nematode community structure was related to metal pollution, but also to the hydromorphology of the sites (Heininger et al. 2007). Interestingly, predatory and omnivorous genera, such as *Mononchus* and *Tobrilus*, appeared more abundantly at sites with high rather than low metal pollution, perhaps a result of reduced competition.

Insect larvae, which in streams are a dominant taxon at the boundary of meiofauna and macrofauna, display a graded and fairly predictable response to metal pollution. Since chironomids appear to be rather resistant to heavy metal pollution, they dominated (80% of all insects) at the most grossly polluted stations (Winner et al. 1980). Hence, the authors suggest that the percentage of midge larvae in samples is a useful index for assessing this type of pollution.

Studies on physiological processes in meiobenthic organisms impaired by toxic metal compounds are, thus far, rare. Binding of metals in mucus might be interpreted as a defence mechanism and could play a major role, but detailed studies are lacking. In the *Enoplus* spp. (Nematoda) the metabolically active cuticle and hypodermis are the main organs that uptake and sequester metals (Howell 1983). Considering the significant physiological and ecological impacts of metals on the macrobenthos (e.g., tributyltin = TBT), detailed research on their impacts on suitable meiofauna indicator species and their physiological reactions (see Schratzberger et al. 2002b) are urgently required in order to better understand the patterns and pathways of metal pollution in meiofauna. In streams and rivers, lead, a ubiquitously present metal of environmental relevance, should also be included in meiofaunal impact studies.
8.8.1.3. Toxicity of Pesticides

Similar to heavy metals, pesticides (herbicides, fungicides and insecticides) are ubiquitous in the environment, since they are often slow to degrade and are thus long-lived. Due to their intensive use, not only in agriculture, they tend to accumulate in freshwater runoffs and coastal marine sediments. Their adsorption into the biofilms of sediment surfaces means that meiofauna provide relevant test organisms not only for acute toxicity tests but also for life-cycle toxicity, including several-generation bioassays. The continuous development of function-designed pesticides contrasts sharply with the few studies that have investigated on their effects on marine meiofauna, as noted by Coull and Chandler (1992, see their Table IV). Many of these few studies were performed in the aqueous phase, which usually results in a lower endpoint. As with heavy metals, the tests organisms appear less sensitive in the presence of sediment, so that threshold concentrations become rather problematic. Some general features from selected marine studies will be presented here without claiming any completeness. For details of the situation in freshwater meiobenthos, the reader should consult the review by Höss et al. (2006) and references therein.

Pesticide toxicity is rarely expressed as a direct indicator of survival. In tests with modern pesticides it is the exception rather than the rule that exposure to environmentally relevant or recommended concentrations induces direct mortality. Atrazine, a common herbicide, has been introduced into mesocosms with estuarine sediments at concentrations near the threshold proposed by environmental authorities. Rather exceptionally, this caused a 70% population decrease in several harpacticoid species, while nematodes were on average barely affected (Bejarano et al. 2005). Usually, the damage symptoms are more concealed, as shown in the lifecycle bioassay with *Amphiascus tenuiremis* (Harpacticoida) using Fipronil (Cary et al. 2004). A deceptive indication of this rather obscure pollution impact is that egg-producing females often seem less sensitive to the short-term impact of PCBs and other lipophilic toxicants than males (Carman and Todaro 1996; Bejarano et al. 2005). This is probably because the noxious substances are sequestered and deposited into the lipid-rich yolk of the eggs. Under realistic concentrations these widely used insecticides caused no significant lethality, but did cause sex-specific reproductive dysfunctions. In certain mating combinations there was an 80% decrease in successful reproduction, while in other combinations the reproductive success was not impaired, but the developmental time of the eggs was delayed. When these subtle, adverse effects act over several generations the ecological consequences become disastrous and massively change the population structure. Similarly adverse effects, be it a reduction in survival or in reproductive success, have also been recorded in other studies for Fipronil (Chandler et al. 2004a), and for Chlorpyrifos (Green and Chandler 1996; Green et al. 1996). Only a few experiments with licensed pesticides lacked direct toxic effects, at least through one generation: the sediment-associated insecticide Fenvalerate seems to bind so tightly to sediment surfaces that its impact on *A. tenuiremis* was negligible, at least under the conditions applied (Strawbridge et al. 1992).
Species react differently to the same pollutant, an obvious fact evidenced by experiments of Bejarano and Chandler (2003), and one that should caution us about making any rash generalizations. For example, *Amphiascus tenuiremis*, the model harpacticoid for many bioassays, was exposed to similar concentrations of Atrazine to the mesocosm harpacticoids tested by Bejarano et al. (2005, see above). Through two generations neither survival nor developmental time of *Amphiascus* were massively affected. However, reproductive failures by the decreasing number of hatching nauplii were recorded. These life history effects, which often increase from one generation to the next, will, under natural conditions, obliterate the population as certainly as direct mortality.

The incorporation of molecular genetics into pollution studies has revealed details of intrapopulation variability that might explain different adaptive capacities along pollution gradients. Toxicants have been shown to alter regular gene expression (Schizas et al. 2001; Staton et al. 2001). Genetically (mitochondrially) different lineages within an estuarine population of *Microarthridion littorale* (Harpacticoida) showed different survival in toxic concentrations of the organophosphate Chlorpyrifos (see above) in the laboratory (Schizas et al. 2001). This corresponded to their prevailing field occurrence in a pollution gradient in the field (Schizas et al. 2002). These interrelations between population genetics, distribution and ecotoxicology might be a field of extreme importance in the future.

Since copepods are an important food source for juvenile fish (see Sect. 9.4.2), and many pesticides are not biodegradable, the problem of pesticide bioaccumulation through the food chain is of high relevance in polluted environments. Transfer of the insecticide Guthion, an organophosphate, to copepod-feeding juvenile spot (*Leiostomus xanthurus*) resulted in a twofold concentration in the fish over the amount in the sediments (DiPinto 1996). When feeding on contaminated sediment particles, bioenrichment in the fish was clearly higher. Also, from other studies it emerges that sediment-associated particulate organic carbon is a main transfer route of lipophilic pollutants to both sediment-screening meiofauna (e.g., the copepod *A. tenuiremis*) or sediment-ingesting macrobenthos and fish (Wirth et al. 1994). The question of whether the fish can modify the pesticide accumulation by their metabolism or excretion remains unanswered. Considering the metabolically highly active cuticles of nematodes, their notably sediment-associated biology, and their ubiquity and abundance, more representatives of this dominant taxon need to be included in future studies on pesticide toxicity.

*More detailed reading:* Zullini (1976); Platt et al. (1984); Heip (1980b); Heip et al. (1988); Bouquegneau and Joiris (1988); Warwick et al. (1990a); Coull and Chandler (1992) Warwick (1993); Kennedy and Jacoby (1999); Chandler (2004); Austen and Widdicombe (2006); Neher and Darby (2006); for freshwater: Burton et al 2001; Höss et al. (2006); Heininger et al (2007)
Box 8.9  Tiny, But Powerful: Meiofauna as Pollution Indicators

What are the main characteristics that make meiofauna superior to most macrofauna when assessing ecosystem health?

- Ubiquitous occurrence
- Rich populations and numerous species—even in small samples—allowing for reliable statistics
- High turnover of generations permits control over several generations in a short time period
- Saves handling time, space and money

These inherent advantages of meiofauna can provide rapid and reproducible answers about the effects of pollution. Studies with meiofauna cover all typical procedures. (1) Field studies of the polluted sites, supported by computer-based multivariate analyses. Identification at a higher taxon level does not cause much information loss and can enable convincing and quick assessments of community changes after pollution incidents. (2) Toxicity bioassays with significant test organisms can explore and quantify uptake rates within short time periods, and determine sublethal reactions to deterioration or recovery over generations. (3) New analytical, histological and genetic methods can show pollution damage in single animals. (4) Mesocosm experiments combine the advantages of sediment-based field studies with those of laboratory assays. They include “realistic” changes in toxicant concentrations due to bacterial uptake and metabolism, accumulation by biofilm adsorption, and incorporate various chemical reactions into the test system.

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