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MEIOBENTHOS

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Introduction

Meiobenthos live in all aquatic environments. They are important for the remineralization of organic matter, and they are crucial members of marine food chains. These small (less than 1 mm) invertebrates have representatives from 20 metazoan (multicellular) phyla and three protistan (unicellular) phyla. With their ubiquitous distribution in nature, high abundances (millions per square meter), intimate association with sediments, rapid reproduction and rapid life histories, the meiobenthos have also emerged as valuable sentinels of pollution.

Definitions and Included Taxa

Meio (Greek, pronounced 'myo') means smaller, thus meiobenthos are the smaller benthos. They are smaller than the more visually obvious macrobenthos (e.g., segmented worms, echinoderms, clams, snails, etc.). Conversely, they are larger than the microbenthos – a term restricted primarily to Protista, unicellular algae, and bacteria. Meiofauna are small invertebrate animals that live in or on sediments, or on structures attached to substrates in aquatic environments. Meiobenthos (*benthos* = bottom living) refers specifically to those meiofauna that live on or in sediments. Meiofauna is the more encompassing word. By size, meiofauna are traditionally defined as invertebrates less than 1 mm in size and able to be retained on sieve meshes of 31–64 μm.

Nineteen of the 34 multicellular animal phyla (**Table 1**) and three protistan (unicellular) phyla, i.e., Foraminifera, Rhizopoda, and Ciliophora, have meiofaunal representatives. Of these multicellular (metazoan) phyla, some are always meiofaunal in size (permanent meiofauna), whereas others are meiofaunal in size only during the early part of their life (temporary meiofauna) (**Table 2**). These are the larvae and/or juveniles of macrobenthic species (e.g., Annelida, Mollusca, Echinodermata). Members of the phylum Nematoda are the most abundant meiofaunal organisms, and copepods (Arthropoda, Crustacea) or Foraminifera are typically second in abundance worldwide. Representative meiofauna taxa are illustrated schematically in **Figure 1**.

The books listed under Further Reading by Higgins and Theil and by Giere, and any invertebrate zoology text, should allow one to identify

Table 1 A list of meiobenthic taxa (Phyla of the Kingdom Animalia). Currently, 19 phyla (**bold**) from the 34 recognized phyla of the Kingdom Animalia have meiofaunal representatives. Of these 19 phyla, only five are exclusively meiofaunal (***bold italics***).

Phyla	*Free-living*			*Symbiotic*
	Marine	*Freshwater*	*Terrestrial*	
Porifera	Yes	Yes	No	No
Placozoa	Endemic	No	No	No
Cnidaria	Yes	Yes	No	Yes
Ctenophora	Endemic	No	No	No
Plathelminthes	Yes	Yes	Yes	Yes
Orthonectida	No	No	No	Endemic (marine)
Rhombozoa	No	No	No	Endemic (marine)
Cycliophora	No	No	No	Endemic (marine)
Acanthocephala	No	No	No	Endemic
Nemertea	Yes	Yes	Yes	Yes
Nematomorpha	No	No	No	Endemic
Gnathostomulida	Endemic	No	No	No
Kinorhyncha	Endemic	No	No	No
Loricifera	Endemic	No	No	No
Nematoda	Yes	Yes	Yes	Yes
Rotifera	Yes	Yes	Yes	Yes
Gastrotricha	Yes	Yes	No	No
Entoprocta	Yes	Yes	No	Yes
Priapulida	Endemic	No	No	No
Pogonophora	Endemic	No	No	No
Echiura	Endemic	No	No	No
Sipuncula	Yes	No	Yes	No
Annelida	Yes	Yes	Yes	Yes
Arthropoda	Yes	Yes	Yes	Yes
Tardigrada	Yes	Yes	Yes	No
Onychophora	No	No	Endemic	No
Mollusca	Yes	Yes	Yes	Yes
Phoronida	Endemic	No	No	No
Bryozoa	Yes	Yes	No	No
Brachiopoda	Endemic	No	No	No
Echinodermata	Endemic	No	No	No
Chaetognatha	Endemic	No	No	No
Hemichordata	Endemic	No	No	No
Chordata	Yes	Yes	Yes	Yes

(Modified from RP Higgins, unpublished, with permission.)

field-collected meiofauna to phylum. Identification to the family, genus, and species level requires specialized literature. Good places to start are chapters on specific phyla in the two texts listed, and also the International Association of Meiobenthologists website: http://www.mtsu.edu/meio

Where Do Meiofauna Live?

Meiofauna occupy a variety of habitats from high-altitude lakes to the deepest ocean depths. In fresh water they occur in beaches, wetlands, streams, rivers, and even the bottoms of our deepest lakes. In marine habitats they occur from the intertidal splash zone to the deepest trenches. Wherever one looks in the aquatic environment, meiofauna are likely to be found. This holds true even in heavily polluted or anoxic sediments where the only living multicellular species are often a few meiofaunal taxa.

Sediment Habitats

Sediments, from the softest muds to the coarsest shell gravels and cobbles, harbor abundant meiofauna. Meiofauna associated with sediments live 'on' or 'in' the sediment. Those living on top of the sediment are epifaunal (or epibenthic) and are adapted to moving over sediment surfaces. Those living 'in' the sediment may burrow into the sediment (burrowing meiofauna), displacing sediment particles as they move, or they may move in the interstices between sediment grains and be called interstitial meiofauna (see **Table 2**). The interstitial fauna are restricted to sediments where there is sufficient space to move between the particles;

Table 2 Types of the meiofauna

Permanent meiofauna: always meiofaunal size
Interstitial: moves between sediment particles
Burrowing: displaces sediment particles
Epibenthic
  On sediment surfaces
  On plants or animals
Temporary meiofauna: meiofaunal size in early life only
Larvae or juveniles of macrofauna: mostly bivalve molluscs and polychaete worms

typically sands and gravels. Sediments where the median particle diameter is below 125 μm provide little room for meiofauna to move between particles, and thus are inhabited by burrowing and epibenthic taxa. In those taxa having both interstitial and burrowing representatives (e.g., Nematoda, Copepoda, Turbellaria), there are often stark differences in the morphologies of the mud dwellers and sand dwellers. The sand fauna tend to be slender, since they must maneuver through narrow interstitial openings, whereas the mud fauna are not restricted to a particular morphology and are generally larger. Since sandy habitats often occur in areas with high wave and tidal action, most interstitial fauna have adhesive glands for attaching to sand grains so that they will not be washed away. They also tend to have a low number of eggs because their reduced body size cannot support large egg masses.

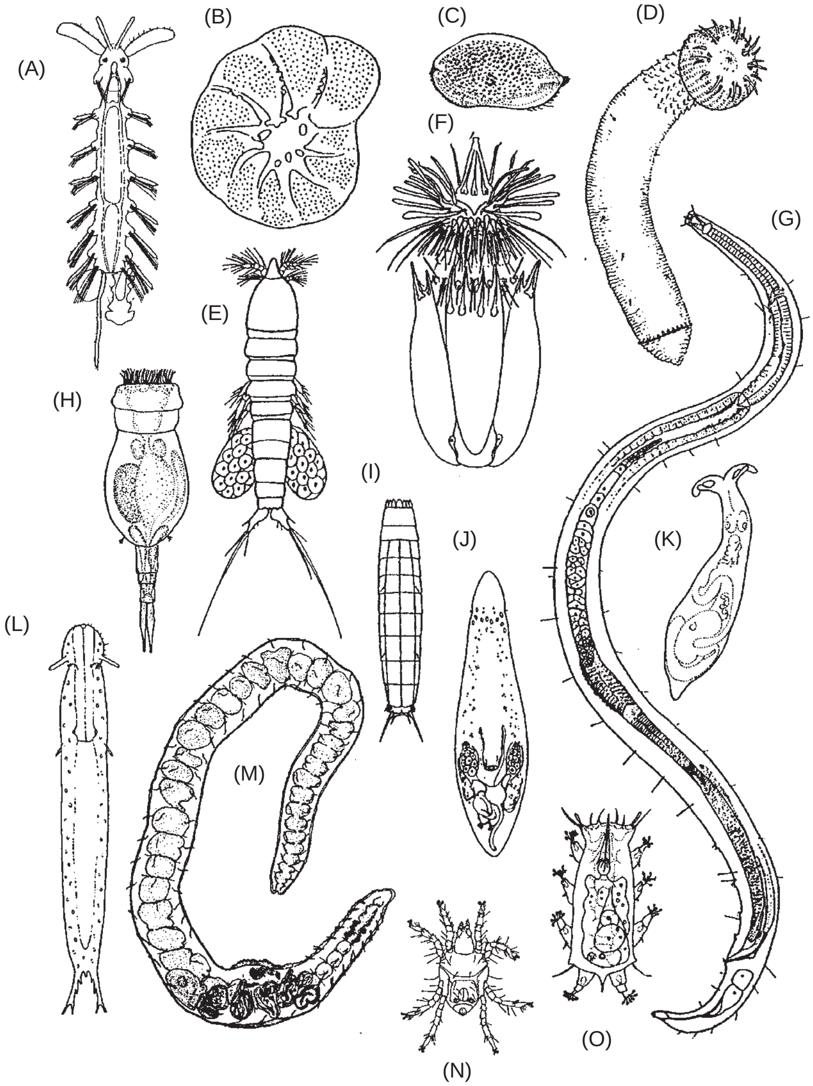

Figure 1 Schematic diagrams of representative meiofaunal animals: (A) Annelida, Polychaeta; (B) Foraminifera; (C) Crustacea, Ostracoda; (D) Priapulida; (E) Crustacea, Copepoda; (F) Loricifera; (G) Nematoda; (H) Rotifera; (I) Kinorhyncha; (J) Plathelminthes, Turbellaria; (K) Mollusca, Gastropoda; (L) Gastrotricha; (M) Annelida, Oligochaeta; (N) Arthropoda, Halacaroidea; (O) Tardigrada. The animals are not drawn to scale. (Modified from Higgins and Thiel (1988).)

Other Habitats

Meiofauna also occupy several ‘above sediment’ habitats, including rooted aquatic vegetation, moss, algae, sea ice, and various animal structures such as coral crevices, worm tubes, and echinoderm spines. Still other meiofauna are symbionts living commensally in animal tubes. Those meiofaunal assemblages living above the bottom, for example, in or on fouling communities, or on various animal structures, differ from sediment dwellers by having species composition and adaptive morphologies specific to particular epibenthic habitats.

Collection and Extraction of Meiofauna

Qualitative sampling of meiofauna will not allow estimation of abundance per unit area, but it is useful for a general assessment of faunal richness or to accumulate one or several species for experimental work. Qualitative samples of sediment are taken by scooping sediment arbitrarily with some device (shovel, hands, grab sampler, dredge), whereas qualitative samples of meiofauna living on structures are taken by collecting the structure itself. Such samples can be sieved live at the collection site, be taken to a laboratory for extraction of the fauna by physical or chemical means, or be preserved in their entirety for future examination. Quantitative meiofauna sampling requires that the sampling area be accurately known. For sediments, this typically involves pushing a core tube of known diameter into the sediment to a preselected depth, collecting all the sediment within the core, and ultimately counting all the fauna in the known area or volume.

Quantitative samples are typically preserved in formaldehyde or alcohol and subsequently counted and identified under a microscope. They are often stained with a protein stain (e.g., Rose Bengal) to help distinguish the animals from surrounding sediment and organic debris. Meiofaunal abundance values are preferably expressed as number per $10\,\mathrm{cm}^2$, but also as number per m^2.

There are multiple ways of extracting meiofauna from sediments and surfaces. For live qualitative sediment samples, many species will be attracted to a focused directional light source (preferably cold fiberoptic light so as not to heat the sediments unduly) if sieved sediments are spread in a thin layer with a centimeter or so of overlying water. Sieved sediment can also be put into funnels, where established salinity and/or heat gradients will drive the fauna down the funnel and into a collecting dish. For animals clinging to surfaces, chemical relaxants – or fresh water for marine samples – will cause some fauna to release their purchase and be washed into overlying water where they can be collected onto sieves of appropriate size. For preserved quantitative samples, meiofauna can be separated from the sediments by decantation (swirling the sediment in a container and pouring off the less dense animals after the mineral particles have settled), elutriation (where water is passed through a sample continuously so that sediment is kept in suspension and the lighter animals come off with the flow), or by centrifugation in a density gradient solution so that the sediment (or debris) remains in one layer and the animals in another. All the products of extractions are sieved through a fine mesh (32–100 μm depending on the objective) and the portion retained on the mesh is observed, counted and identified under a microscope.

Distribution of Meiofauna

Geographic Distribution

Meiofauna inhabit some of the most dynamic environments imaginable (such as exposed high-energy shores) and these animals have traditionally been considered sedentary. Emphasis has centered on adaptations for remaining in close proximity to the substratum, particularly because pelagic larvae are almost nonexistent in the permanent meiofauna. Development, morphology, and biology all seem designed to ensure that the organism remains in or on the substratum. On the basis of such observations, one would expect limited worldwide distribution patterns for species. However, numerous species (identified by morphology, not by molecular genetic technologies) appear to be cosmopolitan. Plate tectonics has been invoked as a potential mechanism to describe pan-oceanic and worldwide meiofaunal distributions, as have dispersal via birds, rafting on drifting materials, transport in the ballast of sailing vessels, and dispersal by suspension in the water column. On a local scale, meiofaunal dispersal is either a passive process of mechanical removal due to current scour or one in which the animals actively migrate to the water column. Animals occupying the sediment surface are obviously scoured much more easily than those living deeper in the sediment. The abundance of eroded species in the water column at any given time is a function of the magnitude of local current velocity and sediment erodability.

Large-scale Spatial Distribution

Meiofauna are rarely evenly distributed on, or in, a substrate. On the large scale (meters to kilometers) gradients in physical factors (e.g., salinity, tidal exposure, sediment grain size, oxygen concentrations) are primarily responsible for variances in abundance, whereas on smaller (centimeter) scales both physical and biological factors have been reported as important. Large-scale gradients lead to zonation of the fauna. For example, certain meiofauna species are confined to specific areas along salinity gradients in estuaries, across intertidal sandy and muddy habitats, and across the water depth gradient in lakes and in the ocean. With water depth, faunal changes are primarily a function of food availability (e.g., organic content of sediment), sediment type, temperature, and oxygen availability. Interestingly, the meiofauna at similar ocean depths are usually similar to each other all over the world. The same families and/or genera comprise a significant portion of the fauna at similar depths except in the Mediterranean and the Arctic, where many of the 'deep sea' genera also occur into shallower (<500 m) depths.

Small-scale Spatial Distribution

Meiobenthos also exhibit spatial variation (patchiness) on a small (millimeter to centimeter) scale. A variety of factors have been suggested for the observed small-scale patchiness including: (1) microspatial variation in physical factors (oxygen, grain size); (2) food distribution; (3) physical structures in the habitat (worm tubes, algae, mud balls, etc.); (4) predation/disturbance, where a predator eats one patch of animals but not another; (5) interspecific competition, where species segregate themselves spatially to avoid competition for a resource; and (6) aggregations, where individuals come together for mating. While we presently lack a framework for experimentally testing how these factors effect microspatial distribution in the field, we know that species are aggregated more often than not. Small-scale zonation also takes place vertically in sediment. Here the vertical distribution of the fauna is controlled primarily by the level of oxygen in the sediment layers. Most meiofauna require oxygen to survive, but certain adapted species can tolerate low oxygen or no oxygen. Species living in such sediments that can tolerate hydrogen sulfide, a known animal toxin, are called the 'sulfide fauna' or the thiobios. Copepods are typically the meiobenthic taxon most sensitive to decreased oxygen, and generally are confined to oxic sediments. Gnathostomulida primarily live in mild sulfidic and low oxic sediments, as do some Nematoda, Turbellaria, Ciliophora, Gastrotricha and Oligochaeta (see **Table 1**). While oxygen content is the ultimate factor controlling most meiofaunal vertical distribution, desiccation can also be important, particularly in intertidal marine beaches. As sand dries at low tide, the fauna face desiccation stress regardless of the oxygen content. Meiofauna therefore migrate downward on an ebbing tide and upward on a flooding tide, and this happens more at midday in the summer, when drying is greatest, than at midnight in the winter.

Abundance and Diversity of Meiofauna

On the average there are a million meiofaunal organisms per square meter of sediment surface, with a dry weight biomass of $0.75\text{–}2\,\mathrm{g\,m^{-2}}$ in shallow (<100 m) waters. Highest abundance values come from intertidal muddy estuarine habitats (6–12 million per m^2), lowest values from the deep sea (hundreds to thousands per m^2). In general, sediment grain size is the primary factor affecting the abundance and species composition of meiofaunal organisms within a given depth range. Different species occur in muddy versus sandy versus phytal habitats. In areas where temperature varies seasonally, meiobenthos abundance and species composition also vary seasonally. Typically, maximum abundances occur in the warmer months of the year, but individual species may reach maximum abundance at other times. Year-to-year variability in abundance also can be greater than within-year seasonal variability.

The highest known species diversity for a meiofaunal assemblage has been recorded for copepods from algal holdfast communities. Shallow-water algal frond assemblages and deep-sea sediments also yield high species diversities. Even though meiofaunal abundance in the deep sea is greatly reduced compared to shallow sediments, there are many different and exotic species. In shallow-water sedimentary habitats, meiofaunal diversity appears similar worldwide, with ecologically equivalent species in different geographic regions. These communities usually have four to ten predominant species. While the database is limited and there are always difficulties interpreting diversity data, there appears to be a standard diversity range for most shallow-water meiofaunal assemblages. There is no evidence that meiofaunal species diversity increases toward the tropics. Pollution or other disturbances, such as hypoxia/anoxia, tend to decrease diversity.

Functional Role of Meiofauna

Meiofauna appear to have two major functional roles in aquatic ecosystems: to serve as food for organisms higher in the food web, and to facilitate mineralization of organic material and enhance nutrient regeneration. In addition, because they exhibit high sensitivity and rapid response to anthropogenic disturbance, they are excellent sentinels of pollution.

Food for Higher Trophic Levels

Meiofauna are very important nutritionally to a variety of animals that could not survive without them. Many predators go though an obligatory meiofaunal feeding stage, and copepods appear to be the major meiofauna prey item for most of these predators. These copepods primarily live in muddy sediment or on plants. Thus most predation on meiofauna takes place in muddy substrates or in areas with substantial sea grass or macroalgae. In muds, the meiofauna prey are restricted to the upper few millimeters or centimeters of oxidized sediment. Thus bottom-feeding predators only need to take a shallow bite to obtain abundant food. On aquatic plants, fish predation on meiofauna is analogous to birds eating insects on a tree. Over 90 species of juvenile fish are known to eat meiofauna, making them the major meiofaunal predators. Other predators are shrimp (prawns) and some bottom-feeding birds.

Mineralization and Nutrient Regeneration

Meiofauna are important in stimulating bacterial growth, which then enhances remineralization (the conversion of organic nitrogen, phosphorus, and carbon to their inorganic forms). Meiofauna package organic molecules and, because of their relatively short life span (months) and high metabolic rate, this packaged material is returned to the system rapidly (compare, for example, the carbon tied up in a clam that lives for 2–5 years). Meiofaunal nutrients then become part of the well-known microbial loop in which they are utilized by bacteria and can be converted into dissolved organic carbon for use by higher trophic levels and/or remineralized for primary producers. Meiofauna typically have less than 20% of the standing biomass of the larger, more visible, macrofauna, but they turn over as much or more carbon per year. These processes are important in all kinds of habitats, but they are probably most important in those sediments with high amounts of organic matter, i.e., muds.

Meiofauna and Pollution

Sediments are the ultimate repository for most of the persistent pollutants released to the ecosphere. Upon entering aquatic environments, most toxicants associate with dissolved organics, suspended silts, clays, and organic particulates and eventually accumulate in sediments. Meiofauna, of course, are intimately associated with this muddy-sediment geochemical soup, as they spend their entire life cycle there and have limited ability to leave. Because meiofauna reproduce very rapidly (often in 2–4 weeks), pollution effects on meiofaunal populations can be detected quickly and early in the history of contamination of a site. There have been three general approaches to using meiofauna to assess pollution: field studies, laboratory studies, and studies using replicas of the controlled natural environment (microcosm/mesocosm studies). In field studies, samples are typically collected from a polluted site and from a reference site, and differences in community (or genetic) structure between the sites are assessed. Laboratory studies usually examine the lethal effects (e.g., how many individuals die after exposure to specific dose levels of a contaminant) or sublethal effects (e.g., changes in egg production, embryonic development time, hatching success, or genetic diversity of contaminants singly or in mixture. Meiobenthic community responses to pollutants in micro/mesocosms are measurable and reproducible over reasonable time and spatial scales (owing to small organism size and rapid production/turnover), and are more effectively assessed than macrobenthos for toxicant-induced effects since meiofauna spend their entire life cycle in sediments and are not reliant on recruitment of a planktonic larval stage. After years of neglect, meiofauna are becoming more popular subjects of pollution studies.

See also

Benthic Foraminifera. Benthic Organisms Overview. Carbon Sequestration via Direct Injection. Deep-sea Fauna. Fish Feeding and Foraging. Macrobenthos. Microbial Loops. Microphytobenthos. Pollution: Effects on Marine Communities. Salt Marshes and Mud Flats. Sandy Beaches, Biology of. Sea Ice: Overview.

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MESOPELAGIC FISHES

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Introduction

'Meso' meaning intermediate and mesopelagic (or midwater) fish refers to fish that live in the intermediate pelagic water masses between the euphotic zone at 100 m depth and the deep bathypelagic zone where no light is visible at 1000 m. Most mesopelagic species make extensive vertical migrations into the epipelagic zone at night, where they prey on plankton and each other, and thereafter migrate down several hundred meters to their daytime depths. Some species are distributed worldwide, and many are circumpolar, especially in the Southern Hemisphere.

Much research on distribution and natural history of mesopelagic fish was conducted in the 1970s, when FAO (Food and Agriculture Organization) searched for new unexplored commercial resources. The total biomass was at that time estimated to be around one billion tonnes with highest abundance in the Indian Ocean (about 300 million tonnes) approximately 10 times the biomass of the world's total fish catch. No large fisheries were, however, developed on mesopelagic fish resources, perhaps due to the combination of technology limitations and a high proportion of wax-esters, of limited nutritional value, in many species. From 1990 there was renewed interest in these species in connection with interdisciplinary ecosystem studies, when vertically and diel migrating sound-scattering layers (SSLs) turned out to be high densities of mesopelagic fish. These findings formed the basis for studies of the life history and adaptations of mesopelagic fish in the context of general ecological theory.

The thirty identified families of mesopelagic fish are listed in **Table 1** and typical morphologies are shown on **Figure 1**. The taxonomic arrangements of the families differ between various classification

Table 1 Families of mesopelagic fish with corresponding number of genera

Family	*Number of genera*	*Family*	*Number of genera*
Argentinidae	2	Alepisauridae	1
Bathylagidae	2	Scopelarchidae	5
Opisthoproctidae	4	Evermannellidae	3
Gonostomatidae	20	Giganturidae	2
Sternoptychidae	3	Nemichthyidae	ca.5
Stomiatidae	2	Trachypteridae	3
Chauliodontidae	1	Regalecidae	2
Astronesthidae	6	Lophotidae	2
Melanostomiatidae	ca.15	Melamphaeidae	2
Malacosteidae	4	Anoplogasteridae	2
Idiacanthidae	1	Chiasmodontidae	5
Myctophidae	ca.30	Gempylidae	20
Paralepididae	5	Trichiuridae	8
Omosudidae	1	Centrolophidae	1
Anotopteridae	1	Tetragonuridae	1

Adapted from Gjøsaeter and Kawaguchi (1980).