Meiobenthology

The Microscopic Motile Fauna
of Aquatic Sediments

Olav Giere

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The Microscopic Motile Fauna of Aquatic Sediments

2nd revised and extended edition with
125 Figures, 20 Tables, and 41 Information Boxes

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To Gaby,
to whom I owe it all.

Preface to the Second Edition

Also bestimmt die Gestalt die Lebensweise des Thieres,
und die Weise zu leben sie wirkt auf alle Gestalten mächtig zurück.

So the shape of an animal patterns its manner of living,
likewise their manner of living exerts on the animals' shape
massive effects.

GOETHE 1806: *Metamorphose der Thiere*

Encouraged by the friendly acceptance of the first edition and stimulated by numerous requests and comments from the community of meiobenthologists, this second edition updates my monograph on meiobenthology. The revised text emphasizes new discoveries and developments of relevance; it has been extended by adding chapters on meiofauna in areas not covered before, such as the polar regions, mangroves, and hydrothermal vents. As I attempted to keep up with the actual literature for the whole field of meiobenthos—taxonomy and ecology, marine and freshwater—I became a little discouraged upon noticing the flood of literature that had appeared in the few years after the publication of the first edition. Has there been a multiplication of new meiobenthologists or an inflation of their industrious efforts? How could I compile this plethora of new data; how to select, what to omit? The need to extract general information from the details, and to modify and amalgamate them within a greater context; this difficult "condensation" process was the key to my approach. It forced me to be selective, to focus on one goal: to write a readable compendium that will serve the interested biologist, the fellow benthologist and the student alike. Avoiding a style with constructions that are too sophisticated should also enhance the comprehension of those readers that are not natively familiar with the English language.

Since the first edition, meiofaunal research has made, I believe, major progress in three general areas: (a) systematics, diversity, and distribution; (b) ecology, food webs and energy flow; and (c) environmental aspects, including studies of anthropogenic impacts.

(a) In the area of systematics, diversity and distribution, molecular biological studies suggest that some of the “smaller” meiobenthic groups, such as Kinorhyncha, Gastrotricha and Rotifera, hold key positions in metazoan phylogeny, linking various invertebrate lines into new units (e.g., Ecdysozoa, Scalidophora, Cycloneuralia, Lophotrochozoa). Genetic fine-scale diversification has become an indispensable tool for understanding distribution processes and biogeographic patterns. With enhanced studies in exotic and remote areas, the meiobenthos continues to be a haven for the discovery of unknown animals, even of high taxonomic rank, e.g., Micrognathozoa. Reports on meiofauna from polar or tropical regions, deep-sea bottoms or hydrothermal vents were limited in the first edition due to the scarcity of pertinent studies. Recent comprehensive publications have now recognized these formerly exotic areas as being in the research mainstream, and are covered here in separate chapters. Problems of principal biological relevance, such as the study of distribution patterns or the relation of body size to distribution, have been tackled using meiofauna as tools. The high number of meiobenthic species found under even extreme or impoverished ecological conditions puts meiobenthos at the forefront of biodiversity and “census of life” studies. Taxonomic, functional and genetic diversity as influenced by ecological and/or anthropogenic variables are widely acknowledged matters of concern. Molecular screening methods allow large numbers of species to be recorded upon expending reasonable effort.

(b) Today, essays on aquatic environments mostly consider the relevant role of meiobenthos. Mucus agglutinations and microorganisms are increasingly recognized to be important components that structure the sediment texture and provide the basis for many meiobenthic food chains. Trophic fluxes can be followed using new techniques, such as by assessing isotopic signatures. Metabolic pathways visualized by fluorescence imaging enable us to broaden our limited knowledge of the physiology of meiobenthos. Combined with advanced statistics, such as multivariate analyses, we can achieve results that link meiobenthos to general ecological paradigms.

(c) The reactions of biota to environmental threats are increasingly based on evaluations of the meiofauna, underlining their inherent advantages (small size, ubiquity, abundance). With improved processing and culturing methods, pollution experiments are now often based on meiobenthic animals, apply population dynamics and use micro-/mesocosm studies. Standardized bioassays include meiofauna and have become commercially available. The increased role of meiofauna in this field is reflected by new chapters on the impact of metal compounds and pesticides. The use of molecular techniques can alleviate the problem of rapid mass identification, e.g., in nematodes.

All of these research fields tie meiobenthology closer to the “mainstream,” which should be a main goal of future meiobenthic research. If this second edition can synthesize these modern scientific achievements, meiobenthology could indeed play a key role in assessing the health of our environment, and will not just represent a playground for singular interests.

Several comprehensive publications on meiobenthos published in the last few years are contributing to this goal. Of broad interest are monographic publications on freshwater meiobenthos (Hakenkamp and Palmer 2000; Hakenkamp et al. 2002; Robertson et al. 2000a; Rundle et al. 2002). The new edition of the classic treatise *Methods for the Study of Marine Benthos* (Eleftheriou and McIntyre 2005) contains competent contributions to sediment analysis, sampling strategies and meiofauna techniques (Somerfield et al. 2005). It also covers statistical and analytical methods that assess ecosystem functioning and measure energy flow through benthic populations. Therefore, in this edition of *Meiobenthology* I have condensed the information in some chapters referring to "Methods for the Study of Marine Benthos." Lesser known are the meiofauna reviews of Galhano (1970, in Portuguese) and Gal'tsova (1991, in Russian), which were not mentioned in the first edition. In other chapters of this edition (e.g., on polluted sites), the scope has been expanded by adding short accounts of the impacts of metals and pesticides on meiobenthos. The most conspicuous novelty is the highlighted boxes, which either contain the essence of a particular section or comment on special aspects.

The figures have been redesigned for higher clarity, and some outdated paragraphs have been shortened or omitted. To maximize readability not all of the publications on which I drew are cited; on the other hand, on several occasions the same publication is cited in a different context in order to make the chapters independently readable and understandable. The resulting reference list is meant to provide an archive of detailed studies in all fields of meiobenthology. A comprehensive index and a glossary explaining specific terms facilitate the use of this book. Because of their ease of accessibility for the general reader, I accentuate references in widely distributed, English-dominated journals. As much as all this may help to improve the distribution and didactic impact of this book, I especially hope, for the sake of the student reader, that Springer-Verlag publishes this new edition at a competitive price that is affordable to all interested in the great world of small organisms. I hope that this edition will be considered as readable and received as warmly by the readers as the 1993 edition.

Despite all the care that I have taken, I could not consider every contribution, and so I apologize especially to those colleagues who have published in less common native languages or in journals with restricted distributions, whose results have not been considered here. My particular regrets remain realizing how much valuable knowledge is "hidden" to most of us in the numerous publications that have appeared in Russian over the last few years, much of it unnoticed by many of us. Mistakes in the first edition, for which I apologize, have hopefully been eliminated. I regret and take the responsibility for remaining omissions or erroneous interpretations.

Should this book draw the attention of benthic ecologists to the relevance of meiobenthos and foster further research in this field, it has accomplished its goals. Perhaps it represents the last chance to write a monographic textbook that amalgamates bits of information into a coherent context before electronic databases, pictures and information networks produce a glut of innumerable details and publications—an information jungle in which the beginner especially can easily become lost.

Meiobenthology is now increasingly represented on the Internet: the International Association of Meiobenthologists (I.A.M.) and also many colleagues have often designed comprehensive homepages with address and publication lists. New editions of the I.A.M. newsletter *Psammonalia* are regularly published online (http://www.meiofauna.org/) and include pictures and even short movie galleries. Also, CD-ROMs and databases of computer-based pictorial identification keys have attained increasing importance (European Limnofauna; European Register of Marine Species, ERMS; separate databases for Nematoda, Harpacticoida, Turbellaria).

With this book I conclude many of my activities in meiobenthology. To express my feelings I could do worse than adopting the words of a good friend and protagonist of meiobenthos research, Prof. Bruce C. Coull, who upon his retirement wonderfully characterized his feelings and probably those of many other fellow meiobenthologists of our peer group: "I maintain an interest in all things meiofaunal and it has been a great life studying them. I hope that the next generation of researchers will learn much more about these creature friends and that the researchers have as much fun as I have had trying to understand our ubiquitous and omnipresent aquatic denizens."

Acknowledgements The second edition has been carefully proof-read again by my friend Robert P. Higgins (Ashville, NC, USA). His dedication and encouragement constantly accompanied me while writing this text. Important chapters have been kindly reviewed by two other good friends and experts, Bruce C. Coull (Columbia, SC, USA) and Walter Traunspurger (Bielefeld, Germany). I owe a large intellectual debt to all those many colleagues who invaluably helped me by sending literature, giving comments and, most importantly, kept encouraging me to complete this work. There are far too many to mention them all here by name. I thank Mrs. M. Hänel for her detailed drawings and particularly Mrs. A. Kröger (both Hamburg) for her most valuable and patient computer skills when designing the figures. Finally, Springer-Verlag (Heidelberg, Berlin) is to be thanked for its continuous interest in this project and its "author-friendly" support throughout the correspondence.

Hamburg, July 2008 Olav Giere

Preface to the First Edition

Studies on meiobenthos, the motile microscopic fauna of aquatic sediments, are gaining in importance, revealing trophic cycles and allowing the impacts of anthropogenic factors to be assessed. The bottom of the sea, the banks of rivers and the shores of lakes contain higher concentrations of nutrients, more microorganisms and a richer fauna than the water column. Calculations on the role of benthic organisms reveal that the "small food web", i.e., microorganisms, protozoans, microphytobenthos, and smaller metazoans, play a dominant role in the turnover of organic matter (Kuipers et al. 1981). New animal groups—even those of high taxonomic status—are often of meiobenthic size and continue to be described. Two of the most recent animal groups ranked as phyla, the Gnathostomulida and the Loricifera, represent typical meiobenthos.

Up to now, a textbook introducing the microscopic organisms of the sediments, their ecological demands and biological properties has not existed, despite the significance of meiobenthos indicated above. A recent book entitled *Introduction to the Study of Meiofauna* (Higgins and Thiel 1988) gives valuable outlines for practical investigation, and *Stygofauna Mundi*, a monograph edited by Botosaneanu (1986a), focuses on zoogeographical aspects of mainly freshwater forms, but neither was intended to be a comprehensive text on the subject of meiobenthology.

The purpose of this book is to provide a general overview of the framework and the theoretical background of the scientific field of meiobenthology. The first of three major parts describes the habitat of meiobenthos and some of the methods used for its investigation; the second part deals with morphological and systematic aspects of meiofauna, and the third part reports on the meiofauna of selected biotopes and on community and synecological aspects of meiobenthos. However, a monographic text cannot include an adequate survey of general benthic ecology, or be a textbook on the zoology of microscopic animal groups. The primary purpose of this text is to provide an ecologically oriented scientific basis for meiobenthic studies. Further advice for practical investigations is found in important compilations by Higgins and Thiel (1988), Holme and McIntyre (1984), and Gray (1981). Hence, aspects of sampling procedures and strategies, statistical treatment and fauna processing will be treated here only briefly. In these fields, the present work should be considered a supplement to the books mentioned above and instead focuses on some critical hints, methodological limitations, and a few neglected practical aspects.

Writing this book was particularly difficult because the literature on meiofauna is so widely dispersed in journals and congress proceedings and has so rapidly increased in volume that complete coverage is impossible. Regardless of my efforts, therefore, there is no pretence that this text is absolutely comprehensive. Where it is important for the general context, the major chapters of the book contain some overlap in terms of information. This is deliberate; it provides the reader with chapters that are complete in themselves and avoids the need for too many cross-references. Also, in order to maintain a readable, coherent style, citations of specific references had to be restricted. Thus, the "reference list" of this text does not represent all of the sources drawn upon during the production of this book.

The selection of topics and the emphasis given to them is admittedly subjective. In particular, the brief treatment of freshwater meiobenthos (Chapter 8.2) by no means reflects the exhaustive achievements and importance of this field of meiobenthology. This book does not include the nanobenthos, since this represents a microbiota that is completely different from the meiobenthos in its size range, methodology, and taxonomical composition (mainly prokaryotes, often autotrophic protists and fungi). Where appropriate, references compiled in a "Recommended reading" paragraph are given at the ends of many chapters. They will serve as supplementary information and, hopefully, will compensate for my own subjectivity. Should incorrect or misunderstood data be reported in the text, I would be most grateful to be informed of this.

This book resulted from a series of lectures for advanced students given by the author over a period of several years at the University of Hamburg. Studying the tiny organisms living in sand and mud fascinated many of the students and provided the encouragement and persistent stimulus needed to write this book. It will achieve its goal if it further promotes interest in the diverse and cryptic microscopic world of meiobenthic animals, emphasizes their ecological importance, from both theoretical and practical viewpoints, and contributes to the awareness that small animals often play a key role in large ecosystems, which are becoming increasingly threatened.

Acknowledgements I am deeply obliged to Dr. Robert P. Higgins (Washington, DC), who critically reviewed the entire text, and not only for linguistic flaws. My thanks go out to my graduate students who supported me in selecting figures and designing graphs. I am grateful to several of my colleagues for their valuable comments on parts of the text, and for providing me with manuscripts that were sometimes still in press and for other helpful hints. It was my intention to include only originals or redrawn figures. This was possible through the patient work of A. Mantel and M. Hänel (both in Hamburg), for which I am most grateful.

Hamburg, July 1993 Olav Giere

Contents

Chapter 1
Introduction to Meiobenthology

1.1 Meiobenthos and Meiofauna: Definitions

The terms "macrobenthos" and "microbenthos" were already well established when in 1942 Molly F. Mare coined the term "meiobenthos" to define an assemblage of benthic metazoans that can be distinguished from macrobenthos by their small sizes (note that the Greek "μειος" means "smaller"). Therefore, the study of meiobenthos per se is a relatively new component of benthic research, despite the fact that meiobenthic animals have been known about since the early days of microscopy. This book will mainly focus on metazoan meiofauna, which mirrors the author's field of expertise. Hence, the term "meiobenthos" is used here synonymously to "meiofauna." However, an ecological picture cannot be drawn without also considering relevant benthic protists (e.g., ciliates, foraminiferans, amoebozoans), and microalgae (e.g., diatoms).

Today, members of the meiofauna are considered mobile and sometimes also haptosessile benthic animals, smaller than macrofauna but larger than microfauna (the latter term is now restricted mostly to Protozoa). The formal size boundaries of meiofauna are operationally defined, based on the standardized mesh width of sieves with 500 µm (1,000 µm) as upper and 44 µm (63 µm) as lower limits: all fauna that pass through the coarse sieve but are retained by the finer sieve during sieving are considered meiofauna. In a recent move, a lower size limit of 31 µm has been suggested by deep-sea meiobenthologists in order to quantitatively retain even the smallest meiofaunal organisms (mainly nematodes). Using biomass as a measure, meiofauna (in freshwater) have been defined to include all mobile benthic organisms with masses of between 2 and 20 µg (Hakenkamp et al. 2002). What began as an arbitrarily defined size-range of benthic invertebrates has since been supported by studies on the size spectra of marine benthic fauna. Quantitative size-taxon studies (Schwinghamer 1981a; Warwick 1984; Warwick et al. 1986a; Duplisea and Hargrave 1996—see Sect. 9.2) infer that the (marine) meiofauna represent a separate biologically and ecologically defined group of animals, a concept well known in the case of the (interstitial) meiofauna of sands (Remane 1933, see Sect. 1.2). In addition to the "permanent" meiofauna, members of the "temporary" meiofauna belong to the meiofaunal size category only as newly settled larvae that later grow

O. Giere, *Meiobenthology*, 2nd edition, doi: 10.1007/b106489,

to become macrofauna. An exact upper size limit that will be passed by these temporarily small organisms (often juvenile molluscs and annelids) is difficult to define.

Meiofauna are mostly found in and on soft sediments, but also on and among epilithic plants and other hard substrates (e.g., animal tubes). Even the surfaces of barren rocks with their biofilm and detritus cover are suitable habitats. Under each footprint of moist shore sediment we often find 50,000–100,000 meiobenthic animals! Indeed, it is unclear why the meiobenthos was not recognized earlier as a valid intermediate between the micro- and the macrobenthos. It seems inconsistent with the fact that the microscopic fauna in the water column had long been considered an established faunistic assemblage. Personally, I believe that bare sand bottoms and beaches and the often odiferous muds were considered unlikely habitats for diverse fauna of minute dimensions.

More detailed reading: Warwick (1989), Palmer et al. (2006), Rundle et al. (2002).

Box 1.1 Meiofauna, Meiobenthos: Definitions

The term “meiofauna” denotes microscopically small, motile aquatic animals living mostly in and on soft substrates at all depths in the marine and freshwater realm. Although originally restricted to small metazoans, ecological connections suggest that larger protozoans (ciliates, amoebozoans) should also be included in the scope of meiofauna. In the context of this book, this wider definition is used synonymously with meiobenthos. Formally defined by sieve mesh sizes of between 44 and 500 mm, meiobenthos is increasingly considered an ecological unit of its own, an important link between micro- and macrobenthos. In contrast to permanent meiobenthos, the newly settled larvae of many macrobenthic animals are temporary meiofauna.

1.2 A History of Meiobenthology

Taxonomic descriptions and biological investigations of minute benthic animals were being published by the mid nineteenth century. One of the first of these was on the discovery of a minute aberrant mollusc, the aplacophoran *Chaetoderma* by Lovén in 1844, then described as a new worm genus, and the Kinorhyncha described by Dujardin in 1851. In 1901, Kovalevsky studied Microhedylidae (Gastropoda) in the Eastern Mediterranean, and in 1904, Giard described the first archiannelid *Protodrilus* from the coast of Normandy. He even stated that the microscopic fauna were so rich “that it would take years to study them.” However, these pioneers of meiofauna considered only isolated taxa—often the exceptional species of known invertebrate groups—not their ecological niches and community aspects.

Since then, field investigations were biased towards commercially interesting macrofauna. Consequently, a suitable methodology for specifically sampling the smaller benthic animals had to be developed. It was Remane who first used fine-meshed plankton nets to filter the "coastal ground water," and he used dredges with sacks of fine gauze to perform equally pioneering studies of the microscopic fauna of (eulittoral) muddy bottoms ("pelos") and of the small organisms associated with surfaces of aquatic plants ("phyton")). Remane summarized this work in a monograph entitled *Verteilung und Organisation der benthonischen Mikrofauna der Kieler Bucht* (1933), where he first used the word "*Sandlückenfauna*." The corresponding term "interstitial fauna," introduced by Nicholls (1935), comprised all animals living in interstices, not only those of meiobenthic size, e.g,. polychaetes in a pebble beach. Aside from his important descriptions of new kinds of animals, the significance of Remane's work is reflected by his contention that the meiobenthic fauna of sand were not merely a loose aggregation of isolated forms, but "a biocoenosis different not only in species number and occurrence, but also in characteristics of form and function" (Figs. 8.11 and 8.12). In his 1952 paper, Remane embodied this concept in the word "Lebensformtypus," which has since been incorporated into the terminology of general ecology. The ubiquity and complexity of this smaller benthos became much clearer with the development of effective grabs (Petersen 1913) and dredges (Mortensen 1925) for sampling subtidal bottoms.

With improved methods (e.g., Moore and Neill 1930; Krogh and Spärck 1936), studies on the small benthos soon emerged from many parts of the world. From Remane's school came numerous German scientists of considerable influence in meiofaunal research, e.g., Ax, Gerlach, Noodt, to name just a few. Through their work Remane's stimulus even proliferated to further generations of meiobenthologists (Westheide, Schminke, Riemann) in Germany. From Britain, Moore (1930, 1931), Nicholls (1935) and Mare (1942) initiated the study of meiofauna. At the beginning of the 1960s Boaden and Gray were among the first to perform experiments with marine meiofauna. In 1969, McIntyre compiled the first review, *Ecology of Marine Meiobenthos*, which is still a valuable source of information, particularly for data on meiofauna from tropical areas. By studying the fauna of the Normandy coast of the Channel, the Swedish researcher Swedmark focused attention on the rich interstitial fauna, and described many hitherto unknown species. His review *The Interstitial Fauna of Marine Sand* (1964) is considered a classic among early meiofaunal literature. Working along the shores of the Mediterranean Sea, Delamare Deboutteville concentrated his research into the meiobenthos on the brackish transition areas between the marine and freshwater realms. He was the first to conduct meiofaunal research along the African shores. His book *Biologie des Eaux Souterraines Littorales et Continentales* (1960) is another much-esteemed compendium of meiofaunal research.

What about North America, now one of the main centers of meiofaunal research? The early marine meiofaunal studies were linked to just a few names, e.g., Pennak, Sanders, and Zinn, who discovered important new crustacean groups. Some European scientists working in the US also contributed to the further development of this field: the studies of the Austrians Riedl, Wieser and Rieger in the 1950–1980s stimulated several American students to become meiobenthologists. The 1960s saw the beginning of American investigations directed primarily at ecology (e.g., Tietjen), which continue to be a major thrust of American meiobenthology, and are mostly concentrated along the Atlantic and Gulf coasts of the United States. Beginning in the 1970s the school of Coull began investigating the soft-bottom meiofauna, often addressing environmental problems (disturbance, predation, pollution) and using field experimental methods in estuarine soft bottoms. Its impact drew the attention of general marine benthologists to meiofauna.

The development of meiobenthology in the freshwater realm went separate ways, used different methods, and even produced a separate nomenclature. Still now, research on freshwater meiobenthos is not well coupled with its marine counterpart, although both Remane and Delamare Deboutteville often emphasized the connections between marine and freshwater meiofauna, especially those of a zoogeographical and evolutionary nature. Similar to the situation in the marine field, important taxonomic work was performed early in the nineteenth century, especially on benthic freshwater copepods (e.g., the works of Sars, Claus, Lang, Gurney), but freshwater meiobenthology, as an ecological discipline, started later. It developed independently with the Russian Sassuchin and colleagues (1927), who sampled at a river shore. They first described the "psammon," i.e., the fauna and flora of sand. Today, this term is specified as "mesopsammon," the fauna between sand grains (= interstitial fauna of sands), in contrast to the mostly macrobenthic "epipsammon" (i.e., species that live burrowing in the sand) and "endopsammon" (species that live burroweing in the sand). Wiszniewski (1934) conducted similar studies in Polish rivers and lakes that emphasized the important role of rotifers (see Sect. 8.7).

While in England, Germany, France and Belgium early papers on the freshwater psammon remained rather isolated and mainly taxonomic in nature, it was the American Pennak who included a wider faunal spectrum in his ecological and faunistic considerations. His monograph *Ecology of the Microscopic Metazoa Inhabiting the Sandy Beaches of Some Wisconsin Lakes* (1940) is one of the classic publications in freshwater meiobenthology. His ecological comparison of freshwater and marine interstitial fauna (1951) provided valuable insights into the characteristics of these two biomes, an approach later continued in the USA by Palmer and Strayer.

Related to the research of Delamare Deboutteville were the investigations of Angelier (1953) on the river shores and banks in the south of France exposed during the dry season. Detailed granulometric and physiographic descriptions of the biotopes are a characteristic of this work. The importance of the hydrological regime was the subject of the meiobenthos studies by Ruttner-Kolisko (beginning in 1953) in Austrian mountain streams and rivers.

In Switzerland Chappuis started a series of investigations (beginning in 1942) on the fauna of the groundwater. He found the "stygobios" to be a distinct faunal element (see Sect. 8.2.1). The "hyporheic" biotopes beneath streams and rivers were the research domain of Karaman (1935), Orghidan (1955) and collaborators. They were attracted by the interesting subterranean fauna of karstic rivers in

Southeast Europe and contributed much to the early knowledge of cave meiobenthos, today also termed “troglobitic” fauna. From the 1960s Danielopol worked intensively on hyporheic and lacustrine meiobenthos, mainly in Austria. Although specializing in ostracods, he and his colleague Stock from Holland also focused on general evolutionary aspects, discussing the colonization pathways for subterranean habitats (see Sect. 8.7.2).

The ecology of groundwater fauna has been well covered in a volume edited by Gibert et al. (1994). A summary of methods for studying freshwater meiofauna has been provided by Palmer et al. (2006). Based mainly on lake meiofauna, Rundle et al. (2002) provided a competent review of freshwater meiobenthos. Meiofauna of lotic ecosystems (streams) is covered in a special volume edited by Robertson et al. (2000a,c). Enhancing our insight into their similarities and differences will hopefully reduce the historical separation between marine and freshwater meiofaunal research.

Today, several hundred scientists are working to expand our knowledge of meiofauna from alpine lakes to the deep-sea floor, from tropical reefs to polar sea ice. However, despite an increasing number of meiobenthologists working in Africa, South America, Asia and Australia, the meiobenthos in these continents is as yet largely unknown. Studies of the deep-sea meiobenthos gain increasing momentum with the development of sophisticated maneuverable vehicles.

As in other biological sciences, the structure of meiobenthological research evolved from isolated and individualistic taxonomic descriptions to assessments of abundance and distribution principles worked out by teams. These were the foundation for ecological research that, after implementing sophisticated statistical methods, could tackle complex problems such as pathways of distribution, community functioning and the impact of disturbances. From there, studies on environmental effects and on anthropogenic disturbance and pollution using meiofauna as sentinels were a logical consequence. The future of meiobenthology (see Chap. 10) will largely depend on how well we understand how to incorporate the specific potentials of meiobenthic animals into mainstream benthic research. The adoption of molecular methods will decisively contribute to future development. We should address the importance of global climate change and advocate more strongly than before the value of using the ubiquitous and speciose meiofauna to assess the health of ecosystems.

Most meiobenthologists are members of the *International Association of Meiobenthologists* (IAM) (http://www.meiofauna.org/) and thus receive its newsletter *Psammonalia* for information on current fields of interest, members’ research projects and recent literature. The triennial conferences of the IAM are important occasions for the mutual exchange of results, experiences and developments, and members from countries that are now starting to perform meiobenthic research are increasingly participating in these conferences. The website provides information on upcoming events, new results and the e-mail addresses of all of the members. Scientists from remote places that are often cut off from the mainstream of meiofaunal research can also use such electronic media to easily contact their colleagues and access recent literature. The development of electronic species registers, identification guides, and expert lists (e.g., the European Register of Marine Species, ERMS; NEMYS) has enabled easier access in order to solve the diversity problem of meiofauna. Thus, due to the increasing "globalization" of meiofaunal research through new technical achievements, meiofaunal research will be better dispersed into areas hampered by their social or geographical isolation.

> *More detailed reading*: Remane (1933); Pennak (1940); Swedmark (1964); Delamare Deboutteville (1960); Ax (1966); Schwoerbel (1967); McIntyre (1969); Coull and Chandler (1992); Gibert et al. (eds. 1994); Robertson et al. (2000c); Rundle et al. (2002).

Box 1.2 Meiobenthology: A Young Research History

Meiofaunal research, especially meiobenthic ecology, as initiated by Remane, is a fairly young field. Aside from singular and scattered early descriptions of strange tiny organisms, the field of marine meiofaunal research originated in the first decades of the twentieth century in Europe, starting with taxonomic and basic ecological work. More complex ecological approaches were characteristic of research carried out between 1960 and 1980 in Europe and particularly in the US. Freshwater studies began independently in eastern European rivers, Swiss streams, and North American lakes. Marine and freshwater studies of meiobenthos developed along different lines and only recently prompted the ecological parallels a common nomenclature. Reasons for the relatively late start of multidirectional meiofaunal research may include the inconspicuous nature of meiobenthic organisms and their unspectacular habitats. This may have confounded the real phylogenetic and ecological roles of meiofauna. Today, the International Meiofauna Association and its triennial conferences bring together work in all fields of meiofauna research and most scientists that are studying meiobenthos.

Chapter 2
The Biotope: Factors and Study Methods

2.1 Abiotic Factors (Sediment Physiography)

2.1.1 Sediment Pores and Particles

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

Aside from pore volume, the external surface area of the sediment particles is an important determinant of meiobenthic life. It directly defines the area available for the establishment of biofilms (mucus secretions of bacteria, fungi, diatoms, fauna), which, under natural conditions, form the matrix into which the sediment particles are embedded. Thus, particle surface is an important parameter for microscopic animal life. This internal surface is unbelievably large: for a 1-m^3 stream gravel it has been calculated to amount to about 400 m^2. One gram of dry fine sand with a median particle diameter of 63–300 µm may have a total surface area of 8–12.5 m^2; if it consists mostly of diatom shells, this value can even exceed 20 m^2, whereas for 1 g of coarse-grained calcareous sand a value of just 1.8 m^2 was calculated (Suess 1973; Mayer and Rossi 1982).

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

O. Giere, *Meiobenthology*, 2nd edition, doi: 10.1007/b106489,

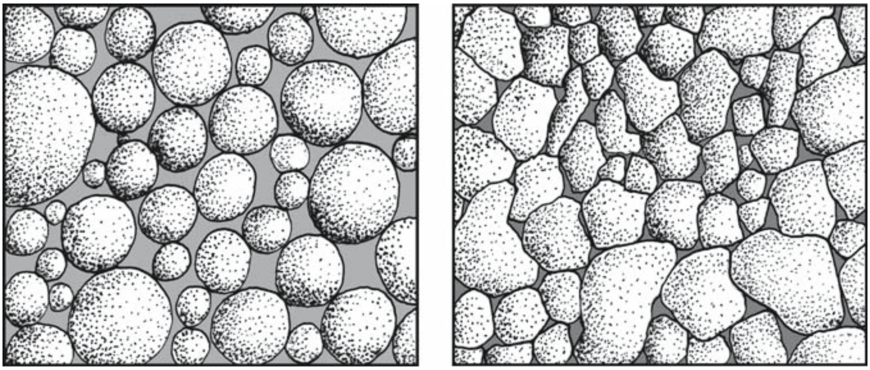
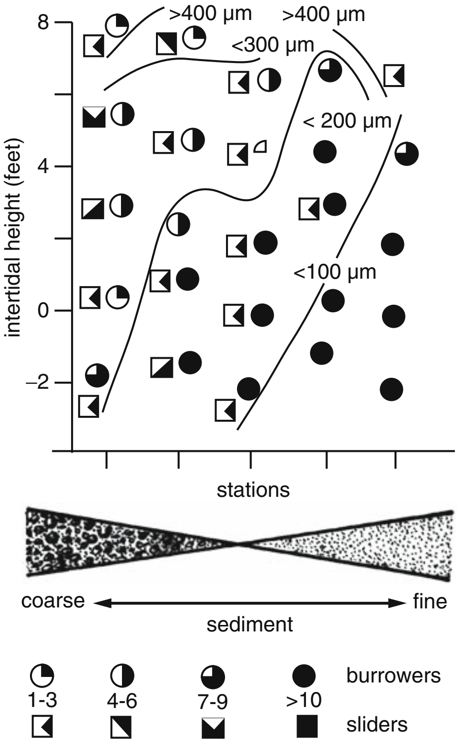


Fig. 2.1 The pore system in sediments consisting of grains with a round shape (glass beads; *left*) vs. natural grains of angular shape (*right*); note differences in pore space due to different packing. (After Conrad 1976; modified)

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

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

Fig. 2.2 Distribution pattern of meiofaunal locomotory groups in the intertidal of a sandy shore. *Black areas in circles or squares* relate to the number of species per sample (250 cm^3) that belong to the same locomotor type; *lines* indicate areas of identical median grain size. (After Wieser 1959)



2.1.2 Granulometric Characteristics

2.1.2.1 Grain Size Composition

Grain size analysis is fundamental to all ecological aspects of meiobenthic work. Although the fractionation of the sediment into different size groups does not reflect the natural composition, it provides a basis for reference and an important comparative framework. Techniques of sediment analysis are well covered in Bale and Kenny (2005); only some additional practical hints are presented here. Granulometry is usually based on the rather tedious procedure of the fractionated sieving of a sufficiently large sample. Recently sieving has been replaced by electronic procedures (modified Coulter counters, laser diffraction counters) with higher accuracy and throughput. Inherent inaccuracies with sieving (underrepresentation in the finer fractions) are based on effects of the adhesion of particles to the mesh fibers (Logan 1993). Salt-containing marine samples are mostly wet sieved, especially when fecal pellets consolidate fine sediment. However, the faster technique of dry sieving is often preferred (80 °C, 24 h) and is sufficiently accurate if agglutination is avoided and the salt content of the sample is corrected for. The inaccuracies involved in these procedures are acceptable for most ecological questions. The silt-clay fraction (“mud content”) passing through the 63-µm or 44-µm sieve is an important ecological parameter that determines the biological and mechanical properties of the sediment, but is usually not differentiated any further. After sieving, its proportion is determined by the loss of weight. However, it can be refined by performing a fractionated analysis of the settling velocity using elaborate soil science methods.

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

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

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

Block histograms or ternary diagrams (triangular coordinates) are the usual methods used to illustrate particle size distribution (Krumbein 1939; Gray 1981; Bale and Kenny 2005). The relevant granulometric parameters can be computer-calculated using specific software (e.g., Gradistat; Blott and Pye 2001) or calculated by simple mathematical methods: the fractions are computed as cumulative percentages starting with the coarsest fraction. These values are listed for further mathematical treatment or plotted as cumulative frequency curves (Fig. 2.3). It is apparent that the use of the φ notation (abscissa) has the advantage of giving relatively more detailed information on the important finer particles, and it also produces equidistant intervals that are relevant for the assessment of the following important statistical indices.

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

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

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

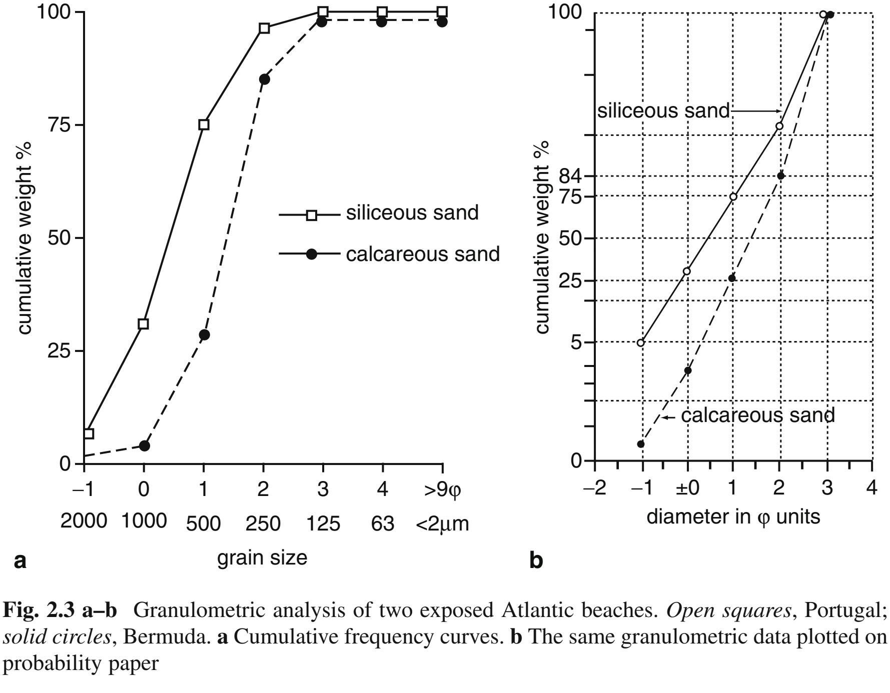


Fig. 2.3 a–b Granulometric analysis of two exposed Atlantic beaches. *Open squares*, Portugal; *solid circles*, Bermuda. **a** Cumulative frequency curves. **b** The same granulometric data plotted on probability paper

Table 2.1 Sediment sorting classes (Gray 1981)

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

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

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

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

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

the "graphic mean" $M_z = \dfrac{(\varphi\,16 + \varphi\,50 + \varphi\,84)}{3}$

the "inclusive quartile deviation or "inclusive sorting coefficient:"

$$QD_I = \frac{\varphi\,84 - \varphi\,16}{4} + \frac{\varphi\,95 - \varphi\,5}{6.6},$$

or the "inclusive graphic skewness:" $Sk_I = \dfrac{\varphi\,16 + \varphi\,84 - 2\varphi\,50}{2(\varphi\,84 - \varphi\,16)}$,

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

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

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

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

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

Box 2.1 To See a World in a Grain of Sand

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

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

2.1.3 The Sediment–Water Regime

2.1.3.1 Exposure, Sediment Agitation, and Erosion

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

Current velocity is not directly proportional to agitation and erosion. Turbulent water currents reduce particle suspension (McNair et al. 1997); particles with a diameter of approximately 180 μm are most easily eroded (Sanders 1958). A threshold of around 200 μm, earlier defined as a “critical grain size” for the occurrence of many animals (see Sect. 2.1.1), is of prime importance for the water contents of sediments. The lower average grain size threshold for the existence of an interstitial assemblage is often reported to be 150 µm. In freshwater sediments, 250 µm has been considered the size limit for the circulation of interstitial water (Rutter–Kolisko 1961).

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

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

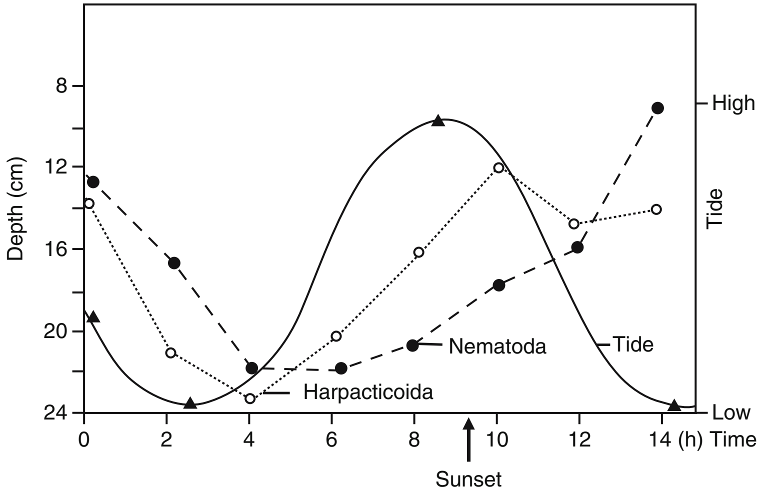


Fig. 2.4 Migration of beach meiofauna in relation to the tidal cycle. (McLachlan et al. 1977)