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Michaela Schratzberger *Editors*

New Horizons in Meiobenthos Research

Profiles, Patterns and Potentials

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Preface

Discover, Discuss, Develop—
Crossing Established Boundaries

Introduction

The variety, quantity and distribution of life on Earth, its biodiversity, are the basis of our existence. For many centuries, researchers have been attempting to capture the world's biodiversity and most of this research has initially been based on large-sized, conspicuous organisms. However, the famous dictum by Linnaeus (1739) "*No wonders are greater than the smallest ones*" [1] is still valid today. Over 90% of animal life on Earth is smaller than your fingernail (Naskrecki 2005)! This remarkably underlines the necessity of integrating in our studies organisms of all sizes, including those that are invisible to the naked human eye. This 'small life' is mostly aquatic and mainly marine: here, bottom-living invertebrates, the meiobenthos, represent diverse assemblages of minute animals that emerge as an increasingly relevant link between the microbial and the macroscopic world.

The great mentors of meiobenthology, Remane (1933) and Mare (1942), saw 'interstitial fauna' and 'meiobenthos', respectively, as rather exotic and somewhat isolated groups occurring in specific habitats. However, subsequent research in diverse biotopes revealed the numerous and complex interactions of meiobenthos with other organisms, and with the physical and chemical environment: meiobenthos plays a critical role in the benthos with many links to the micro- and macro-world, and often with a pioneering role, especially when environments change. Thus, the position of meiofauna in benthic systems reflects the classical perception of Alexander von Humboldt (1803; English version 1811) who, on his numerous travels, realised that in the entire scenery of nature "*everything is interrelatedness*" [2]. Up to now, the

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[1] *"Inga underwärk äro större än de minste".*

[2] "Alles ist Wechselwirkung".

complex interactions of meiofauna with all other benthic organisms, this ‘theorem of interconnection’, have often been disregarded or underestimated.

Meiobenthology has developed into a wide field, with more and more researchers studying cross-disciplinary aspects. This shift in perspectives motivated this book: a multifaceted compilation of contemporary meiobenthology. The aim is to give an integral view of this fascinating biological discipline, with emphasis on rapidly developing topics and techniques of future relevance.

Knowledge of meiofauna has expanded to such a degree that developing the expertise necessary to conduct meiobenthos research at the cutting edge of the entire discipline is virtually impossible. This, in combination with the increasing complexity of the questions addressed, means that on a collective level, meiobenthos research is becoming more cross-disciplinary and collaborative. On an individual level, researchers are required to consider the bigger picture, much of which lies well outside their specific area of expertise. The value of bringing together multiple disciplines, and of working at the intersections of disciplines, is that each brings to the table a unique and distinct set of tools and approaches.

Since the last compilation (Giere 2009), meiobenthology has advanced rapidly with the development of new methods and amazing progress in digitisation. New horizons for impactful research are emerging, as evident in the progress of freshwater meiobenthology (Majdi et al. 2020), and in the growing understanding of physiological and ecological processes affecting meiobenthos and their roles in aquatic ecosystems (Schratzberger and Ingels 2018). Accelerating environmental threats force us to adopt a wider cross-disciplinary perspective to gain a more comprehensive and integral understanding of ecosystems, using modern, sophisticated methods. These include computer-supported mathematics and models that can simulate the processes underlying nature’s responses to environmental dynamics and human-caused change, and require innovative experimental approaches to identify the factors affecting such responses.

This book does not aim to represent another textbook or a review covering all aspects of meiobenthology. Rather, it attempts to address and summarise recent progress in various fields of forthcoming importance, thus emphasising the role of meiofauna in the world of benthos. Scientifically rigorous, this compilation seeks, on the basis of well-founded knowledge, to outline new horizons for future meiobenthology. A selection of seminal chapters seeks to encourage future studies in this fascinating field. The initial chapters discuss general topics that frame the presence of meiofauna. These include evolutionary processes determining the diversification of meiobenthos, biochemical pathways underlying and driving meiobenthic life, the biofilms and their prokaryotic world forming the basis of all meiobenthic life, as well as molecular-biological processes determining bacteria-symbiotic interactions with meiofauna. The following chapter identifies the factors driving patterns of meiofauna diversity and distribution, and addresses the causes and consequences of shifts in those patterns. Demonstrating the numerous parallels in marine and limnetic meiobenthology, the ecological relevance of freshwater meiofauna is underlined within the complex network of organisms in different limnetic systems (streams, rivers, lakes). In a rapidly changing world, multifaceted ecological effects play a central role. Hence, the effects of the most widespread and persistent anthropogenic disturbances on meiobenthic species, populations and communities in the ocean are considered in a conceptually comprehensive central chapter. Corresponding to the introductory chapter, where the origins of meiofauna are reflected, the circle of chapters closes by emphasising the often extreme conditions under which these amazingly differentiated microscopic organisms exist, with the focus on adaptations of meiofauna in difficult to access or ‘exotic’ biotopes of high general relevance such as the deep sea, the polar regions and the often disregarded subterranean world.

The rapidly increasing knowledge of meiobenthos, both theoretical and applied, renders an attempt to cover these broad topics by a single-author book hardly possible. Therefore, in order to meet the ambitious goal of compiling a treatise that reflects the wide scope of contemporary meiobenthology, leading specialists in the various disciplines of meiobenthic research have come together to present the current state of knowledge, and outline directions for further research. The different background, perspectives and experiences of over thirty participating authors are reflected by the varying structure and style of the chapters. Despite, or maybe because of, this diversity, the chapters emphasise the shared curiosity, commitment and imagination of those who wrote them: curiosity to ask the scientific questions, commitment to interact with others to address those scientific questions in all their complexity and to offer answers, and imagination to move from listing data to generating understanding. We hope that the chapters, individually and collectively, inspire the next generation of meiobenthologists to pursue alternative lines of evidence, offer new interpretations of existing data, ask new questions, and find alternate explanations, all of which will help meiobenthos research to move forward towards new horizons.

Trying to create rather self-contained chapters, a certain overlap is not only unavoidable, but is welcomed to attain independent topical units. Succinct text sections are often supported by illustrations and compilations: figures, tables, flowcharts and graphs. This way, we hope to keep complex information manageable and, importantly, intellectually attractive. For ease of use, each chapter has its own, separate reference list. We are confident that the authors of this book, well known in their numerous often diverging research fields, achieve our common goal: stimulating and directing innovative and relevant future research and highlighting how and where meiobenthology can become integral to general benthology.

Conceptually, this book was conceived at the 17th International Meiofauna Conference in July 2019 in Évora (Portugal), where, during a memorable lunch break in the ‘refectory’ of a historic monastery, the first plans and suggestions found a markedly positive echo. Therefore, it is our pleasure to dedicate this work to Professora Helena Adão, the lead organiser of this inspiring conference.

Hamburg, Germany — Olav Giere
Lowestoft, UK — Michaela Schratzberger
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Contents

Chapter 1
Evolution of Bilateria from a Meiofauna Perspective—Miniaturization in the Focus

Katrine Worsaae, Jakob Vinther, and Martin Vinther Sørensen

Abstract Meiofaunal life forms are found all over the animal tree of life, and miniaturization seems to have occurred within otherwise macrofaunal clades multiple times. While sponges, comb jellies and cnidarians suggest a macroscopic ancestry for Metazoa, several phyla are exclusively meiofaunal, however, and may evidence a wider microscopic ancestry of some major groups, such as Ecdysozoa and Spiralia/Lophotrochozoa. This is an unsolved debate, which should be tackled from a synthesis of zoomorphological, palaeontological, molecular and phylogenetic approaches to test alternative scenarios. Advances in microscopic techniques have led to a renaissance in anatomical studies that allows for new and detailed examination of both extant and extinct meiofauna, revealing an unseen wealth of information. Likewise, the rapid development in genomic sequencing and analytical tools makes detailed reconstructions of meiofauna genomes feasible. The anticipated flood of new morphological and molecular data on meiofauna will broaden integrative and comparative studies and hopefully allow scientists of this generation to answer the long-debated questions of how the animal kingdom evolved and ramified into today's amazing diversity of life. In this enormously complex tree of life, what is the significance of minute creatures represented by meiofauna?

1.1 Introduction

Animals are the most diverse and disparate kingdom of multicellular organisms, thanks to their heterotrophic lifestyle, diverse feeding strategies and modes of

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motility. Animals, macroscopic or microscopic, have shaped in their evolutionary process the biosphere by developing complex ecosystems and habitats. This includes sediments, the seafloor and water column and even land and air. Meiofaunal animals contribute to ecosystems as primary consumers and recycle organic detritus in terrestrial soils and aquatic sediments. Microscopic animals capable of passing a 0.5 mm mesh and being retained on a 44 μm-mesh are categorized as meiofauna (Giere 2009; but see Ptatscheck et al. 2020). While juvenile macrofauna may belong to this category temporarily, a diversity of animal species and groups lives their entire life cycle as part of the "permanent" meiofauna. With several phyla being exclusively meiofaunal across the tree of life, meiofauna has been speculated to represent an archaic community from which bilaterian evolution started. If true, it would have ramifications for palaeobiological scenarios and body plan evolution (Vinther 2015). For example, the fossil record may not reveal the true origins of the earliest inceptions of metazoan life if too small to be preserved. Understanding the evolutionary drivers of animal diversity and disparity requires understanding the size and shared anatomy of ancestors.

Almost all major lineages in the tree of life contain meiofaunal representatives (Fig. 1.1), which attests to a clear adaptive trend towards a successful life strategy in spite of the several inherent constraints it also poses. Phylogenetic inference studies (bracketing) reveal that many meiofaunal groups, in particular those found within otherwise macroscopic phyla, have originated secondarily through miniaturization. Nonetheless, recent phylogenomic studies have found several meiofaunal phyla branching off at the deeper nodes of Bilateria and Spiralia/Lophotrochozoa (Fig. 1.1). These include the acoelomorph worms, which have been recovered as sister group to the remaining Bilateria (Cannon et al. 2016), as well as the Gnathifera consistently recovered as sister group to the remainder of Spiralia (Struck et al. 2014; Laumer et al. 2015a, 2019; Marlétaz et al. 2019). Moreover, within Ecdysozoa several microscopic phyla exist that subtend macroscopic branches (Laumer et al. 2015a, 2019; Borner et al. 2014; Campbell et al. 2011).

Could this imply that small body size may be ancestral for Bilateria? While microscopic phyla are widespread, a complicating factor is that each of these deep branching meiofaunal clades also accommodates extant macrofaunal taxa, i.e. (i) Xenoturbellida in Xenacoelomorpha, (ii) Chaetognatha and Acanthocephala in Gnathifera, (iii) Priapulida in Scalidophora and (iv) Nematomorpha and some Nematoda in Nematoida.

Can the fossil record, which will be in the focus of this chapter, be of any use in resolving these issues? Fossilization tends to favour macroscopic organisms, which is somewhat of a limitation but offers the possibility to reveal whether stem groups to microscopic phyla were once macroscopic. Still, there are some unique taphonomic windows preserving meiofauna that trace this lifestyle back in time, even to the Cambrian Explosion (Butterfield and Harvey 2012; Baliński et al. 2013; Harvey and Butterfield 2017). There are also some macroscopic fossil taxa that could be stem groups for some microscopic phyla (Peel et al. 2013).

Another perspective that complements morphology and the fossil record is the exploration of microscopic organisms at the genomic level. Body size and cell size

Fig. 1.1 Metazoan tree of life. Images showing meiofauna representatives of exclusively meiofaunal lineages, within macroscopic lineages (mixed with meiofauna), and representatives of exclusively macrofaunal lineages (original)

have been shown to sometimes correlate with genome size, e.g. in Copepoda and free-living flatworms, and loss of morphological complexity or features may be accompanied by changes in the genetic architecture. However, overall, genome size and architecture are highly variable and seemingly influenced by a range of different factors which are not easily linked to morphological miniaturization (Martín-Durán et al. 2021). Nonetheless, with the accumulation of genomic data on meiofauna organisms, functional and comparative genomics may yield new evolutionary insights.

Thus, several future frontiers exist for understanding the role of meiofauna in animal evolution. We here outline how this subject can be examined from multiple disciplines, including phylogenetics, comparative zoomorphology, genomics and palaeontology. We believe the answers should be sought through their synthesis.

1.2 Where to Find Meiofauna on the Metazoan Tree of Life?

Most of the exclusively meiofaunal organisms were historically lumped together in groups such as “Nemathelminthes” or “Aschelminthes”, suggestive of a common origin. However, it has become clear that the immense anatomical diversity among meiofaunal taxa is evidence for a wide phylogenetic distribution with clear indication of independent evolution in many cases. As modern phylogenetic approaches using genetic evidence have advanced to include meiofauna, testing of evolutionary relationships has further corroborated that meiofauna evolved through multiple evolutionary events across the tree of life (Nielsen 2012; Laumer et al. 2015a; Giribet and Edgecombe 2020) (Fig. 1.1).

When thinking of the origin of meiofaunal organisms in an evolutionary perspective, a robust phylogeny is crucial. Reconstruction of the tree topology allows for distinguishing between clades of exclusively meiofaunal organisms and clades accommodating both meio- and macrofaunal animals. In the latter case, we need to ask ourselves if these clades evolved from a microscopic or macroscopic ancestor, and also if enlargement or miniaturization happened multiple times within the clade. The deepest branches (more appropriately successive sister lineages) in the animal tree of life—the sponges, the placozoans, and the phylogenetically controversial comb jellies—do not accommodate any meiofaunal organisms. The first examples of meiofaunal clades appear within the cnidarian lineages where we find well-known meiofaunal hydrozoans such as *Halammohydra* and *Protohydra* (Schmidt-Rhaesa 2020a, b). Most cnidarian phylogenies support that Hydrozoa is a derived clade within Medusozoa (Bridge et al. 1995; Kayal et al. 2018). This suggests that ancestral cnidarians were macroscopic organisms, and that *Halammohydra*, *Protohydra* and other meiofaunal hydrozoans are results of miniaturization.

The remaining metazoans are united in the large clade Bilateria exhibiting bilateral symmetry and triploblastic bodies, i.e. with tissues derived from the three germ layers: endoderm, ectoderm and mesoderm. Biologically, we also see a shift from mainly a sessile benthic or passive pelagic lifestyle, towards free-living and actively moving benthic and pelagic animals. Being motile with a through-gut offers new modes of life and effective consumption. The rampant diversification of bilaterian phyla as evidenced by the fossil record in the earliest Cambrian (~541 ma) coincides with the first carnivores represented by grasping spines of chaetognath-like spiralians (Caron and Cheung 2019; Vinther and Parry 2019) as well as trace fossils attributed to priapulid-like ecdysozoans (Sperling et al. 2013). It is not unlikely that the emergence of predators kick-started an arms race forcing animals to quickly adapt, evolve new defence mechanisms and explore new habitats for resources or refuge. This shift in lifestyle and biology must be facilitated by anatomical architecture and genomic regulation. Hunting and escaping are contingent upon detection and speed. They result in centralization of nervous systems and formation of brains and ganglia and sensory organs (e.g. olfaction, mechano- and photo-sensing). This novel regionalization along the body axis is evidenced by expansions of transcription factors, such as the three *Hox* gene classes "*anterior*", "*central*" and "*posterior*". Whereas "*anterior*" and "*posterior*" are present in cnidarians also, "*central*" is present exclusively in bilaterians (Hejnol and Martindale 2009).

Bilateria are divided into the smaller clade Xenacoelomorpha and the diverse Nephrozoa that accommodates all remaining bilaterians. Xenacoelomorpha is a relative novelty in metazoan systematics and includes the two former flatworm groups Acoela and Nemertodermatida, and the enigmatic Xenoturbellida that also originally were considered to be flatworms (Westblad 1949). Xenacoelomorpha have been recognized as a monophyletic assemblage for about a decade, even though recent spermatological results might question the monophyly of the group (Buckland-Nicks et al. 2019). Also, it is still debated whether they are nested within Deuterostomia (Philippe et al. 2011, 2019) or are basal bilaterians (Hejnol et al. 2009; Cannon et al. 2016; Laumer et al. 2019). In the present chapter, we follow the early divergence hypothesis and consider Xenacoelomorpha as early bilaterians and as sister group to Nephrozoa (Fig. 1.1), but acknowledge that this debate is far from over.

Acoela and Nemertodermatida (collectively referred to as Acoelomorpha) include mostly meiobenthic species, and even though some species may grow to a centimetre in body length, it is fair to consider the group meiofaunal. Species of Xenoturbellida, on the other hand, are all macroscopic and divided into a group of smaller (2–5 cm) shallow water species and another taxon with considerably larger (10–25 cm) deep-sea species (Rouse et al. 2016). This leaves it uncertain whether the acoelomorphs evolved and miniaturized from a macroscopic ancestor, or if Xenacoelomorpha represents an ancestrally meiofaunal clade. With a possible sister group relationship to all other bilaterians, this question is obviously an important one to resolve.

Nephrozoa is divided into the two well-supported clades Deuterostomia and Protostomia—a classification that was already recognized by Haeckel (1866). The deuterostomes include predominantly macrofaunal clades like echinoderms, hemichordates and chordates, whereas occasional meiofaunal species, such as the meiobenthic enteropneust *Meioglossus psammophilus* (Worsaae et al. 2012), appear to be the result of miniaturization. The vast majority of diversity is contained in the other nephrozoan clade, the Protostomia, which is divided into the two large clades Ecdysozoa (8 phyla) and Spiralia (> 14 phyla) (Fig. 1.1).

Ecdysozoa is a very well-supported clade, supported by target gene phylogenies, more comprehensive phylogenomic studies, as well as several robust morphological autapomorphies (Eernisse et al. 1992; Giribet et al. 2000; Hejnol et al. 2009; Holton and Pisani 2010; Mallatt et al. 2010). The latter includes the moulting of cuticle induced by the steroidal hormone ecdysone, the loss of a ciliary primary larva, which has been replaced by either direct development or secondary larvae, and the loss of feeding and locomotory cilia. Morphology suggests that the ecdysozoans can be subdivided into the predominantly meiofaunal clade Cycloneuralia with organisms characterized by the presence of a ring-shaped brain that wraps around the pharynx. This clade includes the groups Nematoda and Nematomorpha (collectively Nematoida) and Kinorhyncha, Priapulida and Loricifera (collectively Scalidophora) (Figs. 1.1 and 1.2).

The remaining ecdysozoans form the clade Panarthropoda, uniting Tardigrada, Onychophora and Arthropoda. Phylogenomic analyses are still indecisive about the relationships within Ecdysozoa. Especially nematodes and tardigrades often tend to obscure the analyses, since, here, they can appear as sister taxa (e.g. Hejnol et al. 2009; Laumer et al. 2015a), which is difficult to accept from a morphological point of view. However, these analyses often suffer from a biased taxon sampling with an overrepresentation of arthropods and nematodes, whereas other taxa, such as kinorhynchs and loriciferans, have been under-sampled, represented by single species, or in certain cases not included at all. Furthermore, nematodes and tardigrades are long-branched terminals in molecular phylogenies. Their higher molecular substitution rates can be hard to model and accommodate for. But when accounting for such artefacts, minimizing potential long-branch attraction, nematodes and tardigrades do not form a clade (e.g. Rota-Stabelli et al. 2013; Borner et al. 2014).

Despite the phylogenetic uncertainties, it would be fair to speculate about the common ancestor of all Ecdysozoa to be of meiofaunal size, since

- Tardigrada may be a sister to all other panarthropods;
- Scalidophora is dominated by two entirely meiofaunal phyla, Kinorhyncha and Loricifera;
- Priapulida include meiofaunal (or at least “close to meiofaunal”) genera such as *Tubiluchus*, *Meiopriapulus* and *Maccabeus*;
- Nematoida accommodate the entirely macrofaunal and endoparasitic nematomorphs, but also the nematodes in which deep branching clades are meiofaunal free-living animals (De Ley and Blaxter 2002);
- Nematoda as trace fossils have been dated back to the Early Ordovician (470 million years ago (Mya) (Baliński et al. 2013)) or even Late Ediacaran (555–542 Mya) (Poinar 2011; Parry et al. 2017), while also molecular analyses have pointed to an origin of nematode evolution at roughly 500–550 Mya (Rota-Stabelli et al. 2013; Vanfleteren et al. 1994).

However, meiofaunal origins are contradicted by the rich macrofaunal ecdysozoan fossil fauna. The fossil record includes famous Cambrian signature animals like the stem euarthropods *Opabinia*, *Anomalocaris* and *Pambdelurion*, a variety of macroscopic lobopodian-grade total group panarthropods. Several bona fide scalidophoran fossils exist, including the fauna of palaeoscolecid worms that could be cycloneuralian, scalidophoran or even nematoid/panarthropod stem groups (Dzik and Krumbiegel 1989; Yang et al. 2020). For the mixed meio- and macrofaunal Priapulida, we also know several macroscopic stem group species, such as the well-known Cambrian *Ottoia prolifica*. Even the entirely meiofaunal phylum Loricifera might have had macroscopic ancestors, as suggested by the more than 120 mm long *Sirilorica,* proposed as stem group loriciferan (Peel et al. 2013). The occurrence

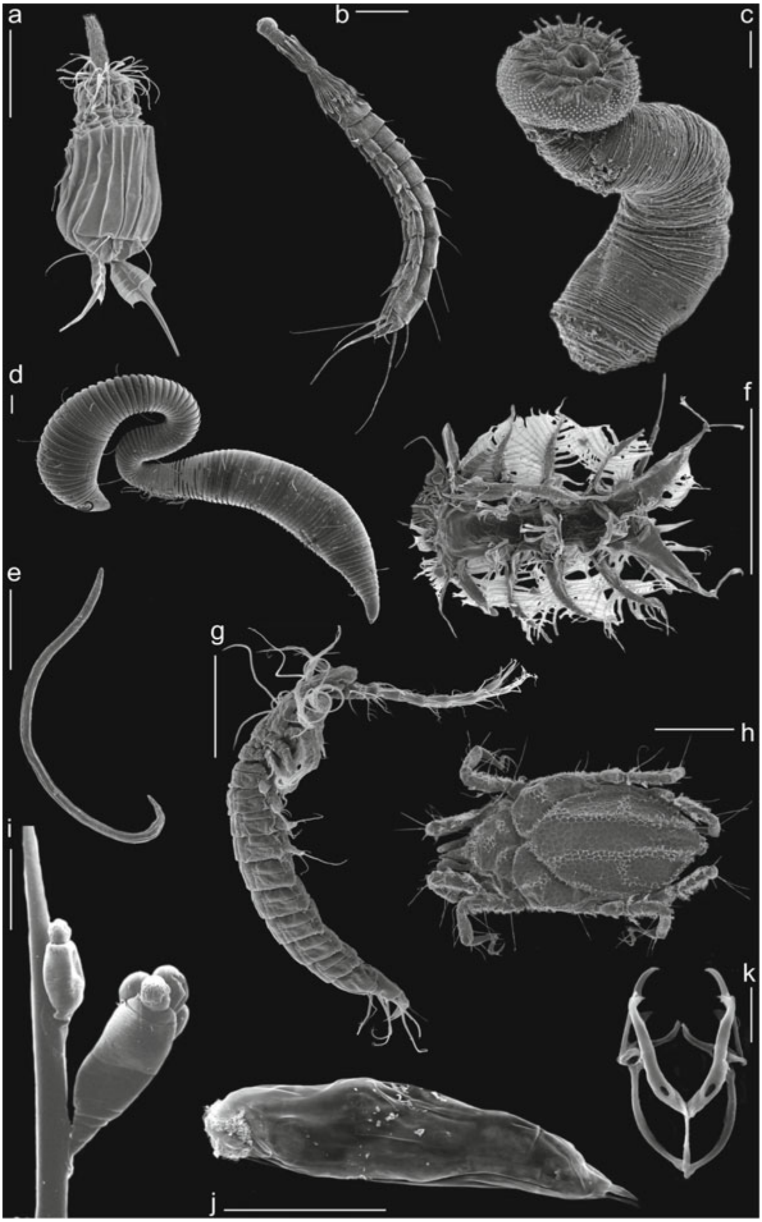

Fig. 1.2 Scanning electron micrographs on meiofauna (originals unless other stated) **a** Loricifera: *Armorloricus elegans*, Higgins larva; **b** Kinorhyncha: *Triodontoderes anulap*; **c** Priapulida: *Meiopriapulus fijiensis;* **d** Nematoda: *Epsilonema* sp.; **e** Nematoda: *Thalassomonhystera vandoverae*; **f** Tardigrada: *Neostygarctus oceanopolis*; **g** Mystacocarida: *Derocheilocaris remanei* (photograph credits: Jørgen Olesen); **h** Halacaridae: *Acarothrix grandocularis*; **i** Cycliophora: *Symbion americanus*, feeding stages (photograph credits: Matthias Obst); **j**, **k**. Rotifera: *Encentrum astridae*, whole animals + jaws. Scale bars: a, d, k, 10 µm; b, c, e–j, 100 µm

of macroscopic stem group species obviously does not necessarily refute a meiofaunal origin of Ecdysozoa, but then they should be considered as representing tips on the phylogenetic tree. But we should always ask ourselves how the "meiofauna hypothesis" would look like if those macroscopic lineages had survived until today. Among arthropods, which (arguably) were ancestrally macroscopic, there are several independent switches to meiofaunal modes of life.

The other large protostome clade, Spiralia, is supported by a stereotypical cleavage pattern during the early embryology, the so-called spiral cleavage. This character is not uncontroversial because many spiralian species have modified/different cleavage patterns. Moreover, the embryology is still only known from a restricted number of representatives, some of which show deviation from the spiral cleavage pattern (Hejnol 2010; Martín-Durán and Marlétaz 2020). However, Spiralia are also well-supported in phylogenomic analyses (Laumer et al. 2015a, 2019; Marlétaz et al. 2019), and there are no reasons to question its monophyly. The basal branching order in Spiralia has been a topic of intense debate during the last decade, but we are moving closer to a consensus by consistently identifying the Gnathifera as the sister group to all other Spiralia. Gnathifera accommodates the two exclusively meiofaunal phyla Gnathostomulida and Micrognathozoa, plus the Rotifera that includes free-living meiofaunal organisms and the derived clade of macroscopic, endoparasitic Acanthocephala (Figs. 1.1 and 1.3). Gnathifera is morphologically well-supported by the presence of chitinous pharyngeal mouth parts, forming a jaw apparatus, in which the central forceps-like elements appear with the same tubular ultrastructure (Rieger and Tyler 1995; Kristensen and Funch 2000). Such jaws are present in all gnathiferans, except the acanthocephalans, which have lost them together with their mouth opening as an adaptation to an endoparasitic lifestyle.

While it remains uncertain whether spiralians derived from meiofaunal ancestors, up to now it appeared reasonable to consider the gnathiferan ancestor as meiofaunal. However, recently even this hypothesis became weakened by new studies demonstrating phylogenetic affinities between gnathiferans and chaetognaths. The phylogenetic position of Chaetognatha has been contentious in both molecular and morphological studies. Until recently, it was even disputed to which of the top clades they belong, to the deuterostome or protostome branch? However, recent studies revealed that the *Hox* protein gene *MedPost*, that so far had been considered unique for chaetognaths, is present in rotifers as well, suggesting a closer relationship (Fröbius and Funch, 2017). This affinity was confirmed by a subsequent transcriptomic phylogenetic study, which substantiated the relationship between Chaetognatha and the gnathiferan taxa (Marlétaz et al. 2019; Laumer et al. 2019) (Fig. 1.1). Additional evidence is provided by the fossil record with studies suggesting that the Cambrian taxon *Amiskwia* was equipped with internal, pharyngeal hard parts that could be homologized with the gnathiferan jaws (Caron and Cheung 2019; Vinther and Parry 2019) and, thus, representing a taxon with a combination of gnathiferan and chaetognath characters (see further discussion below in Sect. 1.6.1). With Chaetognatha accommodating a mix of nearly microscopic, i.e. millimetre long, planktonic species and much larger, up to 12 cm long benthic species, it becomes uncertain whether

Fig. 1.3 Light micrographs of meiofauna. Anterior end pointing to the left or upwards. **a** Cnidaria: *Halammohydra* sp. **b** Hemichordata: *Meioglossus psammophilus.* **c** Nemertea: *Cephalothrix* sp. **d** Entoprocta: *Loxosomella* sp. **e** Gastrotricha: *Xenotrichula velox*. **f** Micrognathozoa: *Limnognathia maerski*. **g** Rotifera*: Seison nebaliae*. **h** Gnathostomulida: Onychognathiidae sp. **i** Mollusca: *Helminthope* sp. **j** Annelida: *Diurodrilus* sp. **k** Annelida: *Pharyngocirrus* sp. **l** Platyhelminthes: *Acanthomacrostomum* sp. **m** Platyhelminthes: *Schizorhynchidae* sp. Abbreviations: ag, adhesive glands; e, eye; j, sclerotonized jaws; s, calcareous spicule in body wall; sc, scale; p, proboscis; at, adhesive tail. Scale bars: a–e, g–m. 100 µm; F. 10 µm (originals)

gnathiferans derived from meio- or macrofaunal ancestors and it will also depend on the exact phylogenetic placement among the other gnathiferans.

Further muddying the waters, it is the fact that remaining spiralian taxa are still not fully resolved. While Marletaz et al. (2019) place the gastrotrichs among the lophophorates, several other phylogenomic studies recovered a sister group relationship between Platyhelminthes and Gastrotricha—a clade referred to as Rouphozoa (Struck et al. 2014; Laumer et al. 2015a) (Fig. 1.1). Whereas all gastrotrichs are meiofaunal, we have much more size variation within Platyhelminthes, and especially the parasitic Neodermata can grow to considerable sizes. However, platyhelminth phylogeny is relatively well-understood, and the deepest branches within the phylum are represented by free-living, meiofaunal flatworms (Laumer et al. 2015b). This would suggest that the rouphozoan ancestor was meiofaunal.

The phylogenetic relationships get more blurred as we move further into Spiralia. A potentially monophyletic, but yet disputed clade, is the Polyzoa that accommodates Cycliophora, Bryozoa and Entoprocta (Fig. 1.1). Whereas all cycliophoran life stages are exclusively meiofaunal, and entoprocts balance right at the limit between meio- and macrofaunal, bryozoans form colonies that definitely are macroscopic, even though the single individuals in the colonies have meiofaunal size, perhaps except for the Phylactolaemata. The polyzoan phyla are often recovered together with two other lophophore-bearing phyla, the brachiopods and phoronids. As such, the particular sessile and lophophore-bearing morphology could have evolved only once in a common ancestor to a clade that is termed Lophophorata. But this may still be premature since both Polyzoa and Lophophorata are highly sensitive to the phylogenetic reconstruction methods and data used (Laumer et al. 2019; Marlétaz et al. 2019). Hence, it requires further studies and careful examination of previous studies to reconstruct the evolution of size and life strategy among the lophophorates.

The remaining spiralians are dominated by the two diverse phyla Mollusca and Annelida alongside Nemertea (Figs. 1.1 and 1.3). Their interrelationship is highly controversial (Laumer et al. 2015a, 2019). While meiofaunal representatives occur in most major molluscan lineages, phylogenetic bracketing and the fossil record clearly show that molluscs successfully evolved and radiated as a macrofaunal body plan. The most successful diversification of meiofaunal molluscs happened within the Aplacophora, in which the majority of the ca. 425 species are smaller than a few millimetres (Bergmeier and Jörger 2020). Morphological hypotheses had for a long time been influencing hypotheses for how the ancestral mollusc may have looked like, with either monoplacophorans or aplacophorans being the most ancestral representative among living species, and thus representing the “Urmollusk”. Molecular phylogenetic studies now corroborate a topology in which two major clades exist, the Aculifera and the Conchifera (Vinther et al. 2012; Kocot et al. 2020). Fossil evidence shows that aplacophorans evolved from ancestors with a slug-like appearance and eight overlapping shell plates, like polyplacophorans today (Vinther et al. 2012). The fossil record suggests that the molluscan common ancestor was slug-like, covered by sclerites and harbouring a single valve, while taxa such as the naked *Odontogriphus* and sclerite-covered *Wiwaxia* with their more primitive radula resolve as stem group molluscs (Vinther et al. 2017).

The other major Spiralian phylum, the Annelida, also shows huge diversity, morphological variation, and size ranges from less than 500 µm and up to 3 m. Annelida is perhaps the phylum presenting the highest number of independent miniaturization events—within orders, families and genera across the annelid tree (Worsaae 2020; Worsaae et al. 2021). Exclusively meiofaunal (or interstitial) annelid families have been, for a period, grouped as "archiannelids" and discussed to represent a successive sister group (often incorrectly termed a "stem group") from which the macrofaunal lineages had evolved (e.g. Hermans 1969). However, both morphological and later phylogenomic data have disputed the similarity and common origin of the meiofaunal families. Although their exact positions in the annelid tree are not conclusively resolved, all deep branching annelid clades are macrofaunal (Andrade et al. 2015; Laumer et al. 2015a, b; Struck et al. 2015; Helm et al. 2018; Martín-Durán et al. 2021). Also the Cambrian fossil record comprises several macroscopic stem lineages (Parry et al. 2016; Vinther et al. 2011) plus even an early, macroscopic, crown group member attributable to the palaeo-annelids (Chen et al. 2020).

1.3 Do Common Structural and Functional Traits Exist in Meiofauna?

Whereas size and diameter, in particular, define an animal as meiofaunal, other similar features (or absences) frequently occur. From an ecological perspective, the highest diversity of meiofauna is found in soft sandy sediments. This environment is generally referred to as the interstitial realm. Pore spaces between the sand grains restrict the feasible diameter (but not the length) of its inhabitants. Therefore, the body shape is often elongated, and body appendages are either absent or reduced in number or length, as they become disadvantageous for moving between sand grains (Figs. 1.2 and 1.3). Interstitial organisms move by muscular contractions (ecdysozoans) or ciliary gliding (acoels and spiralians), and many groups possess specialized adhesive structures, such as duo-glands, tails, toes, claws or suction discs (Fig. 1.3) (Giere 2009 and references herein).

Whether related to inherent, developmental or spatial constraints, coelomic cavities are often lacking or less developed in meiofauna—especially among meiofaunal phyla. Originally thought to have evolutionary and phylogenetic bearing, the phylogenetic distribution of coeloms, as we currently understand the tree of life, reveals them as being highly interchangeable and their development easily being suppressed (Bartolomaeus et al. 2009). Also, mesodermal tissues and organs are often missing (e.g. blood vascular system) or developed in a less complex state (in, e.g. nephridia and gonoducts) (Bartolomaeus and Quast 2005; Worsaae and Kristensen 2005; Schmidt-Rhaesa 2007).

The neural architecture in meiofauna is often comparably simple, e.g. showing a reduced number of cord commissures and glial cells, the brain lacking mushroom bodies or distinct regionalization and less complex sensory organs such as eyes

(Schmidt-Rhaesa et al. 2015; Bekkouche and Worsaae 2016a, b; Kerbl et al. 2016a; Gąsiorowski et al., 2017). This lack of structural complexity may be compensated for by a higher diversity of neurotransmitters (Kerbl et al. 2017; Martín-Durán et al. 2021).

Asexual reproduction, hermaphroditism and internal fertilization are fairly common among meiofauna (Giere 2009; Worsaae et al. 2012, 2020, 2021; Fontaneto 2019). Most meiofaunal groups exhibit direct development. With their small body size, the numbers of eggs are often limited, eggs may be adapted for desiccation prevention (Guil 2011), or embryos may be nursed through brooding (Giere 2009; Schmidt-Rhaesa 2020a, b).

For many of these organ systems, there is a clear relationship to size—whether it is rheological properties of water or the volume dependency on gas and nitrogen exchange. Being smaller often also means having fewer cells (Loriciferans is a notable exception), which limits the complexity of organs. These organ systems may therefore primarily reflect body size rather than reveal evolutionary relationships. Some of these traits also resemble those of larval or juvenile stages of macrofauna where organ systems such as nephridia, coeloms or nervous systems may not yet be fully developed, indicative of their dependence on size. None the less, the anatomical resemblance of macrofaunal larvae and juveniles to several meiofaunal groups may still hold clues to the evolutionary trajectories that lead to miniaturization.

It is clear that miniaturization is a frequent phenomenon that has happened convergently in most animal phyla. However, with (i) the many exclusively meiofaunal phyla, (ii) the current phylogenetic uncertainty and iii) the incomplete morphological, genomic and palaeontological records, much remains to conclusively establish the true antiquity of any meiofaunal taxon as well as the evolutionary role of miniaturization.

1.4 Pathways Towards a Secondarily Miniaturized Body

Although some meiofauna lineages may represent ancestrally small body designs, multiple meiofaunal taxa are indisputably nested within phylogenetic clades of macroscopic phyla or families (e.g. within Annelida; Laumer et al. 2015a; Struck et al. 2015; Worsaae et al. 2018, 2021; Worsaae 2020) and must hereby represent coincidences of regressive evolution in the form of miniaturization (Hanken and Wake 1993). Highly diversified evolutionary pathways may lead to a miniaturized outcome, the two overall theoretical pathways being either a "stepwise" miniaturization or a "one-step" miniaturization (Westheide 1987). Whereas the first evolutionary theory relies on independent mutations, losses and gains in an adaptation to a new niche, the latter theory suggests an evolutionary short-cut through heterochrony, leading to paedomorphosis (underdevelopment) (e.g. Garstang 1922; Gould 1977). The outcome is characterized by "paedomorphic" traits, theoretically resembling those of a juvenile ancestor (inferred from juvenile characteristics of closely related macrofaunal taxa) (Martynov et al. 2020).

1.4.1 Paedomorphosis

Paedomorphosis is usually considered to be the outcome of one of three underlying processes (Smith 2001; McNamara 2012), all of which involve changes in developmental rate or timing:

progenesis: an early offset of development
neoteny: a decelerated rate of development
postdisplacement: a late onset of development.

The theory of progenesis has been discussed and specified by Gould (1977), Smith (2001) and McNamara (2012) (and should be prioritized to "hypomorphosis" as named by Reilly et al. 1997). The early offset of somatic growth is often proposed to be coupled with or even caused by an early or accelerated sexual maturation (e.g. Westheide 1987), because many animals arrest their somatic growth when sexually maturing. Progenesis has been a popular explanation for the origin of the small-sized meiofauna taxa, especially those that show resemblance to larval or juvenile stages of macrofaunal taxa (Westheide 1987; Worsaae and Kristensen 2005). Since many macrofaunal taxa already have a temporary meiofaunal larval or juvenile life stage, it would "only" take a fast sexual maturation and successive arrest of somatic development to become part of the permanent meiofauna.

The two other scenarios cannot as easily explain meiofauna origin since they do not infer an overall reduction of somatic growth and size. Neoteny has been often used as an explanation for delayed development or retention of juvenile features into adulthood, e.g. the hairless body and slow development of humans compared to non-human primates (e.g. Rice 2002). Postdisplacement characterizes features that are delayed in their development relative to their ancestor and may not be completed when the descendant reaches maturity.

However, neither of these three scenarios can be clearly defined since they do not reflect the evolutionary and genetically controlled processes per se, but rather the appearance of the descendant's morphology. Moreover, these theoretical changes can morphologically act on a complete scale (entire organism) or a local scale (selected tissues or characteristics), which further complicates their definition and mutual distinction. Finally, with the increasing knowledge of the genetic mechanisms controlling development, it seems likely that a variety of genetic changes or modifications of regulatory networks may lead to a paedomorphic phenotype. Hence, it is rarely possible to predict the specific evolutionary process leading to a paedomorphic meiofaunal taxon, when judging from comparative phenotypic traits and the phylogenetic context. So, one may be restrained to using the common descriptive term "paedomorphosis", rather than more refined terms of hypothetical processes (Martynov et al. 2020).

1.4.2 Genetic Mechanisms Underlying Paedomorphosis

Meiofaunal taxa (e.g. within Annelida, Tardigrada, Rotifera, Gastrotricha and Nematoda) often possess small-sized genomes (*C. elegans* Sequencing Consortium 1998; Gregory et al. 2000, 2007; Hashimoto et al. 2016; Yoshida et al. 2017, Martín-Durán et al. 2021). Yet, several macrofaunal and parasitic taxa also exhibit tiny genomes (Seo et al. 2001; Slyusarev et al. 2020; Martín-Durán et al. 2021 and references herein), whereas the simple-looking meiofaunal acoels have relatively large genomes (Arimoto et al. 2019) exceeding the size of their macrofaunal sister group Xenoturbellida (Gregory et al. 2007). Thus, genome size is clearly highly variable, and so far, it has not been possible to link specific genetic changes with the origin of paedomorphic meiofauna.

Reconstructing such potential genetic changes on an evolutionary scale is challenging. The general lack of closely related macrofaunal and meiofaunal sister species hampers comparative genomic studies, and the complexity of genetic interplay and control during development are ever amazing. Moreover, changes affecting a variety of developmental processes such as cell division and differentiation may lead to evolutionary paedomorphosis, although these mechanisms are not directly controlling the timing of explicit events (Moss 2007). In this context, a recent genomic study (Martín-Durán et al. 2021) of the miniaturized meiofaunal annelid, *Dimorphilus gyrociliatus*, revealed a miniaturized, highly compacted and conserved genome with a few gene losses explaining the change of certain morphological structures. Interestingly, this genome also presented a divergent *Myc* pathway, which is a key physiological regulator of growth, proliferation and genome stability in animals.

Relevant genetic insights into miniaturization might be gained from intraspecific studies of species exhibiting sexual dimorphism in the form of paedomorphic males (Vollrath 1998), such as the finding of sex-specific expression patterns of metamorphic genes in the insect *Xenos vesparum* (Chafino et al. 2018). Meiofaunal, miniaturized males are found in, e.g. annelids, cycliophorans or rotifers (Ricci and Melone 1998; Obst and Funch 2003; Worsaae and Rouse 2010; Kerbl et al. 2016b), and comparative molecular studies of their dimorphic sexes will likely be informative.

Also, experimental approaches exploring distinct timing mechanisms have turned out to be very promising. Especially *Caenorhabditis elegans* with its meticulously mapped genome and engineering options has facilitated striking discoveries, especially of "heterochronic genes" orchestrating developmental timing (e.g. lin-4 and lin-28) (e.g. Ambros and Horvitz 1984; Thummel 2001; Moss 2007). Although timing mechanisms may not exist to regulate all aspects and scales of development, their presence is supported by the discovery of the "heterochronic genes" in *C. elegans.* These genes not only prove the existence of an explicit regulation of developmental timing but may also aid to achieve synchrony and succession of developmental events, such as emergence of patterns and organ formation (Moss 2007 and references herein). Although timing may also emerge from other aspects of developmental regulation, the genetic or epigenetic changes in the "heterochronic genes" may affect pathways not too different from the evolutionary heterochrony scenarios hypothesized to cause paedomorphosis.

No doubt, with all these potential evolutionary trajectories towards paedomorphosis, it will be challenging to establish genetic causality through comparative analyses. Yet, the technical progress in morphology, phylogenomics and comparative genomics is now opening a window for a broader and integrative search for the genetic causality of paedomorphosis.

1.5 What Can the Fossils Tell Us?

To understand body plan evolution, much can be learned from looking at the tree of extant life. For example, sponges share traits with the animal sister group, the choanoflagellates, and have less differentiated tissues and organs than eumetazoan taxa. More often, however, extant diversity is a poor representation of a lineage and its trajectory as it splits from its sister clade. Hence, the fossil record would be the only testament. To illustrate this, birds and crocodiles are morphologically distinct, but are sister taxa. By comparing their extant diversity, one could never establish how birds became birds. Their ancestral ecology can only vaguely be pondered about, and even the way some branches evolved to fill unique roles in the past (e.g. giant quadruped herbivores or the independent evolution of flight in pterosaurs) would be but a fantasy. Returning to meiofauna, how representatives are living clades for reconstructing their origin? Extant phylogenetic bracketing (Witmer 1995) may help to establish shared antiquity between clades and, along with molecular clock estimates, could help to date the minimal temporal origin (e.g. Rota-Stabelli et al. 2013).

However, there may still be long branches between meiofaunal clades and their split to their nearest extant sister taxon. Palaeontological evidence is therefore of importance for complementing the neontological framework. As with any other line of evidence, palaeontological data come with its strengths and its weaknesses. Fossils typically preserve limited aspects of an organism, even under truly exceptional circumstances. Furthermore, available windows into the past are scattered and feature their own biased set of filters governing what is recorded, where and how. Charismatic fossils are of course macroscopic, but in fact there is a just as diverse fossil record documenting bacteria, pollen, single-celled eukaryotes and indeed even microscopic animals such as meiofauna (Fig. 1.4). Hence, to appreciate what the fossil record has revealed and what may be in store is key to appreciate taphonomical pathways.

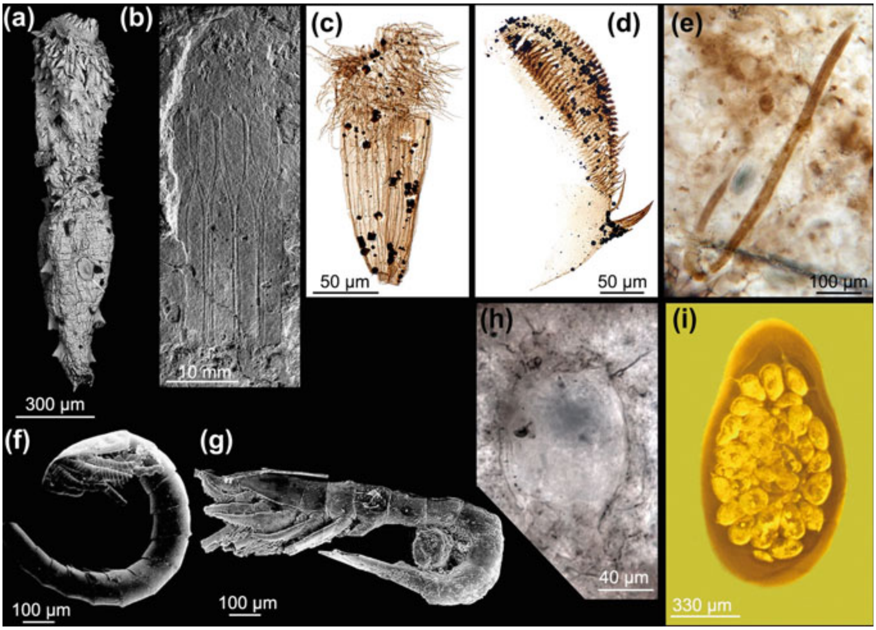

Fig. 1.4 Taphonomic windows and fossil representatives of meiofauna and putative stem groups. **a**, **f**, **g** Orsten-type preservation. **c**, **d** Small carbonaceous fossils. **e** and **i**: Chert and **h** Amber. **a** The putative stem group kinorhynch, *Eokinorhynchus rarus* from the Early Cambrian (~535 million years old) Xinli section, Sichuan, China. **b** The macroscopic stem group loriciferan, *Sirilorica carlsbergi* from the Early Cambrian (~518 million years) Sirius Passet Lagerstätte, North Greenland. **c** The meiofaunal loriciferan *Eolorica deadwoodensis* from the Late Cambrian Deadwood Formation (485–497 million years old). **d** Mandible of anostracan grade crustacean from the Late Cambrian Deadwood Formation (485–497 million years old), Saskatchewan, Canada. **e** The nematode *Palaeonema phyticum* from the Early Devonian (~410 million years old) Rhynie Chert, Scotland. **f** The pancrustacean *Scara anulata* from the Late Cambrian (485–497 million years old) Alum shale, Kinnekulle, Sweden. **g** The pancrustacean *Martinsonia elongata* from the Late Cambrian (485–497 million years old) Alum shale, Kinnekulle, Sweden. **h** A putative rotifer from the Middle-Late Jurassic hot spring-cherts of the Deseado Massif, Patagonia, Argentina. **i** The rhabdocoel flatworm *Palaeosoma balticus* from the Eocene (~40 million years old) of the Kaliningrad region, Russia. Image credits and courtesy: **a** open access CC 4.0; **b** Tae Yoon Park, Korean Polar Research Institute; **c** Nicholas Butterfield and Thomas Harvey, Cambridge and Leicester University; **d** Nicholas Butterfield, Cambridge University; **e** George Poinar Jr.; **f**, **g** Palaeontological Research Open Access https://doi.org/10.2517/prpsj.7.71; **h** Juan Garcia Massini; **i** George Poinar Jr

1.5.1 Taphonomy and Windows to Preservation of Meiofauna

Taphonomy is the study of fossil preservation. Whereas trace fossils support the presence of meiofaunal bilaterians already in the Late Ediacaran, these burrow morphologies can only provide limited information on the animal creating them (Parry et al. 2017). On the other hand, fossils most often comprise only the most resistant remains, such as biomineralized bones and shells, yet under the right circumstances, it is possible to preserve more delicate tissues that are more decay-prone (Parry et al. 2018). Several conditions and burial pathways may facilitate exceptional preservation. Most universal is the need for rapid burial and anoxia, slowing down decay and disarticulation. The rapid formation of an impermeable environment and alternative anaerobic metabolic pathways generate steep chemical gradients that can cause mineralization around, or within, carcasses and stabilization of more labile organic molecules (Parry et al. 2018). A couple of taphonomic windows have been particularly instrumental in tracing meiofauna back in time and are the result of very different mechanisms for high fidelity preservation. For more ancient marine records, these include the Orsten localities and the Small Carbonaceous Fossil (SCF) window. For younger occurrences, hydrothermal vent cherts (Poinar et al. 2008; Massini et al. 2016; Dunlop and Garwood 2018) and amber (Waggonar and Poinar 1993; Bertolani and Grimaldi 2000; Huys et al. 2016; Poinar and Nelson 2019) have been crucial windows into terrestrial and limnic environments.

1.5.1.1 Orsten Preservation

During the Cambrian period, diagenetic phosphate deposition was a widespread phenomenon. The phosphate precipitated on the seafloor as the sediment became anoxic and reducing, often replacing or infilling minute skeletons of various mineralogical nature, but also soft tissues such as coprolites and certain meiofauna. When encountered in limestones, phosphatic microfossils can be extracted using weak acetic acid.

Most phosphatic microfossils are skeletal and are not considered particularly exceptional (termed small shelly fossils). However, the discovery of soft-bodied organisms preserved at cuticular and even cellular fidelity is more notable. The first and best-known occurrence is the Orsten fauna, from the Late Cambrian alum shale across the Baltic craton, but mainly from Kinnekulle in Sweden (Müller and Walossek 1985; Waloszek 2003; Maeda et al. 2011). Older and younger occurrences now extend this window back to the Earliest Cambrian (Dong et al. 2005; Zhang et al. 2007, 2015; Han et al. 2017; Shao et al. 2018) and up into the Ordovician (Siveter et al. 1995).

Famous Orsten fossils comprise various panarthropods (Euarthropoda, Onychophora and Tardigrada and the descendants of the common ancestor) in articulation although their delicate nature often leads to disarticulation upon extraction from the rock. Pancrustaceans (all crustacean lineages plus hexapods) are the most diverse and abundant faunal elements (Fig. 1.4f, g) and often include both adult stages and nauplius larvae and intermediates. The pancrustacean fauna allows for tracing several lineages back to the Cambrian (Branchiopoda, Cephalocarida, Thecostraca and Pentastomida). In contrast, Burgess Shale-type deposits preserve macroscopic organisms and document several abundant stem and crown euarthropods, but no apparent crown group pancrustaceans. The fossil record is a strong indicator for pancrustaceans having ancestrally been small-bodied members of the zooplankton and meiobenthos.

Non-euarthropod microfossils also occur in the Orsten window, including lobopodians (Maas et al. 2007a, b; Zhang et al. 2016), tardigrades (Maas and Waloszek 2001) as well as some cycloneuralians with putative nematode and kinorhynch affinities (Fig. 1.4a) (Dong et al. 2005; Maas et al. 2007a, b; Zhang et al. 2015; Shao et al. 2018) and the extinct palaeoscolecids (Dong et al. 2013). The prevalence of ecdysozoan microfossils underlined some of the potential biases inherent with Orsten-type preservation. The chitinous cuticle of ecdyzosozoans may make these either more prone to phosphatization or more resistant to rapid decay for time periods long enough to enter the conditions leading to phosphatization within the sediment. Cellular details also occur in some of the oldest deposits (Dong et al. 2004), preserving embryos of mainly cnidarian affinities (Dong et al. 2013) as well as their chitinous periderm. Some peculiar organisms still await further scrutiny, such as the putative deuterostome *Saccorhytus* (Han et al. 2017), which has been used as evidence for a microscopic ancestry of deuterostomes (but see Liu et al. 2022).

1.5.1.2 Small Carbonaceous Fossils

Organic preservation is not uncommon in the fossil record (e.g. coal, oil and gas are the products of buried fossil organic matter) and includes microfossils. Since organic material is essentially carbon dioxide that has been reduced to form larger molecules, the key is to protect organic molecules from enzymes, oxidation and hydrolysis. However, different organic molecules are more likely to degrade or be consumed faster and may never survive to enter the geological record. Most unstable are nucleic acids (DNA/RNA) and peptide chains (proteins), while a range of more robust organic molecules have a survival potential, including long-chained hydrocarbons and lipids, such as waxy substances or cholesterol/hopanoids and large, cross-linked/polymerized molecules such as melanin, lignin and sporopollenin (Ellington and Logan 1991; Parry et al. 2018). The latter class of molecules explains the prevalence of pollen and plant material occurring as microfossils and melanin associated with exceptionally preserved skin, hair and feathers in vertebrates (Vinther et al. 2008; Vinther 2020). Chitinous tissues also preserve and occur as microfossils (Butterfield and Harvey 2012). Chitin is less stable, however, and seems to preserve mainly through secondary cross-linking with lipids in the pore water fluids to form kerogen (Stankiewicz et al. 1998, 2000). As organic material is buried, the increasing pressure and temperature lead to both fragmentation and condensation reactions, generating oil and gas and more stable coke, eventually becoming graphite. For these reasons, organic microfossils are generally obtained from fairly shallow-depth deposits where they retain some volume and are not too brittle from having been cooked.

Small Carbonaceous microfossils (SCF) have been described from a range of Early and Mid-Cambrian sites preserving sponge spicules, chaetognath grasping spines, wiwaxiid sclerites, polychaete chaetae and scales, various cuticular fragments, scalidophoran scalids and arthropod limb elements (Stankiewicz et al. 1998; Slater et al. 2018a, b).

As with the Orsten window, the SCF window yields pancrustaceans (Fig. 1.4d) and corroborates their meiofaunal ancestry, documenting appendages reminiscent to modern branchiopod filtering elements and copepod mandibles (Harvey et al. 2012; Harvey and Pedder 2013). While most scalidophoran and ecdysozoan microfossils are elements derived from macroscopic organisms (Caron et al. 2013; Smith et al. 2015), a remarkable discovery of a fully articulated and microscopic loriciferan with lorica (Fig. 1.4c), introvert and scalids from the Late Cambrian Deadwood formation (Harvey and Butterfield 2017) illustrates the great potential for future exploration of the SCF window.

1.5.1.3 Entombed Meiofauna

Another pathway for high fidelity preservation is rapid precipitation of mineral cements (siliceous opal/chert, Fig. 1.4e, h) or immersion into viscous organic substances that are stable over geological time (tar or tree resin, Fig. 1.4i) (Parry et al. 2018).

Cherts are amorphous silica derived from opal. Such deposits are common as late-forming concretions but can form directly in evaporative and hydrothermal settings when super-saturated. Cherts are the most important record for Precambrian unicellular life and record prokaryotic cells back to the Archaean (4000–2500 million years), although some previous claims may instead be pseudofossils (Braiser et al. 2006; Donoghue 2020). The most notable fossil locality is the Early Devonian Rhynie Chert in Scotland (~410 million years old), preserving a shallow water environment near a hydrothermal vent system. Early vascular plants with cellular detail, fungi and arthropods are encountered here along with the oldest unequivocal record of a nematode (Fig. 1.4e) (Poinar et al. 2008). Younger hot spring-cherts from the Jurassic (Fig. 1.4h) preserve putative rotiferan loricae and bodies (Massini et al. 2016) which await more detailed description.

Amber is another remarkable taphonomic window, which becomes significant from the Cretaceous and onwards, although some Triassic records are noteworthy (Schmidt et al. 2012). Amber is derived from tree resins, rich in diterpenes and trienes, which polymerize and cross-link into stable macromolecules. Notable is of course the diversity of insect inclusions commonly retained in these, but meiofaunal elements also occur, including tardigrades (Cooper 1964; Mapalo et al. 2021), rotifers (Waggoner and Poinar 1993), nematodes (Poinar 2011) and even platyhelminths (Poinar 2003) (Fig. 1.4i).

A peculiar window of preservation that can be placed in this category is the bioimmersion of meiofauna into the cocoon walls of leeches from the Permian (~270 million years) and onwards (McLoughlin et al. 2016). A well-preserved Early Cretaceous nematode suffered such a fate (Manum et al. 1994).

1.6 Taphonomic Biases May Explain Distribution Patterns of Fossil Meiofauna

The nature of preservation explains the absence of many meiofaunal groups and the overrepresentation of others. Taxa with chitinous cuticles dominate both the Orsten and SCF windows. They do allow us to trace microscopic cycloneuralian lineages and possibly kinorhynchs back to the Early Cambrian (541–529 million years), while microscopic loriciferans were in existence in the Late Cambrian (485–497 million years). Pancrustacean zooplankton is known from the Cambrian (521–514 million years ago). Several meiofaunal groups, although lacking decay-resistant features or a robust cuticle, such as rotifers with their proteinaceous lorica, are still recorded in fossils from younger Jurassic cherts (Massini et al. 2016) and amber (Waggoner and Poinar 1993), which may be indicative of a more recent origin but again could be the result of the inherent biases in preservation as such deposits are not available or discovered from this time. A possible rotiferan stem lineage is offered by *Inquicus fellatus* (Vinther and Parry 2019; Cong et al. 2017), see below. Meiofaunal annelid chaetae may preserve, but the body is unlikely to preserve, rendering such occurrences non-informative. Any meiofauna that is entirely soft-bodied is unlikely to preserve in a taxonomically informative state, though traces hereof may persist (Knaust 2020).

1.6.1 Fossil Evidence for Macroscopic Ancestries to Meiofauna

A central question remains as to whether meiofauna may have been a cradle for macroscopic bilaterians, given their distribution among spiralians and ecdysozoans with phyla that are entirely microscopic (Struck et al. 2014; Laumer et al. 2015a) as previously discussed. But given the numerous cases of secondary miniaturization, the meiofaunal realm might altogether represent a derived pool in which many early diverging phyla ended up as a consequence of competition and evolutionary refuge, rather than an adaptive cradle of origin (Laumer et al. 2015a; Vinther 2015). An obvious test for this is to trace microscopic lineages back in time and see if they always have been microscopic or not.

While a Late Cambrian meiofaunal loriciferan has been discovered, there are Early Cambrian macroscopic forms suggested to represent stem loriciferans (*Sirilorica* from the Early Cambrian Sirius Passet Lagerstätte in Northern Greenland, Fig. 1.4b, Peel 2010a, b, 2013). Specimens collected range up to more than 120 mm in length (J. Vinther, pers. obs.). The hexaradial introvert scalid arrangement aligns *Sirilorica* with the arrangement observed in loriciferans, nematoids and tardigrades in contrast to pentaradial kinorhynchs and priapulids.

With chaetognaths as probable members of the Gnathifera, another group of microscopic phyla are facing scrutiny as to their ancestral nature. Fossil evidence corroborates the links between chaetognaths and gnathiferans as mentioned earlier.

Amiskwia from the Burgess Shale has been debated as a possible chaetognath (Walcott 1911) but was later dismissed for its lack of grasping spines to instead represent a pelagic nemertean (Owre and Bayer 1962) or of uncertain affinity (Conway Morris 1977). Two independent studies demonstrated that *Amiskwia* preserves a robust jaw apparatus (Caron and Cheung 2019; Vinther and Parry 2019) that include bilateral elements and a symmetrical basal plate reminiscent of the condition observed in gnathostomulids. While the first study argued for *Amiskwia* being a stem chaetognath, the latter one argued for a stem gnathostomulid affinity with the otherwise chaetognath anatomy being convergent. Irrespective of these differing positions, tracing chaetognaths back in time to their shared origin with gnathiferans as macroscopic forms provide evidence, albeit not conclusive, for a macroscopic ancestry of gnathiferans while potentially, some or all, gnathiferans could be the result of a single, shared miniaturization event depending on where chaetognaths should be placed among the Gnathifera. Another taxon worth mentioning is the sessile and relatively large (3.3 mm long) taxon *Inquicus fellatus* (Cong et al. 2017), which appears to possess a jaw apparatus and a subterminal gut, hence possibly a gnathiferan, perhaps related to rotiferans (Cong et al. 2017; Vinther and Parry 2019).

The fossil record may eventually provide evidence for other phyla having been macroscopic in the past or been genuinely microscopic since their dawn. As such, the fossil record, as vestigial and interpretable it may be, is a crucial piece of the puzzle for understanding and resolving the origin and evolution of meiofauna.

1.7 Meiofauna Evolution—How to Trace Back Animal Miniatures

The origin and early evolution of meiofauna is one of the most fundamental questions in meiofauna research. Living animals and their relationship to each other provide important insights into the potential sequence of events that led to the establishment of specific morphologies. Linked to these morphologies is a vast diversity of functions and interactions of meiofauna with their habitat and other biota. However, compared to larger-sized benthic organisms, many meiofauna taxa are poorly studied with regard to their morphology, systematics, population structure, biogeography and biology (see chapters in this book). This leaves many research frontiers unaddressed that relate to the fundamental questions of:

- *How did meiofauna evolve?*
- *How has natural selection modified meiofauna over evolutionary time?*

Evolution is the unifying theory that explains all biological science. All life is connected, and none of it can be fully understood without understanding its evolution. Research on evolution therefore relies on many other fields in the biological sciences, and there is a wide variety of methodologies and research tools to tackle complex and often unresolved questions. Our questions of "*where from?*", "*along* *which pathways?"* and "*at what time periods?"*, all of which are of genuine human interest, can only be addressed successfully by collaborating specialists studying the diverse aspects of meiofauna evolution with diverse methods. As we learned from this chapter, successfully resolving questions regarding meiofauna evolution requires integration of geological/paleontological, climatic, ontogenetic and morphological data ranging from microscopic to macroscopic scales. Findings from developmental biology, genomics, functional ecology, genetics and ethology also have to be considered.

The analysis and interpretation of the time scales at which meiofauna evolution is occurring remain challenging, partly because short-term changes are predictable, whereas long-term evolution is not. We cannot directly observe processes at macroecological time scales. Instead, we collect and interpret data from many related scientific fields and connect and interpret their diverse bodies of evidence to form a robust thread of scientific deduction as a basis of highest probability. As heterogeneous as the research fields involved will be the novel methods not only advancing but also promoting future research on the phylogenetic role of meiofauna. Some examples could be:

- Cryo-fixation of tissue preserving unseen ultrastructural details.
- High-resolution microscopy techniques such as serial block-face scanning electron microscopy combined with computational analysis tools, enabling faster, better and three-dimensional anatomical reconstructions.
- New staining and scanning analyses of minute biomineralized remnants in fossils.
- Optimized protocols for acquiring high-quality genomic data from minute organisms with limited amount of high molecular weight input DNA.
- Better bioinformatic pipelines for genomic data and analyses.

When discussing animal evolution and addressing the plethora of open questions, which ones have the potential to put meiobenthic organisms and their connections with macrofauna in a critical, complementing position? As almost all major animal groups include meiobenthic representatives, some more general aspects and questions may include:

- The possibility of Xenacoelomorpha as sister group to Bilateria,
- The role of Scalidodophora within Ecdysozoa,
- The phylogenetic position of Tardigrada,
- The position of Chaetognatha and evolution of Gnathifera,
- The potential monophyly of Polyzoa,
- Trochozoa with ancestors of meiobenthic size,
- The role of miniaturization and paedomorphosis, e.g. at the origin of larger clades and within phyla such as Annelida,
- Fossils of meiofaunal size as derivates or origin of macrofauna,
- Genomic signatures of miniaturization.

The inevitable reliance on an indirect, combined approach renders pertinent evolutionary research complex, especially when dealing with minute meiobenthic organisms. On the other hand, multiple deductive approaches that use varied, often independent, methods of investigation increase the probability of achieving resilient results and avoid reasoning in merely likely (abductive) derivations (the advantage of "triangulation" sensu Munafò and Smith 2018).

Supported by novel computational power, the numerous, heterogeneous pieces comprising the puzzle of meiofauna evolution will be put together to form a more coherent picture. In interdisciplinary collaboration, network processes will elucidate the role and often still rather vague position of meiobenthos in the tree of life. Most challenging and fascinating, this has the potential of stimulating many other studies in various biological fields. Pursuing major open questions on meiofauna evolution will moreover generate significant ramifications into macro-evolutionary research:

- Morphologists and evolutionary biologists wanting to understand diversification, biogeography and adaptation to different environments.
- Geochemists and microbiologist seeking to understand how meiofauna have shaped biogeochemical processes.
- Palaeontologists seeking to constrain the timing and nature of animal evolution.
- Molecular biologists wanting to characterize the link between genomic and phenotypic organization.

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Chapter 2
Meiofauna Shaping Biogeochemical Processes

Stefano Bonaglia and Francisco J. A. Nascimento

Abstract Biogeochemical processes at the sediment–water interface are essential for the functioning of marine ecosystems. It is a central question in benthic ecology how these processes are controlled and mediated by biotic factors. Particularly, the role of meiobenthos, the most abundant and diverse faunal component in these systems, is little understood and requires more attention. In this chapter, we discuss the impact of meiofauna bioturbation in marine sediments on significant mechanisms and processes in (a) carbon degradation and oxygen penetration, (b) sulfide dynamics, and (c) nitrogen cycling. Particularly in the growing hypoxic areas of the seafloor where meiofauna is often the only animal group present, the role and bioturbative activities of this central component of the benthos need further scrutiny regarding the decrease of oxygen and increase of toxic hydrogen sulfide. These knowledge gaps in the interaction between meiofauna and marine biogeochemistry are the background for our concluding outlines: We present current research frontiers in order to assess the role of meiofauna as regulators of geochemical processes and microbial activities. These goals require combination of quantitative and qualitative meiobenthos investigations with state-of-the-art experimental work.

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2.1 Sediment Biogeochemistry—Of Basic Relevance to Meiobenthos

Marine sediments cover 71% of our planet surface (Emerson and Hedges 2008). This vast surface area makes sedimentary habitats the most widespread, yet underexplored environments on our planet. By definition, marine sediment is a type of substrate produced by chemical and mechanical weathering of rocks and shells of dead organisms into particles that are moved by different forces (e.g., air, water, ice) and accumulate on the seafloor. Besides this enormous pool of inorganic particles, sediments—and the derived sedimentary rocks—also host the largest reservoir of organic carbon on the planet (Hedges and Keil 1995). Organic matter within the sediments is composed of both living organisms (e.g., microbes, protists, meio-, macro-, and megafauna) and of dead organic matter, also known as detritus or particulate organic matter (POM).

What is happening between the grains of marine sediments? The processes involved are inseparably linked to the dynamics occurring in the pelagic realm, where sunlight and dissolved nutrients sustain rapidly growing phytoplankton, which, in turn, is continuously grazed by protozoans and zooplankton. This is what constitutes marine productivity (Hedges and Keil 1995). The average depth of the ocean is ca. 3700 m. Some seminal works demonstrated that only 1% to 4% of marine primary production is settling to sediment depths (Martin et al. 1987). Thus, physical, chemical, and biological composition of marine sediments is intimately connected with processes and conditions that happen in the overlying water column.

Diagenesis refers to physical, chemical and biological forces that lead to sediment alterations (Berner 1980). For decades, the consensual picture of diagenesis was that physical changes lead to chemical changes, which finally determine biological features of ecosystems (Fig. 2.1a). In the 80s, however, Robert Aller and Erik Kristensen started reporting evidence that macrofauna (and to a lesser extent meiofauna) with their sediment reworking activities affect sediment geochemistry and physical properties (Aller 1982; Aller and Aller 1992; Kristensen and Blackburn 1987). In the following decades, studies on bioturbation mainly concentrated on macrofauna omitting the impacts of meiofauna bioturbation. The main reasons why macrofauna outcompeted meiofauna in this type of studies are twofold. Beside technical reasons, large animals were expected to alter microbial pathways and process rates more intensively and with clearly measurable end-points.

Only recently, studies on meiofauna bioturbation started emerging again. Experiments conducted with Baltic Sea sediments showed that meiofauna significantly affect ecosystem functions as they double nitrogen removal by denitrification (Bonaglia et al. 2014), stimulate by up to 50% organic matter mineralization (Nascimento et al. 2012), and alter pathways of hydrocarbon degradation (Näslund et al. 2010). Very recently, it was further demonstrated that meiofauna can increase benthic oxygenation and help removing toxic hydrogen sulfide from hypoxic sediments (Bonaglia et al. 2020). These studies helped abolish the earlier sequential paradigm, i.e., physical properties influence sediment chemistry, which in turn allows specific

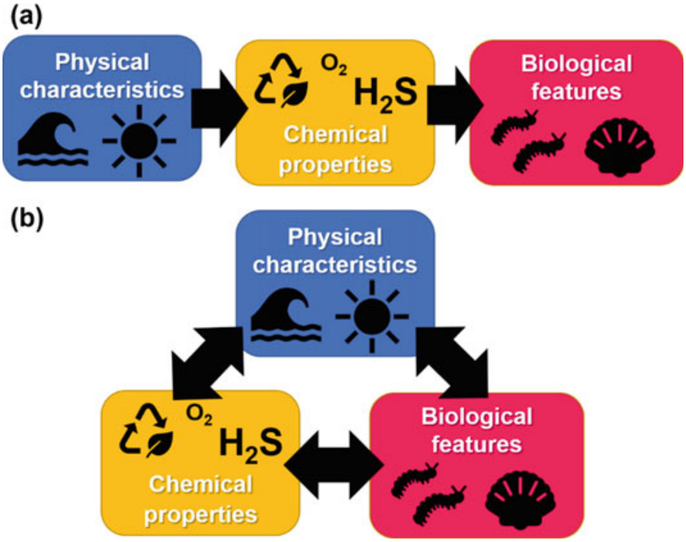


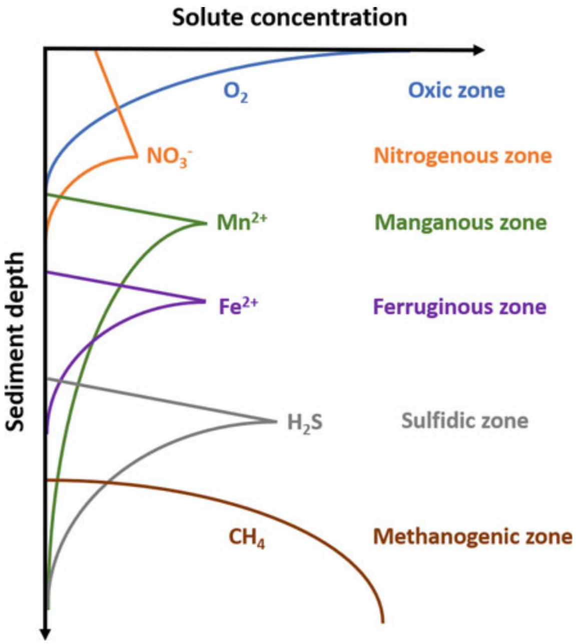
Fig. 2.1 Diagrammatic comparison of earlier (**a**) and recent (**b**) conceptions of benthic interactions in marine research. Original

benthic communities to thrive. Instead, they introduced an interacting paradigm in which physical, chemical, and biological properties mutually affect each other (Fig. 2.1).

Most fast-growing microorganisms and metazoan communities inhabiting the seafloor are heterotrophs or organotrophs, i.e., organisms that utilize settling organic material as food and energy. During diagenesis, these organisms sustain 30 to > 99% degradation of the organic matter deposited on the sediment surface (Henrichs 1992). In the absence of these players, the seafloor would be an enormous repository of undecomposed organic matter. While most heterotrophic organisms metabolize and respire the largest fraction of the available organic carbon to carbon dioxide (CO_2) through aerobic respiration with oxygen (O_2) (for more details, see Sect. 2.3), many meiofauna organisms can respire other compounds than O_2 or can "hold their breath" for long time (see Chap. 4).

Different benthic habitats obviously have different biogeochemical regimes. Benthic biogeochemical processes (and their relative importance) mainly depend on organic carbon content (both quantity and quality), on oxygen conditions and on microbial communities. While most carbon becomes already degraded in the water column, this process continues in the sediment fueled by a variety of electron acceptors (Fig. 2.2). The energetically most favorable carbon degradation process uses oxygen and is generally carried out in the topmost oxic zone (Fig. 2.2). When O_2 is gone, microbes start respiring nitrate (NO_3^-), which, energetically, constitutes a pretty good substitute of O_2. At these depths, we already encounter the accumulation of the so-called reduced compounds, products of redox respiration processes, such as ammonium. When also NO_3^- is depleted, microbes get energy from the respiration of

Fig. 2.2 Simplified schematic chemical zonation of marine sediments indicating the specific dominating respiratory pathways. Modified after Canfield and Thamdrup (2009)



manganese and iron oxides, which produce and accumulate reduced dissolved metals (Fig. 2.2). Below these layers called nitrogenous, manganous and ferruginous zones, respectively, microorganisms use sulfate for energy, which is reduced to hydrogen sulfide (Fig. 2.2). Finally, very specialized microorganisms (so-called Archaea) can respire CO_2 and use it to oxidize organic matter into methane (CH_4).

Depending on latitude and water depth, the seafloor hosts very different quantity and quality of organic matter for the heterotrophic meiofaunal organisms. For example, shallower sediments contain much more organic material than deeper ones, which is reflected in the oxygen penetration through the sediment layers (Glud 2008). The higher the organic carbon content and lability, the less oxygen penetration; in contrast, the lower organic carbon content, the more oxygen stays unused and, thus, penetrates deeper (Glud 2008). Organic matter quality can be classified in different types such as dead organic matter (algal detritus, zooplankton carcasses, etc.), living organic matter like biogenic structures (mucus) and living organisms (bacteria, protists) that meiofauna can feed upon. Thus, it strongly influences community composition of organisms. Carbonic gases such as CO_2 and CH_4, which derive from microbial and infaunal respiratory processes, are emitted from the sediment to the water column and depending on the conditions may reach the atmosphere and act as “greenhouse gases.” All carbon that is not respired to CO_2 and CH_4 by benthic organisms is stored, preserved, sequestered, or also “buried” in sediments. This carbon preservation fraction enters the long-term geological cycle. In the marine environment, it was estimated to be less than 0.5% efficient, meaning that $< 0.5\%$ of modern oceanic productivity is preserved in sediment repositories (Hedges and Keil 1995).

Marine and especially coastal sediments are not only repositories for the nutritious organic matter, but they are also important sinks for organic pollutants. Especially important and environmentally relevant are organic pollutants such as microplastics and pharmaceuticals. Nowadays, microplastics are becoming a common feature in marine sediments (Kvale et al. 2020), especially in anthropologically impacted coastal sediments. Whether meiofauna organisms will adapt and cope with this new impact or alternatively become threatened is currently under debate (see Chap. 7). It is important to note that while we start understanding the role of meiofauna in degrading natural organic carbon (see Sect. 2.3, below), no studies have so far addressed the impact that meiofauna bioturbation and activity may have on transformation of microplastics and their ultimate fate.

In a pristine world, the benthic realm would represent a stable and self-regulated environment mostly dominated by oxic processes with bioturbation, maintenance reactions, predation, and other ecological pathways dominating. However, the currently changing global conditions force us to resolve many open questions arising from the emerging impacts, which affect biogeochemistry and ecosystem functioning.

2.2 The Concept of Meiofauna bioturbation—The "Benthic Fusion"

The term "bioturbation" sensu Kristensen et al. (2012) defines how benthic organisms affect the sediments they inhabit and encompasses "*all transport processes carried out by animals that directly or indirectly affect sediment matrices.*" Regarding these processes infaunal organisms are often divided into five functional groups depending on their modes of sediment reworking (François et al. 1997; Kristensen et al. 2012; Maire et al. 2008):

- Gallery-diffusors,
- biodiffusors,
- upward conveyors,
- downward conveyors, and
- regenerators.

Infauna acting as gallery-diffusors and biodiffusors normally move sediment particles randomly over short distances through diffuse transport (Meysman et al. 2003). On the other hand, downward and upward conveyors move particles between the sediment surface and deeper layers by non-local transport. While downward conveyors feed at the sediment surface and relocate particles to the deeper egestion layer, upward conveyors feed under the surface and move sediment particles in the opposite direction (Kristensen et al. 2012). Lastly, infaunal regenerators create particle movement to the sediment or to the overlying water column through digging or through passive non-local transport resulting from burrow desertion (Gardner et al. 1987; Kristensen et al. 2012).

In marine sediments, the community structure and diversity of infauna determine the predominant mode and intensity of bioturbation. It seems that the impact of bioturbation on ecosystem processes depends rather on functional richness than on species diversity (Mermillod-Blondin 2011; Meysman et al. 2006; Solan et al. 2004). However, it should be noted that the above functional groups of bioturbators have been defined based on macrofauna studies (Dauwe et al. 1998; Maire et al. 2016; Sandnes et al. 2000). In contrast, for meiofauna, there is, as yet, virtually no information on different bioturbative modes. Clarifying these should be a much needed and exciting "frontier field" of future meiofauna research.

Regarding meiofauna, the organisms are often smaller than the surrounding sediment particles. Nevertheless, their population density affects sediment reworking. Bioturbation by meiofauna (Fig. 2.3), or meiobioturbation, as an active process was first identified and clearly distinguished from macrofauna bioturbation by Cullen (1973): "*meiobenthic bioturbation is a factor to be considered, in addition to the better known physical and biological marine processes.*" He suggested that macrobenthic burrows and sediment reworking (back then called *lebensspuren*) should be regarded as a short-lived phenomenon, which would likely not persist for more than a few days, because of the constant activity and presence of ubiquitous meiofauna, which would essentially destroy the results of this macrofauna activity. Thus, bioturbation with its complex and ever fluctuating interactions, is a strong example of "the benthic fusion" that is linking life histories of meio- and macrobenthos. For decades, these realms have been considered as rather independent fields.

Meiobioturbation is then a term that encompasses multiple biological processes performed by meiofauna in sediments, that carry oxygen, nutrients and solutes from the overlying water down to sediments (Coull 1999). These include the reworking and aggregation of sediment particles, the formation of microburrows through the

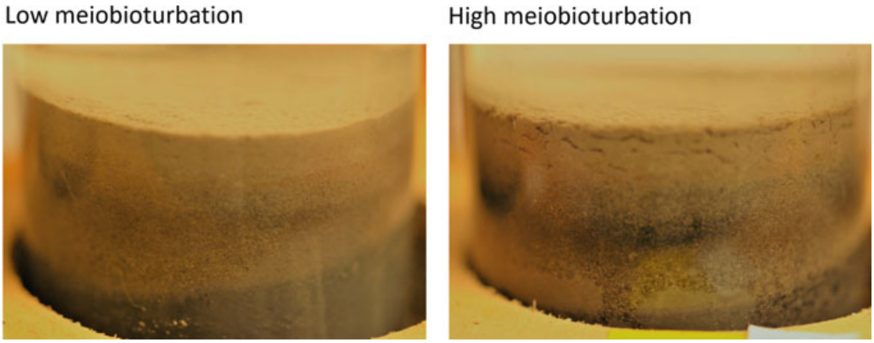


Fig. 2.3 Visual impact of meiofauna bioturbation: left–low intensity: about 130 ind.10^{-3} m^{-2}; right–high intensity: about 850 ind.10^{-3} m^{-2} (Bonaglia et al. 2014). Original

binding of particles with mucus and other substances and feeding activities that result in ingestion and excretion of particles and macromolecules important for bacterial production (Chandler and Fleeger 1984; Kristensen et al. 2012; Schratzberger and Ingels 2018). The combined result of these activities impacts sediment hydrodynamics and sediment physical properties such as permeability, granulometry, and stability (Coull 1973; Schratzberger and Ingels 2018). Until recently the effects of meiobioturbation were considered to be local and small scale, but work by Murray et al. (2002) has indicated that such impacts on sediment proprieties are significant at a global scale, due to meiofauna's ubiquitous distribution and high abundances.

Meiofauna activities in the sediments can have important consequences for the vertical biogeochemical zonation of sediments, especially the balance between oxic and anoxic sediment processes (Bonaglia et al. 2020; Fenchel 1996). Because of its impact on sediment porosity and permeability, meiobioturbation can attain an important role in mediating the rates of nutrient cycling and biogeochemical fluxes (Aller and Aller 1992; Bonaglia et al. 2020, 2014). Especially the seminal work by Aller and Aller (1992), quantifying meiobioturbation, demonstrated that meiofauna enhances solute transport by a factor of two when compared to defaunated sediments. Later, these findings were confirmed by field studies that used inert tracers to estimate the effect of meiofauna on solute transport (Berg et al. 2001; Rysgaard et al. 2000). This quantification can be performed by measuring solute transport sustained by molecular diffusivity (Ds) and biodiffusivity (Db) in sediments inhabited by meiofauna compared to defaunated sediments governed only by molecular diffusivity. Meiofauna biodiffusivity is clearly enhanced by increasing meiofauna abundance/biomass (Fig. 2.4). Using variations of this approach, metazoan meiofauna in Arctic sediments was found to increase transport of solutes by 1.5–3.1 times (Rysgaard et al. 2000). In addition, by combining microchamber experiments, microsensor measurements and empirical modeling, Glud et al. (1995) further demonstrated that large densities of ciliates and nematodes enhance interstitial solute transport by a factor of 1.1 to 10× in surface sediments and benthic microbial mats (Glud and Fenchel 1999; Glud et al. 1995).

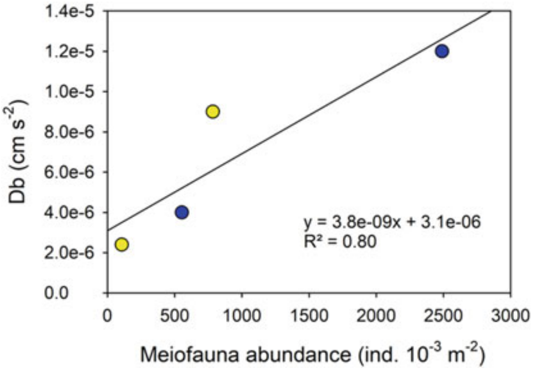


Fig. 2.4 Relationship between meiofauna abundance and biodiffusivity (Db). Yellow dots are from Bonaglia et al. (2014) and blue dots are from Rysgaard et al. (2000). With permission of Bonaglia et al. (2020)

More recently, a number of studies have directly quantified meiobioturbation intensity. Bouchet and Seuront (2020) showed that in surface sediments reworking rates by foraminifera can range between 11.5 and 65 $cm^2 \cdot m^{-2} \cdot day^{-1}$ depending on the taxa. Extrapolating to population level, the authors estimate foraminifera sediment reworking rates in intertidal mudflat habitats to be comparable to those by polychaete and bivalve macroinvertebrate populations. In the same temperate intertidal sediments, it was further demonstrated that foraminiferal bioturbation was significantly reduced when individuals were exposed to high temperature regimes above 32 °C (Deldicq et al. 2021).

Experimental approaches manipulating entire meiofauna communities have been useful to quantify the effect of total meiobioturbation on oxygen distribution in the sediment (Bonaglia et al. 2020, 2014). These works indicate that meiofauna significantly increased oxygen penetration depth (OPD) when compared to sediments with very low meiofauna abundances. The experimental impact of meiofauna abundance on OPD was, however, variable and ranging from 12% (Bonaglia et al. 2014) to 85% (Bonaglia et al. 2020). OPD enhancement by meiofauna is likely to be in the higher ranges of this interval, as the latter study simulated more natural environmental conditions. In this latter experiment with undisturbed, recently hypoxic sediment, OPD increased by 85% after 5 days when meiofauna was added, an effect mirroring the rapid initial colonization by meiofauna. Even after 22 days, the OPD enhancement, although decreasing, was still 62%, significantly indicating that meiofauna effects on oxygen transport to deeper sediment layers is pervasive through time (Bonaglia et al. 2020).

This change in oxygen dynamics has important structural and functional impacts in benthic ecosystems. Meiofauna activities in the sediment not only significantly change bacterial abundance, community structure and composition (Bonaglia et al. 2020; Lacoste et al. 2018; Nascimento et al. 2012; Näslund et al. 2010), they also seem to modulate the biotic interactions between macrofauna and bacterial communities (Lacoste et al. 2018). The ecological consequences of these meiofauna-mediated alterations in the physical, chemical and biological characteristics of marine sediments can have important consequences for global ecosystem processes and biogeochemical cycles (Meysman et al. 2006) and are our next topic of discussion.

2.3 Meiofauna and Dominant Chemical Cycling Processes

2.3.1 Carbon Cycle

Most of the global marine carbon is produced and consumed in photic pelagic environments (approximately 50 Pg C y^{-1}) and less than 4% of this carbon reaches the ocean floor (2 Pg C y^{-1}), mostly in a highly degraded form (Martin et al. 1987; Middelburg 2019). Despite this efficient pelagic degradation, marine sediments are central to the functioning of global carbon cycle (Atwood et al. 2020; Middelburg

2019). Since sediment-buried organic carbon can be sequestered for millions of years (Estes et al. 2019; Mcleod et al. 2011), marine sediments harbor is one of the largest carbon reservoirs on our planet and is inhabited by some of the most efficient heterotrophic communities on Earth (Middelburg 2019). Settling organic carbon and its mineralization is vital for the maintenance, growth and reproduction of all benthic heterotrophs including meiofauna (Albert et al. 2021). However, to empirically quantify the contribution of meiofauna for carbon cycling is not a trivial task and needs a short methodological detour.

The amount of carbon mineralized in sediments depends on multiple factors including organic matter quality and quantity, sediment type and the biological communities living in these sediments (Glud 2008; Song et al. 2016). It is usually indirectly measured by the rate at which total oxygen is taken up (TOU) or consumed. TOU is a complex, summative parameter. It encompasses respiration by macro-, meiofauna, and microorganism, but also oxygen transport processes resulting from bioturbation, bioirrigation, and chemical oxygen demand. A subunit of TOU is the diffusive oxygen uptake (DOU): the sum of oxygen consumption by microbial respiration and chemical re-oxidation processes. Therefore, the difference between TOU and DOU allows to estimate the oxygen consumption and carbon mineralization of the benthic fauna, including bioturbation and bioirrigation as side effects (Glud 2008; Kristensen et al. 2012).

The use of this comparative oxygen method allowed for a number of important ecological insights in benthic metabolism: Oxygen consumption and carbon mineralization of the benthos strongly correlate with their biomass (Middelburg 2019). In marine sediments, infauna normally accounts for 10–25% of the total biomass and direct oxygen consumption. The most important components of the fauna-mediated TOU are aerobic microbial activity and chemical oxidation, stimulated by bioirrigation and bioturbation (Glud 2008).

In general, there is consensus that meiofauna only makes a small direct contribution (a few %) to C mineralization (Schratzberger and Ingels 2018). Nevertheless, meiofauna's contribution to carbon mineralization and oxygen consumption seems to increase with water depth (Rex et al. 2006; Snelgrove et al. 2018). Using benthic respiration data, meiofauna has been reported to account for similar sediment oxygen demand as macrofauna (approximately 12% together) at depths between 500 and 1200 m in the Pacific Ocean (Leduc et al. 2016). Also, the meiofauna biomass correlated positively with sediment oxygen demand in the same deep-sea area (Pilditch et al. 2015). In shallow sediments, the importance of meiofauna in sustaining carbon mineralization compared to that of macrofauna seems to follow a seasonal pattern, i.e., increasing meiofauna activity in spring after the settling of the spring bloom (Franco et al. 2010). Due to their fast metabolism and short generation times (Coull 1999) in meiofauna, the time-lag between secondary production and settling of phytodetritus is short (Olafsson and Elmgren 1997). This enables these communities to quickly respond and mineralize carbon while macrobenthic densities and biomass are still seasonally low.

As stated above, assessing meiofauna metabolism is a complex and demanding task. While the above data are based on summative and indirect calculations, first direct measurements with microelectrodes yielded differing results. They indicated that in earlier calculations total oxygen consumption was significantly higher than in recent data derived from direct measurements of single individuals (Maciute et al. 2021). The modeling data of Braeckman et al. (2013) also suggested a lower carbon turnover in meiofauna than assumed from earlier estimations. A relatively minor direct contribution of meiofauna to carbon mineralization has been confirmed by other studies that used isotope tracing to quantify direct carbon assimilation by meiofauna in marine ecosystems (Middelburg et al. 2000).

Summarizing, these works confirm that the importance of meiofauna for organic matter mineralization through direct grazing and carbon assimilation is limited. This pattern is consistent and independent of the geographical area or carbon source. Collected experimental and field data indicate that usually in marine ecosystems meiofauna assimilate less than 3–4% of total labeled carbon from phytodetritus (Nascimento et al. 2008, 2012; Olafsson et al. 1999), polar sediments (Braeckman et al. 2018, 2019; Urban-Malinga and Moens 2006), and deep-sea ecosystems (Moodley et al. 2005; Van Oevelen et al. 2012, 2006). However, this contribution can become larger when measuring carbon assimilation in short-time frames (Middelburg et al. 2000; Moodley et al. 2002).

Conversely, the facilitation effects of meiofauna to microbial processes involved in carbon mineralization (aerobic degradation and denitrification) are high and generally recognized (Fig. 2.5). As mentioned before, mineralization of detritus is to a large extent a microbial process. However, several lines of evidence show that this process is enhanced by positive interactions between meiofauna and microorganisms. Although difficult to quantify, these supporting processes mediated by meiofauna have been suggested in many earlier studies (Cullen 1973; Findlay and Tenore 1982; Moens et al. 2005) based on the degradation rates of carbon. More recently, Nascimento et al. (2012) calculated, using radioisotope techniques, that this effect could be as high as 50%, and that it depended on meiofaunal abundance (Fig. 2.5). A comparable increase (30%) in the decomposition rate of macroalgal detritus was found by Alkemade et al. (1992) to result from stimulation of microbial processes by nematode activity.

This positive effect on carbon mineralization by microbial communities is mediated through a number of different mechanisms:

- Meiofauna grazing on microbial populations can keep microbes in an active growth phase, resulting in higher carbon requirement and consequent enhancement of carbon mineralization rates (Alkemade et al. 1992; Lillebø et al. 1999).
- Meiobioturbation increases solute transports and breaking down of detritus that facilitate microbial activity by catalyzing carbon degradation processes. These provide microbes with both carbonaceous substrate and critical electron acceptors (Aller and Aller 1992; Bonaglia et al. 2014).

Additionally, high turnover rates of meiofauna increase the rate of nutrients supply to microorganism with potential benefits to carbon degradation (Coull 1999) and provide sediment microbial communities with important sources of carbon in

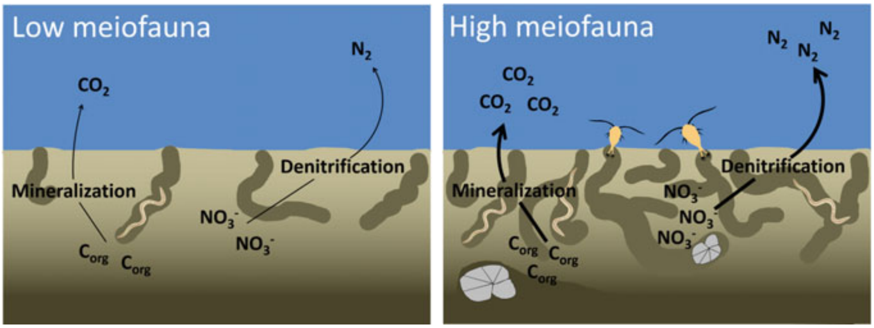


Fig. 2.5 Conceptual scheme illustrating the main stimulatory effects of meiofauna activity on microbial processes involved in carbon degradation such as aerobic mineralization and denitrification. Original

the form of mucus (Coull 1973), fecal pellets, or carcasses which may enhance heterotrophic microbial metabolism (Schratzberger and Ingels 2018).

2.3.2 Sulfur Cycle

In marine sediments, sulfur and oxygen cycling are closely linked. The interface between the oxic zone and the sulfidic zone is an unstable, much fluctuating environment that is often, but incorrectly called the suboxic zone. This is the zone where molecular oxygen is absent, but metal oxides (iron and manganese) and nitrate may still be present to keep the conditions oxidized. A better definition of sediment layers is given through the geochemical conditions present in the sediment (Fig. 2.2; Canfield and Thamdrup (2009).

In principle, when oxygen is completely consumed by aerobic respiration and by other geochemical oxidation processes, anaerobic respiration processes take place. Only when all other favorable electron acceptors (i.e., nitrate, manganese and iron) have been consumed, sulfate is used in microbial respiratory pathways leading to the production and potential accumulation of hydrogen sulfide (H_2S) in this sulfidic layer (Fig. 2.2). When O_2^- and/or NO_3^- are available, hydrogen sulfide can be re-oxidized to sulfate by sulfide-oxidizing microorganisms (both Bacteria and Archaea).

Hydrogen sulfide, the main reductive product of sulfate metabolism, is toxic to most aerobic meiofauna. At high concentrations, H_2S is also toxic to the few specialized meiofauna with an aberrant metabolism such as certain protists and metazoan meiobenthos like Loricifera that can live under fully anaerobic conditions (Fenchel 2012). Far more widespread in the sulfidic zone are aerobic organisms that can live, often in high abundance, under slightly sulfidic conditions, the so-called thiobios (Boaden and Platt 1971), e.g., marine nematodes and oligochaetes (see Muschiol et al. 2015; Ott et al. 2004; Sogin et al. 2020); for more details, see Chap. 4 of this book, and overview in (Giere 2009). Often thiobiotic species have been found to live in symbiosis with chemosynthetic bacteria where the partners interact in complex metabolic pathways.

Beside this direct effect on sulfur cycling, it was previously suggested (Wetzel et al. 1995) and only recently demonstrated that meiofauna, through their bioturbative burrowing activity, have the capacity to push sulfides deeper down into the sediment. Bonaglia et al. (2020) could demonstrate that in short-term periods (six days exposure) meiofauna can enhance the thickness of the sulfide-free sediment layer by 68% and decrease the sulfide flux by a factor of 22. In hypoxic sediments, meiofauna can coexist with cable bacteria (Bonaglia et al. 2020). These multicellular filamentous prokaryotes have a global distribution in marine sediments and are electrically conductive. Cable bacteria transfer electrons vertically from different layers of the sediment, thus connecting sulfide oxidation at deeper layers with oxygen reduction at the sediment surface (Malkin et al. 2014). These ecosystem engineers can thus take advantage and thrive on H_2S and have a strong impact on the biogeochemistry of hypoxic habitats (Pfeffer et al. 2012). The electrical coupling of H_2S oxidation to O_2 reduction by cable bacteria can even occur over centimeter distances (Nielsen et al. 2010), thus removing free H_2S from sediments. It is not clear whether the above described bioturbative effects on sulfur cycle are solely due to meiofauna or to the combined activity of meiofauna and cable bacteria and require further investigations.

2.3.3 Nitrogen Cycle

Nitrogen (N) cycling is perhaps the most complex of all element cycles on Earth and its transformation pathways from one chemical compound to another are almost exclusively carried out by microorganisms (Canfield et al. 2005). Nitrogen cycling in sandy and muddy sediments is particularly intense in the top mm layers, coinciding with the oxic and nitrogenous zones (Fig. 2.6). In both the upper oxic and deeper anoxic sediment layers, N cycling is initiated by microbial degradation of particulate organic nitrogen (PON, e.g., algal detritus, fecal pellets, etc.). This involves the breakdown of macromolecules (proteins, nucleic acids, etc.) into ammonium by the ammonification process (Bonaglia 2015).

In oxic sediments, ammonium is either assimilated by benthic organisms or oxidized while oxygen is reduced by the nitrification process, which leads to production of nitrate (Fig. 2.6). Even in well-oxygenated sediments, anoxia usually occurs after few millimeters (coastal sediments) or centimeters (deep-sea sediments) (Glud 2008). Thus, nitrification is generally constrained to the sediment surface, but can become very important in deeper sediment layers in the presence of burrowing animals (Kristensen and Kostka 2005). It has been suggested that meiofauna may promote sedimentary nitrification by increasing solute transport and reactions in the oxic zone of the sediments (Aller and Aller 1992). Later, this “enhancement effect” by meiofauna has been supported by experiments in Baltic Sea sediments (Prast et al.

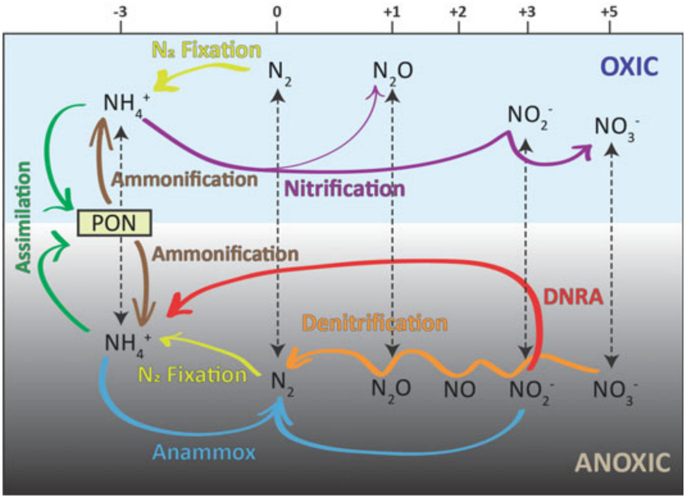


Fig. 2.6 Schematic of benthic N cycle and microbial pathways mediating it. Numbers on *x*-axis represent the oxidation state of nitrogen (N atom) in the molecules. PON = particulate organic nitrogen, DNRA = dissimilatory nitrate reduction to ammonium. With permission of Bonaglia (2015)

2007) where the addition of ciliates caused higher nitrification rates and abundances of nitrifying bacteria.

It is well documented that bacterivorous nematodes obtain nitrogen that greatly exceed their requirements, which is then excreted in the form of ammonium (Lee and Atkinson 1977; Wright and Newall 1976). Evidence from soil ecology has shown that C/N ratios in bacterial-feeding nematodes (ca. 5.9) are 43% higher than those in bacteria (ca. 4.1), and that the N surplus is secreted as ammonium (Ferris et al. 1997). Ammonium, dissolved in the porewater, is then cycled through different pathways:

- it can be aerobically nitrified, i.e., converted in to nitrate by nitrification; this process is generally stimulated by larger bioturbators such as polychaete worms and bivalves with an intense effect on nitrogen cycling (Kristensen et al. 1985; Kristensen and Kostka 2005).
- it can be directly assimilated by microorganisms;
- it can flow back to the water column;
- it may be sequestered by physical sorption onto clay sediment particles;
- it can be oxidized anaerobically through the anammox process (Dalsgaard and Thamdrup 2002; Thamdrup and Dalsgaard 2002). This anaerobic nitrate removal process is reaching high contribution of nitrogen loss in deep-sea sediments with low organic carbon content (Thamdrup 2012);
- it can be temporarily removed, together with nitrate, by algal and plant uptake.

Regarding nitrate, bioturbators increase its diffusion rate down into the sediment from the upper water column. Nitrate also develops by nitrification inside the sediment (Kristensen et al. 1985; Pelegri and Blackburn 1995). Most nitrate, however, is partly or entirely removed by the denitrification process—the respiratory reduction to nitrous oxide (N_2O, a potent but overlooked greenhouse gas) or dinitrogen gas—in the absence of oxygen and presence of electron donors such as organic carbon, reduced iron or sulfide (Canfield et al. 2005; Thamdrup 2012). The reaction couple "nitrification–denitrification" is a vital ecosystem process as it converts biologically available nitrogen (ammonium and nitrate) into less bioavailable nitrogen (gaseous compounds) and thus alleviates ecosystem nutrient loading and potential eutrophication of water bodies (Fig. 2.6).

Bonaglia et al. (2014) tested how meiofauna activities such as bioturbation and bioirrigation affect microbial nitrogen cycling, and particularly the vital nitrification–denitrification process: marine muddy sediments with abundant and diverse meiofauna double nitrogen loss rates compared to sediments with low abundances and less diverse meiofauna. This stimulation can be related to a significant enhancement of microbial nitrification–denitrification coupling. High abundance and biodiversity of meiofauna, and particularly nematodes, may promote denitrification and nitrogen loss via two mechanisms:

(1) excretion of ammonium (Ferris et al. 1997), which directly stimulates nitrification;
(2) bioturbation and mixing of oxidized solutes such as oxygen and nitrate (Bonaglia et al. 2014), which promote nitrification and denitrification, respectively. Especially important is the creation of more endogenous nitrogen at the oxic–anoxic interface, where nitrifiers are mainly active, which fosters nitrification rates and lead to enhanced denitrification rates.

The fact that certain meiofauna taxa can carry out nitrate respiration instead of oxic respiration is a fascinating topic. Hentschel et al (1999) indicated that the nematodes *Stilbonema* sp. and *Laxus oneistus* have capacity to denitrify, and that the process was carried out by their associated bacterial ectosymbionts (see Chap. 4). However, incubation experiments with randomly picked Baltic Sea nematodes did not result in any detectable denitrification rate (Bonaglia et al. 2014) suggesting that the capacity for nematode-associated nitrate reduction is species-specific. Not only prokaryotes (Bacteria and Archaea), but also eukaryotes belonging to the subphylum Foraminifera (Risgaard-Petersen et al. 2006) and to the order Gromiida (Piña-Ochoa et al. 2010) can carry out direct denitrification. Interestingly, these organisms, all being Rhizaria within the SAR (Stramenopila, Alveolata and Rhizaria) supertaxon, have the capacity to accumulate and respire with nitrate instead of oxygen, a trait that was suggested being of ancient origin (Piña-Ochoa et al. 2010). This unique feature enables some Rhizaria to respire even when favorable electron acceptors are absent from the environment, i.e., when completely anoxic conditions are present. Recently, it was further indicated that denitrification is the preferred respiration pathway in some benthic Foraminifera from the Peruvian oxygen minimum zone (Glock et al. 2019).

Nitrate is an efficient electron acceptor and the most favorable after oxygen. Thus, many microorganisms and SARs compete for it. In highly eutrophic and organic-rich sediments (An and Gardner 2002) and in hypereutrophic pelagic environments (Broman et al. 2021), nitrate can be converted back to ammonium by the dissimilatory nitrate reduction to ammonium (DNRA). Contrarily to denitrification, this antagonistic nitrate reduction process retains bioavailable nitrogen in the ecosystem, with strong implications for eutrophication (Burgin and Hamilton 2007). In short-term experiments, abundant copepods from silty intertidal sediments enhanced DNRA rates, possibly through interaction with bacteria and diatoms (Stock et al. 2014).

These links between meiofauna ecology and N cycling provide important insights into marine benthic ecosystem functions. But they need further scrutiny by complex manipulative experiments.

2.4 Knowledge Gaps and New Research Horizons

Meiofauna research in the field covered by this chapter has progressed significantly in the last two decades. However, there is still a number of critically important questions that today remain unanswered. Regarding meiofauna-biogeochemical research, we suggest a number of frontiers that would contribute to resolve relevant knowledge gaps.

Methane oxidation: A relatively unexplored, but relevant, question is the effect of meiobioturbation on sediment to water fluxes of greenhouse gases like methane (CH_4) and nitrous oxide (N_2O). While even the impact of macrofauna on these fuxes is relatively unknown, there is virtually no information regarding meiofauna. As for sulfides, meiofauna may have an analogous mitigating effect on these fluxes by enhancing CH_4 oxidation in the oxic and nitrogenous sediment zones (Fig. 2.6). The need to decrease greenhouse gas emissions will necessitate a comprehensive mechanistic understanding of these emissions from marine sediments, particularly considering the role of meiofauna in carbon and nitrogen cycling.

Microplastics: The direct and indirect effects of meiofauna activity on emerging contaminants polluting the ocean, is another topic that will require attention in the future. For example, pollutants such as microplastics often constitute only a minute fraction of carbon budgets in marine sediments, but when present in high concentrations they may potentially affect ecosystem processes and carbon cycling (Ladewig et al. 2021). However, there is almost no literature regarding microplastic ingestion by marine nematodes or the consequences of such particle ingestion to meiofauna populations and their overall carbon uptake and storage. Recent literature has shown that microplastics can function as an additional carbon source to benthic microbial communities not only due to their carbon content, but also through their capacity of sorbing other organic contaminants (Ladewig et al. 2021; Nauendorf et al. 2016; Romera-Castillo et al. 2018). There is a clear knowledge gap on the consequences of increasing microplastic exposure to benthic community structure and function.

Future work in this area should focus on investigating these hypotheses also in the context of meiofauna-mediated microbial interactions.

Nitrogen cycling: As yet it is unknown, whether meiofauna have a stimulatory effect on anaerobic ammonium oxidation and nitrogen fixation activity. The former process would be particularly important in deep-sea sediments, where meiofauna outcompetes macrofauna both in terms of numbers and in terms of biomass. Also, the photosynthetic activity of micro-algae living at the sediment surface, and that of bacteria associated with major plant communities can introduce a relevant amount (15 Tg N y^{-1}) of nitrogen (Capone 1983). Even inside sandy sediments, nitrogen fixation was shown to occur resulting from the metabolic activity of sulfate reducing bacteria. This mechanism was particularly intensive in well-mixed and bioturbated sediments (Bertics et al. 2010). Thus, in shallow coastal sediments also, the usually abundant meiofauna might strongly contribute to and influence nitrogen fixation through their bioturbative activities.

Phosphorus and silicon cycling: The impact of meiofauna on these entire element cycles has not been considered yet. Phosphorus is an element that limits primary production in the ocean and controls eutrophication in coastal systems. Its benthic cycling is largely governed by redox conditions such as oxygen and sulfide concentrations. Biogenic silica (a mineral containing silicon) is often abundant and well preserved in aquatic sediments (Conley and Schelske 2001), but bioturbation can return large quantities of this element to the water column where it may favor diatom blooms.

2.5 Conclusions

We here evidence the important role of meiofauna in mediating biogeochemical cycles in marine sediments. While in most contexts the direct, quantifiable effect of meiofauna on carbon and nitrogen cycling is relatively small, the indirect role of meiofauna in these processes through bioturbation and interaction with prokaryotes at multiple scales is undeniable. Today, meiobenthos is acknowledged to be an important mediator of sediment biogeochemical cycles and benthic ecosystem processes, particularly in habitats exposed to anthropogenic pressure (hypoxic sediments, heavily polluted sediments, hypereutrophic environments) where they may dominate the benthos in abundance and biomass. With the increase of such habitats, the relationship between meiofauna and biogeochemical processes may attain a decisive role. This cognition underlines that the knowledge gaps indicated above represent crucial research frontiers. They should be urgently addressed not only for allowing a deeper understanding of the functional cycles in marine ecosystems, but also for assessing their hazards and potential resilience under continuous change.

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Chapter 3
Meiofauna and Biofilms—The Slimy Universe

Nabil Majdi, Cédric Hubas, Tom Moens, and Daniela Zeppilli

Abstract Biofilms develop in and on any wet substrate from mountainous rocks splashed by glacier-fed streams to deep-sea hydrothermal vents. Biofilms are not only hotspots of microbial diversity, but they also house astonishing abundances of meiofaunal organisms that find in a few-mm thick biofilm a proper shelter and a wealth of food items. This tiny 'slimy universe' represents a coherent and predictable framework to investigate responses of complex biological communities at convenient experimental scales. Therefore in this chapter, we proposed to explore three questions to identify frontiers of meiofauna–biofilm research: (1) What are the Benefits of Living in the Slimy Universe? (2) How do Meiofauna Contribute to Biofilm Functions? (3) What are Applied Aspects of Research on Biofilm—Meiofauna? It appears that meiofauna is key players in biofilm food webs, obviously finding there a diversity of nutritive food items. However, studies should further investigate the feeding preferences of the meiofauna and their role in fluxes of energy to the upper-ends of those food webs (the macroscopic world). Biofilms offer shelter for meiofauna against flow erosion, desiccation, temperature fluctuation, UV-radiation and predation. Whilst we have evidence of biofilm-compatible life-styles in some meiofaunal taxa like chromadorid nematodes, we lack knowledge on how the microbial world behaves when it is exposed to meiofaunal grazers. At small scales, meiofauna tends to stimulate biofilm functions both directly when grazing on some microbes and indirectly through poking holes in the cohesive matrix and through their excretion and

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secretions. However, to gain a comprehensive understanding of how benthos functions we urgently need to assess at a larger-scale, the consequences of meiofaunal control on microbially-mediated ecosystem processes. Finally, biofilm–meiofauna interactions show encouraging premices for a number of rewarding environmental applications like epuration of wastewater, remediation of xenobiotics, restoration of contaminated sites and consolidation of sediments.

3.1 Introduction—The Slimy Universe

Biofilms are what most of us would call ‘slime’, but more scientifically speaking, they define a complex assemblage of microorganisms growing on a surface and becoming so prominent that they may form clearly observable macroscopic structures. Biofilms are probably the oldest and most successful form of collective life on our planet (the fossil stromatolites of Shark Bay, Australia, are estimated to be 3.5 billion years old, thus proving that extensive microbial biofilms had already evolved less than 0.5 billion years after the origin of the very first life on earth; Schopf et al. 2007). Biofilms contain mind-blowing numbers of organisms (Flemming and Wuertz 2019 estimate 40–80% of ca. 1.2×10^{30} prokaryote cells on Earth which are organized in biofilms), and they are extremely dynamic and diverse in their physico-chemical structure, their ecological functions and their species composition (e.g. Decho 2000; Consalvey et al. 2004; Romaní et al. 2004; Battin et al. 2016). This reflects the textural diversity of the substrates they colonize and the environmental diversity they are able to cope with (e.g. Cardinale et al. 2002; Lyautey et al. 2003; Boulêtreau et al. 2014).

Perhaps you have slipped whilst hopping from one slime-covered rock to another across a stream or on a rocky shore or you observed extensive goldish or greenish ‘smears’ on the surface of intertidal muds (Fig. 3.1). More generally, when given enough time, a biofilm layer will appear on almost any moist surface and in the interstices of coarse and fine sedimentary beds. But complex biofilms may form in the most unhospitable places for life as well: from biological soil crusts populated by nematodes, tardigrades and micro-arthropods in the most arid deserts (Darby and Neher 2016), to microalgal mats growing on snow or glaciers and populated with an intriguing meiofauna community dominated by cold-tolerant tardigrades and rotifers (Zawierucha et al. 2021). Biofilms also thrive in chemotrophic ecosystems, e.g. hydrogen sulphide-based bacterial mats floating at the surface of thermomineral cave waters. Here, rich nematode populations were found to develop ecological successions depending on bacterial density (Muschiol et al. 2015). Also under extreme conditions of temperature and pressure, whitish chemotrophic biofilms develop on the ocean floor around hydrothermal vents (Fig. 3.1). These biofilms mostly comprise nematodes and assemblages of harpacticoid copepods (e.g. Dirivultids) with a high degree of endemism (Zeppilli et al. 2018). Dirivultid copepods dwell in bacterial mats growing on hard-substrates or are found associated with engineering macro-invertebrate species (Gollner et al. 2016).

Fig. 3.1 Some examples of epibenthic biofilms. Upper panel: microphytobenthic biofilms coating cobbles in the Garonne River, France (photo N. Majdi). Middle panel: microphytobenthic biofilms coating tidal flats near Yerseke, The Netherlands (BIO-Tide project, photo K. Sabbe). Lower panel: chemotrophic biofilms coating rocks and clams near a deep-sea hydrothermal vent (Lucky Strike, 1700 m water depth, Mid-Atlantic Ridge, MOMARSAT 2012 cruise, photo courtesy of Ifremer)

When organizing into a biofilm, microbes (prokaryotes, unicellular eukaryotes or both) secrete a matrix of exo-polymeric substances (EPS) providing a favourable environment for growth. They can invest as much as 73% of their carbon production into the formation of such matrices (e.g. Goto et al. 1999). The EPS matrix can capture, retain and transform dissolved ions, organic molecules as well as inorganic and organic particles (e.g. Flemming 2016; Bonnineau et al. 2020). The self-organization of biofilm organisms in space and time is remarkable, contributing to form a collective, adaptative barrier against some external constraints like temperature, dessication, sheer stress, pollution and predation (e.g. Sabater et al. 2002; Neu et al. 2003; Risse-Buhl et al. 2017) that would otherwise be quite detrimental to a loosely organized community. When forming biofilms, microbes cooperate and/or compete, but either way, biofilms may be viewed as ‘microbial forums’, where collective exchange of information and chemical communication is key mechanisms (e.g. Decho 1990; Parsek and Greenberg 2005; Nadell et al. 2008). Indeed, biofilms have been the focus of an intense scientific interest, the majority of it directed at their associated economical benefits (e.g. wastewater mitigation, bio-production, biofouling, coastal erosion prevention) and health issues (e.g. antibiotic resistance, infections). Nevertheless, microbial biofilms are also emerging models in ecology as biodiversity hotspots and for their provision of essential ecosystem functions such as photosynthesis, decomposition of organic matter and recycling of nutrients (e.g. Battin et al. 2016).

But biofilms should not be viewed with a scope that is too narrowly focussed on their microbial constituents and their EPS secretions only. As dynamic and productive interface ecosystems, biofilms are a food resource and a refuge for meiofaunal organisms that are either permanently or temporarily associated with the biofilm matrix. Not to mention that the interstitial meiofauna spends their entire life associated with biofilms growing in the interstitial space. In most marine ecosystems, biofilms developping on hard-substrates are quickly and massively colonized by foraminiferans, nematodes and copepods (e.g. Fonsêca-Genevois et al. 2006; Zeppilli et al. 2018). In rivers, thick diatom biofilms may cover stones, cobbles and pebbles (Fig. 3.1), being crowded with diatom-feeding nematodes and bdelloid rotifers filtering out drifting particles (Kathol et al. 2011; Majdi et al. 2011, 2012a). The notion that meiofauna can attain high abundances within a biofilm that is only a few-mm thick testifies to the affinities of many meiofauna with biofilms: up to a dozen million individuals per m^2 were found on stones in the littoral of a lake (Schroeder et al. 2012), and up to 50 million individuals per m^2 were found in diatom biofilms growing on the surface of intertidal muds in salt marsh creeks (Moens unpubl.). However, whilst there is well-grounded consensus about the importance of the ecological functions provided by biofilms (e.g. Lock et al. 1984; Ford and Lock 1987; Winterbourn 1990; Mulholland et al. 1991), suprisingly poorly investigated is the role of biofilm-dwelling meiofauna in mediating these functions. Only recently, broader biofilm food web concepts comprising bacteria, algae, protozoans, meiofauna and macrofauna have been developped (Weitere et al. 2018).

Here, we argue that the slimy universe consisting of microbes and meiofauna is one of meiobenthology’s frontiers but is not restricted to meiobenthology. It will rather become a decisive domain in numerous facets of modern integrative aquatic biology, for example:

- In ecosystem ecology, we foresee that studying biofilm-dwelling meiofauna could shed more light on the fate of carbon, nitrogen and phosphorus (see Chap. 2).
- In functional ecology, one may learn more about the relationships between the different components of diversity (taxonomic, trait-based) and the functioning of ecosystems at a scale quite convenient for the experimentation–modelling–theory loop.
- In sociobiology, much is to be understood about the different ways in which biofilm-forming organisms and biofilm inhabitants communicate and interact which each other.
- In ecotoxicology, studying biofilm-dwelling meiofauna would help refining the toxicokinetics of pesticides which can be sequestered, transformed by the EPS matrix, and then bio-accumulated by the grazing meiofauna (see Chap. 7), and eventually transmitted to higher trophic levels (e.g. fishes).
- In restoration ecology, studying biofilm-dwelling meiofauna can hint at new ways to improve the purification capacities of hydrosystems.
- Last but not least, studying ecological interactions and adaptations of biofilm-dwelling meiofauna can further improve our understanding of the evolutionary consequences of processes such as competition, collaboration and communication between phylogenetically distant organisms.

We foresee an immense potential for further research exploring the fascinating set of meiofaunal interactions within the slimy universe. In this chapter, we try to address three questions to pave our way beyond the frontier of meiofauna–biofilm relationships:

- What are the Benefits of Living in the Slimy Universe?
- How do Meiofauna Contribute to Biofilm Functions?
- What are Applied Aspects of Research on Biofilm–Meiofauna?

3.2 What Are the Benefits of Living in the Slimy Universe?

3.2.1 Main Features of the Slimy Universe

The terms *biofilm, slime, aufwuchs, periphyton, epixylon, epipsammon, epilithon, microbial mats* or even *soil crusts* may be found in the literature and may refer to different assemblages of various viscosities and location (e.g. *epilithon*, or *epilithic biofilm*, defines biological assemblages growing on stony substrates), yet there is currently no consistency in the use of these different terms. However, whether it is a film, a crust or a mat, growing on wood chunks, macrophytes or stones, the general structure of these consortia has a number of similarities with, in the foreground, the secretion of extracellular polymeric substances (EPS) or low-molecular weight metabolites that literally form this ‘slimy universe’. These secretions support a significant number of functions that are common to the various assemblages considered and have been reviewed a number of times (e.g. Decho 2000; Wotton 2004; Battin et al. 2016; Flemming 2016; Decho and Gutierrez 2017).

The idea that all biofilms share common features, and structure is well grounded (e.g. Costerton et al. 1995; Stoodley et al. 2002; Lasa and Penadés 2006; Battin et al. 2007). All biofilms are indeed subject to attachment and dispersion constraints that require adaptation to fluid dynamics (air flow for biological soil crusts, water flow for aquatic biofilms), and all communities must protect themselves from external deleterious factors (e.g. water or air pollution, temperature, salinity, desiccation, UV-radiation and irradiance) by promoting the production of EPS. Thereby, biofilms show similar successional patterns, with simple colonizer forms adhering to the substrate whilst more complex forms emerge through time as a result of immigration and diversification of the community (e.g. Jackson et al. 2001; Lyautey et al. 2005).

These assemblages are also characterized by a high level of complexity and cooperation (or competition) between the different members that compose them: for instance, bacteria use intercellular signalling (*aka.* quorum sensing) to trigger the complex biofilm succession process such as attachment, maturation, aggregation and dispersal (Parsek and Greenberg 2005), and bacteria are involved in a number of synergistic interactions with microalgae such as algal growth and flocculation (Ramanan et al. 2016). But one may note that microalgae also secrete 'allelochemicals' (*aka.* toxins) to inhibit the growth of competitors for space and resources or to deter their predators (Leflaive and Ten-Hage 2007). These complex cross-talks between the different organisms composing biofilm assemblages are an obvious common feature that has been described by van Gemerden (1993) as a 'joint venture'.

Whilst the largely stochastic processes of death, reproduction and immigration from source assemblages are important drivers of biofilm community assembly, interactions such as grazing by protozoans and/or metazoans and quorum sensing are just some of the factors that influence the structure and heterogeneity of biofilms and microbial mats. Environmental features such as topography and pressures (seasonality, desiccation, exposure to radiation, the existence of chemical and energetic gradients) drive microorganisms to organize themselves in space (e.g. in laminated microbial mats), to exclude each other (i.e. soil crusts, stromatolithes) or, by contrast, to associate even more closely, adding a further crucial structuring force to the definition of biofilms. Thus, despite the resulting heterogeneity, from a conceptual point of view, all these assemblages share some common key features and form microscopic landscapes where EPS compounds represent the nodal point from which the relationships between microorganisms, but also between microorganisms and meiofauna, can be explained (Hubas et al. 2018).

In addition, not only do EPS compounds share common characteristics, but species assemblages are also extremely dynamic and can constantly change from one state to another as environmental parameters fluctuate (e.g. Jackson et al. 2001; Boulêtreau et al. 2006; Timoner et al. 2012). Purple bacterial mats growing onto coastal sediments are a good example of this dynamics (Fig. 3.2). Indeed, during episodes of green algae proliferation (i.e. green tides), the sediment becomes progressively anoxic as the algae are deposited and degraded (Hubas et al. 2017). The biogeochemical gradients are gradually modified until H_2S becomes dominant on the sediment surface. Then,

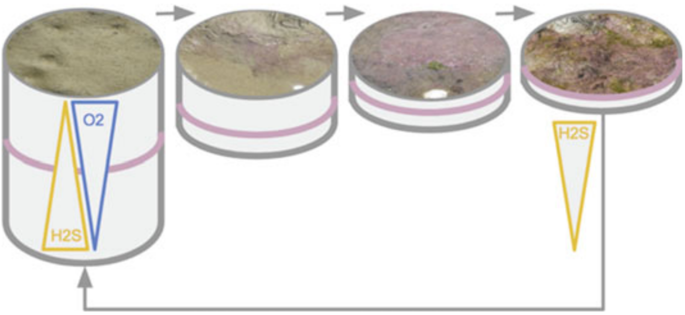

Fig. 3.2 Seasonal development of a photosynthetic microbial community in coastal sediments. The community develops from a typical microphytobenthic mat to a purple anoxygenic bacteria biofilm. From left to right, the images represent the evolution of the sediment surface from winter (left) to the end of summer (right). The pink line indicates the approximate position of the purple anoxygenic bacteria in the sediment core. The depth of the core is proportional to the thickness occupied by the photosynthetic organisms. Adapted from Hubas et al. (2018)

very thick and almost monospecific biofilms, composed of Chromatiaceae of the *Thiohalocapsa* genera, settle on the surface (Hubas et al. 2013). These bacteria, which are usually present deeper inside the sediment, can then massively proliferate at the surface. After the complete degradation of green algae, the purple biofilms generally disappear, and a microbial mat more typical of sandy-muddy sediments gradually returns, dominated by diatoms at the surface (Fig. 3.2).

Independent of the type of ecosystem (i.e. freshwater, marine, terrestrial), the following sections will describe the numerous advantages for meiofauna organisms to live in the microbial slimy universe. Notwithstanding the remarks made above, for the sake of readability, the term ‘biofilm’ (which is the most widely used in the literature) will be used throughout this chapter to refer to this complex and multi-faceted ecosystem.

3.2.2 The Biofilm Food Web

The trophic ecology of meiofauna has been the subject of a number of publications (see Chap. 5), and it is generally assumed that the quantity and quality of food sources are primary factors in structuring meiofauna communities. Biofilms represent a wealth of food sources and beneficial nutrients for meiofaunal organisms. The generous EPS production by biofilms fuels the growth of bacteria that in turn can be grazed by certain species of meiofauna (Pascal et al. 2008; Wu et al. 2019). Moreover, ‘drinking EPS soup’ itself has been considered a significant food source to some meiofaunal organisms too (Decho and Moriarty 1990). Whilst this topic surely requires more research, there is ample evidence that meiofauna uses the high-nutritional quality cells present in the biofilm. For example, diatom cells are rich in essential polyunsaturated fatty acids (e.g. Eicosapentaenoic acid 20:5ω3), and they allocate organic carbon into both triacylglycerol and store the polysaccharide chrysolaminarin (Bohorquez et al. 2013; Gügi et al. 2015). Diatoms are known to be an important resource for many meiofaunal organisms (e.g. Azovsky et al. 2005; De Troch et al. 2005; Moens et al. 2013). Also, cyanobacteria, producing a large number of different monosaccharides, may represent another relevant food source for the meiofauna (Mialet et al. 2013); and green algae (chlorophytes) have been found to be exploited by the biofilm-dwelling meiofauna (Kazemi-Dinan et al. 2014; Neury-Ormanni et al. 2016). The combined use of stable isotopes and fatty acids underlines the role of microphytobenthos and benthic bacteria as the main food sources of nematodes and benthic copepods in intertidal mudflats (Wu et al. 2019; van der Heijden et al. 2019). In freshwater biofilms, dissolved and particulate organic matter, microalgae (often diatoms) and bacteria are important food sources for nematodes (Majdi and Traunspurger 2015; see Chap. 6) and other meiofaunal taxa, such as rotifers, tardigrades, water mites, harpacticoid copepods and oligochaetes (Schmid-Araya et al. 2016).

Interestingly, bacterial communities also tend to form biofilms as a refuge against predation by bacterivores such as free-living protozoans (Arndt et al. 2003). Amongst the anti-predator strategies of bacteria, one can distinguish four categories (Matz 2009):

(1) adherence effects (hydrophilous properties or increased adherence to substrate with pili, fimbriae and flagellae that will affect prey dislodgement),
(2) matrix effects (the EPS coating forms a physical barrier decreasing susceptibility to phagocytosis, or a chemical barrier that disrupts chemotaxis in predators),
(3) density effects (bacteria use quorum sensing to form larger aggregations in response to predation, triggering swarm effects or synergistic toxic effects on predators) and
(4) diversity effects (the self-generated structural complexity in complex assemblages reduces susceptibility to grazing and a collaborative defensive strategy with multiple anti-predator responses).

Some of those anti-predator strategies probably hold true when biofilms face meiofaunal grazers as well, but this topic deserves more exploration. For example, Chan et al. (2020) showed that biofilms of *Pseudomonas aeruginosa* produced an exopolysaccharide to entangle and slow down nematode predators. Herman et al. (2001) also suggested that the trapping of mud particles in the biofilm mucilage decreases grazing efficiency, mainly by macrofauna but perhaps also by meiofauna as well. Biofilms may interfere with the chemotaxis of nematode grazers using volatile organic compounds (Höckelmann et al. 2004). The odds of complex chemical communication in biofilms, such as the elaboration of anti-predator strategies by a disparate assemblage of microbes, are a strong topic in microbiology. We argue that this topic would gain ecological relevance by being more inclusive and comprising the chemical interaction between microbes and their meiofaunal grazers.

Interestingly, meiofaunal grazers do not seem to be a major threat to biofilms, and biofilms may even have some benefits in housing meiofaunal grazers. For example, evidence suggests that meiofaunal grazing ‘opens’ the biofilm matrix with positive effects on resource fluxes, microbial growth and activity as detailed in Sect. 3.3 of this chapter. Moreover, meiofauna has a relatively low grazing impact on biofilm microphytobenthos compared to the grazing pressure of freshwater macro-invertebrates (Majdi et al. 2012b; Graba et al. 2014). Correspondingly, nematode grazing rates in estuarine and intertidal flats were found to be modest (Middelburg et al. 2000; Van Oevelen et al. 2006). However, these observations seem to have a local validity only: other calculations on feeding rates of dominant epistrate-feeding and deposit-feeding nematodes from tidal flats suggested that their grazing rates could attain a significant impact on microphytobenthic production, at least during spring (Rzeznik-Orignac et al. 2003). This would correspond to a recent food web modelling study (van der Heijden et al. 2020) in five different intertidal habitat types. It suggested that meiofauna was more efficiently involved than macrofauna in transferring microphytobenthic carbon to higher trophic levels. These contrasting data on the role of meiofaunal grazing for benthic biofilms need further clarification.

Chemoautotrophic biofilms can be a source of food and support very high densities of meiofauna organisms as well (Zeppilli et al. 2018): in deep-sea hydrothermal vents, *Beggiatoa* bacterial mats might constitute a feasible food source for some nematodes (Zeppilli et al. 2019). By concentrating nematodes, these mats indirectly offer high quality food source to other predators (such as to polynoid annelids). Furthermore, some nematodes thriving in chemoautotrophic biofilms develop symbiotic associations with bacteria (for details see Chap. 4). This is the case in *Oncholaimus dyvae*, which hosts various proteobacterial types on its cuticle and on surfaces of its gut, suggesting some direct or indirect benefits (nutrition or detoxification).

Given its productivity, nutritional quality and the variety of resources it harbours, the biofilm is, therefore, a place that promotes the development of a complex food web comprising several trophic levels and ranging from opportunistic to selective feeders (Weitere et al. 2018): it is not uncommon to find organisms with very specific diets. In these microscopic food webs, microalgal carbon can be passed directly by grazing to herbivorous nematodes such as *Metachromadora remanei*, *Daptonema oxycerca* or even benthic copepods with a high degree of selectivity regarding diatom size, but microalgal carbon could be also transferred indirectly to higher trophic levels such as the predacious nematode *Sphaerolaimus gracilis* that feeds on the herbivorous *D. oxycerca* (Rzeznik-Orignac et al. 2008). In rivers, photosynthetically-fixed carbon has been found to quickly flow to *Chromadorina bioculata* nematodes and chironomid larvae (Majdi et al. 2012b), although a significant part of photosynthetic carbon also leaves the biofilm presumably through the drift of organisms or faecal pellets, or the consumption of biofilm organisms by larger, mobile predators.

Many meiofauna species have a high degree of trophic plasticity to adapt to the potential lack of their preferred food sources in the biofilm (Moens et al. 2004). As shown by Riera and Hubas (2003), free-living nematodes may sometimes prefer an allochthonous food source if it is more available or has superior nutritional qualities than local food sources. As another example, in rivers, rotifers can attain record abundances in biofilms growing on hard-substrates. Still, they may largely rely on filter-feeding the water column rather than exploiting the biofilm (Kathol et al. 2011). The isotopic signature of the whole benthic community can switch towards allochthony in response to resource turnover, or to massive allochthonous inputs, such as observed in forested streams where leaf litter falls in autumn (Majdi and Traunspurger 2017), or in sheltered coastal bays upon massive inputs of macroalgal wrack (Riera and Hubas, 2003). It appears that assessing who feeds on whom in biofilms is a complex task, and we surely need more empirical knowledge to better understand the role of meiofauna in the biofilm food web.

3.2.3 The Biofilm as a Habitat—A Safe Haven in Stressful and Extreme Environments?

Aquatic systems are not always favourable places for the settlement of an exhuberant fauna. For example, flow velocity (and sheer stress) is a recognized, predominant driver of the structure of stream and river communities but also more generally in zones exposed to water currents or wave disturbance. Water flow dictates biofilm metabolic rate by limiting the thickness of the diffusive boundary layer of the mat (e.g. Costerton et al. 1995). Flow determines exchanges with the water column like the emigration/immigration rate of organisms (e.g. Peterson and Stevenson 1992; Majdi et al. 2012a; Tekwani et al. 2013). Of course, the slimy nature of the biofilm reduces considerably its vulnerability to shear stress, because the increased fluid viscosity near the biofilm surface imposes a slower and less turbulent flow (Stewart 2012). Additionaly, the biofilm organisms may engineer the local architecture of the mat, e.g. filamentous diatoms may form large ‘tufty’ structures on top of the mat further reducing flow velocity and biofilm vulnerability to erosion (e.g. Battin et al. 2003; Besemer et al. 2009; Risse-Buhl et al. 2020).

From a macroscopic perspective, biofilms may appear unstable ecosystems, constantly assembling and disassembling; however, at the microscopic scale, they are coherent and predictable frameworks in response to environmental forcing (Ceola et al. 2014). Biofilms tend to shelter meiofauna against such fluctuations (Majdi et al. 2012a; Graba et al. 2014); however, not all species have a life-style compatible with shear stress constraints. For example, Kreuzinger-Janik et al. (2015) showed that exposure to wave action in a lake had a positive short-term effect on the density of biofilm-dwelling meiofauna by favouring the species able to anchor themselves to the substrate like the chromadorid nematode *Punctodora ratzeburgensis*. Similar findings were corroborated in ponds (Croll and Zullini 1972), in rivers with chromadorid nematodes dominating during high flow periods (Majdi et al. 2011), and on epiphytic and ‘hard’ substrates in coastal waters, where Chromadoridae again appear the best adapted nematodes to maintain themselves when exposed to waves, probably by the use of sticky secretions from their caudal glands (Fonsêca-Genevois et al. 2006). Interestingly, nematodes can attain very high densities with a higher proportion of gravide females in free-floating biofilms, suggesting that they may use those floating biofilms as ‘biological rafts’ for downstream dispersal (Gaudes et al. 2006). Recent studies have also shown that biofilms growing on the carapace of loggerhead turtles were housing an abundant and diverse meiofauna community (Ingels et al. 2020), which suggests that those ‘moving biofilms’ may help meiofauna to disperse over long distances.

In intertidal areas, it has been shown that biofilms can act as a protective layer on the sediment surface against the disturbance imposed by the cycle of emersion/immersion (Orvain et al. 2014), EPS composition playing a critical role for protection against dessication and osmotic fluctuation. In streams and rivers, biofilms buffer the effects of droughts (Costerton et al. 1995; Timoner et al. 2012). Further comparing biofilm-dwelling meiofaunal communities, Caramujo et al. (2008) observed a greater abundance of copepods, turbellarians, nematodes and larval chironomids in rivers impacted by droughts that could be linked to changes in algal composition and biofilm growth rate. As another example, Majdi et al. (2020) observed that meiofaunal taxa showing the most outstanding capabilities to cope with desiccation (like tardigrades) benefitted the most from the longest drought periods in Mediterranean streams, and those dessication-resistant meiofauna might help to quickly restore river functions after droughts. The mucilaginous nature of the EPS matrix certainly helps biofilm organisms to withstand moisture fluctuations and also provides additional shelter against UV- radiation (Elasri and Miller 1999).

3.3 How Do Meiofauna Contribute to Biofilm Functions?

3.3.1 Biofilm–Meiofauna Systems: A Trophic Powerhouse?

Studying the response of complex, multitrophic biofilm communities to environmental fluctuations might help to better understand how changes in the structure of species assemblages could transmit to ecosystem functions. Tackling such issues implies a mechanistic understanding of patterns and processes at a scale comprehensive enough to link changes in species assemblages to the ecosystem functions, which are mostly determined by microbes (Pusch et al. 1998). Biofilms are such a landscape where all fundamental ecosystem compartments (producers, decomposers, primary consumers and predators) are at work. From a biogeochemical point of view, biofilms form a micro-world producing its own organic matter through autotrophic fixation of inorganic carbon (CO_2) by algae and cyanobacteria and/or through uptake of dissolved organic carbon (DOC) by decomposers (e.g. bacteria and fungi).

As an example, in headwater streams, subsidized by large amounts of allochthonous DOC originating from soil aquifer and riparian forests (Gessner et al. 1999), benthic biofilms are hotspots of DOC degradation and CO_2 production (Battin et al. 2003; Romaní et al. 2004). Inversely, microphytobenthic (MPB) biofilms in intertidal areas generally show a high autotrophic fixation of inorganic carbon (CO_2), but patterns of net MPB primary production vary strongly in these ecosystems as a result of the high variability and interactions of environmental factors which generally affect the estimation of realistic annual carbon budgets (Hubas et al. 2006; Davoult et al. 2009; Haro et al. 2020). Producers and decomposers are also linked through mutualistic interactions as producers fuel decomposers with labile organic carbon sources, whereas producer growth is dependent on nutrient recycling ensured by decomposers (Danger et al. 2013). In intertidal sediments, bacteria represent up to 88% of benthic community respiration, but a significant part is also sustained by meiofauna activity (Hubas et al. 2006). In addition, it has been shown in those intertidal areas that the contribution of a given benthic compartment (i.e. bacteria or meiofauna) to total secondary production depends on productivity gradients (Fig. 3.3): Contribution of heterotrophic bacteria to material flows is greatest in less productive sandy sediments and decreases towards more productive muddy sediments in favour of the meiofauna and macrofauna. This is presumably based on the permeable nature of the coarser sediments, where organic matter is not retained but rapidly ‘drains through’, not allowing time for meio- and macrofauna to use it.

The complex set of biological interactions occuring in biofilms can indirectly affect carbon dynamics (see also Chap. 2). An illustrative example might be the

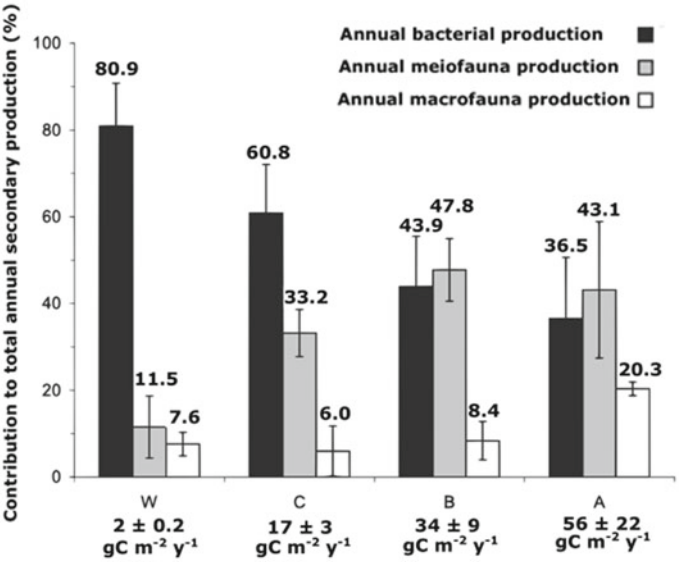

Fig. 3.3 Contribution of the different benthic heterotrophic compartments to total secondary production (in gC m^{-2} y^{-1}) along a productivity gradient. Stations A, B and C correspond to muddy to sandy sediment (median grain sizes are, respectively, 132 ± 54, 215 ± 43 and 251 ± 10 μm) of the Roscoff Aber bay and W to the Wimereux sandy beach (median grain size ~ 200 μm). The total secondary production for each site has been reported at the bottom of the graph. Bacterial production was estimated by the incorporation of radiolabelled thymidine, meiofauna and macrofauna production which were estimated by measurement of the biomasses and biovolumes. All measurements were converted to *C* units using conversion factors. Unpublished results adapted from Hubas (2006)

top-down effect of nematodes on the species composition of both the diatoms and bacteria of an artificial biofilm reared in laboratory conditions (D'Hondt et al. 2018). There are more examples of studies where nematode grazing, even at relatively low rates, may affect the composition (e.g. De Mesel et al. 2004, 2006) or the productivity of microbial assemblages (Traunspurger et al. 1997), but the functional implications are not always well understood.

As another example of top-down controls, we may question the role of 'top-predators'. In biofilms, those top-predators may be in the millimetre range; still, they are expected to perform the same important functions than in other ecosystems: triggering trophic cascades, engineering habitat properties or modifying the behaviour of prey organisms (e.g. Schmitz et al. 2010; e.g. Terborgh and Estes 2010). In benthic environments, there is some evidence that microscopic top-predators have effects on ecosystem processes and community structure through direct predation but also through indirect pathways such as mucus secretions (e.g. Riemann and Helmke 2002; Majdi et al. 2014, 2016; Wilden et al. 2019), excretions (De Troch et al. 2010), construction of burrows (Ings et al. 2017), displacement of sediment particles (Majdi et al. 2015) or dispersion/displacement of microbes (Riemann and Helmke 2002).

There is much debate about how food web architecture and how biodiversity influence emergent properties of ecosystems, notably their productivity and stability (e.g. Johnson et al. 1996; Worm and Duffy 2003; Cusson et al. 2015). Tackling this question is essential to understand and to anticipate and remediate the ecological and societal consequences of global declines in species diversity (Estes et al. 2011). We envisage that biofilm–meiofauna systems could be highly suitable models to tackle such questions given their amenability to experiments and the diversity of biological interactions at play.

3.3.2 On the Roles of Poking Holes

A key aspect of biological interactions is the 'engineering' effect that animals have on their habitats. Like beavers do when creating reservoirs by damming rivers, worms can turn a homogeneous seabed landscape into a mosaic of holes, burrows and excavation patches. Whilst the important ecological (and evolutionary) consequences of bioturbation by macrofauna are well known (Meysman et al. 2006), the consequences of meiofaunal bioturbation (which might be specifically coined 'microbioturbation' or 'meioturbation') are comparatively little studied. With their worm-like morphologies, many meiofaunal species are well adapted to an interstitial life-style, not necessarily pushing aside large sediment particles when moving. But they rather move through interstices and through biofilm matrices. By doing so, they probably modify the cohesiveness (and permeability) of biofilms, thereby affecting the penetration of light and solutes in deeper layers (Pinckney et al. 2003). In addition, the way meiofauna ingest or displace microbes, whilst they forage may further affect the composition of biofilm assemblages.

Collectively, 'meioturbation' has been suggested to have a significant and often stimulatory effect on interstitial biofilm functions (see Chap. 2). Regarding epibenthic biofilms, a similar stimulation of ecosystem functions has been measured in the presence of meiofauna. For example, Mathieu et al. (2007) used microelectrodes to measure oxygen profiles in artificial diatom biofilms incubated with and without free-living nematodes. They showed that with nematodes present (density threshold > 50 ind cm^{-2}), biofilms produced more oxygen under daylight, and even deep biofilm layers were found to produce oxygen at a higher rate than without nematodes. A similar effect was observed by D'Hondt et al. (2018), where nematodes have been found to further alter the community structure and increase the production of diatom biofilms. In another experimental study, the effect of bacterivorous nematodes *Diplolaimelloides meyli* and *D. oschei* on the EPS production by biofilm bacteria and diatoms was investigated (Hubas et al. 2010). Despite expected grazing by nematodes on bacterial cells and on microbial EPS, the biofilm structure (including EPS production) was always stronger in the presence of nematodes. This indicates that links between meiofauna and EPS are not straightforward and include a number of retro-control loops, which make the relationship highly unpredictable. Whether these stimulations of biofilm functions are mainly due to grazing, meioturbation or both, need more studies, but there is consensus that the presence of meiofauna stimulates key biofilm functions.

More specifically, our knowledge on the different suites of foraging behaviour in meiofauna that trigger specific engineering effects is quite fragmentary. Some congruent observations have reported interesting behaviours, e.g. in chromadorid nematodes, that use sticky secretions to collect surrounding particles and form small 'nutritive' pellets that may further be used as a shelter or food supply (Meschkat 1934; Croll and Zullini 1972). These pellets might affect the biofilm architecture (and functions), given the outstanding abundances that biofilm-dwelling chromadorids may attain on hard-substrates. Other biofilm-dwelling organisms are known to build tubes or burrows lined with silky secretions. These burrows modify biofilm architecture locally (Lock et al. 1984; Pringle 1985) and probably affect the distribution of microbial organisms as well. Turbellarians secrete substantial amounts of mucus when moving, and thereby, they might be expected to have conspicuous effects on biofilm and sediment cohesiveness (like in their macroscopic relatives Majdi et al. 2014). The suite of behaviours that leads to meioturbation effects needs to be assessed more thoroughly and in a broader variety of taxa, in order to obtain a better understanding of its influence on benthic processes.

3.3.3 On the Roles of Mucus

Another potential contribution of meiofauna to biofilm function is the 'priming effect' (PE) due to the use of labile exudates (e.g. faecal pellets, mucus) boosting the decomposition of recalcitrant organic matter by microbes. PE, as first studied in soil ecosystems, has been defined by Kuzyakov et al. (2000) as '*strong short-term changes in* *the turnover of soil organic matter caused by comparatively moderate treatments of soil*'. The influence of PEs for DOC mineralization in aquatic ecosystems is a timely topic (Guénet 2010), but studies have mostly assessed PE triggered by the mucilage of autotrophic organisms like diatoms (e.g. Danger et al. 2013).

Here, we argue that PE triggered by animal secretions could be ideally studied using meiofaunal models. Indeed, several species of nematodes secrete mucus trails when moving, and these trails become quickly colonized by bacterial clusters (Riemann and Helmke 2002; Moens et al. 2005). This suggests that nematodes are able to displace or 'prime' the bacteria that surround them or even specifically 'prime' the microbiome they carry with them. These bacteria find ideal conditions for their development in the mucus trails. The nematodes may benefit from this mechanism by 'turning back' and grazing on previous trails. Riemann and Helmke (2002) proposed the hypothesis of such a facilitative interaction between nematodes and bacteria: the enzyme-sharing concept. On the one hand, the nematodes disperse bacterial colonies and the cellulolytic activity of the mucus provide a labile carbon source, which would stimulate bacterial growth (i.e. PE triggered by animal secretions). On the other hand, the proteolytic activity of the bacteria (as well as potential direct nutrition of the nematodes on the bacterial clumps) would be beneficial for the nematodes, which depend on labile nitrogen in their environment. Referring to green algae, Warwick (1981) noticed that the nematode *Praeacanthonchus* was unable to ingest the 'square' active *Tetraselmis* cells but could feed intensively on its slimy spherical resting cells. Although the ecological relevance of these mechanisms at larger scales needs to be confirmed, priming effects triggered by meiofaunal exudates or external enzymatic-symbioses could change the way we conceptualize the sociomicrobiology of biofilms.

3.4 Applied Research on Biofilm–Meiofauna

3.4.1 Improving Water Purification Processes

Inland waters and coastal areas are increasingly impacted by dissolved pollutants (heavy metals, pesticides, pharmaceuticals) as well as by particulate matter (fine-sediment, organic particles, micro-plastics, nano-materials; see Chap. 7) from anthropogenic activities. Biofilms can, depending on the composition and performance of their communities, affect the toxicokinetics (absorption, distribution, biotransformation and elimination) of those contaminants (Bonnineau et al. 2020). Moreover, some species of annelids, nematodes and rotifers can massively colonize contaminated biofilms or thrive in sludge from sewage treatment plants (Fried et al. 2000; Fraschetti et al. 2006; De-ming and Xiao-shou 2014; Monteiro et al. 2019; Bighiu et al. 2020; Rohal et al. 2020). Studies explored the hypothesis that the presence of meiofauna would improve the filtration rate and the lifespan of gravity-driven membrane filtration (GDM) as the meiofaunal activities tend to reduce the clogging of membranes (Derlon et al. 2013; Klein et al. 2016; Lee et al. 2020). It could be shown that the flux of water could be significantly enhanced: e.g. + 119 to 164% flux in the presence of nematodes, + 50% in the presence of oligochaetes. Studies in laboratory microcosms have considered the addition of meiofauna to biofilms (e.g. Nascimento et al. 2012; Bonaglia et al. 2014; Liu et al. 2015, 2017, 2021). Results of these studies show that in the presence of more meiofauna, biofilms denitrify more and retain more dissolved organic carbon.

In the realm ‘biofilms–microorganisms–meiofauna’, our knowledge is often minimal. Basic questions of high theoretical relevance are still open, although they often represent the ‘natural’ pathways biofilms cope with chemical stress:

- To what extent will the contaminants become adsorbed by the EPS matrix, accumulated, metabolized to microbial cells or transferred to the ‘biofilm-fauna’?
- Does meiofauna living in biofilms represent a sink or a source of harmful compounds that is transmitted (bio-accumulated) to the higher levels of the food Web?
- To what extent become (micro)plastic particles, trapped in biofilms and subsequently ingested by the meiofauna (Fueser et al. 2020)?

In experimental designs, one could selectively remove biofilm-dwelling grazers known to accumulate problematic contaminants. One could also apply as ‘useful’ indicators those meiofaunal taxa whose sensitivity, resistance or even accumulation capacity is known. Considered at different operational scales (from use in private aquariums to wastewater treatment plants), biofilm-dweeling meiofauna would indicate problematic pollutants or the restoration status of contaminated sites. Finally, one could assess the potential of self-purification provided by biofilms and their associated meiofauna. Based on these results, this specialized biota could be applied, e.g. for mitigating contaminations in wastewater effluents.

3.4.2 Biogenic Stabilization

The increased mobilization of fine sediments in river and coastal ecosystems due to deforestation and urbanization is a threat to benthic ecosystems. The resulting massive deposition of fine-sediment increases accumulation of particulate organic matter and tends to clogg interstitial spaces (Wood and Armitage 1997; Goatley and Bellwood 2013). Schratzberger and Ingels (2018) conceptualized the ambivalent role of meiofauna in the process of sediment stabilization: meiofauna may increase sediment cohesiveness by increasing EPS production by microbes or by secreting sticky mucus and burrows. On the other hand, meiofauna may decrease sediment cohesiveness when grazing on or moving through the interstitial biofilms. Empirical experiments have supported both aspects: For example, Hubas et al. (2010) showed increased sediment compaction by nematodes stimulating EPS production by bacteria, whereas De Deckere et al. (2001) found decreased stabilization by grazing and bioturbating effects of meiofauna. This exemplifies the need of gaining more evidence on the impact of meiofauna on sediment stabilization in order to formulate better predictions about the fate of sediments in aquatic ecosystems. Furthermore, meiofauna may affect both the permeability of biofilms for dissolved particles and the chemical diversity of biofilm exopolymers. Particles entering the EPS matrix may become affected and/or entrapped on hard-surfaces under the influence of meiobenthos. Unravelling such meiofauna-mediated processes of sediment stabilization represents potentially high relevance and a frontier that needs urgent investigation. More knowledge about the relation between meiofauna and EPS production or composition in biofilms may lead to important future applications, e.g. mitigation of fine-sediment deposition or erosion. Similarly, the role of biological interactions at a meiofaunal scale in the restoration of ecotones (e.g. mangroves, riparian forests) would help to reduce sediment displacement—a research frontier of high future relevance.

Finally, biogenic stabilization has also been suggested for applications trying to mitigate desertification. It may be considered an anecdotal suggestion, but recent technologies have been proposed spraying nanoscopic tubular frameworks inoculated with eutrophicated lake water containing cyanobacteria to stimulate the development of a biological crust which slows down the erosion of superficial sand layers (Li et al. 2020). Would those ‘artificial ecosystems’ be sustainable and could they benefit from the presence of desiccation-resistant meiofauna like tardigrades or nematodes to initiate trophic retro-controls or to further spread the algal crust vertically?

3.5 Frontiers and Future Horizons

Biofilms are fascinating microbiological structures that show some analogies with multicellular organization. Since meiofauna are important components in biofilms, we explored in this chapter three questions to identify frontiers of meiofauna–biofilm research:

(1) What are the Benefits of Living in the Slimy Universe?
(2) How do Meiofauna Contribute to Biofilm Functions?
(3) What are Applied Aspects of Research on Biofilm–Meiofauna?

The short history of this scientific field may account for the frequent lack of evident answers. However, we may conclude identifying the following scientific frontiers in this field:

- Meiofauna benefits from biofilms in two ways: firstly, biofilms are a hotspot of microbial diversity and thus constitute an ideal resource for microbivorous as well as predatory meiofauna. However, we need more evidence to differentiate the relative importance of each resource as diet of meiofaunal organisms, and whether microbes may adopt defence strategies to repel meiofaunal grazers. Secondly, we have evidence that biofilms offer shelter to meiofauna against flow disturbance and moisture fluctuation. Biofilms probably also protect meiofauna from long-term desiccation, UV-radiation, chemical stress and predation effects, but these topics are little studied so far.

- Meiofauna contributes to biofilm function: when grazing on microbes meiofauna affect microbially-mediated processes. Thus, future insights on the feeding selectivity of meiofaunal organisms would reveal how top-down controls can structure biofilm functions.
- Meiofauna acts also indirectly on biofilm functions through poking holes in the cohesive matrix, as well as emitting secretions. Overall, these indirect controls have the potential to stimulate microbial processes. As bioturbation increases solute fluxes, labile secretions tend to stimulate the remineralization of recalcitrant organic matter. These fluxes are, thus, mostly bottom-up driven. But without quantification of those controls at larger scales we are not yet in the position to refine these animal-effects on ecosystem processes.
- The domain of biofilms and meiofauna has a large potential for environmental applications (e.g. epuration of wastewater, remediation of xenobiotics, restoration of contaminated sites, sediment stabilization). Details in this complex relationship between meiofaunal grazers and their biofilm habitat–resource are, as yet, mostly unexplored.
- Based on the small-scale engineering capacities of a biofilm-dwelling meiofauna community, technical applications for their use are probably countless, and there are many fields that could benefit from the study of meiofauna–biofilm relationships with a high potential of rewarding exploitation.

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Chapter 4
Meiofauna Meets Microbes—Chemosynthetic Symbioses

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Abstract Nutritional symbioses of meiofauna with chemosynthetic bacteria occur across the globe, from deep-sea vents and seeps to shallow water sediments. The bacteria provide nutrition to their hosts, and the hosts provide both habitat and the efficient bridging of long redox gradients. In this chapter, we summarize our current understanding of these intricate symbioses, identify knowledge gaps and point out future-oriented research directions in this expanding field. The peak species diversity of meiobenthic hosts of chemosynthetic bacteria is found in shallow water sediments towards the tropics, however in only a few higher taxa, including ciliates, platyhelminths, nematodes and oligochaetes. The degree of association ranges from ectosymbioses, subcuticular endosymbioses to intracellular endosymbioses. Independent of the association type, several modes of nutritional transfer have been documented, even a transfer of nutrients via outer membrane vesicles. The mode of symbiont transmission is independent of association type or nutrient transfer. It can be strictly vertical or a mixed mode depending on the host group, but largely remains unknown. The symbiotic life style has profound influences on morphology and functions in both partners. The mouth and several other key structures related to food uptake or excretion are reduced in members of all host phyla. Several bacterial partners exhibit a strongly modified cell biology with longitudinal division as an adaptation to secure contact with the host. The host immune system, responsible for establishment and maintenance of the symbiotic association, appears highly specific and except for the oligochaetes, allows only one microbial partner across the host phyla. The receptor and effector molecules that ensure the selective presence of the "right", and the effective defence against the "wrong", microbes appear convergent for both nematodes and oligochaetes. In both hosts, the symbionts appear integrated into the host defence. Diverse carbon and energy sources are exploited and the ability to use small organic molecules as carbon source puts the strict autotrophy of these symbiotic consortia in question. Mixotrophy and even heterotrophy are possible,

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and in addition, anaplerosis seems to play an important role in inorganic carbon acquisition. Among the symbionts, the Gammaproteobacterium *Ca.* Thiosymbion stands out with an extremely broad physiological spectrum that includes nitrogen fixation in some hosts. This flexibility has enabled it to associate with phylogenetically unrelated host groups and adopt all possible life styles, from ectosymbiont to intracellular endosymbiont. Frontiers and challenges of future research in this field include the still unresolved taxonomic diversity of these symbioses, their puzzling evolutionary dynamics, the lack of cultivable representatives, and the unknown scale of their global influence in permeable sediments, one of the largest global habitats.

4.1 Introducing a Special Relation

The living world runs on solar energy: photosynthesis is the dominating process that converts oxidized inorganic carbon into reduced organic carbon compounds as the building blocks of life. However, the greater part of the surface, and even more of the volume, of the biosphere is lightless. Life in the vast volume of water, sediment and crustal rock below the euphotic zone depends on the production by photosynthetic organisms inhabiting ecosystems that receive enough sunlight where a surplus build-up of organic matter can be sustained.

Whilst the existence of alternative ways to reduce inorganic carbon for production of organic matter has been acknowledged for some time, it was considered an insignificant part of global production. The discovery of abundant deep-sea hot vents where microbes utilized reduced compounds to incorporate inorganic carbon renewed the interest in such alternative ways of carbon fixation (see Chap. 2). The main pathway is the oxidation of reduced sulphur compounds, mainly hydrogen sulphide, as an energy-yielding process. Many of the microorganisms involved in this chemolithoautotrophic production live in symbiosis with animals. They provide a plentiful, stable and safe environment for their bacterial partners and in turn are nourished by the microbial production. The ecological and physiological processes that evolved in these symbioses seemed to be restricted to the lightless deep sea.

However, in the wake of the discoveries in the deep ocean, scientists turned their attention to shallow water ecosystems where reduced compounds, such as sulphide are abundant on sheltered sedimentary coasts and in subtidal shelf areas. These habitats revealed an astonishing diversity of animal-microbe symbioses comparable to those in the deep sea (Dubilier et al. 2008; Sogin et al. 2020). Surprisingly, both hosts and symbionts differed from those found in the deep. At deep water vents and seeps the hosts of thiotrophic symbioses are represented by macrofauna, whereas in shallow water, they belong, with the exception of bivalve molluscs, to the meiobenthos, including various taxa of e.g., Ciliata, Nematoda, and Annelida (Fig. 4.1).

Higher taxa that make up the chemosynthetic meiofauna are different from those in the deep sea. Of the four groups included in this chapter, amongst Platyhelminthes and Nematoda so far, no symbiotic representatives have been found around deep-sea hot vents and seeps, although symbiotic nematodes occur in bathyal habitats.

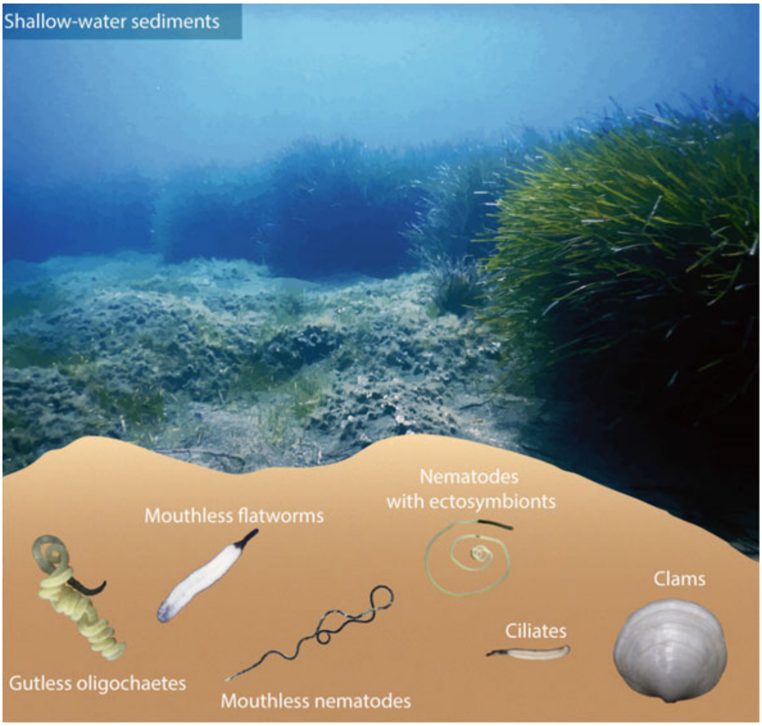

Fig. 4.1 Overview of chemosynthetic meiofauna. Today, a wide range of chemosynthetic organisms live in sediments surrounding seagrass meadows and coral reefs. Many of the taxa are small, like the gutless oligochaetes (*Olavius* and *Inanidrilus*), mouthless flatworms (*Paracatenula*) and nematodes (Stilbonematinae with ectosymbionts, mouthless *Astomonema* with endosymbionts), and single-celled ciliates (*Kentrophoros*). These habitats also support larger fauna, such as clams (lucinids and *Solemya*, latter not shown). Image credits: Seagrass meadow, Y. Sato; *Olavius algarvensis*, A. Gruhl; *Kentrophoros*, B. K. B. Seah; and Stilbonematid, U. Dirks. Modified after Sogin et al. (2020)

Symbiotic Ciliata and Annelida are represented by taxonomic groups that differ from those in deep water.

Complex animal life evolved with the Precambrian oxygenation of the oceans some 850–540 Ma ago, (see Chap. 1). The intimate relationship with bacteria that may have existed a billion years prior to the origin of the eukaryotic cell shaped the evolution of animal diversity to the present day (McFall-Ngai et al. 2013). The oldest chemosynthetic symbioses documented so far are the marine catenulid flatworms (*Paracatenula*) and lucinid mussels, with estimated ages of 500–400 million years (Gruber-Vodicka et al. 2011; Stanley 2014). The fossil lucinids were probably already associated with chemosynthetic symbionts as they are showing imprints of enlarged gills that, in the present relatives, house the symbionts (Stanley 2014). With the evolution of terrestrial vegetation and export into coastal sediments, available carbon and energy sources diversified. A second major organic input was provided by the evolution of seagrasses in the Late Cretaceous Tethys Sea (65–100 Ma). It should be noted that chemosynthetic production in these shallow water systems is not independent of light and photosynthesis since the energy for inorganic carbon fixation is ultimately derived from bacterial decomposition of organic matter.

Numerous meiofauna organisms have developed mutualistic associations with microbiota enabling the colonization of new niches. This process resulted in the evolution of novel metabolisms and tissue adaptations. In these associations, microbial symbionts colonized meiofauna hosts via various routes. The fact that most multicellular organisms harbour a variety of microorganisms, the microbiome, is already textbook knowledge substantiated by a great number of studies. In meiofauna, however, such studies are rare for those organisms that are not in an obvious symbiotic relationship. A study on the microbiome in marine free-living nematodes (Schuelke et al. 2018) did not find correlations with either geographic location, habitat, feeding type, or phylogenetic position of the host, but on host species level identified putative pathogenic, parasitic, or symbiotic interactions.

4.1.1 Why Study Chemosynthetic Symbioses in Meiofauna?

There are both advantages and drawbacks when choosing meiofauna as the preferred research objects.

Advantages are:

(1) Easily accessible, most known chemosynthetic meiofauna live in shallow water where no costly equipment, ships, robots, submersibles, etc., are needed for sample collection.
(2) All stages of integration of the microbial symbiont into the holobiont are represented: ectosymbiosis, extracorporal to intracellular endosymbiosis.
(3) High diversity, all types and many species may be found together in a few handfuls of sediment, raising the question of niche partitioning/niche diversification.
(4) Sampling is possible without exposing the objects to excessive stress (temperature, pressure) as is the case in deep-sea sampling.
(5) Possibility of keeping the objects alive for extended periods under near-natural conditions.
(6) Ease of experimental manipulation (small size, no high-pressure chambers needed); possibility of work with high numbers of individuals increases statistical power of arising data sets.

Disadvantages are:

(7) Small size/low biomass, but genetic and biochemical techniques become increasingly sensitive.
(8) Identification is often difficult, tedious, requiring microscopical preparations; knowledge of specialists is necessary, risk of misidentification.

(9) Information on biology is scarce due to limitations in observing the objects under (near) natural conditions.

We discuss symbiont transmission and integration, cell biology of symbionts, the immunological basis of symbiont recognition and maintenance, and, finally, the physiology of the holobionts. We highlight recent advances in the study of meiofauna chemosynthetic symbioses. In a final section, we identify challenges in understanding the intricate relationships between eukaryotes and their prokaryotic partners and map frontiers for the advancement of science in meiofauna and general biology. For explanation of terms used see Box 4.1.

Box 4.1 Definitions

Autotroph—an organism capable of synthesizing its own food from inorganic substances using light or chemical energy.
Heterotroph—an organism feeding on sources of organic carbon.
Chemosynthesis—synthesis of organic compounds using energy derived from inorganic chemical reactions.
Chemolithoautotroph—a chemosynthetic organism that obtains energy from the oxidation of inorganic compounds and uses inorganic carbon as sole source of carbon.
Chemolithoheterothroph—a chemosynthetic organism that obtains energy from the oxidation of inorganic compounds and uses organic compounds as a source of carbon.
Ectosymbiont—a partner in a symbiotic relationship that lives on the surface of its host.
Endosymbiont—an organism that lives within the body or cells of another organism.
Holobiont—an assemblage of a (often eukaryotic) host and another (often prokaryotic) species living in or on it, together forming an ecological unit.
Morphospecies—a species whose taxonomic definition is based on morphological characters.

4.2 Ecological Settings

All microorganisms using energy sources alternative to light depend on chemical gradients between electron donors and acceptors. The quantitatively most important of these is the redox gradient from sulphide to sulphate, which provides the highest energetic yield. In sharp gradients over a few millimetres, non-symbiotic microorganisms dominate, some of them with a (limited) capability to move or with other adaptations (e.g., *Beggiatoa*, *Thioploca*, cable bacteria).

Both, highest diversity and numbers of chemosynthetic meiofauna, are found in sediments where the redox gradient stretches over several centimetres. Here, the association with a motile host appears to be a selective advantage for microorganisms despite the tribute they have to pay for the transportation service (Giere et al. 1991; Ott et al. 1991). In some of the sediments containing the most diverse symbiotic meiofauna, sulphide is not detectable in the field and appears only when sediment is kept under stagnant conditions in the laboratory. Here, obviously, production and removal of sulphide by both biotic and abiotic processes, such as percolation of oxic water, is in perfect balance.

Prime habitats for the groups included in this chapter (marine Catenulida, Stilbonematinae, Astomonematinae, and Phallodrilinae) are subtidal sediments. Here, the silt and clay fractions are sufficiently low to allow both interstitial metazoan life and percolation of water through subtidal pumping preventing stagnation and sulphide build-up. There are, though, a few reports of Stilbonematinae and Astomonematinae from deeper shelf water (Ansari et al. 2016; Ingole et al. 2010) or in continental slope canyons (Leduc 2013; Tchesunov et al. 2012).

Highest abundance and diversity are found in tropical to warm-temperate climates. Especially rich are back-reef sediments where locally produced sand often has a coarser grain size than the hydrodynamic situation would predict, while at the same time the organic fraction is high. There is some evidence that the sediment near and within seagrass beds supports a more diverse and abundant meiofauna with thiotrophic symbioses than bare sediments do. Seagrasses provide shallow water sediments with both fresh and decaying organic material, available to fuel chemosynthesis via remineralization. Decaying seagrass might e.g., be the source for CO and H_2, and by stabilizing the habitat it also enhances development of chemical gradients. Seagrass material incorporated into sediments increases the surface area of the redoxcline in a three-dimensional way, enhances development of micro-niches and, thus, fosters local diversity. Furthermore, seagrasses often have seasonal dynamics, adding temporal variation to the habitats of many chemosynthetic symbioses. In addition, the root system provides valuable protective habitats for meiofauna like annelids but also macrofauna like the lucinids. All these factors might have contributed to the high diversity of chemosynthetic hosts we encounter today that are often linked to seagrass stands, and to the underlying rampant radiations of chemosynthetic meiofauna in several host groups over the last 100 million years alongside the evolution of seagrasses.

So far, the marine Catenulida and Phallodrilinae have been found predominantly under tropical to warm temperate conditions. Stilbonematinae and Astomonematinae have also been recorded from cold temperate and even subpolar locations, albeit in much lower abundance and diversity than in warmer climates. Also, reports of Stilbonematinae and Astomonematinae in canyons originate from cold deep areas. *Kentrophoros* appears to be ubiquitous in sheltered sulfidic sediments.

All thiotrophic symbionts store large amounts of elemental sulphur and polyhydroxyalkanoates (PHA) in intracellular vesicles causing the hosts to appear bright white in incident light, and facilitating their detection in live samples under low magnification.

4.3 Introduction to the Organisms Included in this Chapter

The hosts in chemosymbiotic meiofauna belong to diverse and unrelated taxa. Here, we present them ordered from the lowest to the highest degree of functional intimacy with their microbial symbionts.

Stilbonematinae (Nematoda, Chromadorea, Desmodorida, Desmodoridae) are a taxon classified presently as a subfamily, comprising 12 genera with approximately 50 species, both numbers which tend to increase. The slender, cylindrical worms are 3 to almost 10 mm long and 30–50 μm in diameter. Except for two monotypic genera from bathyal canyons, all other known species have been reported from intertidal or shallow subtidal sands. A synapomorphic character is the possession of complex glandular sense organs (GSO) that play an important role in host-symbiont recognition and adhesion. Despite their close molecular relationship, they show a large morphological diversity with regard to the structure of the cuticle, the pharynx and especially the arrangement of the coat of ectosymbiotic sulphur-oxidizing Gammaproteobacteria. The symbionts belong to the *Candidatus* genus Thiosymbion and are host-species specific. Mucus-embedded bacteria are attached to the host cuticle and are, therefore, directly exposed to the environment. Worms migrate between oxic and sulfidic layers. For several host species, there is evidence (gut content, stable isotope ratio) that the bacteria constitute all or at least the bulk of the host nutrition.

Kentrophoros (Ciliata, Karyorelictea), a worm-shaped ciliate genus comprising 17 species, is characterized by the lack of an oral apparatus (“mouth”). The ribbon-shaped body has a dense coat of ectosymbiotic sulphur bacteria on one side. The symbiont-bearing surface is non-ciliated, while the other side is covered with somatic kineties. Folding of the symbiont-bearing body surface provides some separation from the environment. *Kentrophoros* consumes its symbionts by direct phagocytosis into digestive vacuoles. The symbiotic Gammaproteobacteria *Ca.* Kentron is chemolithoheterotrophic in contrast to the autotrophic microbial partners in most thiotrophic symbioses.

Gutless oligochaetes/clitellates (Annelida, Clitellata, Tubificidae, Phallodrilinae). This monophyletic taxon comprises over 100 described species worldwide. They are 100–200 μm in diameter and up to 4 cm long. They are found in tropical and subtropical soft sediments with redox gradients, e.g., in mangroves, coral reefs, or seagrass meadows, as well as in coastal upwelling zones. Both, digestive tract and excretory organs, are completely reduced. Between cuticle and epidermis, they contain a species-specific consortium of extracellular symbionts with a gammaproteobacterial sulphur oxidizer *Ca.* Thiosymbion as numerically dominant symbiont phylotype in all but one species (exception *Inanidrilus exumae*; Bergin et al. 2018). Additional symbiont phylotypes can be other sulphur oxidizers, sulphate-reducing Deltaproteobacteria or Alphaproteobacteria. In at least one species (*Olavius algarvensis*; Dubilier et al. 2001), syntrophic sulphur cycling occurs between gamma- and deltaproteobacterial symbionts. Additionally, spirochaetes with unclear functional roles (heterotrophic, possibly parasitic) can occur. As in Stilbonematinae, the worms migrate between oxic and sulfidic layers (Giere and Langheld 1987). Transmission of bacteria from host to host is apparently vertically. There are indications that the majority of sulphur oxidation takes place under oxic conditions.

Astomonematinae (Nematoda, Chromadorea, Monhysterida, Siphonolaimidae). The subfamily comprises two genera, *Astomonema* and *Parastomonema*. The very slender worms lack a mouth and pharynx. The majority of the body is occupied by large endosymbiotic bacteria, which are located in either the lumen or the cells of a gut rudiment. Like in the Stilbonematinae and the gutless oligochaetes, the symbionts belong to *Ca*. Thiosymbion. Little is known about the ecology of the Astomonematinae. For the type species, *Astomonema jenneri*, an association with the tubes of sediment-dwelling Annelida has been reported.

Paracatenula is a genus of marine catenulid flatworms, lacking a mouth. Except for the anterior-most region (rostrum), the body is filled with a mass of symbiocytes (trophosome) that contain large Alphaproteobacteria packed with sulphur and polyhydroxybutyric acid (PHB) inclusions which constitute the primary energy storage for the holobiont. Transfer of nutrition from symbiont to host is via outer membrane vesicles. The mechanism of infection of new stem cells for trophosome growth is still unclear. Reproduction of the host is mainly by vegetative fission where symbiont transmission is vertical.

4.4 Symbiont Transmission and Physical Integration in Chemosymbiotic Meiofauna

Chemosynthetic symbioses vary widely in terms of quality, specificity, and integration (Dubilier et al. 2008; Sogin et al. 2020). In most cases, the symbionts are the primary source of energy and nutrients for the host. However, further symbiont functions can add to the host's benefit or even constitute the main "currency" in the association. Sulphur-oxidizing symbionts, for example, remove poisonous sulphide allowing their host to live in sulphide-rich habitats without own detoxification mechanisms. While some host taxa have very specific, single symbiont phylotypes, other associations can involve several partners. Chemosymbioses cover a wide range from very low to high stabilities over time, between individuals or between geographical locations. In this section, we explore the physical interaction between the symbiotic partners. Focussing on structural host adaptations, such as specific organs or cells for hosting symbionts, as well as symbiont transmission mechanisms, we compare the different levels of host-symbiont integration and discuss their significance for both the interactions between the partners and the evolution of their symbioses.

One of the main characteristics of symbiosis is the degree of integration or physical connection between the partners. Commonly, ectosymbioses in which the symbionts are on the surface of the host are juxtaposed with endosymbioses in which symbionts reside within the host body. In the latter case, symbionts occur in specific host organs, tissues or compartments (e.g., body cavities). On a finer scale, the symbiont location can be either intra- or extracellular (e.g., between cells in a tissue or in acellular, fluid-filled compartments). Intracellular symbionts may occur in specialized cells, called bacteriocytes, where they either occur freely in the cytoplasm, or are enclosed by the cell membrane into vesicles or vacuoles, called symbiosomes. Intracellular symbionts can be restricted within their host cell to certain parts of the cytoplasm or associated with specific cell structures, compartments or organelles, such as cytoskeleton, ER, or mitochondria (Fig. 4.2).

Host and symbiont structures forming and mediating the physical interaction between the partners are collectively referred to as the host-symbiont interface. We expect the structure of the host-symbiont interface to both shape and be shaped by the quality and quantity of physiological interactions between the partners. Nutrient transfer, for example, depends on the number, structure, and function of barriers

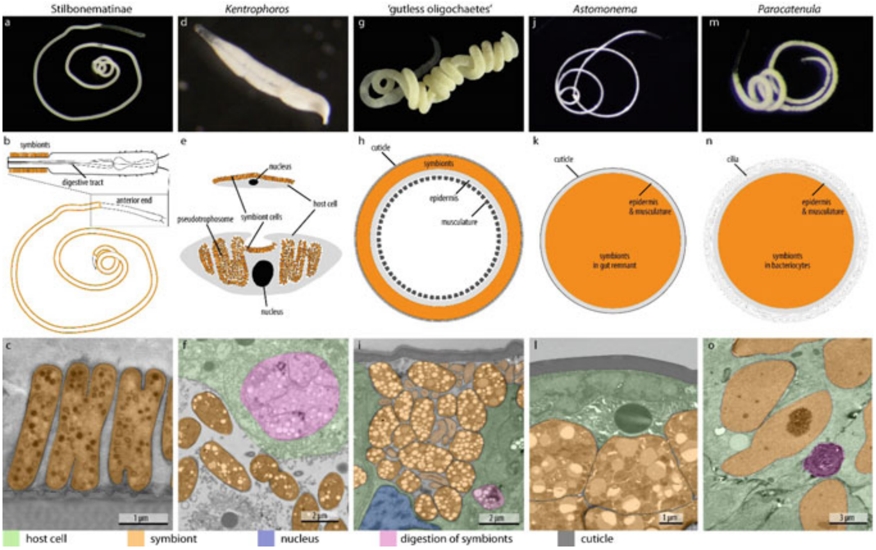

Fig. 4.2 Chemosymbiotic meiofauna and the integration of their symbionts into their body plans. Top row: low magnification micrographs of live holobionts. Middle row: schematic drawings indicating the location of the symbionts on or in the body of the host. Bottom row: False-coloured transmission electron microscopy of the symbionts on or in the host tissues. **a–c** Stilbonematinae; **d–f** *Kentrophoros*; **g–i** 'gutless oligochaetes'; **j–l** *Astomonema*; **m–o** *Paracatenula*. From Sogin et al. 2020, modified and supplemented. Photos courtesy of U. Dirks (Stilbonematid) and B. K. B. Seah (*Kentrophoros*)

(membranes, cell walls, tissue layers) that these substances have to pass on their way between the partners. In many cases, environmental substrates required by the symbionts have to either pass host structures, or be transported by the host, enabling the latter to exert control over the symbionts' access to these substances. Conversely, the location of the symbionts as well as the characteristics of their cell wall and membrane determine, for example, their visibility to the host immune defence.

Finally, animal-microbe symbioses show a wide variety of transmission strategies (Bright and Bulgheresi 2010; Russell 2019). In order to achieve continuity of the symbiotic association over time, the hosts have to either pass on the symbionts directly or evolve other mechanisms that ensure the reliable establishment of a consistent symbiont community after an aposymbiotic life cycle stage.

4.4.1 Host-Symbiont Interfaces and Transmission in the Different Taxa

All members of the nematode subfamily **Stilbonematinae** carry dense coats of coccoid, rod-shaped or filamentous *Ca.* Thiosymbion bacteria on their cuticles (Bayer et al. 2009; Ott et al. 2004; Scharhauser et al. 2020). However, the connection of the symbionts to the host cuticle differs between species. In species of *Stilbonema* and *Leptonemella,* the bacterial coat is multi-layered and the bacteria are embedded in a mucous matrix, the exact composition and origin of which is unclear. It could be both parts of the cuticle and a secretion of the bacterial cells. Monolayered coats are found, for example, in the genera *Laxus*, *Catanema,* and *Robbea.* Within these, the symbionts are typically rod-shaped and attach with one end to the cuticle. A mucous matrix has been shown in some cases. More complex coats of filamentous bacteria are present in the genera *Eubostrichus* and *Adelphus.* Here, the symbionts are attached with either one or both ends and often arrange in regular spiral patterns along the host body. Stilbonematinae have fully functional intestinal tracts and are suspected to feed on their symbionts. The mode of transmission of ectosymbionts in Stilbonematinae has not been demonstrated directly. However, high consistency of host species and associated symbiont phylotypes as well as congruence between symbiont and host phylogenies make a vertical transmission likely (Zimmermann et al. 2016). In Stilbonematinae, stability of the symbiont population does not only have to be achieved across generations, but also across life-cycle stages, as the cuticle is shed four times in the regular moults. The mechanisms of 'inter-' and 'intra-generational' transmission could differ, for example feeding on exuviae after moult versus egg-smearing.

In the ciliate ***Kentrophoros,*** the gammaproteobacterial *Ca.* Kentron symbionts densely cover the dorsal surface of the body. The currently 17 distinguished morphospecies differ in the degree of involution of the dorsal surface, amongst other characters. In species with flat or slightly rolled-up dorsal surfaces, the ectosymbiont coat is monolayered. In some species, the involuted dorsal surface forms pouches packed with symbionts (Seah et al. 2020, 2017). The enclosed space, termed "pseudotrophosome", however, still communicates with the outside via a small pore or slit. Attached symbionts appear to be connected to the host cell membrane (called pellicle in ciliates) and proximally embedded in a mucous matrix (Foissner 1995). *Kentrophoros* has reduced its cytostome (the cellular feeding apparatus) and symbionts are digested by phagocytosis via the entire symbiont-covered surface. Symbiont transmission is not documented, but reproduction of the hosts seems to happen mainly by fission, during which also the symbiont population would simply be distributed to the daughter cells, thus resulting in vertical transmission. Partial incongruence between symbiont and host phylogenies, however, indicates at least occasional horizontal transmission or host-switching (Seah et al. 2017). Thus, we have to assume a mixed mode of transmission. Whether horizontal transmission happens directly between individuals, for example during conjugation, or mainly as environmental uptake is currently unknown.

Gutless oligochaetes harbour their symbiotic bacteria in spaces between the epidermis and the cuticle. The cuticle is secreted by epidermal cells and is connected to protrusions of their apical surfaces via spot-like hemidesmosomes. This 'symbiont space' is formed by connected invaginations and surface extrusions of the epidermal cells. Regularly repeated constrictions of the symbiont space are visible as annuli, a type of secondary segmentation that occurs in a regular pattern of around seven annuli per segment. The composition of the symbiotic consortium differs between body regions. Whereas in the postgenital (trunk) region all symbiont phylotypes are present and intermixed, the symbiont space in the pregenital region (tip) is much narrower and only contains the smaller morphotype symbionts, excluding *Ca.* Thiosymbion. There is evidence that symbionts are regularly digested by phagocytosis (Giere and Langheld 1987). All gutless oligochaetes reproduce exclusively sexually. Despite a high potential for regeneration, fragmentation of worms never results in proliferation. Individuals can regenerate the post-genital trunk region, but tip regeneration only happens in cases where the prostomium or first segment was amputated. As typical clitellates, gutless oligochaetes are hermaphrodites and self-fertilization does not seem to play a role. Sperm transferred during copulation is stored in spermathecae and used to fertilize oocytes during or directly after oviposition. During the reproductive season, gutless oligochaetes develop prominent structures, so-called "genital pads". These are formed by ventrally located epidermal swellings of the genital segments that are filled with abundant symbionts. In most species, the genital pads surround or adjoin the female genital opening so that they rupture and release their contents onto the egg surface. In newly deposited eggs, the symbionts are located in the fluid-filled space of the cocoon, surrounding the embryo. During embryogenesis, they get incorporated into the epidermis once the cuticle forms (for details of symbiont transfer in *Inanidrilus leukodermatus* see Krieger 2000).

In the siphonolaimid nematode genus ***Astomonema***, the buccal region and intestinal tract are reduced and the body (behind the head region) is filled with endosymbiotic bacteria. In those species studied in detail by electron microscopy, different situations have been described. In *A. jenneri* two morphotypes of bacteria occur, one smaller and one larger type. The symbionts reside intracellularly in cells interpreted as gut rudiment (Ott et al. 1982). Contrarily, in *A. southwardorum* the cells of the single symbiont morphotype are surrounded by a layer of eukaryotic cells interpreted as gut lining (Giere et al. 1995). The modality of nutrient transfer is unresolved as no evidence for phagocytotic digestion has been found. In both *A. southwardorum* and *A. jenneri,* the intestinal cells appear amorphous with very electron-lucent cytoplasm and few organelles. The mode of symbiont transmission is not known for any *Astomonema* species.

The catenulid flatworm ***Paracatenula*** houses intracellular *Ca.* Riegeria symbionts in specialized bacteriocytes in the trunk region of the body, also termed 'trophosome' (Dirks et al. 2011; Ott et al. 1982). The body wall consists of epidermal cells, musculature and neoblasts; large bacteriocytes fill almost the entire inner lumen of the worms (Gruber-Vodicka et al. 2011; Leisch et al. 2011). Each bacteriocyte, which, in turn, is surrounded by a vacuolar membrane, contains numerous symbionts. Interestingly, bacteriocytes themselves do not divide, but are formed, like all differentiated cells in platyhelminths, from dividing pluripotent stem cells, so-called neoblasts. *Ca.* Riegeria symbionts divide within the bacteriocytes, but how the newly formed bacteriocytes are infected is not known. In terms of nutrient transfer, digestion of entire symbionts by the bacteriocytes via phagocytosis seems to play a minor role: phagolysosomal structures in bacteriocytes are very rare compared to other nutritional symbioses in which transfer via phagocytosis is the major pathway (Jäckle et al. 2019). There is also no evidence for transporter-mediated exchange of nutrients. Instead, nutrients are likely transferred via outer membrane vesicles (OMVs) which are abundantly found in the vacuolar spaces that surround the symbionts. Reproduction of the holobionts in *Paracatenula* happens mostly by asexual fission; sexual reproduction has never been documented (Dirks et al. 2012). Fragmentation in the trophosome region results in division of the bacteriocyte population to the daughter animals. Highly congruent co-diversification patterns support strict vertical transmission (Gruber-Vodicka et al. 2011).

4.5 Structure and Function of Host—Symbiont Interfaces

In chemosymbiotic meiofauna, we see a wide range of host-symbiont interfaces. In ectosymbioses, the symbionts are firmly attached to the cuticle (in the case of nematodes) or cell membrane (in the case of ciliates). Based on the ultrastructure, it seems reasonable that this contact is mediated by both partners, i.e., by secretion of glycocalyx by the host, mucus that could come from both partners, and specific cell polarity and surface structures by the symbiont. The symbionts have direct and unrestricted access to environmental substrates from the sediment pore water. Thus, host control of symbiont proliferation can only happen via host behavioural adaptions, harvesting of symbionts, or immunological interaction. Conversely, symbiont secretion products will hardly be efficiently taken up by the host, limiting nutrient transfer pathways in these systems to intra- or extracellular symbiont digestion. In the extracellular endosymbioses, represented here by the gutless oligochaetes and *Astomonema southwardorum*, direct uptake of substrates is still possible, but symbionts are in a slightly more restricted compartment (subcuticular space and gut) where the chemical composition may differ from the surrounding pore water. Intracellular symbionts in *Paracatenula* experience a much higher level of host control. For example, considering that bacteriocytes do not divide, symbiont cell proliferation needs to be restricted. Substrate provisioning happens via the bacteriocyte cytoplasm and is, thus, potentially highly regulated by the host. Conversely, nutrient transfer has been shown to happen via exchange of OMVs, a process that is putatively controlled by the symbionts and not the host (Jäckle et al. 2019).

4.5.1 Symbiosis as a One-Way Street?

So, do the differences in the extent of host-symbiont integration represent adaptations to specific biological conditions or can they be interpreted as stages in an evolutionary series of increasingly higher integration and dependency, culminating in an organelle-like role of the symbionts? Naturally, in each symbiotic system, the partners have co-evolved based on their biological properties and environmental conditions. Thus, a specific degree of integration may be an optimal, evolutionary stable strategy. For example, a certain openness for horizontally acquired symbionts may not indicate an evolutionary young association, but can be an adaptation to unstable conditions or enable the animal to easily move into new habitats and take advantage of locally well-adapted pools of potential symbionts (Russell 2019). Hosts often evolve mechanisms to control symbionts by separating them or confining them to certain cellular or body compartments, a concept termed compartmentalization (Chomicki et al. 2020b). This may help the host to control symbiont reproduction, prevent infection, “punish” or “reward” symbionts based on their performance. However, some mechanistic explanations suggest that a pathway to higher integration and dependence may be a common phenomenon in mutualistic symbioses (Bennett and Moran 2015). For example, hosts may get locked into an association at some point by having adopted so many changes and losses that they cannot easily revert back. On the symbiont side, reduction of effective population size by strict vertical transmission can lead to genome reduction and accumulation of deleterious mutations, leading to reduced performance outside the host (Fisher et al. 2017).

In the known chemosynthetic meiofauna taxa, the phylogenetic positions of the hosts provide clear evidence that these associations have evolved multiple times independently. However, each taxon (i.e. gutless oligochaetes, Stilbonematinae, Astomonematinae, *Kentrophoros, Paracatenula*) is a well-defined monophylum including only symbiotic species within its higher taxon of non-symbiotic relatives. This shows that in meiofaunal chemosymbioses the hosts, once the association is firmly established, hardly ever revert to a non-symbiotic lifestyle. Also, signs for adaptive radiations are seen in some of the chemosymbiotic meiofaunal taxa, suggesting a strong selective advantage of these symbiotic associations (Seah et al. 2017). Dependence is not always symmetrical between hosts and symbionts. This is shown, for example, in Stilbonematinae and gutless oligochaetes, whose gammaproteobacterial symbionts have repeatedly switched between major host lineages (Zimmermann et al. 2016). An interesting question is whether chemosymbioses are particularly prone to strong dependence phenomena, which might have further implications. For example, highly dependent mutualists are suspected to be less adaptable towards new and fluctuating environmental conditions (Chomicki et al. 2020a), a possible explanation for the rarity or lack of chemosynthetic taxa in cold-temperate or limnic habitats.

4.6 Symbiotic Associations Are a Window into Environmental Bacterial Cell Biology

Symbiotic associations between animals and bacteria face the challenge to coordinate the rapid cell cycle of the bacteria within the cell- and the-life cycle of the eukaryote. Ectosymbionts for example need to ensure that their bacterial offspring stays in contact with the animal host, to continue the symbiotic association. Endosymbionts on the other hand need to be able to cope with the host's immune system and strike the balance of growing without "overrunning" the host, and in the case of chemosynthetic symbioses grow enough to satisfy the metabolic demand of the host. To understand these symbiotic associations, one really needs to understand the bacterial cell biology. Research in this field has shown that sophisticated systems are in place to ensure that bacteria keep their shape and can propagate it to their offspring over generations. Despite the misleading simplicity, multiple molecular systems interact with each other to ensure a coordinated cell cycle. In rod-shaped bacteria like *Escherichia coli*, the cell cycle has two morphologically distinct phases. Initially, the rod-shaped cell elongates, along the whole length of the cell. Key to this is the protein MreB, a homologue of the eukaryotic actin protein. MreB binds to the cytoplasmic face of the inner membrane and coordinates cell elongation. Its binding behaviour lets MreB ”sense” the local curvature of the cell wall and ultimately maintains the rod shape (reviewed in Shi et al. 2018). The cell elongation is followed by the actual septation process. This centres around the bacterial tubulin homologue FtsZ. FtsZ, a GTPase, is the first protein to localize to the future division site where it self-polymerizes into a ring-like structure termed the Z-ring. It recruits approximately 30 more proteins into a macromolecular complex called the divisome, which organizes the cell wall constriction, peptidoglycan synthesis and overall formation of the two new poles, until the two daughter cells are separated (reviewed in McQuillen and Xiao 2020). Research in the last decades has highlighted the complexity of this whole process, but most research was limited to a handful of cultivable model organisms. Symbiotic associations with a low diversity, however, are ideal to gain insights into the cell cycle of uncultivable environmental bacteria.

Among the chemosynthetic associations, nematodes of the sub-family **Stilbonematinae** are the ideal model to study bacterial cell division. The association is highly specific, and each worm species carries a monoculture of a single symbiont on its cuticle (Fig. 4.3) The symbionts are still in contact with the environment and therefore need to cope with both the symbiotic and the free-living aspect simultaneously, and, finally, one can easily remove the symbiont monoculture from its host for experimentation. The symbionts do rely on the host for transport through their habitat and have therefore evolved strategies to ensure that the contact with the host is transmitted to the offspring upon cell division.

The nematode *Eubostrichus fertilis* carries one of the most complex but also aesthetically appealing bacterial coats (Fig. 4.3a, b). Under the microscope, the worm has a rope-like appearance, which is due to the symbionts on its cuticle. The bacterium is crescent-shaped and attaches with both cell poles to the worm’s cuticle. However, the bacteria span one order of magnitude in length, ranging from 4 to 45 μm in length. The shortest bacteria are attached closest to the worm and layered on top

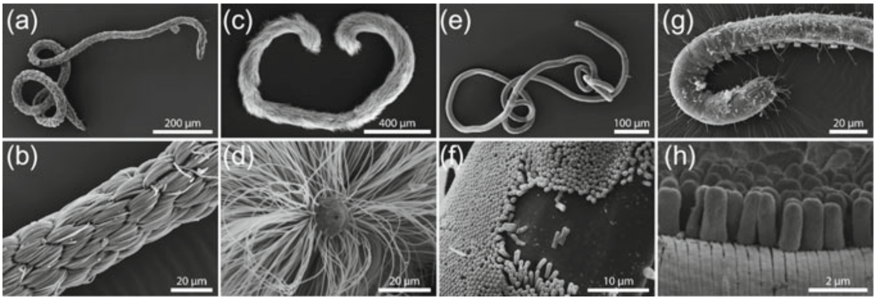

Fig. 4.3 Symbiotic nematodes of the subfamily Stilbonematinae and their ectosymbionts. Overview (**a**) and detail (**b**) of the crescent-shaped bacteria that cover *Eubostrichus fertilis*. The long thin filaments covering *Eubostrichus dianeae* give it a furry appearance (**c**,**d**). The nematode *Laxus oneistus* (**e**) is covered by a monolayer of rod-shaped bacteria (**f**). While the head of *Robbea hypermnestra* (**g**) is symbiont free, the rest of its body is covered with rod-shaped bacteria, arranged in a picket-fence-like manner (**h**)

are longer and longer bacteria (Ott et al. 2014; Pende et al. 2014). Typically, the individual cells of a bacterial population deviate very little from its size-optimum (e.g., *E. coli* approximately 1–4% in length), as the surface-to-volume ratio governs most bacterial processes (reviewed in Young 2010). It is therefore surprising to see such a huge range of cell length within a single *Eubostrichus fertilis* symbiont population. Immunofluorescence marking of the FtsZ protein showed that this population structure is actively maintained, as all cells from 4 to 45 μm length formed Z-rings and underwent cell division (Pende et al. 2014). One explanation for the stark differences in size might be the arrangement itself. The symbiont cells are stacked on top of each other and require reduced sulphur compounds and oxygen from the environment to fuel their metabolism. The topmost cells might simply have better access to these than the bottom ones, therefore growing faster and with this nutrient gradient established, the complex 3D structure is perpetuated further.

The closely related nematode *Eubostrichus dianeae* is similarly covered by long filamentous bacteria, however, they only attach with one pole to the cuticle and grow even longer, up to 120 μm in length (Fig. 4.3c, d). Despite their large cell size, these bacteria are dividing by binary fission (Pende et al. 2014). While bacterial gigantism has been observed in multiple endosymbionts, like nodulating root bacteria, insect symbionts or bacteria inhabiting the surgeonfish gut, these are often under strong host control. Here, cell division is inhibited, resulting in large, polyploid bacteria (Bulgheresi 2016; de Velde et al. 2010; Login et al. 2011; Mendell et al. 2008). As the symbiont still actively divides in a FtsZ-based manner, this makes it not only the longest non-septate bacterial cells that undergo binary fission, but also highlights how the positioning system for the Z-ring can function even in bacteria of extreme length, to reliably find mid-cell. One of the open questions here is how the apically formed daughter cell gets in contact with the host's surface, as, after division, this is far away from the host's cuticle.

The most studied symbiont is that of the nematode *Laxus oneistus* (Fig. 4.3e, f). Based on electron microscopy, Polz et al. (1992) pointed out that the rod-shaped bacteria colonizing this nematode attach with one pole to the host's cuticle where they are arranged like a picket fence. Moreover, they seem to split along their longitudinal axis, instead of transversal like typical rod-shaped bacteria (e.g., *E. coli*). Using a combination of morphometric analyses, transmission electron microscopy and immunofluorescent labelling, Leisch et al. (2012) showed that this symbiont, *Ca.* Thiosymbion oneisti, grows in width instead of length, and the division is mediated by the Z-ring forming at mid-cell, along the length axis.

The arrangement and division mode of the symbiont *Ca.* Thiosymbion hypermnestrae of the co-occurring nematode *Robbea hypermnestra* do look identical at first glance but differ in an important detail (Fig. 4.3g, h). At the basal pole of the symbiont, which attaches to the host cuticle, a patch of FtsZ localizes and initiates cell division earlier than the apical pole, resulting in an asynchronous division. Only later on in the division process, a full Z-ring is formed and cell division will terminate in the upper third of the bacterial cell length (Leisch et al. 2017). Using D-amino acids which are incorporated into the bacterial peptidoglycan layer, and which can be fluorescently labelled, together with immunofluorescent detection of

MreB, Pende et al. (2018) started to dissect the growth mechanisms of these two symbiont species. They showed that MreB is required for septal growth, which starts at the poles, a region typically thought to be inert in model rod-shaped bacteria, and furthermore that growth of new cell wall is mainly in the region of the new septum (Pende et al. 2018). This is in stark contrast to textbook knowledge of model rod-shaped organisms where MreB-based cell elongation occurs along the length of the cell, independently of the FtsZ-driven septal growth. This re-orientation of the division plane not only highlights the flexibility of prokaryotic protein machineries, but it allows both daughter cells to remain in contact with the nematode host throughout the whole division process.

The ectosymbionts of the ciliate ***Kentrophoros*** also show an extraordinary reproduction mode. They are rod-shaped bacteria which attach with one pole to the host. Based on morphological observations, their longitudinal cell division initiates at the distal pole and proceeds unilaterally towards the basal pole (Fenchel and Finlay 1989).

Few insights are available from endosymbionts. For both the symbionts of the mouthless nematode *Astomonema* and the mouthless flatworm *Paracatenula***,** no data are available on growth rates, division strategy or host control. In the case of *Astomonema,* the symbionts are clearly understudied, with the main published work focussing on the phylogenetic identity, their position within the host or the host anatomy (Giere et al. 1995; Musat et al. 2007; Ott et al. 1982; Tchesunov et al. 2012). None of the *Paracatenula* species analysed with electron microscopy showed clear signs of dividing cells (Jäckle et al. 2019; Leisch et al. 2011). However, as the symbiont seems to rely on outer membrane vesicle secretion to supply the host with nutrients, this could be a symbiotic system in which bacterial cell division is under tight host control.

The symbionts of **gutless oligochaetes** seem to be fairly “unconstrained” compared to other endosymbionts. Representing a complex consortium with up to five bacterial types, that occupy the extracellular space between epidermis and cuticle, these endosymbionts show no strictly ordered arrangement like the symbionts of the Stilbonematinae. Not being within cells or cellular compartments, they are exposed to different local micro-niches with varying nutrient supply and bacterial-bacterial interactions. For the main symbiont of the gutless oligochaete *Olavius crassitunicatus,* longitudinal division has been documented, based on transmission electron microscopy (Giere and Krieger 2001).

Methodological improvements in fluorescent imaging, ranging from super-resolution to novel dyes and stains, have rapidly accelerated our understanding of bacterial cell biology and have highlighted the complexity of the processes that control bacterial growth and division. Whilst most of these studies stem from a handful of cultivable model organisms, symbiotic associations have proven ideal to gain broader insights into the cell cycle of uncultivable and environmental bacteria. Most importantly, research on these symbiotic bacteria allows us to evaluate which of the findings that originated from bacterial model organisms are applicable more broadly. The range of biological solutions to the deceptively simple question “How to divide one bacterium into two?” is wide.

4.7 Should I Stay or Should I Go? How Chemosynthetic Bacteria Are Chosen by Their Meiofauna Hosts

Although immunology has so far focussed on pathogenic microbes and on laboratory-reared animals, much can be learned by studying how immune systems cope with beneficial microbes in their natural habitats. In this section, we discuss and compare immune components and mechanisms that likely allow meiofauna to engage in successful relationships with chemosynthetic bacteria (Fig. 4.4). At present, host transcriptomics and proteomics have only been performed for the nematode *L. oneistus* (Bulgheresi 2011; Paredes et al. (2022) and for the oligochaete *O. algarvensis* (Wippler et al. 2016; L. König and Y. Sato, unpublished). This section therefore only reviews the immune systems of these two symbiotic meiofauna worms. Comparing their repertoires to those of the model nematode *Caenorhabditis elegans* and the marine annelid *Capitella capitata*, respectively*,* allows us to identify putative symbiosis-specific components. Finally, we review immunoreceptors and immune effectors, both of which represent host immunity components that directly interact with microbes. Immune signalling pathways, on the other hand, will not be covered here, because the core set of invertebrate immune signalling pathway components is present in both *L. oneistus* and *O. algarvensis* (Bulgheresi 2011; Paredes et al. (2022); L. König and Y. Sato, unpublished).

4.7.1 Immune Receptors

For microbes to associate with their hosts, microbial signals must first be detected by immunoreceptors. These recognize microbial molecules that are essential for microbes, but are absent in multicellular eukaryotes, such as the cell surface molecules lipopolysaccharide (LPS), peptidoglycan, or flagellin. They can also recognize bacteria-derived molecules, such as signal peptides or short-chain fatty acids. Immune receptors include Toll-like receptors (TLRs), G-protein coupled receptors (GPCRs), peptidoglycan-binding receptor proteins (PGRPs) and C-type lectin receptors (CTLRs). In contrast to the former two classes, PGRPs and CTLRs can also directly control the growth of bacteria and may therefore be considered both, immune receptors and effectors. They can activate immune pathways that lead to bacterial death and, at the same time, they can directly agglutinate and immobilize bacteria (as in the case of CTLRs) or kill bacteria by, for example, hydrolysing their peptidoglycan (as in the case of PGRPs).

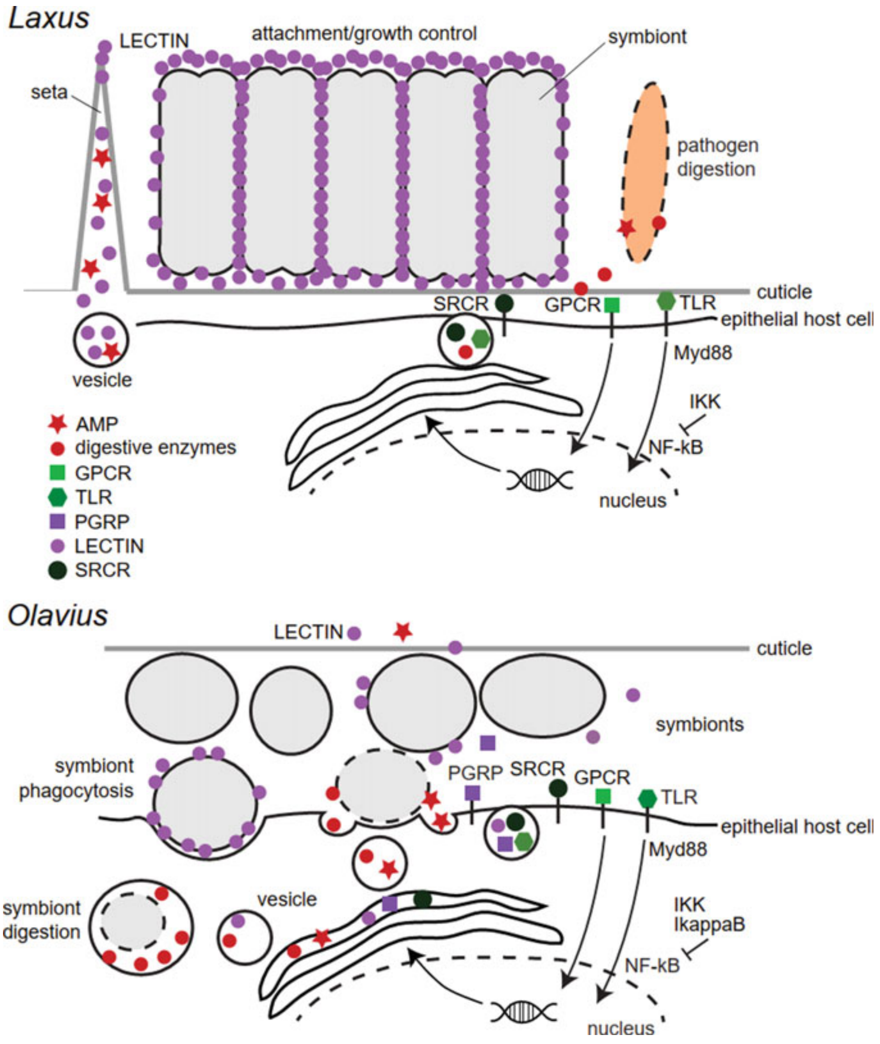

Fig. 4.4 Schematic overview of immune system components present in *Laxus oneistus* and *Olavius algarvensis* transcriptomes. The immune systems of chemosynthetic meiofauna are adapted to maintain their bacterial symbionts (grey) while controlling their symbionts' growth and defending against pathogens. AMP, antimicrobial peptide; ER, endoplasmic reticulum; GPCR, G-protein coupled receptor; LECTIN, C-type lectin receptor; PGRP, peptidoglycan-binding receptor protein; SRCR, scavenger receptor-like cysteine-rich protein; TLR, Toll-like receptor

4.7.2 Toll-Like Receptors (TLRs)

Although functional evidence of the role of TLRs in immunity is only available for model organisms, bacteria are known to modulate the expression of genes encoding

TLR pathway components even in the most basal metazoans, which suggests that microbial recognition is the ancestral function of TLRs.

Canonical, bona fide TLRs are transmembrane receptors with several extracellular leucine-rich repeat (LRR) motifs and an intracellular Toll/interleukin-1 receptor (TIR) domain. The extracellular LRR motifs of TLRs can bind a wide range of microbe-derived signals, but also endogenous ligands derived from damaged cells such as fibronectin (Yu et al. 2010). TLR stimulation ultimately causes the transcription factor NF-kB to enter the nucleus and to switch on the expression of inflammatory antimicrobial peptides (AMPs) or cytokines. In addition to NF-kB signalling, TLR receptors can activate mitogen-activated protein kinase (MAPK) and interferon regulatory factor signalling cascades (Akira et al. 2006; Kawai and Akira 2010).

Initially identified as essential in fruit fly early development (Anderson and Jiirgens 1985), the Toll signalling was later found to protect adult flies from bacterial and fungal pathogens. Curiously, although one Toll homolog (Tol-1) was identified in *C. elegans*, this nematode lacks key proteins of the canonical TLR-signalling cascade including the NF-kB transcription factor (Pujol et al. 2001). Moreover, rather than being required to kill pathogens, *C. elegans tol-1* is necessary for the development of chemosensory neurons that nematodes need to sense and avoid pathogens (Brandt and Ringstad 2015; Pradel et al. 2007).

One bona fide TLR was found to be expressed in *L. oneistus* and two were found in *O. algarvensis* (L. König and Y. Sato, unpublished). In addition to complete TLRs, *L. oneistus* and *O. algarvensis*, encode for a similar number of TIR-only or LRR-only-containing proteins, reported to be related to TLR proteins (Brennan and Gilmore 2018). Therefore, besides their TLRs, it is possible that both symbiotic worms use LRR-containing proteins in combination with other signalling components to interact with microbes.

In neither *L. oneistus* nor *O. algarvensis*, we observed the expansion of the TLR family reported, for example, for humans and for the polychaete *Capitella capitata* (10 TLRs have been identified in our genomes and we confirmed the presence of eight *C. capitata* TLRs out of the 105 previously reported), or the impressive explosion observed in some invertebrates such as sea urchins (Davidson et al. 2008; L. König, unpublished). However, all the key components of the Toll signalling pathway were identified in both *L. oneistus* and *O. algarvensis*, indicating that this pathway is active and may mediate successful host-microbe negotiations (see Wippler et al. 2016).

Concerning what is downstream of the Toll receptors, *L. oneistus* seems to bear a more ancient version of the Toll pathway in comparison to the gutless oligochaete, but a far more complete one when compared to the model nematode *C. elegans*. Most strikingly and in stark contrast to all other nematodes, which notoriously do lack a NF-kB transcription factor, *L. oneistus* encodes one. The presence of a NF-kB1-like protein in the symbiotic nematode suggests that triggering of the Toll pathway might result in the expression of immune effectors, as observed in fruit flies and humans. Whether the presence of this key immune transcription factor enables *Laxus* to wear its symbiont coat awaits to be proven.

4.7.3 G Protein-Coupled Receptors (GPCRs)

GPCRs are central for the perception of external stimuli and the transduction of the signal to the cytoplasm and, therefore, vital for connecting organisms with their environments. GPCRs are characterized by a conserved signature motif consisting of seven transmembrane (TM) spanning helix domains. Upon ligand binding, a conformational change activates the cytoplasmic C-terminal domain, which, in turn, through coupling to heterotrimeric guanine nucleotide-binding regulatory proteins (G proteins), starts the intracellular signalling cascade (de Mendoza et al. 2014; Dierking and Pita 2020). Although there is evidence of the involvement of GPCRs in the immunity of model invertebrates and although, in *C. elegans*, GPCRs present a potential link between the nervous system and immunity, it is as yet unclear if they directly respond to microbes or to microbe-triggered endogenous ligands.

The family of GPCRs represents the largest receptor family in animals. Vertebrate genomes may contain over 1300 GPCRs, whereas in invertebrates, numbers vary unpredictably: from the hundreds of GPCRs found in *Drosophila melanogaster* and sponges to over a thousand in *C. elegans* (Dierking and Pita 2020). As for *L. oneistus* and *O. algarvensis*, 238 and 118 GPCRs were predicted, respectively. In both worms, the largest group of GPCRs are the rhodopsin receptor-like class A GPCRs. Within this GPCR class, both organisms have a relatively high number of FMRFamide receptors (59 in *Laxus* and 20 in *Olavius).* Interestingly, FMRFamide-like receptors have been functionally linked to alterations in microbial pathogen susceptibility in *C. elegans*. In contrast to *Olavius*, *Laxus* also displays an expanded repertoire of neuropeptide Y receptors (NPYR). NPY is found at all levels of the mammalian brain-gut axis and it may control the impact of the gut microbiota on inflammatory processes, pain, brain function and behaviour (Holzer and Farzi 2014). Although the impact of neuropeptides on the gut microbiota-brain interaction awaits elucidation, it is possible that biologically active peptides will emerge as neural and endocrine messengers in orchestrating animal-microbe interactions. Why should FMRFamide-like and Y receptors be more represented in *Laxus* than in gutless oligochaetes? As mentioned in Sec. 4.3 of this chapter, the nematode GSOs are composed of both gland and neuronal cells. Local neuronal regulation of the glandular component of the GSOs might, therefore, allow localized secretion of immune effectors.

4.7.4 Peptidoglycan Receptors (PGRPs)

PGRPs are key innate immunity components known to be involved in many animal-bacteria symbioses, where they mediate symbiont tolerance, control symbiont proliferation or regulate symbiosis establishment and maintenance (Dierking and Pita 2020; Dziarski and Gupta 2018; Royet et al. 2011). PGRP overexpression was observed in the trophosomes of hydrothermal vent tube worms and mussels, but their function within these deep-sea symbioses remains unknown (Bettencourt et al. 2014).

Transmembrane PGRPs that carry intracellular domains often induce an antimicrobial response by activating immune pathways such as the Toll pathway. However, some PGRP receptors bind peptidoglycan without passing on an intracellular signal which results in down-regulation of immunity. Similar to transmembrane PGRPs, secreted PGRPs can induce an antimicrobial response by indirectly activating immune pathways or acting as bacterial growth inhibitors or antimicrobials themselves (Lu et al. 2006). Notably, if they possess amidase activity, they can also dampen the host immune response by cleaving PG into non-immunogenic fragments.

Although six PGRPs were originally identified in *Olavius* (Wippler et al. 2016), a subsequent round of sequencing, assembly and annotation could only identify three (L. König and Y. Sato, unpublished). One corresponds to OalgPGRP2 (Wippler et al. 2016); it contains a signal peptide, an amidase catalytic site and it is homologous to the symbiont PGRP2 of the squid *Euprymna scolopes*. As for the other two PGRPs, they do have amidase catalytic domains, but their N-terminal PGRP domains are incomplete and transmembrane domains are absent. Because the existence of a signal peptide cannot be ruled out, they can either act as intracellular or secreted amidases. All in all, given that all three confirmed *Olavius* PGRPs could function as amidases, they might contribute to symbiont tolerance by digesting immunogenic peptidoglycan fragments, which are released as a by-product of bacterial growth (Wippler et al. 2016). Moreover, *Olavius* PGRPs may also play a role in symbiont population control and host nutrition by contributing to symbiont digestion. Intriguingly, two of the three recently confirmed *Olavius* PGRPs are diaminopimelic acid (DAP)-specific, i.e., they may specifically target the peptidoglycan of Gram-negative bacteria including, for example, *Ca.* Thiosymbion (Schleifer and Kandler 1972; Swaminathan et al. 2006).

Although *C. capitata* has a similar number of PGRPs, namely four, these are absent from all nematodes including *L. oneistus*. Therefore, if PGRPs are likely involved in mediating the *Olavius* symbiosis, they do not seem to be universally required by meiofauna to establish chemosynthetic symbioses.

4.7.5 C-Type Lectin Domain-Containing Proteins (CTLD-Containing Proteins)

The C-type lectin-like domain family contains secreted, as well as transmembrane proteins that differ regarding their tertiary structures, but all share primary and secondary structural homology in their carbohydrate recognition domain (Cummings and McEver 2009). The first described members of this family indeed bound carbohydrates in a calcium-dependent (C-type) manner, and were thus true lectins. However, the carbohydrate recognition domain was subsequently identified also in proteins that did not bind carbohydrates, but other ligands such as proteins and lipids, and also did not require calcium for binding. The term C-type lectin-like domain (CTLD) was thus introduced to reflect the structural similarity to the CRD of bona fide C-type lectins without implying common function. CTLD genes occur in all multicellular eukaryotes and they may constitute more or less expanded and diverse gene families: the human genome contains 100 CTLD genes, the *C. elegans* genome 283 and *D. melanogaster* 56 CTLD genes. Based on their transcriptomes, *L. oneistus* encodes for 117 CTLD-containing proteins, 42 of which are predicted to be secreted and *O. algarvensis* for 49, 11 of which may be secreted (Wippler et al. 2016; L. König and Y. Sato, unpublished). Although nothing is known about CTLD-containing protein localization and function in *Olavius*, in the case of the Stilbonematinae *L. oneistus* and *Stilbonema majum*, we showed recombinant Mermaid CTLs to mediate symbiont aggregation and host-symbiont attachment. Furthermore, *L. oneistus* and *S. majum* Mermaids exclusively localized to symbiont-coated regions of the two nematodes and different isoforms bound the two respective symbionts more or less efficiently (Bulgheresi et al. 2011; Bulgheresi et al. 2006). Although our localization and functional studies suggested that Mermaid CTLs may be involved in the recruitment of specific symbionts by *L. oneistus* and *S. majum*, their transcripts were hardly detectable in our adult nematode transcriptomes. One possibility to explain this apparent under-representation of *mermaid* transcripts in adult nematodes is that Mermaid CTLs expression is limited to hatching and moulting (Paredes et al. 2022) stages. Transcriptomics of all nematode developmental stages will tell us whether Mermaids are exclusively expressed when the symbiosis must be established (during hatching) or re-established (during moulting).

4.7.6 Effector Molecules

Given that antimicrobial peptides (AMPs) are generally not conserved, it is not surprising that most species-specific AMPs identified in model invertebrates are absent from both *L. oneistus* and *O. algarvensis*. However, non-species-specific antimicrobial peptides such as saposin-like proteins were expressed in both worms. Additionally, *L. oneistus* encoded for thaumatin-like (*C. elegans*) and macin-like (*Hydra*) putative AMPs.

Concerning lysozymes, *O. algarvensis* only encodes for an invertebrate-type one, whereas *L. oneistus* almost exclusively encoded for lysozyme-like proteins, namely 12, nine of which are secreted. Given that invertebrate-type lysozymes were upregulated upon bacterial infection in *C. elegans*, how could Thiosymbion withstand host lysozymes? Given that Thiosymbion does not appear to encode for lysozyme inhibitors, it might modify its peptidoglycan to make it invulnerable to enzymatic digestion. Intriguingly, *Ca.* T. oneisti peptidoglycan displays a high degree of O-acetylation and cross-linking of its glycan strands (Wang et al. 2021). However, future studies need to clarify whether these two modifications enable the symbiont to escape host lysozyme-mediated lysis.

Bactericidal permeability-increasing proteins (BPIs) are AMPs that are found in vertebrates and invertebrates and play a crucial role in the innate immune response against Gram-negative bacteria (Chen et al. 2017). Indeed, by binding their LPS, they may literally perforate bacterial membranes. While most research focussed on mammalian BPIs, just a handful of studies have been carried out in invertebrate ones. For example, in the squid *Euprymna scolopes* BPI was expressed in the symbiotic (light) organ and showed bactericidal effects against its symbiont *Vibrio fischeri*. This suggests that the squid expresses BPIs to control the size of the symbiont population (Chen et al. 2017). A total of 16 bona fide BPIs were found to be expressed by *L. oneistus*, but a single one was identified in *O. algarvensis* (König and Sato, unpublished). *Laxus* BPIs are likely secreted from the GSOs onto the nematode cuticle throughout the nematode anteroposterior axis (Bauer 2012). Particularly in the symbiotic region of the cuticle, BPIs co-localized with and embedded in *Ca.* T. oneisti. Obviously, this symbiont is not harmed by these broadband antibiotics, however, more studies are necessary to prove that the *Laxus* BPIs contribute to symbiosis specificity, i.e., that they select out environmental, non-symbiotic bacteria.

4.7.7 Environmental Regulation of Host Immunity

Because immune systems have traditionally been studied in the laboratory, we do not know much about how environmental, abiotic factors affect vertebrate and invertebrate immunity. The transcriptional response of *L. oneistus* to the presence of oxygen has been recently analysed by comparative transcriptomics. Transcripts of innate immune molecules, likely involved in *Ca.* T. oneisti attachment (e.g., CTLD-containing proteins) were more abundant in the absence of oxygen (Paredes et al. 2022), where this ectosymbiont was observed to proliferate more (Paredes et al. 2021). It is therefore conceivable that the nematode expresses more CTLs to retain and/or control a proliferating symbiont. Additionally, overexpression of lectins in anoxia could favour symbiosis establishment in deep sand. Conversely, transcripts encoding for the Toll receptor, an antifungal protein (e.g., endochitinase-B) and two BPIs were more abundant in the presence of oxygen. This could be explained by the fact that we expect microbial pathogens to be more abundant in oxygenated than in anoxic environments.

All in all, the *Laxus* immune system appears to be optimized to resist to potentially deleterious microbes where they most abound (superficial, oxic sand) and to recruit its symbiont *Ca.* T. oneisti where it thrives (deep, reduced sand).

4.7.8 Conclusions

- The ectosymbiotic nematode *L. oneistus* and the endosymbiotic gutless oligochaete *O. algarvensis* engage similar classes of receptors to interact with microbes, the important exception is the PGRPs which are completely absent from nematodes (Fig. 4.4).

- Both worms may use very diverse immune receptors and effectors (e.g., GCPR, CTLD-containing proteins, lysozymes) to achieve highly specific symbioses.
- A mix of symbiont-induced suppression of host immunity and secretion of growth-inhibiting immune effectors (e.g., CTLD-containing proteins, lysozymes) could mediate symbiont population control (Fig. 4.4); additionally, the gutless *Olavius* appears to directly digest its symbiotic partners.
- In *L. oneistus*, symbiont restriction to specific regions of the cuticle could be mediated by neuronal regulation of the epidermal immune system as suggested by the expansion of genes encoding for neuropeptides (e.g., NPY) and neuropeptide receptors (e.g., NPYR).
- The bacterial skin may be regarded as part of the nematode and oligochaete immune system in the sense that symbiont antimicrobials and/or secretion systems likely repel deleterious or non-beneficial environmental microbes.
- Recent transcriptional studies on *L. oneistus* suggest an exquisite sensitivity of its innate immunity to environmental changes. Indeed, abiotic factors such as oxygen may greatly affect both its capacity to withstand pathogens and to establish microbial symbioses.

4.8 New Insights from the Physiology of Chemosynthetic Symbionts in Meiofauna

4.8.1 Carbon and Energy Sources

The discovery of bacterial sulphide (H_2S) oxidation in a mouthless animal host sparked the characterization of chemosynthetic symbioses at deep-sea hydrothermal vents. Soon after, not only sulphide oxidation but also the oxidation of other reduced sulphur species such as thiosulfate was detected in many environments from the deep-sea to shallow water habitats, coupled with the reduction of a suitable electron acceptor such as oxygen or nitrate. In the initial concept of chemosynthesis framed more than four decades ago, the symbionts were interpreted as nutritional symbionts that provide two innovations to the metabolic spectrum of their eukaryote hosts: 1) the ability to use chemolithotrophic energy sources and 2) the ability to build biomass from one-carbon (C1) carbon sources (see Fig. 4.5 for convergent features in meiofaunal symbionts). It was quickly accepted that, in addition to Carbon Dioxide (CO_2), which defines autotrophic metabolism, also methane (CH_4) might be a C1 carbon source in chemosymbiosis, which, strictly speaking, renders these symbionts chemo-organo-heterotrophs. Methane, as single energy and carbon source, plays a major role at deep-sea sites, but has, however, not been shown to play a role in shallow water habitats and in meiofaunal hosts. Another leap forward in our understanding of the diversity of energy sources was the discovery of hydrogen use in deep-sea mussels that also prompted the discovery of hydrogen use in shallow water symbioses (Kleiner et al. 2015; Petersen et al. 2011). An additional energy source, and the only substrate that, so far, has been only shown in shallow water hosts and not in deep-sea habitats is carbon monoxide (CO), an energy-rich but toxic compound that likely is ubiquitous in decaying seagrass materials around the globe (Kleiner et al. 2015). In addition to these energy sources based on the oxidation of reduced inorganic or C1 organic compounds such as sulphide and methane, a diverse range of more complex organic substrates have been shown to fuel chemosynthetic symbioses in deep-sea environments. In oil-rich sediments of the Gulf of Mexico, chemosynthetic mussel hosts, for example, draw a substantial amount of carbon and energy from short-chain alkanes such as propane or butane (Rubin-Blum et al. 2017). The impact of these hydrocarbons as energy and/or carbon sources is a current frontier in chemosynthesis research and has received quite some attention, as it connects chemosynthetic symbioses and bioremediation, for example, in oil-contaminated shallow water habitats.

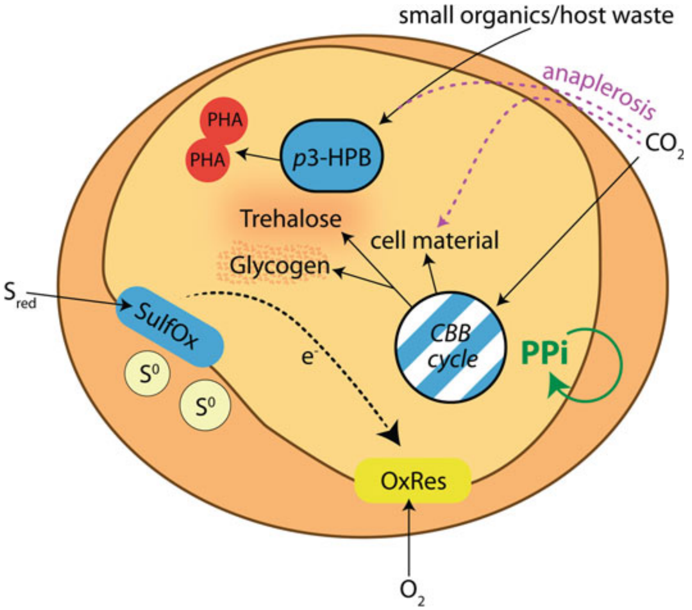

Fig. 4.5 Convergence in major parts of the metabolism characterizes shallow water chemosynthetic symbionts. Depicted are central metabolic features present in all thiotrophic symbionts of meiofaunal hosts. Anaplerosis indicates several carboxylation reactions that lead to a significant top-up to the total carbon budget that is very cheap compared to the same amount of carbon fixed via the Calvin-Benson-Bassham (CBB) cycle. S_{red}, reduced sulphur species; SulfOx, oxidation of reduced sulphur compounds; PHA, polyhydroxyalcanoates; PPi, Pyrophosphate; p3-HPB, partial 3-hydroxypropionate bicycle; CBB cycle, Calvin-Benson-Bassham cycle

4.8.2 Autotrophs, Mixotrophs or Heterotrophs?

These complex carbon and energy sources point to a conundrum in chemosynthesis research: Where to place the consortia in the spectrum from autotrophy to heterotrophy? In the symbioses that are clearly within an autotrophic framework, symbiont carbon fixation via Calvin-Benson-Bassham cycle (CBB) is the main carbon source. CBB has in fact been shown in most symbiont groups from both the deep sea and shallow waters, apart from the methane and alkane oxidizers. Other pathways for carbon fixation such as the reverse tricarboxylic acid cycle (rTCA) pathway have been documented as well, and some deep-sea symbionts are apparently able to use more than one carbon fixation pathway (Hinzke et al. 2021; Kleiner et al. 2012; Rubin-Blum et al. 2017). In shallow-water meiofaunal hosts, carbon fixation via the CBB dominates carbon source (Fig. 4.5).

In addition to CBB-based autotrophy, many chemosynthetic symbionts, particularly in shallow water environments, can also make use of small organic molecules as substrates (Fig. 4.5). These compounds are, for example, propionate or acetate, and symbionts also express transporters for their specific uptake (Jäckle et al. 2019; Kleiner et al. 2012; Paredes et al. 2021). Unrelated symbionts in *Paracatenula* and gutless oligochaetes, for example, express an incomplete 3-hydroxypropionate bicycle (3-HPB) that can be used for the heterotrophic assimilation of these small organic acids (Fig. 4.5; Jäckle et al. 2019; Kleiner et al. 2012; Paredes et al. 2021). These substrates can be connected to a role of the symbionts in host waste recycling. This is a logical conclusion, given that important and well-researched host groups such as the gutless oligochaetes lack a gut, and excretory organs. Recent data from stable isotope analyses of the chemosynthetic consortia on one hand and the habitat's biochemistry on the other hand, however, suggest that such "small organic substrates" can also come from the environment. The fermentation of the substrates could be performed by the hosts, by environmental organisms, or by the symbionts themselves. A major source for these external substrates is, for example, seagrass. Recent observations show that many seagrasses massively export metabolites into sediments, both directly as simple sugars or indirectly via the slow decay of the dead plant biomass that has been accumulated in a peat-like fashion (Sogin et al. 2019).

The use and importance of such heterotrophic resources in chemosynthesis were long overlooked. This comes as no surprise, given the fact that their use might be buried in the complexity of the overall metabolism of the symbionts present in a given host. Only very recent technical innovations, that allow to track stable isotope data for different members of chemosynthetic communities, have shown that some members of these communities clearly have a non-autotrophic signature for their carbon source (Kleiner et al. 2018). The data also shows that this additional carbon source appears to have a strong effect on the overall carbon budget in the gutless oligochaete *O. algarvensis*, as the host signature can only be explained by an even mix of both types of carbon uptake (Kleiner et al. 2018). In extreme cases, these symbiont groups likely provide a substantial part of their holobionts' carbon budget and would effectively put this chemosynthetic holobiont on the heterotrophic part of the spectrum, despite a large autotrophic potential in their symbionts. The most extreme case of heterotrophy in chemosymbioses was discovered in the meiofaunal ciliate *Kentrophoros* that showed that their *Ca.* Kentron symbionts have no pathway for autotrophic carbon fixation, but rather express an array of importers of small organic substrates including small C3 and C4 organic acids as well as sugars that fuel a completely heterotrophic metabolism (Seah et al. 2019). Initially thought to be a protist-only phenomenon, the striking observation that a Kentron symbiont has apparently replaced the Thiosymbion (Gamma1) symbiont in a gutless oligochaete species from the Caribbean also points to the importance of such chemoorganoheterotrophic lifestyles in meiofaunal animal hosts.

4.8.3 Anaplerosis as a New Force to Reckon with in Chemosymbiosis

The observation that the *Ca.* Kentron symbionts lack an autotrophic pathway for carbon fixation came as a particular surprise, as experiments that were already conducted in the early days of chemosynthetic symbiosis research in Kentron; *Kentrophoros* symbioses showed strong signals of carbon fixation in physiological experiments (Fenchel and Finlay 1989). Both the genomic and expression data from *Ca.* Kentron, but also from *Ca.* Thiosymbion and *Ca.* Riegeria, the alphaproteobacterial symbiont in *Paracatenula* flatworms, showed that a process called "anaplerosis" could explain the conflicting results between sensitive tracer experiments based on using radioactive CO_2 and the recent metabolic reconstructions (Jäckle et al. 2019; Paredes et al. 2021; Seah et al. 2019). Anaplerosis is the replenishment of intermediates for the TCA cycle. These pathways that fuel the TCA all involve carboxylation steps and therefore the fixation of carbon from CO_2. Anaplerosis is a ubiquitous process and is, for example, also taking place in human mitochondria. In most animal hosts, the anaplerotic additions to the total carbon pool are minor and make up less than one percent of the total carbon uptake into the system via heterotrophic nutrition. Both in the *Ca.* Kentron symbionts that lack an autotrophic carbon fixation pathway, but also in the *Ca.* Riegeria symbionts that massively express CBB-based autotrophy, several such carboxylation steps fuel the central carbon metabolism (Jäckle et al. 2019; Seah et al. 2019). When constantly supplied by a high flux of turned over substrate, pathways such as the "incomplete 3-HBP pathway" the Ethyl-Malonyl-CoA pathway can add substantial amounts of carbon to the total carbon budget. In *Kentrophoros*, this apparently reaches such high levels that the positive signal from radiotracer-based analytics can be mistaken for signatures of a chemoautotrophic lifestyle (Fenchel and Finlay 1989; Seah et al. 2019).

The recent expansion of available genomic resources for symbionts has revealed that anaplerosis is widespread in the metabolism of chemosynthetic symbionts. Anaplerotic pathways and carboxylation steps have been detected in all meiofaunal systems investigated (see Fig. 4.5; *Kentrophoros*, *Paracatenula*, gutless oligochaetes, and Stilbonematinae). The advantage of a massive integration of anaplerotic carboxylation into the symbiont's carbon metabolism and the host-symbiont carbon cycling could be the low energy demand per mol carbon fixed. It is a highly efficient supplement to the already accumulated carbon in the system, be it from auto- or heterotrophy or from host waste recycling. These insights are very similar to what has been suggested for efficient free-living heterotrophs that make most of light in the coastal ocean (see e.g., review by Moran and Miller 2007). They point to a much larger role of anaplerosis on carbon budgets across marine habitats that is starting to get more and more attention (Braun et al. 2021).

4.8.4 A Call for Precise and Detailed Physiological Data

In symbionts with versatile genomes, which can use complex organic substrates, the type of metabolic input, be it autotrophic or heterotrophic, cannot be determined by genomic analyses alone. This recent insight in chemosynthetic research is a prime example for the need of e.g., community-resolved stable isotope analyses that can differentiate and resolve e.g., carbon sources that are the two deltaproteobacterial symbionts in *O. algarvensis*. Both have a very similar genomic potential, but one effectively contributes as a net heterotroph and one as a clear autotroph (Kleiner et al. 2018). Particularly in the sediments around seagrasses that are rich in sugars and other plant materials (Sogin et al. 2019), such analyses must be considered imperative if any conclusion on the overall status of the holobiont and the contributions of any given symbiont is drawn.

4.8.5 Nitrogen Sources

Animals have high demands of nitrogen. Therefore, it was a revelation of recent meio- and macro-faunal chemosynthetic symbiosis research to see that symbionts from shallow water sediments are capable of fixing N_2 even within the tissue of their hosts (Petersen et al. 2017; Paredes et al. 2021). While this is essential in nitrogen-limited environments, the major nitrogen source for most symbionts still appears to be ammonium. The mode of nitrogen fixation is not stably retained throughout symbionts, not even within a single symbiotic genus such as *Ca.* Thiosymbion where only some members can fix nitrogen. The host supply with nitrogen and with amino acids are tightly coupled processes. All chemoautotrophic symbionts are fully self-reliant on amino acid production and can provide their hosts with all essential and non-essential amino acids. This complete potential for de-novo production of amino acids is in stark contrast to the nutritional symbioses present in terrestrial systems, e.g., in insects. Selection for a fully autonomous metabolism in the bacterial symbionts seems to prevent integration of amino acid synthesis and metabolism into the host's metabolism. However, for most chemosynthetic symbioses details of amino acid supply remain unresolved.

4.8.6 *Biomass Transfer and Storage*

Typically, chemosynthetic symbionts are food items for their hosts, and as such form the natural stocks to 'harvest' and consume. The standing stock of symbionts also forms the storage reservoirs that hosts can draw on when environmental resources are limited and symbiont populations are not growing. Most symbioses, including the gutless oligochaetes, some Stilbonematinae and *Kentrophoros,* digest their symbionts at high rates. They share this with their deep-sea counterparts such as giant tube worms or *Bathymodiolus* mussels. Digestions can happen in the gut as in Stilbonematinae, or through phagocytosis and lysosomal digestions such as in gutless oligochaetes and *Kentrophoros*. In contrast to this, the *Paracatenula* symbiosis has developed a different way to transfer large amounts of biomass from the symbionts to the host. The bacterial symbionts massively secrete OMVs which the host takes up via phagocytosis. Unlike the crop harvest model typical for most chemosynthetic symbioses, the *Paracatenula* symbiosis rather functions like a battery-and-current system, where the symbionts are a rechargeable storage unit that can supply a current of OMVs for nutrition. Hence, the symbionts become only very rarely digested, they rather develop massive and versatile storage inclusions comparable to fat cells and other specialized storage cell types in metazoans (Jäckle et al. 2019). A similar pattern likely applies to *Astomonema* nematodes that also have very large symbionts, but of a lineage of the gammaproteobacterial *Ca.* Thiosymbion that is specific to this host genus. The *Astomonema* Thiosymbion are much larger than the host cells and the symbionts are completely filled with storage vesicles (Fig. 4.2). Similar to *Paracatenula*, the *Astomonema* symbiont populations show few signs of symbiont digestion in electron microscopy data, suggesting a convergent role for these symbiont lineages from different bacterial phyla as nutritional and storage symbionts (Leisch pers. comm.; Giere et al. 1995; Ott et al. 1982).

4.8.7 *The Role of the Hosts*

While in these symbioses many details are known about the metabolic role of the bacterial partners, the hosts' input in carbon uptake and total carbon and energy budget remains as yet far less resolved. Meiofaunal animals have long been suggested to take up dissolved organic substrates. This is especially important and needs to be considered in those representatives with an open and soft body surface or epidermis such as ciliates, flatworms, or annelids. Nematodes, on the other hand, with their dense and multi-layered cuticle, are relatively unlikely to live of dissolved organic matter, particularly those groups lacking a gut. Proteomic approaches that capture expression and also generate host and symbiont-specific stable isotope data are promising tools to explore the host role.

4.8.8 *Ca. Thiosymbion—The Archetypical Chemosynthetic Symbiont in Meiofaunal Hosts*

While the autotrophic symbionts *Ca.* Riegeria in flatworms and the heterotrophic *Ca.* Kentron symbionts in *Kentrophoros* represent two extremes of a broad spectrum ranging from pure autotrophy to pure heterotrophy, the entire metabolic spectrum is largely covered by *Ca.* Thiosymbion, one of the most successful and archetypical chemosynthetic symbionts. Associated with three unrelated host groups and more than a hundred host species (see Table 4.1 and Fig. 4.2; Musat et al. 2007; Scharhauser et al. 2020; Zimmermann et al. 2016), *Ca.* Thiosymbion:

- can use both nitrate and oxygen as electron acceptors,
- utilizes a wide range of carbon sources,
- uses anaplerosis to top up carbon,
- can fix nitrogen,
- has multiple options to store carbon and energy (Kleiner et al. 2018, 2012; Paredes et al. 2021),
- can flexibly employ all of the metabolic pathways mentioned above in the typical oxic to anoxic gradients, and, at least when associated with *Laxus oneistus*, appears to prefer anoxic conditions (Paredes et al. 2021).

4.9 Intricate Symbiotic Relationships—Present Frontiers, Emerging Challenges, and Future Research

The study of chemosynthetic symbioses in meiofauna has produced an appreciable number of fundamental insights into topics of general relevance in cell biology, immunology and physiology. Nevertheless, many questions still remain unanswered, opening new horizons for research and posing challenges for methodology. Below, we outline some of these, pertaining to the distribution of chemosynthetic symbioses amongst meiofauna groups, the pathways that led to the intimate symbioses that we observe today, the interactions between partners, the mechanisms for acquisition and maintenance of symbionts, the physiology behind the partnerships and, lastly, the role of chemosynthetic symbioses in their ecosystem.

- Up to now, chemosynthetic symbioses have been found **in a few meiofauna groups** only, (karyorelictid ciliates, catenulid platyhelminthes, nematoda, and oligochaetes). Are there more to be discovered? Currently, it is unclear if abundant and well-studied taxa such as Gnathostomulida, Gastrotricha, Kinorhyncha or the diverse interstitial crustacea have symbiotic representatives, although many of those co-occur with symbiotic species and live in environments favourable for chemosynthetic bacteria. Similarly, which traits enable the most successful symbiotic bacterium, *Ca.* Thiosymbion, to colonize most diverse hosts and adopt all lifestyles from ectosymbiont to intracellular endosymbiont? Comparative

Table 4.1 Host-symbiont interfaces and transmission in the different taxa

Taxon	Symbiont(s) (main type)	Type of association (single vs multiple phylotypes per host species etc.)	Symbiont location	Exchange of substances	Transmission mode
Kentrophoros	Gammaproteobacterial SOX (Ca. Kentron)	Single	Extracellular, on cell membrane	Phagocytosis, digestion	Vertical, by division
Paracatenula	Alphaproteobacterial SOX (Ca. Riegeria)	Single	Intracellular, in mesodermal? Bacteriocytes	OMV secretion, some digestion	Vertical, mainly by asexual fission
Stilbonematinae	Gammaproteobacterial SOX (Ca. Thiosymbion)	Single	Extracellular, on the cuticle	Digestion, in some species	Likely mixed
Astomonema	Gammaproteobacterial SOX (Ca. Thiosymbion)	Mostly single	Intracellular, in gut rudiment Extracellular, in gut lumen	Phagocytosis, digestion	Not known
Gutless oligochaetes	Gammaproteobacterial SOX (Ca. Thiosymbion, except *Inanidrilus exumae*)	Main symbiont phylotype and additional "secondary" symbionts (Gamma-, Alpha-, Deltaproteobacteria)	Extracellular, below cuticle	Phagocytosis, digestion by epidermis cells	Mostly vertical

SOX = sulfur-oxidizing
OMV = outer membrane vesicle

approaches could allow us to identify traits that either foster or prohibit symbiotic interactions in either symbiotic partner.

- What were **the evolutionary starting points and pathways that led to the establishment** of the symbioses? Are the symbiotic bacteria survivors from an ancestral microbial menu of the hosts, as seems probable in *Astomonema*? Are they the descendants of pathogens that the host succeeded to keep in check and finding an agreement with the “attacker”, as may be the case in Vestimentifera and *Paracatenula*? Have the microbes just “hitched a ride” on the moving host that has proven to be beneficial to both partners as in *Kentrophoros* or the Stilbonematinae? Understanding the evolutionary background of many clades likely enables us to generalize the dynamics of host microbe associations along the mutualist to parasite spectrum (see Box 4.2).

Box 4.2 How and why did such symbioses evolve?

Expand food sources—Many animals feed on bacteria, and it is likely that the consumption of chemosynthetic bacteria by animals was a major driver for the first encounter of the two partners.

Expand symbiont habitat—Space is highly limited in highly productive environments, and a bacterium that colonizes animal epithelia or cuticles conquers large new habitats.

Expand host habitat—Sulphide detoxification by chemosynthetic symbionts might help to expand the range of the animal host. This effect likely is limited by the quick diffusion of sulphide into animal tissue and only very thick coats might mitigate sulphide stress for a significant period.

Expand symbiont access to resources—Oxygen and sulphide is the optimal red/ox couple, but are spatially separated. An animal host can easily traverse the gradient and provide access to both oxygen and sulphide much more efficiently than if the symbiont was on its own.

Provide buffering capacity—The symbionts can use host carbon and nitrogen waste as substrates, which makes them more independent from environmental conditions.

Provide shelter—Free-living bacterial populations are under pressure for exploitation, both from viruses as well as bacterial and animal predation. Intracellular endosymbionts are fully sheltered from many of these attacks, and even ectosymbionts are much more sheltered, for example, via biofilm formation, physical barriers such as invaginations or chemical barriers such as an extracellular matrix.

- None of the symbiotic meiofauna species has been cultivated over several sexual generations or for an extended period of time yet. This is a major challenge for methodology. Efforts must continue to overcome this shortcoming and thus pave the way to **creating model organisms**, that can be physiologically and genetically manipulated. The recent successes with cultivation approaches for both *Paracatenula* flatworms and gutless oligochaetes (Gruber-Vodicka and Gruhl, pers. comm) are promising and might open new avenues, for example, in immunology and experimental physiology to gain a mechanistic understanding of meiofaunal animals that live in obligate symbiosis.

- In order to fully understand interactions between symbiotic partners, we need a **holistic approach**, combining high-resolution structural data with gene expression and chemical information. In this respect, the small size of meiofaunal organisms is both a challenge and a blessing. Nucleotide, protein and metabolite extraction as well as detection and sequencing methods are more difficult and prone to systematic error the smaller the amount of starting material is. However, low-input library protocols and sensitive sequencing methods are constantly improving towards detection of low-abundance transcripts and assembly of genomes from single cells. Chemical imaging approaches like EDX (Energy Dispersive X-Ray), Raman, SIMS (Secondary-Ion Mass Spectrometry) techniques and especially MALDI-MSI (Matrix-Assisted Laser Desorption Ionization-Mass Spectrometry Imaging) allow quantitative label-free imaging of elements or biomolecules. Here the challenges lie in the balance between spatial resolution and analytical range and in the necessary combination with structural imaging to provide the morphological framework. On the structural side, small organisms are much easier to image in full size than larger organisms. Modern 3D techniques like FIB-SEM (Focused Ion Beam-Scanning Electron Microscopy) allow acquisition of volumetric data sets at ultrastructural level of detail. New light microscopy techniques such as lattice light sheet microscopy make acquisition of near-isotropic 3D data near the diffraction limit possible, thus in the range of bacterial cells. Subcellular imaging can be achieved with new structured illumination or other super-resolution techniques. These are currently highly innovative fields and it is important to follow this progress and its potential for the study of meiofaunal organisms.
- Throughout their lives, meiofauna animals, just like us, need to **communicate with microbes,** and to decide whether to escape, destroy or cooperate. The study of meiofauna immune systems revealed that at least some of the underlying molecules are also at work in vertebrates, including humans. This was highlighted by the discovery of the Mermaid lectins in *L. oneistus*. The carbohydrate recognition domain of this family of proteins is structurally and functionally so similar to the human immunoreceptor DC-SIGN that it can compete with it and block pathogen uptake and transmission by human cells. The potential for discovering, for example, new AMPs by studying symbiotic meiofauna is vast, as it is that of understanding the role of neuropeptide signalling in immunity. Not before we succeed in cultivating and **genetically manipulating** symbiotic meiofauna, will it become possible to understand which receptors, pathways and effectors are responsible for symbiosis establishment and maintenance of highly specific symbioses.

- Can these **autonomous and efficient bio-factories inform synthetic biology**? Nutritional symbioses in insects, where symbionts provide a limited set of metabolic functions exhibit streamlining of the symbiont genomes where genomes lose most genes and only retain the very few metabolic functions necessary for the hosts. This drastic reduction can lead to a point of decay that was observed in many insect symbioses, but such deleterious reduction of the genome is rare in chemosynthetic symbionts. In fact, only two host groups, the deep sea Vesicomyidae clams and the *Paracatenula* flatworms, show pronounced symbiont genome streamlining compared to the free-living prokaryotic relatives. However, in both cases the symbiont genomes remain autonomous for carbon metabolism, amino acid and vitamin synthesis and the two symbiont groups are able to satisfy the full nutritional needs of their animal hosts with a common share of approximately 700 genes. The genomes of chemosynthetic symbionts are smaller than those of most free-living bacteria with highly streamlined genomes, and at the same time are tailored to serve as nutrition. Maybe one day we can learn from these symbionts how to efficiently provide nutrition for animal livestock or humans from recycled waste and at the same time detoxify problematic side products such as sulphide?
- What is the **influence of chemosynthetic symbioses in meiofauna on the conditions in the interstitial environment**? Is there an effect on flux rates in biogeochemical cycles, especially the sulphur or nitrogen cycle? In many cases, the density of symbiotic meiofauna is probably too low to leave a signature. In tropical back-reef sediments, however, chemosynthetic meiofauna can drastically outnumber non-symbiotic interstitial organisms and their role in processes which are largely controlled by abiotic physical and chemical forces in other sediments, is still unknown. Human-induced global change such as eutrophication, rising temperature and CO_2 concentrations are expected to result in expansion of sulfidic, hypoxic and oxygen minimum zones in marine habitats (see Chap. 7). How do chemosynthetic symbioses respond and adapt to these changing conditions? Experimental physiological and ecological approaches may help to assess adaptability and resilience in symbiotic systems.
- For most symbiotic meiofauna, little is known about their **reproductive biology**. However, most of them share traits like internal fertilization, direct development, and low number of offspring. With a lack of planktonic dispersal stages, the full life cycle is effectively locked into the sediment. This raises the questions of how their populations are structured and the effective range of dispersal in both space and time.
- In a symbiosis context, it is a completely **open frontier how population structure** and **dispersal** are linked to the acquired pool of symbionts. As many symbiotic meiofauna systems show a degree of horizontal symbiont uptake, answering these questions will help to identify the key traits that select for a successful association. The comparison between different hosts should allow to differentiate between host- and symbiont-driven selection.

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Chapter 5
Marine Meiofauna Diversity and Biogeography—Paradigms and Challenges

Ann Vanreusel, Pedro Martínez Arbizu, and Moriaki Yasuhara

Abstract Scientists studying the biodiversity and biogeography of meiofauna encounter many uncertainties regarding the causes and consequences of natural and anthropogenic-driven changes in biodiversity patterns they observe worldwide. Recently developed novel analytical and computational technologies are facilitating more systematic and integrated approaches to the study of meiofauna biodiversity. In this chapter, we reflect on the state of the art in biodiversity and biogeography research with a focus on the most abundant and diverse meiofauna taxa including nematodes and copepods. Other occasionally abundant meiofauna taxa such as carbonate-shelled crustacean ostracods and protist foraminiferans, which are present in the fossil record, allow meiobenthologists to understand the links between shifts in biodiversity and major historical events in the marine environment. Sample-size dependency and the lack of standardization across benthic surveys currently hamper the integration of disparate meiofauna studies into wider research of seafloor biodiversity and biogeography. We discuss habitat-specific meiofauna biodiversity patterns that are observed at different scales and identify the main drivers of such patterns. Important factors include physical characteristics of the seafloor, biogeochemical processes, ecosystem productivity, geographical location, but also the interactions of meiofauna with other ecosystem components including their prey, their predators, competitors,

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and habitat facilitators. We discuss the importance of meiobenthic biodiversity for ecosystem functioning and touch on the biogeography of dominant meiofauna taxa by looking at what we know about the importance of endemism versus cosmopolitanism, the growing insights in population genetics and cryptic speciation, the phylogenic processes underpinning them, and critical gaps in our knowledge. We conclude by identifying some dynamic areas of research and inquiry for future generations of meiobenthologists studying the biodiversity and biogeography of meiofauna.

5.1 Why Study the Biodiversity and Biogeography of Meiofauna?

One of the major challenges in ecological research today is to identify the causes and effects of natural and human-driven changes in marine biodiversity patterns. Particularly urgent is the need to better understand and quantify different aspects of biodiversity and identify the role of anthropogenic activities and their consequences such as global warming, deoxygenation, acidification, eutrophication, overfishing, and pollution in local, regional, and global declines of biodiversity for all major components of the marine realm (Sala and Knowlton 2006; Mieszkowska et al. 2014; Luypaert et al. 2019), including the microscopically small meiofauna (see Chap. 7). The United Nation's Convention on Biological Diversity of 1992 defines biological diversity as "*the variability among living organisms from all sources including, inter alia, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species, and of ecosystems*" (Josefsson 2018).

In ecological research on meiofauna, biodiversity is generally represented by the number of species and their equitability or evenness in a given sample, location, or area. Depending on the context, biodiversity is obviously much more than species counts and includes different sources of biological variability, such as genes, ecosystems, phylogeny, and functional traits (Turnhout and Purvis 2020). The metrics that represent biodiversity seem almost infinite, each of them emphasizing particular features of the biodiversity concept, which refers to a biological entity comprising multiple components (e.g., a community represented by different species) (Hill 1973; Ellison 2010; Chao et al. 2020). Biodiversity is studied in many different ways and at a variety of levels of biological organization. These range from counts of taxonomic or functional units per surface area or volume (for meiofauna traditionally expressed as number of taxa per 10 cm^2 surface area) to dominance (i.e., numbers of the most abundant taxon), and from alpha (sample or site) to beta (turnover) to gamma (large scale) diversity (Fig. 5.1), and include different temporal and spatial scales of sampling (Whittaker 1972).

Several abundant meiofauna taxa, especially nematodes and copepods, are known to comprise numerous co-occurring species (from about 10 to more than 100) in a relatively small sample of sediment (10 cm^2 surface area), yet many meiofauna

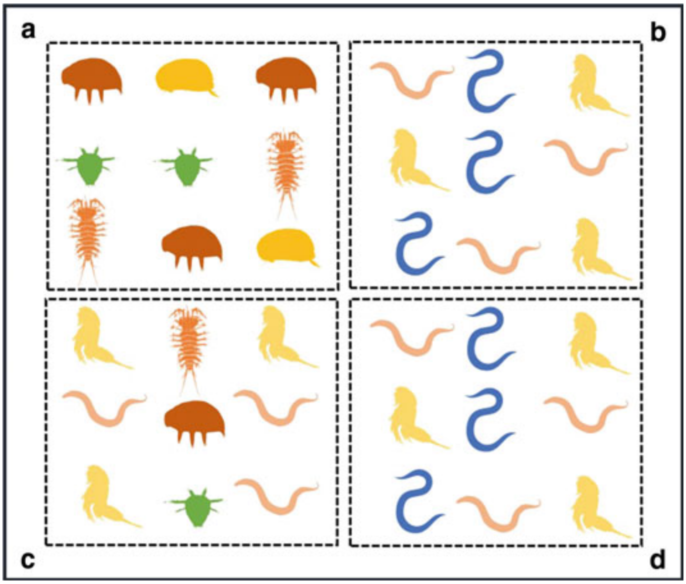

Fig. 5.1 Visualization of alpha, beta, and gamma diversity. The large box in solid line represents a region; the 4 small boxes labeled **a**, **b**, **c**, and **d** are samples from 4 different locations (sites) representative for the region. The different colored drawings illustrate different species or taxonomic units. Gamma diversity is calculated based on all species from within the large box representing the region. Alpha diversity is calculated for each small box separately and represents the site diversity. Beta diversity refers to differences between the sites (small boxes) and is a measure for how many species are shared between two sites. For example, sites **a** and **b** share no species and have a maximum turnover or beta diversity while sites **b** and **d** have a minimum beta diversity since they are identical in species composition

taxa are among the least known in terms of their diversity (Appeltans et al. 2012), suggesting that a large proportion of meiofauna species remains taxonomically undescribed. Understanding drivers of large-scale diversity patterns, i.e., the biogeography of meiofauna, requires knowledge of their dispersal, their evolutionary history, and their ability to adapt to prevailing environmental conditions (see Chap. 7). Is everything everywhere or do we find highly specialized taxa that are endemic to specific ecosystems in distinct areas? The high abundance of some meiofauna taxa, their ubiquitous presence, and their high taxonomic diversity have generated a set of interesting paradigms but also created challenges when interpreting contrasting patterns of meiofauna distribution.

Scientists studying the biodiversity and biogeography of meiofauna indeed encounter many uncertainties regarding the causes and consequences of changing biodiversity patterns they observe worldwide. Some of these uncertainties may remain unresolved in the short term. At the same time, innovative sampling approaches and recently developed novel analytical and computational technologies are facilitating more systematic and integrated approaches to the study of meiofauna distribution and biogeography. In this chapter, we reflect on the state of the art in biodiversity and biogeography research with a focus on the most abundant and diverse meiofauna taxa including nematodes and copepods. Both taxa generally co-occur in the benthos under the same prevailing conditions despite being characterized by different functional traits linked to their distinctive morphology, life history, and physiology. Other occasionally abundant taxa composing the meiofauna are carbonate-shelled crustacean ostracods and foraminiferans, an important protist group. Generally present in the fossil record, studying those taxa allows meiobenthologists to understand the links between shifts in biodiversity and major historical events in the marine environment. Carbonate-shelled ostracods and foraminiferans are also susceptible to the effects of climate change and in particular ocean acidification (Yamada and Ikeda 1999; Fabry et al. 2008; see Chap. 7). Several additional permanent meiofauna taxa, including kinorhynchs, gastrotrichs, tardigrades, turbellarians, and loriciferans, are either rare in most environments or occur in such low abundances that they are largely outnumbered by the previously mentioned taxa in terms of their diversity. Nevertheless, poorly-studied rare taxa also represent interesting cases for comparison with the more abundant taxa to understand biodiversity and biogeography patterns, and the factors and processes driving them.

In this chapter, we

- Reflect on the biodiversity concept within the context of meiofauna biology and ecology, including generally applied approaches to measure biodiversity and some novel methodological and analytical developments, and identify the issues that currently hamper the integration of meiofauna biodiversity data across scales of space and time (e.g., sample size dependency, lack of standardization; Sect. 5.2);
- Discuss, for the most abundant meiofauna taxa, the biodiversity patterns that are observed at different biogeographical scales (Sect. 5.3);
- Reveal similarities and differences in meiofauna biodiversity patterns among habitats and identify the main drivers including physical characteristics of the substrate, biogeochemical processes, ecosystem productivity, water depth, geographic location, alongside biotic interactions of meiofauna with other ecosystem components including predator–prey relationships, competition, and facilitation (Sect. 5.4);
- Examine the importance of meiobenthic biodiversity for ecosystem functioning with an emphasis on the mediating role of meiofauna interacting with other ecosystem components from micro- to megabenthos (Sect. 5.5).
- Consider long-term changes of taxa for which we have a paleo-record (Sect. 5.6).
- Reflect on the biogeography of meiobenthic taxa by looking at what we know about the importance of endemism versus cosmopolitanism, the growing insights in population genetics and cryptic speciation, the phylogenic processes underpinning them, and the gaps in our knowledge (Sect. 5.7).
- Finally, we put forward future perspectives and challenges and present some major opportunities for biodiversity and biogeography research of meiofauna (Sect. 5.8).

5.2 Studying an Invisible World: Sampling and Measuring Meiofauna Biodiversity

Nematoda is one of the most remarkable and widely studied invertebrate phylum on our planet. Still, many aspects of their biodiversity and biogeography in marine environments are poorly understood. Currently, one of the major research questions remains the reason behind the success of nematodes as one of the most abundant and diverse metazoan taxa across aquatic and terrestrial ecosystems (Schratzberger et al. 2019; Traunspurger 2021). Combining soil nematode habitat associations with a phylogenetic tree based on small sub-unit ribosomal DNA sequences, Holterman et al. (2019) showed that the phylum's success resulted from numerous habitat transitions followed by moderate diversification, rather than from extensive diversification after a limited number of major habitat transitions. Resolving the extent to which the same processes apply within the marine realm would deliver major insights for marine biodiversity research. While taxonomic research on marine nematodes began in the early twentieth century, quantitative biodiversity studies on meiofauna started in the late 1960s early 1970s (see reviews by Heip et al. 1985; Giere 2009). Although also present as epifauna or epibionts on hard substrata occasionally of biological origin (such as coral rubble or macroalgae), nematodes generally dominate invertebrate communities in soft sediments (Giere 2009). Soft sediment meiofauna is traditionally sampled with cores (diameter between 2 and 10 cm) to a sediment depth of 5 to 10 cm. Depending on the substrate, the majority of specimens are generally recorded in the upper 3–5 cm of the sediment, and nematode densities commonly lie between 100 and a few 1000s per 10 cm^2 surface area (varying between the extremes of about 10 to more than 10,000 individuals per 10 cm^2; see below for examples). The second most abundant metazoan group tends to be copepoda, generally representing about 10% of the total meiofauna. This proportion is remarkably constant across water depths, only decreasing by a higher copepod sensitivity to oxygen depletion when oxygen becomes more limited (Kawano et al. 2021). Within the copepoda, the Harpacticoida dominate meiofauna samples in terms of abundance and diversity (George et al. 2020).

Because of their generally high abundances, identifying nematodes from an entire sample can be very time-consuming. For this reason, samples are traditionally subsampled (after randomization) to a maximum of a few 100s of nematode specimens that are subsequently identified at varying levels of taxonomic resolution. Most diversity metrics are sample size dependent, so unless sampling and sub-sampling techniques as well as taxonomic resolutions are standardized, data from different surveys are often not directly comparable (Soetaert and Heip 1990). Given the high nematode diversity, it is estimated that the majority of species remains undescribed to the present day (Mokievsky and Azovsky 2002). Consequently, many ecological studies tend to identify nematodes to genus level only. Although nematode genus composition often reflects macro-ecological patterns observed at species level (Vanreusel et al. 2010; Hauquier et al. 2019), several genera can be represented by numerous species in the same sample (high congeneric species richness), especially in the deep sea (Muthumbi et al. 2011). Furthermore, the lack of species descriptions hampers biogeographic studies, and cryptic speciation is probably common in marine nematodes (although evidence is limited to mainly brackish and only a few marine species; Derycke et al. 2005, 2007, 2008; Bhadury et al. 2008; also see Sect. 5.3 below).

High throughput sequencing (HTS) approaches such as those based on metabarcoding are beginning to address these major drawbacks in meiofauna biodiversity research, while generating new uncertainties. No sub-sampling is required when sequencing sufficiently large samples after extraction from the sediment, and sequences can be analyzed at the highest (genetic) resolution. However, some taxa are still not sequenced or recognized in the bioinformatic pipelines currently used (Avó et al. 2017; Macheriotou et al. 2020; Brandt et al. 2021; Castro et al. 2021). Also, different conclusions can be drawn from analyses using different sequencing techniques (Leasi et al. 2018). DNA sequencing does not differentiate between dead and alive specimens, and therefore, the use of environmental RNA (eRNA), specifically targeting live organisms, is being explored as a tool in meiofauna studies. For instance, Broman et al. (2021) demonstrated a clear response of meiofauna to an organic enrichment gradient along the Baltic coast off Finland using eRNA targeting nematodes, foraminiferans, and ciliates.

The identification of copepods to species level can only be achieved by studying the adult specimens. Copepodites and nauplii are therefore generally excluded from biodiversity comparisons using traditional morphological methods. With the rise of molecular methods such as barcoding and metabarcoding, identification of all developmental stages is theoretically possible (Rossel et al. 2019). However, as for nematodes, the lack of suitable reference libraries is still greatly reducing the applicability of molecular methods (only 12% of the 122 species sequenced in Rossel and Martínez Arbizu 2019 are currently present in GenBank). Most of the species found in the abyss (> 99%) are thought to be new to science (George et al. 2013), but even in relatively well studied areas such as the North Sea, many copepod species remain undescribed (Huys et al. 1992) with only a few recent species descriptions added since 1992. Moreover, molecular methods revealed that 19% of the harpacticoid species in the German Bight, a part of the North Sea, are new to science, and > 8% represent species complexes with high cryptic genetic diversity which is not reflected in the morphology (Rossel and Martínez Arbizu 2019). Lack of comprehensive identification keys for marine harpacticoids also hampers the understanding of species ranges and biogeographical patterns of meiobenthic copepods.

Lacking calcareous skeletal structures, nematodes and copepods, do not generally leave a fossil record that could be used to study past biodiversity changes. Conversely, the shelled ostracods and foraminiferans (alive and as fossils) have been well studied since the nineteenth century, although originally with a focus on taxonomy. They both are an important meiobenthic taxon of interest in most aquatic environments, not only for their living specimens, but especially for their fossil records. Quantitative ecological and paleoecological studies were initiated in the 1950s (e.g., Benson 1959; Benson and Kaesler 1963, Walton 1955). Similar to other meiobenthic taxa, most soft sediment ostracods and foraminiferans live in the top few centimeters of the sediment (Gooday 1986; Jöst et al. 2017), and are therefore sampled in the same way as other meiofauna taxa.

5.3 Meiofauna Biodiversity Patterns Across Benthic Habitats

Single locality (sample, site, or station), or alpha, diversity patterns observed for nematodes and copepods range from samples with a very high number of rare taxa (often occurring as singletons or doubletons in a sample) to samples dominated (> 50% or more of total abundance) by a single or few high-abundance species. Intermediate between these extremes, we often observe assemblages composed of a few abundant species and a significant number of taxa with low abundances. Figure 5.2 illustrates some of the density-biodiversity patterns observed for alpha diversity of nematodes and copepods across habitats. While this figure generalizes the main trends, in each of the habitats shown, specific environmental gradients result in within-habitat shifts of density-diversity relationships. For instance, abyssal plains are generally characterized by low densities (from less than 10 to about 100 individuals per 10 cm^2) and high species richness with no dominant nematode or copepod species present (Hauquier et al. 2019; Rose et al. 2005). However, a gradual increase in particulate organic carbon (POC) fluxes to the seafloor along a surface productivity gradient tends to result in higher abyssal densities because of the higher food input. This often corresponds with an increase in species richness for both copepods and nematodes (Fig. 5.3).

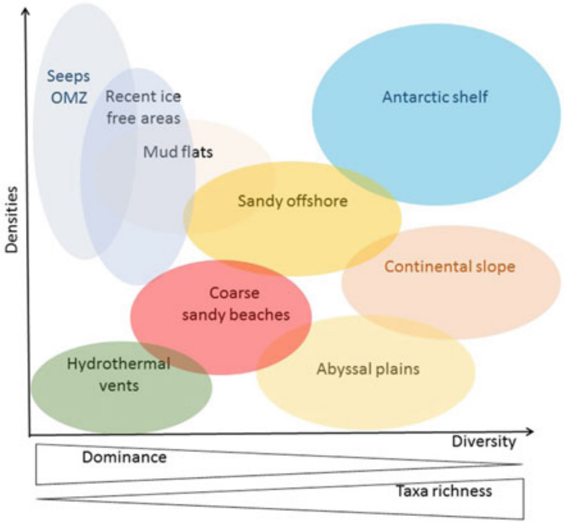

Fig. 5.2 Generalized patterns of density-biodiversity relationship for alpha diversity of marine nematodes and copepods in different habitats (OMZ: Oxygen Minimum Zones)

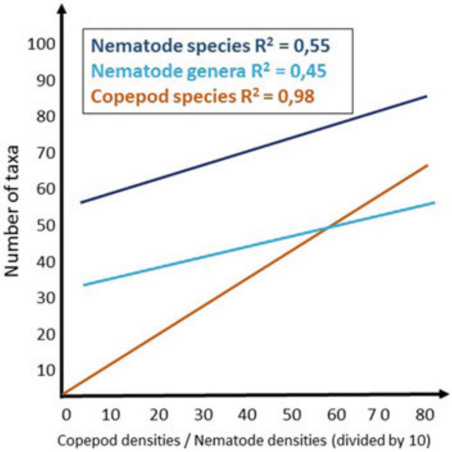

Fig. 5.3 Relationship between nematode species and nematode genera counts and densities (individuals per 10 cm^2) in the abyssal NE Pacific along a particulate organic carbon (POC) gradient in the abyssal North East Pacific (based on data from Hauquier et al. 2019) combined with the relationship between copepod species versus densities from two locations (same depth) in the Angola Basin. Samples with copepod densities below 20 individuals per 10 cm^2 are from an extreme oligothrophic site while samples with densities above 20 individuals per 10 cm^2 are from a site influenced by Benguela Upwelling System (based on George et al. 2013)

Areas that have been depleted of organic matter (OM) for long periods of time, such as permanently ice-covered areas (Rose et al. 2014) or the deepest areas of shallow-water marine caves (Janssen et al. 2013; see Chap. 11), closely resemble abyssal communities in terms of low abundance and high evenness. This contrasts with cold seeps, where methane emanates from soft sediments. Its anaerobic oxidation is coupled to sulfate reduction producing high sulfide concentrations. In these reduced environments, occasionally, very high densities of a single nematode species (up to 10,000 individuals per 10 cm^2) were found, such as *Halomonhystera hermesi* (originally identified as *H. disjuncta*) which was recorded on the subarctic Håkon Mosby mud volcano (Van Gaever et al. 2006; Tchesunov et al. 2014). The high bacterial production on this volcano seems to feed a single opportunistic species that is tolerant to, and even thrives in, extreme sulfidic and anoxic sedimentary conditions. However, not all seeps show the same elevated densities although diversity is in most cases reduced since only a few species seem to survive (Van Gaever et al. 2009; Pape et al. 2011). Also, sediments near shallow hydrothermal vents, such as off Milos (Greece), exhibit low diversity and the dominance of a single nematode species tolerant to the reduced sulfide-rich conditions. Although densities are not of the same magnitude as in the subarctic mud volcano, here too a single free-living marine nematode, *Oncholaimus campylocercoides*, occurred with abundances of up to 600 individuals per 10 cm^2 at the fringe area of the vents, coping with high sulfide concentrations and developing sulfur inclusions in the epidermis (Thiermann et al. 1994, 2000).

While some nematode species may thrive, most copepods and ostracods do not tolerate oxygen depleted sediments (see Chap. 10). Their densities in oxygen-poor sediments are generally very low, and assemblages are represented by a few species only. Copepod assemblages from seeps are often characterized by widely distributed taxa, such as species from the genus *Tisbe* which, for example, was the dominant taxon in chemosynthetic mussel beds in the Gulf of Mexico (Plum et al. 2015). In deep-sea hydrothermal vents, Gollner et al. (2015) reported decreasing copepod species diversity with increased hydrothermal activity. Noticeable is that the functional copepod diversity may increase under intense hydrothermal influence despite the seemingly challenging environmental conditions at vent sites compared to surrounding areas not influenced by vent emissions (Alfaro-Lucas et al. 2020). It is likely that local biochemical conditions and fluid flow intensity resulting from seepage or venting, in combination with the capacity of the dominant species to colonize the reduced environments, are responsible for different diversity patterns observed at different seeps and vents.

Antarctic shelfs too can be characterized by very high nematode densities (> 5000 individuals per 10 cm^2; Veit-Köhler et al. 2018). Depending on the local conditions, nematode assemblages comprise either a few dominant species (Ingels et al. 2006) in addition to several rare taxa or no obvious dominant taxon (Pantó et al. 2021). The availability of food and oxygen seems to drive the patterns observed (Pasotti et al. 2014), as does disturbance from past and present ice scouring (Lee et al. 2001). Moreover, when new ice-free habitats appear as a consequence of glacier and ice shelf collapses, succession can cause shifts in densities and diversity (see Chap. 9). Recently ice-free areas along the Antarctic shelf, for instance, are initially characterized by low densities of colonizing nematodes. Densities of a single or a few rapidly colonizing nematode species then increase before, often after decades, species-rich, highly abundant assemblages develop (Raes et al. 2010; Hauquier et al. 2011, 2015). This observation is in accordance with empirical studies from other habitats, recording the dominance of generalist species at an early stage of succession, followed by colonization of specialists when a diverse resource base has accumulated (Yeakel et al. 2020). The above cases illustrate some of the extreme biodiversity values in Fig. 5.2. Most environments, including sandy or muddy shelf areas, exhibit more moderate average diversity and density. Biodiversity will vary within habitats, depending on local gradients related to different environmental conditions (see Sect. 5.3).

Beta and gamma diversity of meiofauna is less well understood due to the lack of species descriptions and limited numbers of larger-scale studies. Spatial turnover is generally high between distinct habitats. Habitat heterogeneity has a strong positive effect on beta and gamma diversity, both at genus and at lower taxonomic levels (Danovaro et al. 2009; Zeppilli et al. 2011; Leduc et al. 2012a; Schratzberger and Somerfield 2020). A recent regional-scale study of soft sediment nematode communities by Liao et al. (2020), assessing the structuring roles of regional (e.g., dispersal) versus local (e.g., environmental habitat) processes, confirmed the importance of the environment as the first filter that selects a subset of species from the regional species pool. Distance between locations seemed of lower importance for the surface-dwelling species, but when subsurface-dwelling nematodes are included in variation partitioning analyses, the importance of spatial descriptors such as geographical coordinates increases, in addition to the environmental filter (Hauquier et al. 2018).

Metabarcoding methods are being used to reduce limitations resulting from the large number of undescribed species and the unknown degree of cryptic diversity. Using HTS, Macheriotou et al. (2020) evidenced the importance of environmental filtering for nematodes in relatively homogenous abyssal sediments along a 2000 km POC gradient in the North East Pacific. In addition, sympatric speciation and affinity for overlapping habitats were suggested as important processes for diversity based on observations of aggregation and phylogenetic clustering in abyssal nematode amplicon sequence variants (ASVs).

5.4 Environment-Related Drivers of Meiofauna Diversity Patterns

Here we focus on important natural drivers of meiofauna biodiversity. What do we know about the relationship between specific environmental factors and their effect on the diversity of meiofauna taxa?

Substrate type: Sediment granulometry has been one of the most frequently evoked proxies correlating with patterns of nematode and copepod community composition. Multivariate analyses often group (or differentiate) samples based on their species and genus composition according to sediment type (Heip et al. 1985; Vanaverbeke et al. 2011; George et al. 2020). Changes in sediment characteristics are, at least partly, responsible for both nematode and copepod species turnover, because species are highly adapted to the substrate in which they live. For example, more slender copepod species dominate in sandy sediments, living in the interstices between sand grains, while adapted appendages help some copepod and even nematode species such as the members of the families Epsilonematidae and Draconematidae, to attach to hard substrates (Raes et al. 2008). In contrast to taxonomic composition and species turnover, the correlative relationship between granulometry and alpha diversity is less straightforward to explain empirically. Reviewing the wider literature on animal-sediment relationships, Snelgrove and Butman (1994) found little evidence that animal distributions are determined by any of the sediment variables derived from grain size alone. This also applies to meiofauna. Sediment-related primary drivers for biodiversity rather include biochemical processes related to oxygen supply and food input (Vanaverbeke et al. 2011). Shallow silty, organically enriched sediments are often associated with higher densities and lower meiofauna diversity due to the dominance of opportunistic species. Conversely, meiofauna species tend to be more evenly distributed in clean sands, but density is lower because of the generally lower organic matter content in those sediments. Meaningful and predictive explanations for meiofauna distributions are likely to emerge if these are also evaluated relative to the suite of hydrodynamic and sediment transport processes that are responsible for sediment distributions. Also, offshore it seems important to investigate the physical form of the sediments (e.g., bedforms) at a range of spatiotemporal scales, including the details of the grain size distribution when aiming to provide meaningful explanations for the associations of nematodes with their sedimentary environment (Schratzberger and Larcombe 2014).

Organic matter supply and oxygen concentrations: In deep waters, nematode and copepod diversity generally increase with food availability, provided oxygen is not a limiting factor (Bianchelli et al. 2013; George et al. 2013; Hauquier et al. 2019). As shown in Fig. 5.3, both nematode genus and species numbers tend to increase with increasing food densities along a gradient of surface productivity in the North East Pacific abyss. It is likely that the general absence of opportunistic taxa in these food-limited environments prevents an overall increase in dominance, so that an increase in OM content at the seafloor is beneficial to many species. Also, copepod abundance in the abyssal study area in the South East Atlantic is mainly controlled by OM input to oxygen-rich sediments (George et al. 2013). A northern station, influenced by the Benguela upwelling system, had 5 times higher abundances and approximately 3.5 times more species than a southern station located outside the influence of the upwelling system. Remarkably, copepod evenness was only slightly (but significantly) lower in a more productive area, evidencing a clear linear relationship between abundance and diversity of copepods (at nearly constant evenness) in these well oxygenated deep-sea sediments (George et al. 2013). According to several studies, there is not a linear but a parabolic response of diversity to food availability in the deep sea. This is in accordance with the species richness energy hypothesis which suggests that both low and high food availability results in a low local or alpha meiofauna diversity (Leduc et al. 2012b). Indeed, studies from high productivity areas, such as parts of the Southern Ocean (Lins et al. 2018), documented a decrease in diversity due to the dominance of particular nematode species at locations with high food input, despite its abyssal depths. To what extent the decrease in biodiversity is determined by food supply only, or also by an associated decrease in oxygen concentrations or other factors such as shifts in species interactions, is not yet established. In eutrophic environments, oxygen limitation may favor a limited number of more opportunistic nematode species which can thrive on the available food and achieve high densities. However, highly refractory OM content in oxygen-poor sediments, as found in mud flats and mangroves, can depress both diversity and density since both variables may vary from high (Sharma et al. 2021) to very low (Cai et al. 2020). In contrast to nematodes, most other meiofauna taxa, including copepods and ostracods, are often absent or occur in very low abundance in hypoxic and anoxic sediments (Yasuhara and Irizuki 2001; Yasuhara and Yamazaki 2005; Yasuhara et al. 2012a; Yasuhara 2019). Crustaceans are much more sensitive to oxygen depletion and will decrease in density and diversity much more quickly along an oxygen gradient than nematodes (Elmgren 1975; see Chaps. 7 and 11). Neira et al. (2018) recorded a decrease of copepod densities along a gradient of oxygen depletion at the oxygen minimum zone (OMZ) off Costa Rica. No copepods were found at the site with lowest oxygen dissolved concentration (0.05 ml/L) at

400 m depth. Some Harpacticoid families like the Cletodidae, however, show some resistance to low oxygen levels, being the only family able to survive during a two months long anoxic event (Grego et al. 2014).

Temperature: Temperature is a major driver of marine biodiversity (Tittensor et al. 2010). Even in the deep sea, temperature plays an important role in controlling meiofauna biodiversity (Yasuhara et al. 2009; Yasuhara and Danovaro 2016; Jöst et al. 2019; Doi et al. 2021). Physiological tolerance drives the temperature diversity relationship, with fewer species being able to tolerate very cold temperatures (Currie et al. 2004; Yasuhara and Danovaro 2016). Paleontological and biological time series, and modern spatial distribution records of ostracods, foraminiferans, and nematodes all show significant temperature diversity relationships (Cronin and Raymo 1997; Danovaro et al. 2004; Hunt et al. 2005; Yasuhara et al. 2009, 2014; Yasuhara and Danovaro 2016; Jöst et al. 2019). A recent paleontological time series deep-sea benthic Foraminifera by Doi et al. (2021) supported the causality of temperature on diversity, suggesting a major role of bottom-water temperature. For shallow water environments where the effects of global warming are expected to be more prominent, laboratory experiments with nematodes revealed that thermal stress from elevated temperature not only affects the fitness of selected species, but also species interactions, thereby impacting species coexistence and consequently biodiversity (De Meester et al. 2015; Vafeiadou and Moens 2021). Both the amplitude and frequency of diurnal temperature fluctuations affected nematode species interactions (Vafeiadou and Moens 2021). Multiple stressor experiments also demonstrated a combined effect of acidification and warming on meiofauna and nematode structural and functional community descriptors (Meadows et al. 2015; see Chaps. 7 and 11).

Bathymetry: Rex (1973) revealed a parabolic relationship between alpha diversity and water depth for specific macrobenthic taxa such as gastropods. According to this and other studies, diversity reaches a maximum at mid-water depth between 1500 and 2000 m. Some nematode studies evidenced increasing diversity from the shelf break to mid-slope depths (Muthumbi et al. 2011), while others showed that diversity decreases from the mid-slope into abyssal depths (Gambi et al. 2010). Rex et al. (2005) suggested that low abyssal biodiversity resulted from the fact that the benthic fauna there was only a spill-over (sink) from the shallower slope fauna and not a province on its own. However, the presence of abundant nauplii, copepodites, and egg-carrying females was indicative of self-sustaining copepod populations that do not depend on spill-over of individuals from slopes to survive. The vent endemic copepod family Dirivultidae (> 65 species) also diversified in the mid-ocean ridges and not on the slopes (Gollner et al. 2010). For nematodes, biodiversity data spanning the whole bathymetric range from shelf to abyss is limited. The increase of nematode species and genus diversity with increased POC flux in the abyss up to a certain level (Fig. 5.3) is also likely the process responsible for biodiversity increases from the abyss to mid-slope depths (1500–2000 m). From mid-slope to the upper slope, depending on surface productivity, the oxygen minimum (between 1500 and 500 m water depth in general) may impinge on the seafloor which can reduce diversity at the core of the oxygen minimum area and increase the dominance of species adapted to low oxygen concentrations. Furthermore, the presence of strong selective pressures related to gradients of food and oxygen availability, in combination with predation and competition, may have led to an increase in habitat specialization in the lower reaches of oxygen-minimum zones at about 1500 m. This may have supported an increased rate of speciation at mid-water depths (Rogers 2000) and explain the peak in biodiversity at mid-slope depths. For copepods, data on diversity-depth relationships across continuous transects from the shelf to the abyss are also currently lacking. We can only infer from the small volume of diversity-productivity data that does exist that diversity will be attenuated along a transect of increasing depth, following the productivity gradient. Remarkably, meiofauna abundance and diversity increased in several hadal trenches, as these environments act as accumulation areas for OM triggered by lateral transport (Schmidt and Martínez Arbizu 2015; Schmidt et al. 2018; see Chap. 9). Ostracods tend to show a similar parabolic depth diversity relationship. The peak of the curve is shallower in the Arctic and Nordic Seas (several hundreds of meters) than in the North Atlantic (1500–2000 m; Yasuhara et al. 2012b; Jöst et al. 2019).

Disturbance: Measures of nematode diversity have been proposed as potential indicators for disturbance (see reviews by Balsamo et al. 2012; Zeppilli et al. 2015 and Chap. 7 for further references), but such metrics are not always reliable as single indicators of stress. Different natural environmental variables strongly affect meiofauna biodiversity (see sections above), leading to disturbance-biodiversity relationships that are habitat-specific and difficult to unravel. Emerging modeling studies using artificial neural networks may provide new insights. Merckx et al. (2010) modeled both the predictability of free-living marine nematode diversity on the Belgian Continental Shelf (North Sea) as well as the environmental dynamics affecting it, using a large historical database. Reliable predictions were made for evenness and species richness, which were mainly related to the clay and sand fraction of the sediment, and the minimum annual total suspended matter. Variation in species richness was partly explained by disturbance from sand extraction and the amount of gravel of the seabed. To our knowledge, no further attempt has been undertaken to date using such modeling approaches, despite a major development in modeling tools during the last decade. Metabarcoding approaches too have the potential to help identify a baselines against which future changes in meiofauna diversity, both natural and anthropogenic in origin, can be evaluated. On the condition that reference databases are available, metabarcoding can provide a comprehensive and multi-taxon assessment of meiobenthic biodiversity while avoiding the labor-intensive sorting and expert-based morphological identification.

Salinity: Sharp transition zones along strong environmental gradients such as those caused by salinity are known as ecotones. The extent to which ecotones harbor more or fewer meiofauna species than the adjacent environments, which they are connecting, is habitat-specific. For marine nematodes, there is occasional evidence of increased taxonomic distinctness at upper sandy beaches where freshwater and marine species coexist (Gheskiere et al. 2005). Meiofauna diversity patterns along estuarine gradients are not always consistent, but river mouth areas with higher salinity generally have a higher biodiversity of most meiofauna taxa compared to the more brackish and freshwater parts (Soetaert et al. 1995; Whitfield et al. 2012; Broman et al. 2019; Horne et al. 2022). To what extent nematodes species are truly brackish or just tolerant of decreased salinity is unclear at present. It is clear, however, that salinity can limit the dispersion of both marine and freshwater species. Understanding physiological tolerance of these species is a prerequisite to interpret biodiversity patterns along estuarine gradients (see Chap. 7). A noticeable observation was made in the Baltic Sea, where nematode genera classified as predators prevailed under more saline conditions. Network analysis demonstrated more prominent meiofauna-macrofauna associations which were correlated to the higher biodiversity of both size groups (Broman et al. 2019). However, the total number of meiofauna species in estuaries is temporally and spatially variable, and reasons for this are complex. Using eDNA data, Fais et al. (2020) revealed that intertidal meiofaunal communities in the Lima estuary (Portugal) comprised marine taxa, even under oligo- or mesohaline conditions, suggesting they went through a large adaptive effort, compared to the limnetic meiofauna.

Interaction with other ecosystem components: Larger animals belonging to macro- and megafauna affect meiofauna community composition by bioturbating and bio-irrigating the seafloor (Braeckman et al. 2011), providing habitat (Raes et al. 2008; Degen et al. 2012), grazing (Ólafsson 2003), and/or competiting with meiofauna for food (Ólafsson 2003; Nascimento et al. 2011; Ingels et al. 2014). The resultant, combined effect on meiofauna diversity is challenging to ascertain. Meysman et al. (2006) suggested that bioturbation increases the number of habitable niches and the variety of food sources, resulting in higher meiofauna diversity. Recently developed ecological models for larger fauna supported the idea that ecological engineers may enhance community diversity by facilitating colonization and limiting competitive exclusion (Yeakel et al. 2020). To what extent this is applicable to meiofauna is not yet clear. The benthic environment harbors different size classes and is continuously reshaped by larger organisms interacting with their smaller co-inhabitants. Interesting in this context are results from microcosm experiments investigating the effect of meiofauna and their activities on sediment properties and inter- and intraspecific interactions of sediment-dwelling fauna. For example, Piot et al. (2013) found that in the presence of a natural meiofauna community, the interactions between macrofaunal species changed, which subsequently led to modifications of ecosystem properties such as oxygen and nutrient fluxes in the sediment but also microbial abundances.

5.5 The Function of Meiofauna Biodiversity

Positive relationships between nematode biodiversity and benthic prokaryotic activity as a proxy for ecosystem functions in deep-sea sediments suggested that marine diversity loss could have adverse effects on ecosystem functioning (Danovaro et al. 2008; Pusceddu et al. 2014). To what extent these relationships are causal rather than due to other, confounding variables, or are a consequence of reverse causation, remains unclear and requires further experimental testing. However, manipulating the biodiversity of microscopically small organisms in a laboratory approach is not a sinecure. Bonaglia et al. (2014) controlled meiofauna abundances and biodiversity in laboratory microcosms and measured resultant effects on sediment biochemistry. Interactions between meio-, macrofauna and bacteria contributed significantly to the nitrogen cycling in soft sediments. However, the role of biodiversity versus abundance was not disentangled in this experiment. Other experiments also evidenced the effects of meiofauna abundance on specific aspects of ecosystem functioning such as oxygenation of hypoxic sediments and sulfide removal, although the effects of biodiversity were less clear (Bonaglia et al. 2020; see Chap. 2). Mathieu et al. (2007) showed that the activity of nematodes enhanced the net productivity of diatom biofilms, while natural meiofauna communities enhanced the mineralization of organic matter in another experimental setup (Nascimento et al. 2012). Schratzberger and Ingels (2018) reviewed the role of meiofaunal activities in regulating ecosystem processes that provide or support ecosystem services. While empirical evidence is growing on the importance of meiofauna, the specific role of diversity remains a critical knowledge gap. Interesting is the observation that not only biodiversity, but even more so the presence of specific functional traits appears to be crucial for maintaining specific ecosystem functions.

5.6 Looking into the Past to Understand the Future: Fossil Records

Studying temporal variation in marine benthic communities requires continuous and regular sampling. Consequently, long-term studies on benthos including meiofauna are rare (Kitazato et al. 2000; Danovaro et al. 2004; Ruhl et al. 2008; Smith et al. 2009). Currently, the only way to explore temporal variation beyond decadal time scales is by using fossil records. Meiofaunal foraminifera and ostracods are the only groups that have hard, mainly calcareous parts (i.e., shells) that are fossilized and provide good fossil records. In the deep sea, ostracod and foraminiferal fossil diversity changes in accordance with climatic change (Cronin and Raymo 1997; Hunt et al. 2005; Yasuhara and Cronin 2008; Yasuhara et al. 2009, 2014; Doi et al. 2021). Species diversity is generally higher during warmer periods on 10^2 to 10^4 time scales (Yasuhara and Cronin 2008; Yasuhara and Danovaro 2016). Global climate and deep-sea biodiversity curves are remarkably similar on glacial-interglacial time scales, indicating a climatic control of deep-sea biodiversity (Fig. 5.4; Yasuhara et al. 2009). Major climatic events affect meiofauna diversity. There is increasing evidence that the Mid-Brunhes Event (MBE; a major climatic mode shift at approximately 400 to 350 thousand years ago) has affected deep-sea ecosystems substantially, especially in marginal seas such as the Arctic and the Sea of Japan (DeNinno et al. 2015; Cronin et al. 2017; Huang et al. 2018, 2019). In contrast to the majority of marine species, deep-sea benthic foraminifera did not have a major extinction at the Cretaceous/Paleocene (K/Pg) boundary (D'Hondt 2005). Mass extinction of marine foraminifera occurred in the Paleocene-Eocene Thermal Maximum (PETM: approximately 55.5 million years ago; Thomas 2007) during the Cenozoic. An extinction event of certain deep-sea foraminiferan taxa is also known for the Mid-Pleistocene Transition (MPT: approximately 1.2–0.55 million years ago; Hayward et al. 2007). Evidence from bathyal and abyssal foraminiferan fossils indicates that the origin of a latitudinal diversity gradient was at approximately 37 million years ago (Thomas and Gooday 1996; Stuart et al. 2003; Yasuhara et al. 2020). Because of high sedimentation rates in marginal marine environments, highly resolved young meiofaunal fossil records are available, allowing us even to depict the effects of anthropogenic activities. For example, in Osaka Bay and the Gulf of Mexico, man-induced eutrophication and its associated deoxygenation via urbanization and industrialization caused a substantial diversity and/or abundance decline of benthic foraminifera and ostracods (Rabalais et al. 2007; Yasuhara et al. 2007, 2012b, 2019; Tsujimoto et al. 2008; Pitcher et al. 2021).

Recent extensive benthic foraminiferal research resulted in a synthetic Cenozoic paleobiogeographic framework known as the Hopping Hotspots Model (Renema et al. 2008), suggesting that the biodiversity hotspot has moved through the Cenozoic. During the Eocene, highest diversity occurred in the western Tethys (present Mediterranean). Then, the hotspot shifted to the Arabian region from the late Eocene through the Oligocene. By the mid-Miocene, both hotspots had collapsed, the Indo-Australian Archipelago (IAA) hotspot in the southeastern Asian (aka Coral Triangle) emerged and remains until today. Some ostracod data are consistent with this model (Yasuhara et al. 2017a; Shin et al. 2019). Although further data and studies are needed, meiobenthic ostracods and foraminiferans help to understand deep-time diversity and biogeography dynamics by taking advantage of their excellent (i.e., continuous and high abundance) fossil records.

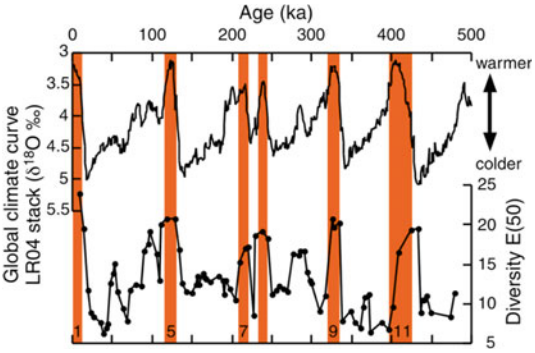

Fig. 5.4 Global paleoclimate (top: oxygen isotope; Lisiecki and Raymo 2005 versus deep-sea ostracod species diversity; bottom: as a standardized diversity measure, rarefaction E(50)) in the Atlantic Ocean. Note the remarkable similarity between global climate and deep-sea diversity curves. Orange areas indicate peak interglacials (warm climate peaks). Modified after Yasuhara et al. (2009)

5.7 Biogeography of Meiofauna: Hypotheses and Evidence

The degree to which meiofauna biodiversity differs between oceans and seas is largely unknown. The lack of biodiversity estimates at species level hampers comparisons of alpha diversity, while the general lack of species descriptions (Appeltans et al. 2012) hampers comparisons of beta and gamma diversity across oceans and seas. Also, latitudinal trends in biodiversity of nematodes are not always straightforward to establish and interpret (Danovaro et al. 2009; Gambi et al. 2010), not even at higher taxonomic levels (Kotwicki et al. 2005). A meta-analysis by Hillebrand (2004) revealed only weak geographical gradients for Nemathelminthes, mainly represented by nematodes. Also, Gobin and Warwick (2006) found that nematode species colonizing artificial hard substrates did not show a trend based on latitude, as diversity was similar for the northern and southern temperate and the tropical areas under investigation. However, in contrast to these shallow water studies, counts of nematode species in the abyssal North Atlantic increased with latitude between 13 to 56°N and were related to the productivity gradient in the North Atlantic (Lambshead et al. 2000). Both, ostracods and foraminiferans show standard latitudinal diversity gradients in shallow-marine and deep-sea systems (Culver and Buzas 2000; Buzas et al. 2002; Yasuhara et al. 2009; Jöst et al. 2019; Chiu et al. 2020). Marginal seas (e.g., Arctic Ocean) tend to lack certain faunal elements (DeNinno et al. 2015). Shallow marine ostracods have more genus-level endemicity among oceans and seas compared to largely cosmopolitan deep-sea ostracod genera.

Since the early days of marine research, it has been acknowledged that many of the small benthic organisms are surprisingly widespread, even to the extent that biogeographical patterns seem absent (Costello et al. 2017; Fontaneto 2019). This observation is commensurate with the ubiquity hypothesis or among meiobenthologists known as the meiofauna paradox: despite their low mobility and their lack of planktonic larval stages, microscopic benthic organisms are often cosmopolitan. Now, we know that there is a wide variety of meiobenthic distribution patterns, ranging from cosmopolitan to endemic. We also know that, depending on specific morphological and life history characteristics, meiobenthic species disperse to varying degrees. According to Fontaneto (2019), important traits for long-distance dispersal in small organisms include dormancy capability, long-term resistance of dormant stages, and the ability to colonize new habitat rapidly. The meiobenthic sized annelid *Dinophilus vorticoides* is a widely distributed species, which lives buried in sediments and lacks pelagic larvae. However, it is also found on macroalgae and ice, likely surviving by forming dormant encystment stages during long-distance rafting (Worsaae et al. 2019). Previously presumed mechanisms for passive transport of meiofauna are now supported by empirical evidence, including resuspension and drifting in the water column, attachment to other fauna (e.g., turtle shells) and flora (e.g., drifting algae), and even survival as aeroplankton (Corrêa et al. 2013; Ptatscheck et al. 2018; Buys et al. 2021). For instance, an unexpectedly dense epibiont community was observed on the back of loggerhead turtles migrating over large distances for reproduction and feeding (Ingels et al. 2020a). Considering the evolutionary age of the taxa involved, dispersal of meiobenthic taxa through turtles is very likely contributing to the cosmopolitan distribution of meiobenthos (Corrêa et al. 2013).

Studying harpacticoid copepods belonging to the deep-sea family Argestidae, Menzel et al. (2011) sampled 113 stations across 12 abyssal regions. They found that many species had a long-range distribution across the Atlantic Ocean and that submarine ridges were not a barrier for dispersal. Pointner et al. (2013) found the same species of deep-sea Paramesochridae distributed in the Atlantic and Pacific abyssal plains.

In addition to limited knowledge on dispersal of meiobenthic taxa, there is also a lack of information on genetic structuring of populations. Given the originally presumed limited dispersal capacity of marine nematodes, prominent genetic differentiation between geographically isolated species was expected previously. However, shared haplotypes and multiple admixture events (when previously diverged or isolated genetic lineages mix) in the population of a *Sabatieria* species (Nematoda) at several widely separated cold seeps in the East Mediterranean revealed gene flow, most likely facilitated by water current transport of individuals and/or eggs (De Groote et al. 2017). In contrast, in the Southern Ocean off the Weddell Sea, gene flow between *Sabatieria* populations and *Desmodora* species was restricted at large geographic distances, questioning the efficiency of transport via currents (Hauquier et al. 2017). However, genetic structuring differed between nematode species from the same geographic area, but with different habitat preferences. Nematodes from surface sediments had a different population genetic structure than those from the deeper layers with the latter exhibiting more complex haplotype networks.

Also, cryptic species are found among several meiofauna groups including not only nematodes and copepods but also nemerteans (Leasi and Norenburg 2014), turbellarians (Tessens et al. 2021) gastrotrichs (Todaro et al. 1996, but Kieneke et al. 2012), and even microscopically small sea slugs (Jörger et al. 2012). Derycke et al. (2016) reported the sympatric occurrence of cryptic nematode species. The coexistence of different bactivorous cryptic species of the nematode species complex *Rhabditis (Pellioditis) marina* was explained by substantial differences in their associated microbiomes and feeding strategies (Derycke et al. 2016). Their performance in combined cultures was compared with that in monospecific cultures at two different salinities, showing that three of the four cryptic species were able to coexist. Salinity had an effect on their interactions, suggesting that abiotic conditions may play an important role in facilitating coexistence between cryptic nematode species and can alter the interspecific interactions between them (De Meester et al. 2011).

5.8 The Future of Meiofauna Biogeography and Biodiversity Research: Gaps in Our Knowledge and Research Frontiers

Biogeography is a multifaceted, multidisciplinary field of study aimed at answering two fundamental questions in science: ***How and why are organisms distributed as they are on Earth?*** (Wen et al. 2013). Addressing these questions from the perspective of meiobenthology is challenging, not only because of the animals' small size and their seemingly wide geographical distribution, but also because many questions concerning the systematics, ecology, and paleontology of meiofauna remain unanswered (see previous sections of this chapter). Yet, meiofauna diversity and biogeography offer many dynamic areas of research and inquiry for future generations of meiobenthologists.

The chapters comprising this book have emphasized the importance of meiofauna as an integral part of marine benthic ecosystems. Although they are not currently considered a major component in food web models in terms of metabolic activity and carbon flow (Gontikaki et al. 2011; Braeckman et al. 2013), their ubiquitous distribution across the globe, their high taxonomic and functional diversity and proven interaction with mega- and macrofauna, and microbiota makes them a non-negligible component of multidisciplinary marine biodiversity research (see Ingels et al. 2020b as a reply to Danovaro et al. 2020). Furthermore, several meiofauna taxa act as excellent model organisms both for experimental research and for modeling approaches to understand fundamental drivers and consequences of biodiversity change.

Many questions in meiofauna diversity and biography remain unanswered, offering horizons for future research and posing challenges for rapidly developing methodology. Most frontiers pertain to the difficulty of generating sufficiently large volumes of reliable distributional, genetic, and phylogenetic meiofauna data:

- ***Overcoming taxonomic challenges***:

  A critical knowledge gap in biodiversity and biogeography research on meiofauna currently is information on the distribution of species, the degree of turnover, population connectivity, and understanding the diversification process. This is mainly due to the identification burden which is, when centered on morphology, time-consuming and expert-based, and therefore not always feasible, affordable, or indeed reliable. Finding rapid, and at the same time standardized and sound, tools for estimating biodiversity at relevant spatial and temporal scales is essential. HTS is offering that first step but still requires a critical and cautious approach. Developing new investigation methods and standardizing them is still ongoing and needs further investments to optimize protocols and validate different techniques. Furthermore, not all questions can be answered with HTS, so training taxonomists with the necessary morphology-based skills remains a necessity for the future. Artificial Intelligence and machine learning may have a role to play in making taxonomy less dependent on the expertise of a limited (and declining) number of taxonomists. By automatizing taxonomic identification through pattern recognition technologies, biodiversity research could become more accessible (MacLeod et al. 2010). The development of automated identification systems that are robust and reliable will take time, however, as has been shown in plankton research (Pastore et al. 2020).

- ***Overcoming analytical challenges***:

  In the next decade, data analytical challenges are emerging as a result of increasing volumes of occurrence data and phylogenetic information. Even for extreme and remote environments, such as trenches and polar seas, access to samples and biodiversity data is growing. Fortunately, data sharing is being facilitated through research financers, journals, and easy to access data platforms (e.g., Genbank, Barcode of Life Data Systems BOLD, Ocean Biodiversity Information System OBIS, World Register of Marine Species WORMS). It seems inevitable that data mining methods will become essential tools for future biogeographic research of meiofauna. The processes involved are not yet perfect due to the lack of standardization and sound quality control of data. Meiofauna phylogenies are increasing in size, and taxonomic breadth and new sequencing techniques generate increasingly vast phylogenetic datasets, yet tools for data mining and integrated analyses of meiofauna are in their infancy. Most existing parametric statistical approaches will need to be improved or developed to handle large and more complex meiofauna data. The need for input from computer scientists is becoming more urgent. As access to reliable big datasets is being ensured, innovative approaches to the study of meiofauna diversity and biography should allow to answer a whole range of crucial research questions beyond the specific meiofauna interest (see below).

- ***The continued search for general patterns of meiofauna diversity and biography***:

  This is particularly challenging because of the tendency of diverse taxa responding differentially to local environmental conditions at varying scales of space and time. Meiofauna biodiversity and biogeography will undoubtedly become an increasingly multidisciplinary and integrative endeavor and become more closely linked to conservation biology (see concluding paragraph below). The current loss of biodiversity causes dramatic changes in the spatial distributions of many species, but the contribution of meiofauna to these global trends remains poorly understood and quantified. Many contemporary drivers of biodiversity change are also recognized as having driven such changes in the past. Therefore, paleobiological investigations reconstructing biogeographic patterns of meiofauna over geological time scales from their fossil records have been increasing steadily. This line of research should be further pursued, given the fact that fossils are the only direct evidence to understand the past biodiversity beyond biological monitoring of a few decades. Paleobiodiversity reconstruction across spatial and temporal scales, using proxy records of paleoenvironment and paleoclimate (such as paleotemperature), will help our understanding of past, present, and future biodiversity and their drivers (Yasuhara et al. 2017b, 2019, 2008). Evidence generated from studies of contemporary and fossil meiofauna will provide the empirical underpinning for predictive models of biodiversity change to address questions including:

- Where are the highest/lowest levels of meiofauna diversity and what factors drive the patterns observed?
- Why are some meiofauna taxa found in certain locations and not others, and what are the processes that generate the patterns in their distribution?
- How have biogeographic patterns of meiofauna been altered in the past, and how are they likely to be altered under various future scenarios?
- Where are changes in meiofauna diversity most pronounced and why?

However, not only the access to large biodiversity datasets is a priority. The use of micro- and mesocosms under controlled conditions is providing us with crucial insights into the interactions of meiofauna with microbiota and macrofauna, while demonstrating the importance of their biodiversity for ecosystem functions such as primary production and mineralization. This kind of experiments would provide further evidence for the consequences of biodiversity loss and natural habitat degradation, and at the same time support the adjustments of model outputs to more realistic descriptions and predictions.

We cannot make meaningful decisions about the conservation of marine life if we do not know what species are where and why. It is clear that meiofauna has a role to play in the discovery and conservation of biodiversity. To some extent, predictive modeling can anticipate the expected impacts of natural and anthropogenic disturbance on seafloor functions coupled to meiofauna biodiversity. Uhlenkott et al. (2020a, b), for example, used random forest models to predict the meiofauna abundance and diversity across the whole German polymetallic nodule contract area in the abyssal Northeast Pacific. They were able to test the suitability of Preservation and Impact Reference Zones that will help in assessing the impacts of future deep-sea mining. Lessons learned from future meiofauna studies need to be applied not only to discover previously unknown species and report their distributions, but to put those findings into a broader ecosystem context. Only then can global biodiversity dynamics be understood in a more holistic, integrated, and consequently more meaningful way.

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Chapter 6
Freshwater Meiofauna—A Biota with Different Rules?

Ignacio Peralta-Maraver, Walter Traunspurger, Anne L. Robertson, Olav Giere, and Nabil Majdi

Abstract Great divergences arise when comparing the ecology of meiofauna in freshwater and marine ecosystems. Emphasizing the main differences between freshwater meiofauna and their marine counterparts, we will go on a stepwise journey through three major frontiers in freshwater research, which in turn are hierarchically interrelated: biodiversity, community organization (e.g. food webs structure), and ecosystem processes (e.g. metabolism and organic carbon breakdown). The starting point of this chapter is one of the utmost frontiers, both in marine and freshwater research: *meiofaunal diversity*. Especially in freshwater ecosystems diversity becomes evident since, here, habitats extend as highly disconnected biotopes, each characterized by an often fundamentally different biocenosis. From the biodiversity level, we move up the theoretical hierarchy to assess the *role of meiofauna* as an integral part of benthic food webs. Recent research underlines the role of freshwater meiofauna as highly connected nodes and shows their pivotal role in the transfer of energy and carbon along food chains. Distributed over all trophic levels, this structure contrasts with the prevailing conception of meiofauna in food webs, where meiofauna often are considered rather marginal units. Finally, we apply allometric principles from the metabolic theory of ecology in order to assess the role of *freshwater meiofauna in the functioning of the benthic systems*. With a novel modelling framework we develop an analytical perspective, showing that secondary production of micro- and meiobenthic communities can predict microbial decomposition rates within the benthic interface. Our results demonstrate that productive micro- and meiobenthos act as catalysers in the system of organic carbon breakdown and recycling. These findings underline the relevance of freshwater meiofauna within the biogeochemical

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carbon cycle. The mechanistic forces behind the processes involved require future experimental research.

6.1 Introduction

In the freshwater realm, meiofaunal-sized organisms occur everywhere in lakes, streams, ponds, groundwaters, puddles, wet soils, mosses, etc. They have been studied since the seventeenth century when the development of microscopes made their observation possible. Linné included freshwater rotifer species in his *Systema Naturae*, and Spallanzani introduced the term ‘Tardigrada’ (meaning ‘slow-walkers’) and he noticed those animals were able to survive desiccation. During the nineteenth and early twentieth century, zoologists showed a broad interest in describing the species of freshwater nematodes, rotifers and micro-crustaceans and other meiofaunal groups from all over the world including some notes on their distribution, behaviour, and ecology (amongst many others: Sars 1867; Hudson and Gosse 1886; de Man 1884; Cobb 1914; Micoletzky 1911). During the first half of the twentieth century, freshwater meiofaunal research moved towards the understanding of species distribution and assessing their ecological importance. For example, Meschkat (1934) provided a first picture of the complex microscopic life in biofilms (or “*Aufwuchs*”), which cover submerged stones in lakes. Altherr (1938) extensively described microscopic communities in abandoned mines, linking species distribution with the presence of water and patches of organic matter or microbial mats. Shortly before Lindeman (1942) first formulated the concepts of food webs and the cyclic nature of trophic fluxes in a lake ecosystem, Pennak (1940) observed that sandy shores of lakes harboured complex communities of micro-metazoans that were presumably using microbes as food and sediment interstices as habitats.

During the 70s and 80s the ubiquity and diversity of meiofauna, and their amenability to laboratory experiments have provided fertile grounds for studies in population dynamics, energetics, functional and community ecology, and biomonitoring of polluting impacts. As underlined also in other chapters of this book, meiofauna are ideal study organisms for understanding the functioning of benthic ecosystems because they can characteristically show how microbial consortia connect with macroscopic processes. But this work, leading to a greater comprehension of the role of meiofauna in ecosystems, has mostly taken place in marine and brackish water biotopes (see general meiofauna textbooks). However, through special issues such as the one by Majdi et al. (2020a) that summarizes our knowledge on the ecological role of freshwater meiofauna, the research efforts also in this field seem to be regaining the long-deserved momentum.

In this chapter, apart from establishing an overview of our current knowledge on freshwater meiofauna with the aim to evidence their contribution in benthic processes, we also want to highlight how this contribution differs from that of their marine counterparts. For example, studies describing body size distribution patterns in streams have rarely found the typical bimodal distribution reported from the marine benthos.

It has been reasoned that in freshwaters, unlike in the marine environment, larval stages of many insect species (e.g. chironomids, mayflies, stoneflies) are important, yet transient, components of the benthic community resulting in a multimodal body size curve.

We will then examine how meiofaunal models can provide valuable new insights and perspectives to main topical areas of freshwater ecological research: biodiversity, food webs, energy fluxes, and ecosystem processes. For a general overview of freshwater meiofauna taxonomy, ecology and participation in ecosystem processes, we recommend the textbooks and journal issues by Robertson et al. (2000), Rundle et al. (2002), Giere (2009), and Majdi et al. (2020a).

6.2 Research on Meiofauna Species—a New 'Frontier in Biodiversity'?

Freshwater meiofaunal assemblages are numerically dominant and surprisingly diverse in lakes and streams (where they may represent a whopping 50–80% share of metazoan species richness, Robertson et al. 2000; Traunspurger et al. 2020). Freshwater meiofaunal communities typically comprise many interstitial groups such as nematodes, rotifers, copepods, annelids, and may form the bulk of all individuals encountered. However, unlike the marine benthos, in freshwater habitats larval stages of many insect groups are common. Especially chironomid larvae are important components of meiofaunal assemblages regarding their total contribution to benthic invertebrate biomass. Furthermore, freshwater habitats are strongly compartmentalized and physically disconnected by terrestrial barriers (Fig. 6.1). Their environmental features can differ fundamentally from one another as we move down from mountainous springs to alluvial plains (e.g. glacier-fed streams or hot springs, forested headwater streams, mosses and peatland patches, ponds and riffles, sandy lake and river shores, muddy alluvial zones and wetlands). Additionally, at smaller scales, biotope patchiness occurs within the same river reach or lake, providing a diversity of potential habitats for meiofauna (e.g. fine or coarse-grained interstitial habitats, microbial biofilms growing on hard stony substrates like cobbles, or on organic substrates such as wood chunks, leaf litter or macrophytes; free-floating biofilms). A freshwater continuum also extends vertically from the surface stream through the benthic zone into the hyporheic zone and eventually into groundwater, providing further habitats (Fig. 6.1).

The great diversity of habitats and the metacommunity dynamics result in unique assemblages of meiofaunal taxa that may be locally quite variable and different from the assemblages in marine habitats. For example, bdelloid rotifers may populate hard-substrates filtering suspended particles as effectively as clams would (Kathol et al. 2011), whilst, in muddy bottoms, they might be largely replaced by detritivorous, burrowing forms such as, annelids and nematodes. Mosses and other

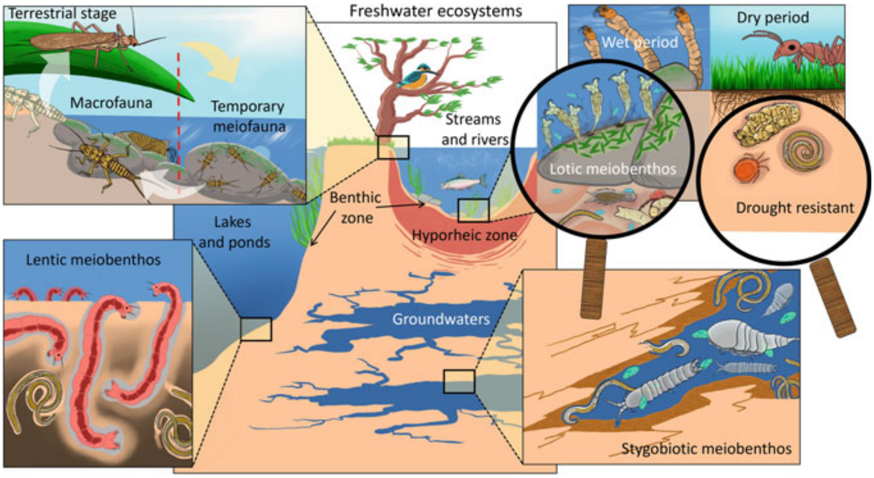

Fig. 6.1 Conceptual depiction of freshwater meiobenthos across a selected variety of freshwater habitat compartments, in part disconnected

ephemeral freshwater habitats comprise a larger share of drought-resistant or terrestrial taxa like springtails, mites, tardigrades, and soil nematode species (Fig. 6.1; e.g. Kreuzinger-Janik et al. 2021). Copepods and cladocerans thrive in ephemeral ponds and basins, including those in urban areas (e.g. Martins et al. 2019). Gastrotrichs, micro-platyhelminths, nematodes, and rotifers flourish in various epiphytic and interstitial biofilm habitats worldwide. Freshwater mites (Hydrachnidia) are surprisingly diverse, being ecto-parasites of aquatic insects and using their host's flying adult stages to disperse (Di Sabatino et al. 2000). The relatively recent discovery in Greenland springs of a completely new class in the Gnatosthomulida clade, Micrognathozoa, exemplifies our limited knowledge of the diversity of freshwater meiofauna (Kristensen 2002). Also in biofilms, species richness and their contribution to freshwater meiofaunal communities remain greatly underestimated, mainly for methodological reasons (see Chap. 3; Zotz and Traunspurger 2016; Balsamo et al. 2020).

Furthermore, groundwaters occurring in unconsolidated sediment aquifers, fractured aquifers, and karst aquifers (including karstic springs) harbour high meiofaunal diversities because the habitat patchiness and low dispersal ability of many groundwater fauna result in a high degree of endemism and ecological specialization. Here, copepod crustaceans are prevalent: a groundwater survey in the early 2000s in the Lessinian region of northern Italy recorded 89 stygobiotic species. More than 50 species were meiofauna, 36 of whom belonged to the Copepoda and many were new to science (Galassi et al. 2009).

Freshwater habitats are often highly disconnected, whether considering across-land distances between lakes or ponds, or flow direction constraints in river networks. While these spatial barriers can be important for larger aquatic organisms, the smallest meiofaunal species tend to easily enter 'resistance stages' enabling them to passively disperse across large distances, supported by wind, rain, drift, and migrating animals (Ptatscheck and Traunspurger 2020). A high dispersal capacity of meiofauna seems a prerequisite for populating disconnected habitats. This is exemplified by cave-dwelling nematodes. Unlike other groundwater animals, most nematode species inhabiting caves are ubiquitous and constitute a transient cave biota, while only a small proportion of the species catalogued show typical troglobiotic traits (Du Preez et al. 2017). Hence, biotopes of freshwater meiofauna represent a complex structural assembly: lateral gradients from terrestrial through riparian to aquatic, horizontal gradients from spring to estuary, finally vertical ones from surface biofilms to the sediment horizon and the deeper hyporheic zone and karst (Fig. 6.1).

Compared to larger organisms, freshwater meiofauna can also be less sensitive to the environmental constraints acting at local and sediment-determined scales. For example, in the hyporheic zone the reduction in oxygen supply and pore-space with depth or under upwelling conditions exert less selective constraints on meiobenthos than on macrobenthos (Strayer et al. 1997; Peralta-Maraver et al. 2018a, 2019a). The ability to populate even the most remote or ephemeral aquatic habitats render freshwater meiofaunal assemblages interesting alternative models for studies on metacommunity patterns. Thus, they feed the debate about processes explaining the observed species richness in a given biotope. Gansfort et al. (2020) recently reviewed 19 metacommunity studies in freshwater, and, although most studies focussed on a limited number of meiofaunal taxa (mostly ostracods), they show that species sorting effects and locally random distribution determine meiofaunal metacommunities. Further studies will doubtlessly reveal the elaborate metacommunity concepts to greatly benefit from incorporating the freshwater meiofaunal compartment.

In the freshwater realm another fundamental contrast to marine meiofaunal assemblages is the common occurrence of temporary meiofauna, i.e. species that start off at meiofaunal size but grow into macrofauna or emerge out of the benthos during their lifespan. This category mostly comprises larval stages of insect species from different orders (mostly Diptera, Plecoptera, Ephemeroptera, Coleoptera, Trichoptera; Fig. 6.1). In inland waters they can greatly influence the spatial and temporal dynamics of meiofaunal assemblages.

Regarding the taxonomic diversity of meiofauna illustrated above and the complex environmental zonation of many freshwater bodies, it is reasonable to assume that the meiofaunal community of a whole lake or of a whole river system can represent one of the most species-rich assemblage of metazoans in a limited spatial area. As a result, even though much effort has been made in recent years to unravel the hidden diversity of freshwater meiofaunal communities (reviewed in Schenk and Fontaneto 2020), traditional taxonomic methods based on morphological features will hardly cover the full range of species found. Using adequate methodologies of sampling and molecular-based identifying all meiofaunal taxa, even the soft-bodied ones, could help avoid potential underestimations of meiofaunal species richness (Schmid-Araya 1997; Kolasa 2002; Tang et al. 2012; Balsamo et al. 2020).

Considering the present scarcity of taxonomic expertise, the recent surge of, and refinement in, molecular-based identification techniques have been proposed as an alternative tool to fill in actual gaps in taxonomy (e.g. Schenk et al. 2020). Nowadays, sequencing has become a standard protocol in developing many biological inventories and monitoring programmes (Baird and Hajibabaei 2012; Leese et al. 2018). However, very few studies have yet addressed shortfalls in freshwater meiofauna diversity sequencing DNA. As recently shown by Schenk and Fontaneto (2020), in ecological research of freshwater meiofauna the use of DNA data and barcoding is presently not well developed.

Yet, this new frontier of diversity assessment in freshwater meiofauna represents a promising avenue of research to link the invisible diversity of meiofauna to conspicuous features of inland water ecosystems. Broad-scale molecular inventories of meiofaunal species could be used for example to tackle 'hot' research topics such as:

- effects of environmental changes on species biogeography,
- detailed recording of potentially invasive species,
- co-occurring networks indicating community structuring or food web processes,
- linkage between biodiversity and ecosystem functions.

Of course, this requires identifying appropriate target genes and primers. For example, candidate target genes for amplification in freshwater meiofauna mainly include ribosomal 18S rRNA and 28S rRNA genes, and the mitochondrial Cytochrome c Oxidase subunit I (COI) gene (reviewed in Schenk and Fontaneto 2020). However, discrepancies might arise when comparing with data acquired with previous methods. Ribosomal genes are preferred because they amplify the broadest range of taxa, but these sequences are generally highly conserved and might fail to discriminate between closely related taxa (Tang et al. 2012; Papakostas et al. 2016; Schenk et al. 2020). Conversely, mitochondrial COI genes possess higher discrimination capacity, but they might even co-amplify with procaryotes and fungi, and inflate real biodiversity values (Weigand and Macher 2018).

In addition, even in up-to-date reference databases of DNA sequences, which determine the accuracy of DNA taxonomy and metabarcoding studies, freshwater meiofauna is underrepresented (Weigand et al. 2019). At the same time, significant advances in molecular-based biodiversity research of freshwater meiofauna advocate for the achievement of complete reference genomes. This implies the challenge of combining morphological identification of model organisms with advanced molecular approaches. Until a very few years ago sequencing the complete genome of an organism was prohibitively costly, not to mention sequencing a whole community. Today, with the ever-decreasing sequencing costs and massive multiplexing capabilities of next-generation-sequencing technologies, molecular barcodes can be generated for thousands of taxa in parallel (Shokralla et al. 2015; Bleidorn 2016). Also, next-generation-sequencing (NGS) methods, in contrast to traditional protocols, permit sequencing completely new organisms for which little genetic information is available (Mardis 2008; Neale and Kremer 2011; Cahais et al. 2012). The use of genomic barcoding has proven to be a powerful method in detecting rare and invasive species in freshwater realms (Brown et al. 2016; Lim et al. 2016). Thus, building complete reference databases in conjunction with applications of NGS techniques might represent the only valid strategy to ensure a future monitoring of diversity, not only in freshwater meiofauna.

6.3 Do Freshwater Meiofauna Hold the Key for Understanding Food Web Topology and Benthic Energy Fluxes?

The trophic role of meiofauna in aquatic food webs tends to underestimate the freshwater compartment. So, here we ask some specific questions of meiofaunal food webs characteristic for freshwater ecosystems:

- How can the taxonomic resolution affect the metrics of food web complexity?
- How does the incorporation of meiofauna into food web analyses affect our view on the connectivity of energy fluxes across terrestrial and freshwater biocenosis?

There is a growing body of research on food web structure involving freshwater meiofauna, which provides some answers to these questions.

In the trophic cycle of ecosystems, the position of meiobenthos is often vaguely defined and mostly lacking larger-scale quantitative evidence. Either they are sweepingly proposed as intermediaries between microbial producers/decomposers and macroscopic organisms (e.g. Schratzberger and Ingles 2018), or, as in most food web studies, the meiobenthic fraction is barely considered. Often, they are also relegated to the level of ‘trophospecies’ within the food web assemblage (aggregation of species that have identical predators and prey). Unfortunately, this undifferentiated conception is symptomatic of both a poor taxonomic definition and a poor knowledge of the feeding habits in meiofaunal species.

As a result, ecologists have often disregarded the role of meiofauna in food web structures (but see Schmid-Araya et al. 2002, 2016). This causes a bias in the interpretation of food web patterns, the metrics of community structure and stability, and ultimately in our understanding of ecosystem functioning. When information on feeding habits is not included, the traditional perception assumes that meiobenthic trophospecies mostly occupy the level of primary consumers (Majdi et al. 2012a; Peters et al. 2012; Schmid-Araya et al. 2016). This is because general allometric scaling principles, inherited from the ‘Metabolic Theory of Ecology’ (Brown et al. 2004), assume that species with small body size occupy low trophic levels (Woodward and Warren 2007; Yvon-Durocher et al. 2011).

Hence, meiofaunal organisms have traditionally been considered as little-connected trophic dead ends in marine ecosystems (Heip and Smol 1975; McIntyre and Murison 1973; Feller 2006). This argument was considered to be supported by the observed high population densities of (marine) meiofauna in sediments that did not seem to be compatible with the expected high predation pressure from large assemblies of macrofauna (shrimps, crabs, polychaetes, ophiuroids, and juvenile fishes

(Castel 1992; Ceccherelli et al. 1994). However, recent studies based on trophic biomarkers such as stable isotopes, are pointing towards a more complex picture.

Freshwater meiofauna are not only primary consumers, but also occupy higher positions in food webs (Schmid-Araya et al. 2016; Majdi and Traunspurger 2017). Many meiofaunal groups (e.g. tardigrades, mites or dorylaimid nematodes) possess a puncturing stylet or piercing-sucking feeding apparatus. Therefore, they can feed on microbes, plants, fungi as well as other meiofaunal organisms, and parasitize animals and plants larger than themselves (e.g. Di Sabatino et al. 2000; Khan and Kim 2007; Hohberg and Traunspurger 2009). For example, freshwater mites (Hydrachnidia) parasitizing aquatic insect larvae occupy top predator positions in food webs (Di Sabatino et al. 2000).

Moreover, within the vast meiofaunal species pool assumed to be microbivorous (i.e. feeding on algae, protozoans or bacteria), diets seem to vary widely. For example, some nematode species seem to prefer certain bacteria species (e.g. Estifanos et al. 2013), or select specific densities of bacteria offered in the laboratory (e.g. Weber and Traunspurger 2013). In the field, nematodes, likely acting as generalist feeders, have been found to opportunistically switch their diet depending on the quantity and quality of prey available (Estifanos et al. 2013; Majdi et al. 2012a; Kazemi-Dinan et al. 2014). There is some evidence that nematodes may even use dissolved organic matter (Höss et al. 2001). This potential trophic flexibility suggests that we should move away from linear schemes for the feeding interactions of meiofauna.

Often meiobenthologists use allometric morphological proxies (body size, morphological traits) to better conceptualize meiofaunal food webs (Weitere et al. 2018; Neury-Ormanni et al. 2020). However, combining several lines of evidence in a holistic manner is a more robust way to better assess the role of meiofauna in freshwater food webs. For example, Schmid-Araya et al. (2016) combined gut content analysis of macro- and meiofauna with stable isotope data of meiofauna to investigate the structure of a stream food web. In addition, information about the community composition (co-occurrence network) was included at an exceptionally high (species-level) taxonomic resolution. Results from this study place meiobenthic species into all trophic levels of the food web. For example, benthic rotifers act as herbivores (i.e. *Proales* sp., *Euchlanis* sp.), microbial feeders (mostly bdelloids), and omnivores including omnivorous predators (i.e. *Dicranophorus* sp.) feeding on other larger ciliates and rotifers. This example also demonstrates that aggregating meiofaunal species into single trophic niches will cause a severe bias of key web properties such as web size, links, linkage density, and predator–prey ratios. In the context of food web ecology these findings are especially relevant because assessment of food web complexity is fundamental to predicting stability and resilience of natural communities (Dunne et al. 2002; Neutel et al. 2007; Sánchez-Carmona et al. 2012).

Meiobenthos contribute considerably to the lengthening of the food chains, the complexity of the food web, and ultimately the transfer of energy and biomass through trophic levels (Schmid-Araya et al. 2016; Fig. 6.2). Therefore, the idea of meiobenthos as a simple trophic intermediary or a dead-end within the food webs should be discarded and replaced by alternative hypotheses that require urgent testing. In this

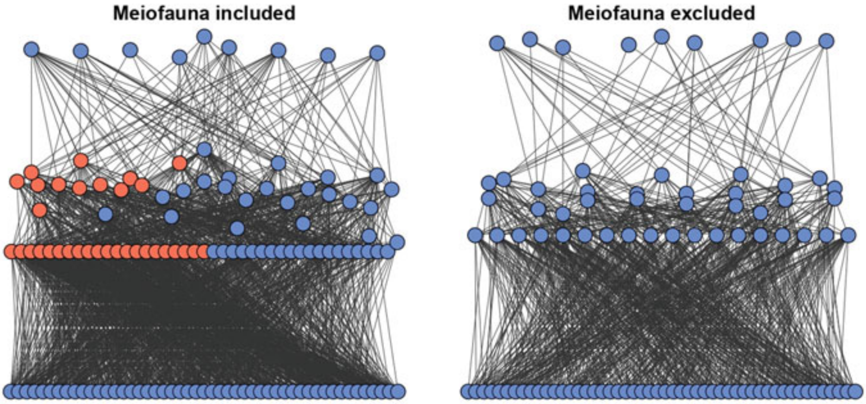

Fig. 6.2 Food web of River Lambourn, UK (summer 2004) indicating trophic interactions between consumers and resources. A comparison of the same community with meiofaunal-sized taxa included (red colour nodes) or excluded. Dots (nodes) represent different species, their links indicated by lines. Location of dots depends on their trophic position. Resources are located in the basal level, followed by primary and secondary consumers, top predators in the upper part. Adapted from Schmid-Araya et al. (2020)

vein, we predict that further significant advances in general food web ecology of benthic systems will necessitate the inclusion of the meiobenthic fraction and their trophic links at a proper, refined scale. Such studies could ideally be performed in manageable freshwater biotopes or in freshwater mesocosms across the globe (urban water bodies, ponds, water reservoirs, etc.).

Information on the role of freshwater meiobenthos as a significant trophic resource for other organisms is limited. Meiofaunal organisms may serve as food for predatory amoebae (Geisen et al. 2015) and may be incidentally ingested by snails grazing on biofilms (Peters et al. 2007). It is intriguing to notice that larvae of *Chironomus riparius* (classified traditionally as a detritivorous deposit-feeder) can feed voraciously on meiofaunal organisms (Ptatscheck et al. 2017). This example demonstrates the way earlier freshwater ecologists have often predefined the trophic preferences even of key actors in energy flows.

Furthermore, a wide range of meiobenthic species has been identified as significant prey for economically important freshwater fish (reviewed in Ptatscheck et al. 2020). For example, juvenile and adult stages of carps, gobiids, and *Tilapia* sp. can feed directly on freshwater meiofauna by filtering them out of sediments (e.g. Weber and Traunspurger 2014, 2015). In aquaculture, freshwater meiofaunal organisms such as copepods, nematodes and rotifers have been extensively used for decades as ‘good quality food’ (reviewed in Ptatscheck et al. 2020).

Interestingly, these trophic interactions between fishes and meiofauna represent a direct link within the food web levels that roughly expands over six orders of magnitude corresponding to a ‘predator–prey body mass ratio’ (PPMR) in the same range as that of whales and krill. Wide PPMRs within the food web have profound implications for the efficiency of energy transfer between benthic predators and prey budgets. The energetic availability, and consequently the metabolic performance and development of predators feeding on low-density resources is constrained by the abundance of large prey. In contrast, those consumers able to exploit swarms of small prey reach a much higher metabolic efficiency (Goldbogen et al. 2019).

In freshwater systems, meiobenthos, such as rotifers, nematodes, oligochaetes, micro-crustaceans and larval chironomids, not only represent the most abundant community of metazoans (Majdi et al. 2020b; Traunspurger et al. 2020), in some benthic habitats they can even dominate in biomass and secondary production (Schmid-Araya et al. 2020; Stead et al. 2005). Furthermore, a number of studies have evidenced de novo synthesis of essential poly-unsaturated fatty acids in common meiofaunal groups such as nematodes, rotifers, and copepods (Lubzens et al. 1985; Menzel et al. 2018; Boyen et al. 2020). Therefore, the ability of benthivorous fish species to 'short-circuit' the food web by including abundant and nutritive meiobenthic organisms in their diet is indeed a highly efficient trophic strategy (Tucker and Rogers 2014). Furthermore, large PPMRs have been suggested to promote persistence of populations in complex food webs and stabilize the diversity of natural ecosystems (Brose et al. 2006). However, the dimension of these interactions between fish and meiobenthos need further scrutiny.

6.4 Inclusion of Meiobenthos, a Pathway Towards New Metabolic Perspectives of Freshwater Ecology?

Communities inhabiting marine and freshwater ecosystems are strongly size- structured, meaning that the abundance (N) of different groups scales powerfully with their body mass (M) (Petchey et al. 2002; Schmid et al. 2000; Perkins et al. 2018; Reiss et al. 2019; Peralta-Maraver et al. 2018b, 2019b). The body mass abundance relationships (M–N) are amongst the most extensively studied patterns in ecology (Blackburn and Gaston 1997; Schmid et al. 2000; Reuman et al. 2008). When individual organisms are clustered into body mass classes, the intercept of the logarithmic relationship provides a proxy for the carrying capacity of the community, while the area under the slope (and intercept) provides a measure of total biomass or biomass spectrum (Fig. 6.3a). Furthermore, the M–N scaling is strongly consistent across habitats of the same type (Schmid et al. 2000). Since deviations from expected scaling indicate the influence of stressors (Petchey et al. 2002) such as anthropogenic contamination (Peralta-Maraver et al. 2019a), M–N scaling coefficients are likely a powerful metric to detect threatened communities.

Under natural conditions, freshwater meiofauna occupy a pivotal position within the standing stock (biomass) described by M–N slope (Fig. 6.3a). Furthermore, their response to disturbance differs from that of macrofauna and, given their small size and potentially high abundance, this can alter the steepness of the M–N slope. For example, macrofauna are scarce within the streambeds of urban water bodies, in

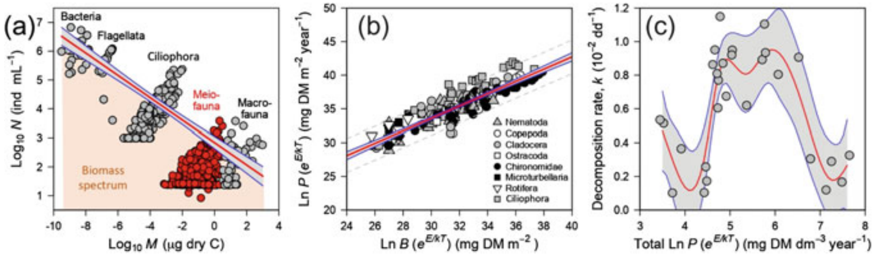

Fig. 6.3 **a** Fitted relationship between body mass (M) and abundance (N) of benthic communities across 30 UK streams. Data expand six orders of magnitude in body size from prokaryotes to macroinvertebrates (from Peralta-Maraver et al. 2019b). **b** Predicted linear relationship between production and biomass for micro- and meiobenthic taxa. Temperature-corrected production (P $e^{E/kT}$) measured in mg DM m^{-2} $year^{-1}$, biomass (B $e^{E/kT}$), measured in mg DM m^{-2}; adapted from Schmid-Araya et al. (2020). **c** Predictions from the generalized additive mixed model relating microbial decomposition of leaf litter (degree $days^{-1}$) as response of secondary production in micro- and meiobenthic communities (Total P) across 30 UK rivers. Scaling coefficients from Schmid-Araya et al. (2020) were used to calculate secondary production of micro- and meiobenthic taxa from reported biomass measurements in Peralta-Maraver et al. (2019b). In all plots, grey areas between blue lines represent the 95% confidence intervals; red line represents fitted predictions

polluted areas, or alluvial plains due to their soft-bottom substrates and frequently hypoxic conditions (Sonne et al. 2018). In contrast, several meiofaunal groups colonize those environments and may even dominate in terms of biomass (Palmer 1990).

In addition to their importance within the standing biomass spectrum, the short life cycles, rapid reproduction rates and dominant abundances of meiofauna in freshwater benthic habitats ensure that these organisms are significant contributors to the total biomass production (permanent meiofauna: ca. 0.3–3 g C/m^2/year, temporary meiofauna: ca. 0.8–5.5 g C/m^2/year) and turnover (Schmid-Araya et al. 2020; Brüchner-Hüttemann et al. 2020). Notwithstanding the body of evidence, and in contrast to studies on macroinvertebrates, only a few studies have quantified empirically the contribution of meiobenthos to the overall production budget of freshwater ecosystems. Indeed, measuring secondary production of microscopic animals demands laborious practises, including tracing development stages of cohorts through time, or assessing species-specific growth rates (Schmid-Araya et al. 2020).

Contrary to the bimodal size spectra distribution of metazoans that is frequently described for marine benthos, more complex modalities prevail in freshwater benthos (Fig. 6.3b). This is probably due to the transient nature of freshwater meiofaunal assemblages comprising a large fluctuating share of temporary meiofauna. Additionally, in temperate zones meiobenthic production ranges can vary greatly with their seasonal changes and export of plant biomass (Majdi et al. 2017) and they can also vary with the small-scale patchiness of stream habitats (Brüchner-Hüttemann et al. 2020). All of these variations demand considerable increase in sampling effort required to obtain reliable estimates. Therefore, in freshwaters, traditional approaches derived from studies on macroinvertebrates might be less suitable for meiofauna.

Current studies on freshwater meiofauna have opted to use allometric scaling relationships to bypass some of the previous issues (reviewed in Schmid-Araya et al. 2020). These models aim to predict production or growth rate as a response to many other variables such as lifespan, temperature, or body size (Benke and Huryn 2010). Their theoretical principles are rooted in the well-established concept of the Metabolic Theory of Ecology (Brown et al. 2004; Sibly et al. 2012). However, in freshwater ecosystems empirical measurements of benthic production showed a weak relationship to individual biomass or temperature (Morin and Bourassa 1992; Benke 1993). In contrast, a new allometric model demonstrates that the temperature-corrected standing biomass powerfully scales with meiobenthic production (Schmid-Araya et al. 2020). Coefficients from this allometric relationship are consistent across benthic habitats both in lakes and rivers, and across nematodes, copepods, cladocerans, ostracods, chironomids, microturbellarians, rotifers, and ciliophoran species (Fig. 6.3b).

Estimates of secondary production integrate information on population density, biomass stock, growth rate, reproduction, and biomass turnover (Benke 1993; Benke and Huryn 2010), and help to explain the organization of natural communities at a local level (e.g. trophic pyramids; O'Gorman et al. 2008). From the perspective of ecosystem functioning, production is the means by which organic carbon and energy become available for transfer from basal to top trophic levels. Hence, production represents a common currency to quantify energy and organic carbon flows between taxonomic groups, trophic levels, and different habitats and/or systems (Dolbeth et al. 2012; Benke and Bruce Wallace 2015). Thus, quantifying meiobenthic production brings us to a central domain of future meiobenthic research: The challenge of assessing the role of meiofauna within the biogeochemical carbon cycle.

Microbially-mediated decomposition of organic substrates, e.g. leaf litter, represents a main entry of bioavailable carbon within benthic food webs. It fuels secondary production in benthic habitats. The diverse microbial consortia inhabiting the streambed pore–spaces are key sites of enzymatic activity and play a leading role during decomposition (Romani et al. 2008; Battin et al. 2016). At the same time, activities of micro- and meiofauna (crawling in the pore–space, digging in the sediment, and grazing on biofilms) promote microbial activity in benthic habitats. Incubation experiments have reported an apparent stimulation of microbial activity and organic matter decomposition with increasing meiofaunal densities (see Chap. 2; Mathieu et al. 2007; Nascimento et al. 2012; Bonaglia et al. 2014; D'Hondt et al. 2018). Based on these premises, we can expect that productive meiobenthic communities promote microbially-mediated decomposition of organic carbon substrates, and therefore, support rapid cycling of allochthonous carbon. Furthermore, recalling secondary production might be used as a common currency of carbon and energy transfer, the microbial decomposition rate enables standardized comparisons across communities and at large spatial scales.

To test our predictions and present an example, we modelled the microbial decomposition of an organic carbon substrate as a response to the secondary production of micro- and meiobenthic communities. For this purpose, we used data provided by Peralta-Maraver et al. (2019b) describing leaf litter decomposition across thirty UK rivers. Their study reports microbial decomposition rates (k) using a standardized bioassay (cotton-strips) as a proxy of leaf litter (Tiegs et al. 2013). In addition, the proxy provides fine-resolution information of the biomass of streambed taxa inhabiting the benthic zone expanding six orders of magnitude in size (from prokaryotes to macroinvertebrates). In essence, length and width of all counted organisms were measured to the nearest micrometre, and transformed into dry carbon (mg C) using allometric relationships. Then, biomass (mg C dm^{-3} of sediment) was obtained from multiplying dry carbon content by individual density (ind dm^{-3} of sediment). Here we consider community data of micro- and meiofauna smaller than 2 mm inhabiting the benthic zone (0–5 cm depth). These data include flagellates, ciliates, and permanent and temporary meiofauna. Biomass data of each taxon were transformed to secondary production using the allometric coefficients provided by Schmid-Araya et al. (2020) for micro- and meiobenthic taxa (Fig. 6.3b). Then, total secondary production of all community taxa was averaged by study site (river) as a measure of total meiobenthic production. Note that the original datasets included other abiotic variables (e.g. latitude, temperature, pH) that were excluded here to facilitate the model performance. Finally, decomposition rates were plotted as response of the total meiobenthic production to explore the shape of the relationship. We could show that decomposition rates follow a convex-curved relationship along the gradient of secondary production, and thus we used non-linear generalized additive mixed modelling (GAM) to fit the observed pattern (Fig. 6.3c). Our results evidence complex trade-off relationships between microbial decomposition and secondary production of micro- and meiobenthic communities in the field.

Our predictions show that productive micro- and meiobenthic communities promote microbial decomposition up to a tipping point at which negative effects come into play and reduce microbial performance (e.g. over-grazing). However, the complexity of processes involved, the various forces behind microbial decomposition and organic carbon cycling defy, as yet, clearly assessed explanations (Peralta-Maraver et al. 2018a). Several pathways come into consideration:

- selective consumption of less active decomposers (Shapiro et al. 2010);
- stimulation of bacterial activity by limiting overgrowth (Traunspurger et al. 1997);
- micro-bioturbation of meiofauna increasing the porosity of microbial mats to nutrients, light and gases (Chap. 2; Pinckney et al. 2003; Mathieu et al. 2007; Otto et al. 2017);
- surface increase of biofilms due to moderate grazing (Neury-Ormanni et al. 2016; Peralta-Maraver et al. 2018a);
- predation–induced recycling of nutrients (microbial loop) (Shapiro et al. 2010);
- dispersal of microbiomes and/or localized priming of bacteria through the deposition of mucus trails and faecal pellets by the meiofauna (Riemann and Helmke 2002).

6.5 Conclusions

Ecologically oriented biodiversity research of freshwater meiofauna not only touches theoretical considerations (e.g. food web topology, diversity-stability). It also affects the practical management of ecosystems. However, the potential use of meiofauna as an efficient tool for monitoring freshwater ecosystems is usually limited by taxonomic impediments. This is changing now with the striking development of genetic sequencing methods that can surmount this limitation. Also in freshwater systems, these powerful genetically-based methods increasingly support the number, efficiency and relevance of those biomonitoring projects that are based on meiofauna assessments: '*meiofauna at the biodiversity frontier*' (e.g. Höss et al. 2011; Semprucci et al. 2015).

Microcosms experiments using meiofauna give insights in physiological processes with the advantages of a broad numerical basis, short experimental times, and convenient repeatability. These studies show that meiofauna species not only represent valuable indicators for a wide range of tolerance limits in ecosystems, with their defined sensitivity against anthropogenic stressors they can also serve as valuable indicators of pollution (e.g. Höss et al. 2004; Gyedu-Ababio and Baird 2006; Brinke et al. 2010, 2011). The large abundances, ubiquity and rapid life cycles characterizing meiofauna make them perfect tracers of pollutants. Additionally, experiments with meiofauna also allow for valuable conclusions on trophic transfer routes and energetic pathways from microbial decomposition rates to macrobenthic predation. Future experimental approaches will define under which circumstances we can expect previously addressed tipping points in microbial decomposition rates in relation to productivity of meiobenthos.

Assessments of secondary production across a broad-range of size spectra prove meiofauna to serve as a powerful indicator of ecosystem structure and processes. Clearly, multiple mechanisms combine to cover these interactions extending from microbial decomposition to top-level predation, but models presented in this chapter offer a novel analytical toolkit to assess these important processes. Considering the effects of environmental drivers (e.g. oxygen concentration) within our models, and their interactions with data on secondary production, will improve our analytical scrutiny. However, theoretical modelling does not substitute the well-designed experiments and survey studies at a fine taxonomic resolution. This combination will still be required to fully understand the role of meiobenthos in the ecosystem functioning: '*the indicative role of meiofauna in benthic ecosystems*'.

Another basic issue is inclusion of meiofaunal organisms into our understanding of the energetic connectivity between terrestrial and aquatic ecosystems, especially relevant under the extremes to be expected in future developments. Interruptions in stream flow are becoming increasingly common worldwide due to climate change and rising pressure on water resources (Datry et al. 2014). In this scenario, studies show that meiofaunal organisms such as tardigrades or nematodes have the potential to quickly recolonize habitats and restore ecological processes even after severe droughts (Majdi et al. 2020b). Thus, we consider particularly freshwater meiofauna as important players when it comes to re-establishing the energetic connectivity between terrestrial and aquatic ecosystems after major disturbances: '*meiofauna as indicator of and basis for ecological regeneration'*.

Summing up, in freshwaters, meiobenthos lives in a closer connection to the terrestrial world. This aquatic-terrestrial link is particularly tight and evident in those organisms with terrestrial adult stages, a life strategy that is very common in freshwater ecosystems, while there are only very few examples from intertidal, mangrove and saltmarsh habitats. This specific aspect underlines freshwater meiofauna as important contributors to the ecosystem complexity and interactivity of benthic habitats, whereas in marine ecosystems, the lines connecting meiobenthos with their ecosystemary neighbours, the microbial world and/or the macrobenthic compartments, often seem weaker, so that in the marine realm meiofauna is often viewed as a trophically less connected entity.

Returning to the basal question underlying this chapter "Freshwater meiofauna—a biota with different rules?" the answer, seen from various perspectives, is affirmative in many ways:

Important differences do occur when comparing biota and biotopes of freshwater meiofauna with their marine counterparts.

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Chapter 7
Hidden Players—Meiofauna Mediate Ecosystem Effects of Anthropogenic Disturbances in the Ocean

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Abstract Humans have used, and had effects on, marine ecosystems throughout history. As the human population and its economic activities increase, these effects intensify. Yet, our awareness and understanding of the long-term, pervasive effects of anthropogenic disturbances on the seafloor, and the resident meiofauna, is far from complete. This chapter summarises research on the responses of marine meiofauna to the most widespread anthropogenic disturbances, including bottom-fishing, pollution, introduction of invasive species, and climate change. Anthropogenic disturbance and natural environmental dynamics interact to cause changes in the response of meiofauna species, either in the short-term, through effects on growth and development, or in the long-term, through genetic selection. Species-specific sensitivity to disturbance can propagate to community-level responses, mediated by shifts in interspecific interactions. Meiofauna responses to anthropogenic disturbance are

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commonly nonlinear and depend on the environmental context in which the disturbance occurs, on the scales at which meiofauna responses are observed, and on the extent to which the disturbance creates novel environments that differ from those to which the resident meiofauna are adapted. Although responses of meiofauna assemblages to anthropogenic disturbance are complex, in general severe disturbance leads to dominance by opportunistic species. The widespread replacement of habitat-specific ecological specialists by broadly-adapted ecological generalists and opportunists often results in biotic and functional homogenisation of once disparate biotas. Their small size, their life history characteristics, and their phylogenetically and functionally diverse species pool, all suggest that meiofauna are resilient, and there is little evidence for the local extinction of meiofauna from anthropogenically disturbed seafloor habitats. It therefore seems likely that meiofauna have the ability to adapt, and thrive, in response to most environmental changes. New horizons for future meiofauna research pertain to the extent to which the resistance or resilience of meiofauna to anthropogenic disturbance buffers ecosystem functioning against further change.

7.1 Disturbance: A Multifaceted Phenomenon

Disturbance is recognised as an event that, regardless of origin, occurs when potentially damaging forces or influences are applied to habitat space occupied by an individual species, population, community, or ecosystem. The forces and resultant changes may harm, displace, or kill organisms, alter or remove consumable resources such as living space and food, and change, degrade, or destroy habitat structure. Prior to the 1990s, a disturbance to an ecosystem was regarded as a discrete event in time (White and Pickett 1985). Since then, the definition of disturbance has broadened, gradually including long-term pressures on ecosystems that may have no foreseeable end, such as climate change (Shukla et al. 2019). Here we follow the notion that disturbance is external to the system of interest and that its effects are manifested as perturbations and stress (Table 7.1).

Disturbance events and how they are distributed through time vary in distinct, quantifiable aspects (Table 7.2). Environmental factors may affect spatial and temporal variability in disturbance regimes.

Table 7.1 Terms used to describe the effects of disturbance (adapted from Rykiel 1985; Parker et al. 1999)

Disturbance consequence	Description
Perturbation	Effect of a disturbance event, altering the physical structure or arrangement of biotic and abiotic elements of ecosystems; may be either temporary or permanent, and can be defined in terms of a change in structure or functions
Stress	Effect of a disturbance event on a biological entity (individual, population, community, food web, etc.), which does not cause mortality; can be defined in terms of a decrease in fitness (i.e. survival and/or reproduction)

Table 7.2 Terms used to describe disturbance regimes (adapted from White and Pickett 1985; Turner 2000; Keane 2017; Ratajczak et al. 2018)

Disturbance characteristic	Description
Source, type	Origin of the disturbance
Intensity	The strength or physical energy of the disturbance per area per time period; characteristic of the disturbance rather than the ecological consequences
Duration	Time period during which the disturbance continues
Frequency	How often the disturbance occurs in a period of time
Return time	Time between disturbances (i.e. the inverse of frequency)
Magnitude	Spatial extent of the disturbance (i.e. area disturbed); can be expressed as area per event, area per time period, or percentage of study area per time period
Timing	Occurrence of disturbance relative to season and/or life cycle of the biological entity in question
Severity	Consequence of the disturbance for the receiving abiotic and biotic environment; is closely related to intensity because more intense disturbances are generally more severe
Variability	Spatial and temporal variability of the characteristics above
Regime	Spatial and temporal patterns of the disturbance over a long period of time; a disturbance regime is characterised by multiple factors including frequency, return time, intensity, and severity

Disturbance responses are often framed within the context of ecological resilience, i.e. the ability of a population, assemblage, or ecosystem affected by disturbance to reorganise and renew itself. Resistance to, and recovery from, disturbance are two important components of resilience (Table 7.3).

Responses of individuals to disturbance include changes in their physiology and/or behaviour that may enhance or reduce rates of survival/mortality and/or recruitment, altering population structure and/or density. Changes in the performance of individuals, either in the short-term through detrimental effects on growth and development, or in the long-term through genetic selection, are possible. Species-specific sensitivities to disturbance propagate through population dynamics to community-level responses, mediated by shifts in interspecific interactions (Supp and Ernest 2014; Fig. 7.1).

Species-level responses to disturbance are most easily interpreted when they are linked to single, clearly defined factors that respond to disturbance, particularly physical or chemical features of their environment. Community-level responses to disturbance are complex as they integrate the responses of numerous populations (Fig. 7.1). However, community responses provide valuable insights into the biological magnitudes of disturbance-induced changes. Inevitably, because of the number of species present, it becomes increasingly difficult to establish well-defined and well-understood causal relationships between disturbance and the composition of entire communities.

Table 7.3 Terms used to describe disturbance responses (adapted from Arnoldi et al. 2018; Falk et al. 2019)

Disturbance response	Description
Resistance	The ability of individuals or their assemblages to tolerate, avoid, or persist in environmental or biological alterations; also referred to as persistence; characterised by low mortality rate
Recovery	Re-establishment of the pre-disturbance population following mortality of the original individuals through recruitment and/or colonisation
Reorganisation	As the intensity, frequency, or magnitude of disturbance increases, both resistance to and recovery from disturbance can be exceeded, and the ecosystem reorganises into an alternative state; alternative states may be transient or permanent
Resilience	Ability to recover following disturbance; this is a key emergent property of individuals, populations, and communities, and recognises that some degree of ecosystem change may reflect processes of adaptation to altered environmental conditions; change is not necessarily an indicator of ecosystem failure

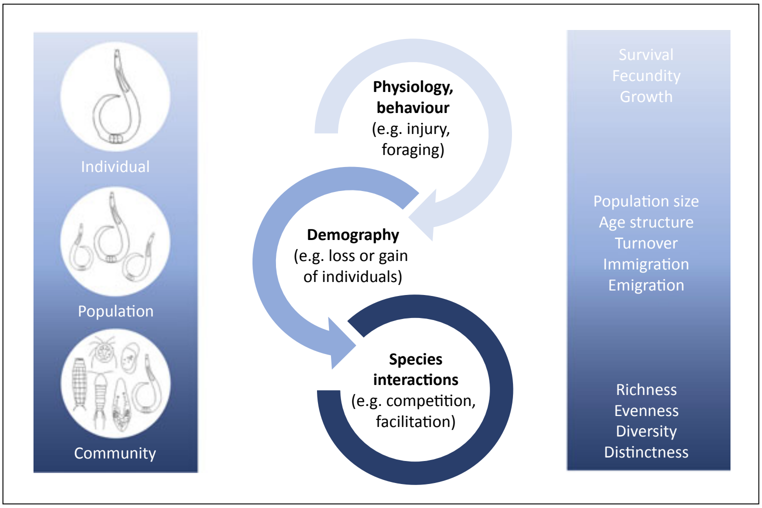

Fig. 7.1 Responses of organisms to disturbance are the result of sequential mechanisms that operate at progressively higher levels of biological organisation (adapted from Falk et al. 2019). See text for details

7.1.1 Under Pressure: Anthropogenic Disturbances in Marine Ecosystems

Disturbance ecology is becoming one of the more valuable lenses through which ecosystem consequences of a rapidly changing world are interpreted. Research on disturbance effects has largely focused on large-sized, visible organisms but most animal life on Earth is small. Over 90% of known species are smaller than a human fingernail (Naskrecki 2005). This 'small life' is dominated by invertebrates with recent estimates placing their proportion as high as 95%, against 5% comprising vertebrate species, and it is mostly aquatic, rather than terrestrial. Aquatic environments cover over 70% of the Earth's surface and are overwhelmingly marine (Charette and Smith 2010). These global overviews are useful, but for a deeper understanding we need to know whether there are differences in threats between different aquatic habitats, and whether similar species are affected by these threats in different ways.

Anthropogenic activities cause many different types of disturbance in all ocean basins (United Nations 2017; Vitousek et al. 1997; Geist and Hawkins 2016). The relative importance of these disturbances varies depending on ecosystem type, species vulnerabilities and spatial context, ranging from global (e.g. overexploitation of populations, introduction of invasive non-native species, climate change), through regional (e.g. non-point-source pollution) to local scales (e.g. point-source pollution) (Box 7.1).

Box 7.1. Major anthropogenic disturbances in the marine ecosystem (adapted from WWF 2020)

Fishing and harvesting

The unsustainable removal of certain species and size classes directly alters the composition and diversity of target and non-target species. These alterations can be amplified by species interactions, which mediate indirect effects through changes in trophic relationships, habitat, etc.

Pollution

Pollution can lead to direct effects by making the environment unsuitable for species and their populations (e.g. oil spills) and/or indirectly by affecting food availability, reproductive performance, etc.

Introduction of invasive species

Direct effects of invasive species include predation of native species and competition for space, food, and other resources. This can result in the fragmentation, destruction, alteration, or complete replacement of native habitats which in turn, can lead to further cascading indirect effects on more species and ecosystem processes.

Climate change

Increases in global ocean temperatures have been linked to decreased ocean productivity, altered food web dynamics, reduced abundances of habitat-forming species and shifting species distributions. In addition, polar regions are experiencing rapid changes in sea ice duration, iceberg disturbance and melt water run-off.

7.1.2 *The Small Majority: Adding Meiofauna to the Bigger Picture*

Here we leverage the knowledge gained in disturbance ecology in a broader context by focusing on the largest ecosystem on Earth by area (i.e. the seafloor), inhabited by meiofauna, some of the most abundant small-sized invertebrates, and investigate how meiofauna mediate ecosystem effects of anthropogenic disturbances.

Marine sediments on continental shelves (above 200 m) and slopes (200–2000 m) occupy approximately 16% of the ocean area, yet they deliver over 80% of global organic matter mineralisation (Middelburg et al. 1997). Metazoan meiofauna inhabiting benthic ecosystems worldwide are the most abundant and phyletically diverse metazoans on Earth (Warwick 1993; Giere 2009). The great abundance and species diversity of meiofauna suggest a high degree of specificity in their choice of the environment (Table 7.4). This, together with their generally short generation times, low mobility and often direct benthic development, results in a wide range of specific and rapid responses to short-term fluctuations of, and longer-term trends in, local environmental conditions (Schratzberger et al. 2000a; Fleeger and Carman 2011). Most meiofauna live in spaces and channels between sediment particles and are, therefore, susceptible to changes in seafloor physico-chemical composition (e.g. texture, bed forms, oxygenation, etc.), biological properties (e.g. biofilms on sediment particles, content of organic matter), and contaminants (Coull and Chandler 1992). The entire life cycle of many meiofauna species can be completed in a matter of weeks (Warwick and Gee 1984), resulting in a much higher production-to-biomass ratio of meiofauna compared with macrofauna. Thus, despite their negligible biomass, meiofauna can make an important contribution to overall benthic productivity (Schratzberger and Ingels 2018).

Meiofauna are relatively easy to sample in large numbers and thus ideal for studies focusing on species richness (alpha-diversity), species turnover (beta-diversity) and comparisons of community similarity in space and time (Table 7.4). However, understanding of meiofauna diversity remains incomplete. Many meiofauna species remain undescribed owing to the lack of taxonomic study, or remain undiscovered due to chronic under-sampling of seafloor habitats and unknown numbers of co-occurring cryptic species (see Chap. 5).

Although functional attributes of meiofauna (such as feeding type, life history, life strategy, growth rates) remain poorly understood, evidence suggests that meiofauna play key roles in the functioning of benthic ecosystems. Meiofauna activities (e.g. movement, ingestion and defecation of food particles, excretion of metabolic wastes), and their stimulating effect on microbiota, modify many physical, chemical and biological sediment properties and processes (Schratzberger and Ingels 2018). These modifications, directly and indirectly, positively and negatively, affect various ecosystem services including sediment stabilisation, biochemical cycling, waste removal and food web dynamics, across spatial and temporal scales (see Chaps. 2 and 5; Schratzberger and Ingels 2018). Meiofauna can mediate ecosystem processes

Table 7.4 Advantages and disadvantages associated with the use of meiofauna in marine disturbance studies (adapted from Schratzberger et al. 2000a)

Advantages	Disadvantages
Small size	
Can be maintained in relatively small volumes of sediment; intensive repeated sampling is possible with minor disruption to the sampling site because the sample size required is small; follow-up studies in the laboratory are possible under controlled and repeatable conditions	Taxonomic problems increase with smaller body size, whereas ecological knowledge decreases; preparation for identification can be time-consuming; a high-power microscope is required for species identification; small-scale spatial variability may be high
Ubiquitous distribution	
Occur in many environments that provide a source of organic carbon, under all climatic conditions, and in habitats that vary from pristine to degraded	Species, population, and community responses to environmental change are not well-documented
High abundance and diversity	
A generally large number of individuals and species give a high intrinsic information value to each sample, and ensure statistical validity of the data; often high species diversity suggests a high degree of specificity in the choice of the environment	High abundance and diversity, together with lack of taxonomic expertise, make the analysis of meiofauna community structure difficult, time-consuming, and labour-intensive; many groups need specialised methods that are rarely employed
Short generation times	
Most species have short life cycles (from days to months) so that changes in community structure can be observed in short-term studies	Population density is affected by a variety of abiotic and biotic factors so that densities may fluctuate over small spatial scales
Direct benthic development, sessile habitat	
Holobenthic lifestyle, general lack of pelagic larvae, and direct contact of many species with the interstitial water make them sensitive to changes in local conditions	Separating meiofauna from the sediment matrix requires a carefully controlled laboratory protocol and the life cycle for most species is unknown (including possibility of producing resting stages that are virtually unaffected by most environmental conditions)

in sediments in the absence of macrofauna, thereby increasing the resilience of those benthic ecosystem processes that are essential for the continued delivery of ecosystem services desired by society. This is of growing importance, since benthic ecosystems are under increasing anthropogenic pressure (Box 7.1).

With the aim of stimulating future research on disturbances in a changing world, here we review the scientific literature to identify frontiers of current knowledge of meiofauna responses to, and their recovery from, the most prominent and widespread anthropogenic disturbances in the sea. We address the following questions:

(i) **How do various types of anthropogenic disturbance affect meiofauna and their habitats?**

We focus on changes to (a) the quality, quantity, complexity, and heterogeneity of the physico-chemical environment, and (b) the fitness, behaviour, composition and distribution of species, their populations and their communities. We attempt to establish how, and to what extent, responses of individuals propagate through species' populations and communities. We include shifts in inter- and intra-specific interactions, recognising that, in general, these cannot be observed directly. Therefore, we infer interactions based on co-occurrence patterns and synchronous population dynamics. The emerging correlative relationships are interpreted to capture biological similarities, functional redundancy or dissimilarities/antagonisms through competition or predation.

(ii) **How do the component processes of meiofauna resistance to, recovery from, and reorganisation following anthropogenic disturbance affect marine ecosystems?**

Our underlying premise is that species, populations, communities, and ecosystems will be best prepared to cope with new or variable conditions induced by disturbance if their altered environment is within the range of variability to which they are adapted. This assumption, however, is being tested and challenged as environmental elements (e.g. atmospheric CO_2 concentrations, biogeochemical cycles, etc.) are moving outside their known historical ranges.

By virtue of their quantitative dominance in marine sediments and robust bodies, nematodes and harpacticoid copepods are the most frequently studied components of the meiofauna. Consequently, the great majority of meiofauna articles published in the peer-reviewed scientific literature to date deal with these taxa, which adds inevitable taxonomic bias to this chapter. However, although the ecological knowledge is scarcer, several other meiofauna taxa can provide useful insights into meiofauna responses to various anthropogenic disturbances (Mirto and Danovaro 2004; Fraschetti et al. 2006).

The disturbance-specific sections that follow (see Sects. 7.2–7.5) are based on large numbers of published studies, conducted in a variety of habitats and locations. Inevitably, study designs and methodologies differ widely among studies, as do the intensities, frequencies and spatial and temporal scales of the disturbances investigated (see Sect. 7.6). We have reviewed many of these studies to illustrate and summarise the range of effects observed, rather than attempting to provide a complete list.

Placing meiofauna responses to anthropogenic disturbances in the wider context of benthic ecosystems emphasises current uncertainties regarding observable versus assumed, direct versus indirect, and single versus interactive consequences of anthropogenic disturbances. This allows us to reflect on our current knowledge about meiofauna, and to identify new horizons for future meiofauna research, which we put forward in the concluding section of this chapter (see Sect. 7.7).

7.2 Fishing for Answers: Response of Meiofauna to Bottom-fishing

General aspects: Bottom-contact fisheries are one of the most widespread anthropogenic sources of direct disturbance to the seafloor and associated biota globally. Halpern et al. (2008) estimated that three-quarters of the world's continental shelf area (approximately 20 million km^2) has been trawled or dredged at least once, and it is the first pass of the gear that is most damaging for the seafloor (Cook et al. 2013) and its biota (Duplisea et al. 2002; Couce et al. 2020). Fishing effort is highly aggregated, reflecting seafloor characteristics and the relative availability of the target species (Table 7.5). For example, while large parts of the European continental shelf are fished at an intensity of less than once in every two years, localised areas may be fished over ten times per year (Eigaard et al. 2017). A wide range of fishing gears and technologies has evolved, allowing fishers to trawl habitats ranging from muddy or sandy sediments, via coarse and mixed sediments to gravel and other hard substrata (Rijnsdorp et al. 2008). Declines of target species in shallow coastal waters have led to expanding fisheries at increasing depths offshore (Roberts 2002; Thurstan et al. 2010).

Different fishing gears are designed to have different levels of seafloor contact or penetration depending on the target species and substrate type, and these factors influence the ecological consequences (Hiddink et al. 2017). Bottom-fishing can cause direct mortality of biota as well as physical changes in sediment composition, topographic complexity, and biogeochemistry (Table 7.6), which in turn can affect seafloor communities (Sciberras et al. 2018). Eigaard et al. (2017) estimated a bottom-fishing intensity of 0.1 year^{-1} to be a critical intensity beyond which bottom-fishing may compromise the integrity of the seafloor and the associated benthic community.

Species-level effects: The small size of meiofauna implies that they are resuspended during bottom-fishing and that their response is mediated primarily via fishing-induced modifications to the seafloor (Table 7.6). Studies have quantified the effects of bottom-fishing on meiofauna using small-scale Before-After-Control-Impact (BACI) experiments or large-scale longer-term studies of areas subject to differing levels of fishing. The response of meiofauna generally depends on the type of fishing gear, the intensity and frequency of fishing and its magnitude relative to other natural disturbances, and the habitat. Given the variety of study designs and habitats investigated, inconsistent effects of fishing practices on total meiofauna densities are

Table 7.5 Disturbance characteristics of bottom-fishing (Halpern et al. 2008; Piet and Quirijns 2009; SPRFMO 2012; Pusceddu et al. 2014; Eigaard et al. 2017; Amoroso et al. 2018)

Disturbance characteristic	Bottom-fishing
Source	Harvesting of aquatic wild animals for commercial purposes using a variety of mobile gears (e.g. trawls, dredges) likely to come in contact with the seafloor or benthic organisms
Attributes (see Table 7.2)	75% of the world's continental shelf area has been trawled or dredged at least once
	Continuous sediment resuspension induced by deep-sea trawling can remove approximately 60–100% of the organic carbon from the trawled area per day
	Fishing effort is highly aggregated; heterogeneous distribution with intensive bottom-fishing in localised areas and lower intensity fishing elsewhere
	Bottom-fishing footprint varies regionally from less than 10% of seafloor area in Australian and New Zealand waters to more than 50% in some European seas
	Distribution of fishing effort is relatively stable over time, especially when determined by morphological features of the seafloor

Table 7.6 Effects of bottom-fishing on the quality, quantity, complexity, and heterogeneity of meiofauna habitat (Jennings and Kaiser 1998; Pilskaln et al. 1998; Cabral et al. 2002; Kaiser et al. 2002, 2006; de Madron et al. 2005; Puig et al. 2012; Pusceddu et al. 2014; Oberle et al. 2016)

Habitat property	Bottom-fishing
Physical	Resuspension of surface sediment and winnowing of fines leads to changes in sediment sorting and grain size; resuspended sediment settles in less frequently trawled areas when trawl tracks are filled in
Chemical	Release of previously buried organic matter and increased organic loading of sediments (discarded bycatch) lead to modified biogeochemical cycles, including shifts towards microbial-dominated, anaerobic food webs
Heterogeneity	'Flattening' of the seafloor reduces the small-scale heterogeneity and topography created by epifauna and flora, large burrowing infauna and demersal fish, and alters hydrodynamic and biogeochemical processes

perhaps unsurprising (Table 7.7; Pranovi et al. 2000; Schratzberger and Jennings 2002; Schratzberger et al. 2002a; Lampadariou et al. 2005; Hinz et al. 2008; Liu et al. 2011; Pusceddu et al. 2014; Ramalho et al. 2020). While short-term, smaller-scale field experiments quantify the immediate effects of bottom-fishing on meiofauna communities, larger-scale surveys at real fishing grounds enable examination of the prolonged effects and their manifestation over many generations. Although each method is not without its own biases, coupling the results from analyses at multiple scales provides insights into the response of meiofauna species, populations, and their assemblages to bottom-fishing (see Sect. 7.6).

The effects of a single passage of a trawl on meiofauna taxa are relatively limited (Alves et al. 2003; Pranovi et al. 2000, 2004), and the presence of nematodes of different developmental stages in experimentally trawled areas suggests a lack of acute effects on reproduction and growth of many species (Schratzberger et al. 2002a). Cumulative effects of repeated hauls, however, result in long-term changes in meiofauna communities. Bottom-fishing influences the number of species, genera, and taxa, affecting physiological, morphological, and behavioural adaptations, and population growth rates, which are reflected in relative reproductive successes, or failures, in fished areas (Table 7.7). Across habitats, nematode diversity decreases with increasing fishing intensity and frequency (Hinz et al. 2008; Schratzberger et al. 2009; Pusceddu et al. 2014; Rosli et al. 2016). The loss of diversity primarily reflects decreased species richness (Schratzberger and Jennings 2002) and/or increased dominance of opportunistic species and genera (Table 7.7).

There has been comparatively little effort to examine how traits other than population growth rates or size make some meiofauna species more vulnerable to bottom-fishing than others. Generally overlooked is the likelihood that variation in physiological traits could make some species more susceptible. Slow-moving nematode species, generally with low respiration rates, are particularly sensitive to experimental physical disturbance (Schratzberger and Warwick 1998a). However, there are currently no investigations of the direct relationships between physiological traits of meiofauna species persisting in fished sediments and trawling intensities. Fished sediments appear to be colonised by meiofauna of larger sizes (individual biomass approximately 60% higher, on average; Table 7.7) than those in unfished sediments at the same depth.

Several studies infer physiological, morphological, and behavioural adaptations of meiofauna to habitat modifications resulting from the release of previously buried organic matter and/or the presence of dead and decomposing animal tissue in fished sediments. The persistence of meiofauna is pertinent to their ability to use the surplus of organic matter either directly or via increased primary production, and to tolerate low levels of oxygen (Tables 7.7 and 7.16). Increased organic loading of the sediment can lead to a shift towards microbial-dominated, anaerobic food chains, causing the proliferation of those meiofauna species that are able to exploit microbial food sources (Hinz et al. 2008) and survive in, or escape from, oxygen-poor sediments (Franco et al. 2008).

Effects on food webs and ecosystems: Results from a modelling study by van de Wolfshaar et al. (2020) indicated that ecological interactions in the benthic food web are important determinants of the effects of bottom-fishing on benthos, and that these indirect feedback effects can, in some cases, even reverse the direct effects of fishing. This can lead to notable increases in abundance of some functional groups. Duplisea et al. (2002) predicted that the largest size classes, with low specific growth rates, would be adversely affected even by relatively low levels of fishing activity.

Table 7.7 Effects of bottom-fishing (including physical disturbance of the seafloor) on the fitness, behaviour, composition, and distribution of meiofauna species, populations, and communities

	Changes in sediment resuspension and granulometry	Changes in organic loading of sediments and food webs	Changes in the heterogeneity and topography of the seafloor
Individual/Species			
Survival	Slow-moving species with generally low respiration rate, fecundity and growth rates are particularly sensitive to experimental physical disturbance (Schratzberger and Warwick 1998a)	Oxygen-tolerant nematode species that are able to use surplus of organic matter (arising from mortality and decomposition of non-target species either directly or via increased primary production) survive and/or increase in oxygen-poor sediments (Ólafsson 1992; Franco et al. 2008; Hinz et al. 2008; Liu et al. 2011; Ingels et al. 2014) Survival rates of harpacticoid copepods are lower than those of nematodes but their recolonisation rates are higher following experimentally induced short-term anoxia in brackish sediments (Guerrini et al. 1998)	
Growth	Large, mature nematode species are successful active migrators and most efficient in exploiting resources in altered sediments (Schratzberger et al. 2004) Trawled coastal sediments are colonised by small-sized nematodes (Lampadariou et al. 2005) whereas deep-sea sediments are colonised by nematodes of larger size than those in untrawled sediments at the same depth (Pusceddu et al. 2014) Modelling reveals a decline of larger size classes, with low specific growth rates, at relatively low levels of trawling while productive smaller meiofauna with short generation times remain relatively unaffected by trawling disturbance (Duplisea et al. 2002)		

(continued)

Table 7.7 (continued)

	Changes in sediment resuspension and granulometry	Changes in organic loading of sediments and food webs	Changes in the heterogeneity and topography of the seafloor
Fecundity	Little evidence exists of direct mortality of meiofauna; nematodes of different developmental stages are present in experimentally fished areas, suggesting minor effects on reproduction and growth of many species (Schratzberger et al. 2002a); nematode assemblages in trawled deep-sea sediments contain a significantly larger proportion of opportunistic species with low maturity index (MI; Pusceddu et al. 2014)		
		Nematode species with rapid dispersal, high reproductive rates, and short generation times are likely to be among early colonists of organically enriched sediments (Ólafsson 1992)	
Behaviour/Species interaction		Surface-dwelling, microalgae-feeding nematode species sensitive to oxygen-poor conditions migrate downwards and opportunistic deposit/bacteria feeders able to withstand altered sediment conditions migrate upwards (Franco et al. 2008)	Mesocosm studies report cascading effects of trawling-induced reduction or removal of large bioturbators on nematode density and community structure; biogeochemical heterogeneity generated by bioturbators benefits many nematode species but a few opportunistic nematode species can proliferate in the absence of bioturbators and increase overall abundance (Ingels et al. 2014). Field investigations imply weak relationships between meiofauna and larger organisms (Austen et al. 2003)

(continued)

Table 7.7 (continued)

	Changes in sediment resuspension and granulometry	Changes in organic loading of sediments and food webs	Changes in the heterogeneity and topography of the seafloor
Population			
Recruitment/Immigration/ Emigration	Nematodes are capable of migrating laterally and vertically into and surviving in up to 10 cm of deposited native and non-native sediment in microcosms (Schratzberger et al. 2000a; Schratzberger et al. 2000b); active immigration of nematodes with high reproductive output and/or high competitive ability can affect the recovery from small-scale physical disturbance (Schratzberger et al. 2004)	Non-selective deposit-feeding and epistrate-feeding nematodes proliferate in organically enriched microcosms (Schratzberger and Warwick 1998b) Decaying fish in sandy sediment attract certain nematode species (Gerlach 1977); meiofauna species are selectively recruited to patches of some species of algae but not to others (Lee et al. 1977)	
Community			
Abundance/Biomass	Fishing-induced changes to the seafloor increase (Liu et al. 2011; Pranovi et al. 2000), decrease (Hinz et al. 2008; Schratzberger and Jennings 2002; Pusceddu et al. 2014), or cause minor change (Lampadariou et al. 2005; Schratzberger et al. 2002a; Ramalho et al. 2020) in total meiofauna abundance Meiofauna biomass changes little in shelf seas (Schratzberger et al. 2002a; Hinz et al. 2008) but declines in the deep sea (Pusceddu et al. 2014) Chronic fishing effects are more pronounced than acute effects (Alves et al. 2003; Pranovi et al. 2000; Pranovi et al. 2004)	Abundance of harpacticoid copepod species in sediments containing dead and decomposing animal tissue is low (Ólafsson 1992)	Total meiofauna abundance decreases with loss of burrowing macrofauna and biogenic structures (Austen and Widdicombe 1998; Tita et al. 2000; Norling and Kautsky 2007; Cerrano et al. 2010; Pillay and Branch 2011; Citadin et al. 2016; Ataide et al. 2014); effects on biomass are generally weaker (Bongiorni et al. 2010)

(continued)

Table 7.7 (continued)

	Changes in sediment resuspension and granulometry	Changes in organic loading of sediments and food webs	Changes in the heterogeneity and topography of the seafloor
Structure/Diversity	Diversity and richness of nematode assemblages and meiofauna are generally lowest in most heavily trawled areas; effects on deep-sea meiofauna are more pronounced than effects on shallow-water meiofauna (Schratzberger and Jennings 2002; Hinz et al. 2008; Pusceddu et al. 2014; Rosli et al. 2016) Taxon evenness declines in response to one-off experimental trawling (Pranovi et al. 2000), effects of repeated trawling on evenness of nematode assemblages are weak (Schratzberger and Jennings 2002) Diversity of nematode assemblages decreases with increasing fishing intensity through increased dominance of opportunistic genera (Pusceddu et al. 2014; Schratzberger et al. 2009) Effects of bottom-trawling on taxonomic distinctness and trophic diversity of nematode genera are generally weak (Schratzberger et al. 2009)		
	Nematode species diversity is highest at intermediate frequencies of experimental physical disturbance of muddy sediments (Schratzberger and Warwick 1998a)	Diversity and evenness of nematode assemblages increase, and dominance declines in sediments containing dead and decomposing animal tissue (Ólafsson 1992)	The presence of bioturbators in mesocosms consistently decreases the abundance of few numerically dominant nematode species and increases evenness, whereas species diversity remains unaltered (Ingels et al. 2014) Species richness declines in the absence of the generally facilitating effect of burrowing macrofauna (Pinto et al. 2006; Braeckman et al. 2011) and corals in the mesophotic zone (Cerrano et al. 2010) and the deep sea (Bongiorni et al. 2010); the spatio-temporal extent of such facilitative effects is currently unclear (Kuhnert et al. 2010) Taxonomic and functional diversity, unique species and communities decrease in structurally homogeneous sediments (Van Gaever et al. 2009; Gingold et al. 2010; Schratzberger and Larcombe 2014; Bianchelli et al. 2016; Zeppilli et al. 2015; Gallucci et al. 2020)

Conversely, the smaller meiofauna, that is very productive and has short generation times, is relatively unaffected by fishing disturbance. There is growing empirical evidence indicating that the predicted changes in meiofauna size spectra are consistent with those that actually occur in fishing grounds, especially in shallow water where repeated intense bottom-fishing tends to select for meiofaunal nematode communities dominated by small-sized colonists that combine high fecundity, short generation times, and continuous asynchronous breeding with a feeding position near the sediment surface (Schratzberger and Jennings 2002; Lampadariou et al. 2005). The benefits of such a survival strategy at high levels of fishing disturbance are clear: continuous dispersal and recolonisation of fished areas are possible. Dominant nematode species in fished deep-sea sediments, for example, differ little from those in shallower sediments in their life history characteristics. However, their mean individual biomass is higher than that of nematodes in unfished sediments, suggesting that the disturbance exerted by bottom-fishing more easily resuspends smaller individuals (Pusceddu et al. 2014). The observed shift towards nematode dominance may relate to their tolerance to decreased oxygen in the deeper sediment layers in highly fished areas resulting from dead and decomposing animals (Table 7.7; Ólafsson 1992; Franco et al. 2008).

The removal of sublittoral epifaunal turfs, biogenic reefs, and burrowing macrofauna is one of the first and most conspicuous effects of bottom-fishing (Table 7.6). Reduction and removal of ecosystem engineers can alter resources for meiofauna, including the quantity and quality of food sources, thereby favouring those species equipped to exploit new trophic conditions. Ingels et al. (2014), for example, used experimental mesocosms to investigate how the effects of reduction and removal of large bioturbators cascade through nematode communities. The biogeochemical heterogeneity generated by bioturbators benefits many meiofauna species. The presence of bioturbators consistently leads to abundance declines of a few numerically dominant nematode species. Fewer, more opportunistic species proliferate in the absence of bioturbators when predation risk and/or competition for food are reduced, thereby affecting nematode density and community structure as part of a trophic cascade of indirect effects. Similarly, in the deep sea where the destructive action of bottom-fishing on cold-water corals alters meiofauna and nematode assemblages, the presence of corals has a facilitating effect on nematode assemblages (Cerrano et al. 2010). Habitat heterogeneity/complexity, mediated by improved quantity and quality of organic matter, and provision of a wide variety of microhabitats and niches for many nematode species, is crucial to preserve meiofaunal biodiversity (Bongiorni et al. 2010). While the abundance of meiofauna is mostly correlated with the quantity of sediment organic matter, species richness of the nematode assemblages is primarily related to the quality of organic matter. Weak effects of bottom-fishing frequency on the trophic diversity of nematode genera suggest that trophic redundancy of meiofauna communities is maintained in fished sediments where ecosystem engineers are absent (Schratzberger et al. 2009). It is therefore possible that these nematode assemblages are functionally resilient to further increases in fishing-induced disturbance.

Can meiofauna sustain chronic fishing effects? Bottom-fishing is so pervasive that it is now effectively impossible to find control systems to investigate effects of bottom-fishing on natural communities and their recovery trajectories (Jackson 2001). Most shelf seas around the world have entered a fished state (sensu Jennings and Kaiser 1998), so that even controlled (i.e. experimental) manipulation of fishing effort may no longer lead to clear responses in meiofauna diversity and community structure. While meiofauna recolonisation of small experimental areas may be a result of active vertical and horizontal immigration (Schratzberger et al. 2000b, 2004), this form of recovery is likely to be negligible in larger and repeatedly fished areas (Schratzberger and Jennings 2002). The persistence of meiofauna in fished sediments worldwide is maintained by their presence in infrequently fished areas and habitats unsuitable for fishing, both of which can act as sources of recruitment via physical transport. Recovery from fishing-induced disturbance is habitat-dependent. Meiofauna in structurally complex habitats (e.g. bioturbated sediment, biogenic reefs) and those that are relatively undisturbed by natural perturbations (e.g. deep-water mud substrata) are generally more adversely affected by bottom-fishing than meiofauna inhabiting unconsolidated sediments in shallow coastal waters. Shallow-water meiofauna are frequently subjected to natural physical disturbance of varying intensity and frequency, and the characteristic species are adapted to the rigours of bottom-fishing. Their response to fishing-induced disturbance is weaker, their changes in abundance, diversity, and biomass small. Competition for resources is a less important structuring force of meiofauna populations in habitats where natural disturbances are frequent and intense. Biological interactions are more likely to be such a force in sheltered, deeper, muddy sediments, and here a decline in species richness with increasing fishing frequency is more apparent (Table 7.7).

Total benthic community biomass and production generally decline with increased fishing frequency and sustained fishing activity, and megafauna are more likely to suffer adverse effects than the smaller macro- and meiofauna (Bergman and van Santbrink 2000; Hiddink et al. 2006; Queirós et al. 2006). A large initial decline in the community production-to-biomass ratio observed in modelling studies (Duplisea et al. 2002), followed by a gradual increase, is consistent with small, fast-growing (meio)fauna with low biomass contributing relatively more to community production as fishing frequency increases. Because respiration rates are inversely related to body size, meiofauna make a disproportionately greater contribution to total benthic community metabolism, and hence to organic matter mineralisation compared to larger-sized animals. Where benthic communities are dominated by small-sized meiofauna, as is the case in deep-sea sediments, meiofauna respiration can represent up to 10% of total benthic metabolism (Soetaert et al. 2009; Leduc et al. 2016).

The generally weak relationship between meiofauna respiration and fishing intensity in deep-sea sediments suggests that biomass is more strongly affected by bottom-fishing than respiration is, because larger organisms account for a substantial proportion of total community biomass, yet make a relatively small contribution to community respiration. Due to the comparatively low respiration rate of large organisms, a fishing-induced shift in favour of smaller (meiofauna) organisms may not, therefore, necessarily result in substantial changes in respiration (Leduc et al. 2016;

Ramalho et al. 2020). Despite their small size and fast life cycles, meiofauna are affected by intensive bottom-fishing, in particular on muddy, deep fishing grounds (Table 7.7). However, the effects of fishing on meiofauna assemblages in shelf seas (e.g. Schratzberger and Jennings 2002) are much more subtle than those on larger macrofauna, certainly in the central North Sea (Bergman and van Santbrink 2000; Jennings et al. 2001; Piet et al. 2001). Given the high rates of recruitment and growth in meiofauna, they would, therefore, be expected to contribute a disproportionally high proportion of benthic biomass, production, and metabolism in heavily fished areas. This, however, would not fully compensate for the loss in production by larger macrofauna, so further reduction in secondary production in chronically fished areas is highly likely (Schratzberger and Somerfield 2020).

7.3 Cohabiting with Harmful Substances: Response of Meiofauna to Pollution

General aspects: Sources, types, and levels of pollution in the marine environment are increasing worldwide (Borja et al. 2011). The range and potential effects of contaminants entering the ocean are vast. Novel contaminants and classes of contaminants, such as nanoparticles, androgens, antiobiotics, and fire-retardants, are continually being added. Although some contaminants may become prevalent, it is likely that many remain at levels too low to induce widespread toxic effects. Most pollution effects, therefore, are relatively localised, centred around sources of contamination such as estuaries, outfalls, and industrial infrastructure. Some newly recognised contaminants such as micro-plastics are becoming ubiquitous and their effects are being studied (Hägerbäumer et al. 2019), although their potential effects on meiofauna have received little attention to date (Gusmão et al. 2016). Here we focus on three main classes of marine pollution (Table 7.8):

- *Nutrients and organic material* released in organic or inorganic form.
- *Persistent pollutants* including halogenated hydrocarbons or organic compounds (e.g. Dichlorodiphenyltrichloroethane DDT, polychlorinated biphenyls PCBs), metals (e.g. iron, manganese, lead, cadmium, zinc, mercury), and metalloids (e.g. arsenic, selenium).
- *Petroleum products and polycyclic aromatic hydrocarbons (PAHs).*

The concentration of pollutants alone does not always reflect their toxicity to the biota. Bioavailability and toxicity of pollutants are affected by their partitioning between the sediment, pore water, and overlying water and this can depend on the sediment organic carbon content (Table 7.9; Di Toro et al. 1991). Some chemicals, for example, may not be bioavailable when bound to organic carbon (Liu et al. 2004; Losi et al. 2013). Furthermore, the bioavailability of heavy metals in sediments depends on environmental factors (e.g. pH, redox potential, salinity; Davies et al. 1991) and biologically mediated processes (e.g. bioturbation, bioaccumulation, trophic transfer, biodegradation, biodeposition; Schratzberger et al. 2000c).

Table 7.8 Disturbance characteristics of pollution (Sandulli and De Nicola Giudici 1991; Danovaro 2003; Borja et al. 2011; Balsamo et al. 2012; Montagna et al. 2002; Gallucci et al. 2015; Gentry et al. 2020)

Disturbance characteristic	Pollution
Source	Introduction of harmful materials into the sea; cause adverse effects on the abiotic and biotic environment; may enter via point sources (e.g. sewage outfall) or non-point sources (e.g. urban run-off); sometimes concentrated in 'hot spots' but are often diffuse
Attributes (see Table 7.2)	***Nutrients*** originate from run-off (approximately 50% sewage, 50% from land use), also aquaculture, and airborne nitrogen oxides; can cause algal blooms; algal decomposition depletes water of oxygen, and releases toxins; enrichment occurs when input of organic matter exceeds an ecosystem's capacity to process it ***Persistent contaminants*** (polychlorinated biphenyls PCBs, metals, Dichlorodiphenyltrichloroethane DDT, etc.) result from industrial and wastewater discharge, pesticides from land use, etc.; poison marine life, especially near major cities or industry; fat-soluble toxins bio-accumulate and bio-magnify in marine food webs ***Oil*** enters the marine environment from natural seepage (43%), transportation (12%), diffuse sources (38%), and offshore oil-drilling (3%); oil seep fauna are adapted to the presence of small oil inputs; oil spills can be large; studies around oil and gas infrastructure are often confounded with an artificial reef effect

Table 7.9 Effects of pollution on the quality, quantity, complexity, and heterogeneity of meiofauna habitat (Di Toro et al. 1991; Sandulli and De Nicola Giudici 1991; Coull and Chandler 1992; La Rosa et al. 2001; Liu et al. 2004, 2015; Dalto et al. 2006; Beyrem et al. 2007; Netto and Valgas 2010; Losi et al. 2013; Rochman et al. 2019; Gambi et al. 2020)

Habitat property	Pollution
Physical	Particulate pollutants alter the physical properties of sediments; pollutants including micro-plastics can change the porosity and heat-transferring capacity of sediments
Chemical	Organic wastes modify the quantity and biochemical composition of sediment organic matter; plastic debris accumulates organic chemicals and trace metals from the surrounding environment; bioaccumulation of metals by algae and seagrasses is a potentially important pathway of contaminant exposure to grazing organisms
Heterogeneity	Changes in sediment texture and transformation of substrate into a flocculent anoxic environment in organically enriched sediments can reduce microhabitat heterogeneity; tensioactive compounds, crude oil, and paraffines reduce habitat heterogeneity in soft sediments and can limit the colonisation of hard bottoms by erect species, thereby reducing physical complexity of the substrate

Studies of the effects of pollution on meiofauna have a long history (Coull and Chandler 1992). Meiofauna has been used in experiments to examine the effects of pollutants (Hägerbäumer et al. 2015), although the majority of studies are spatial field studies comparing sites with differing levels of pollution. Many such studies have found correlations between pollutants and changes in the abundance, diversity and composition of meiofauna (Table 7.10), so that changes in meiofauna communities are often proposed as potential indicators of ecological status. However, although these studies often attribute meiofauna changes to pollution, the relationships are generally confounded by the inherent spatial and temporal variability of the environment. More targeted approaches for impact assessment, such as Before-After-Control-Impact (BACI) studies, are often not applicable for meiofauna because baseline data, necessary to assess the type and severity of ecological effects (Underwood 1991), are missing. For marine meiofauna, direct studies on pollution effects are scarce, and quantitative data is often lacking. Hence, in most cases, links between changes in meiofauna and pollution have to be inferred from work in other habitats, including terrestrial soils and freshwater sediments (e.g. Ekschmitt and Korthals 2006 and references therein). The wealth of knowledge that exists for those habitats about the physiological responses of meiofaunal taxa such as nematodes to toxic substances has yet to be incorporated into marine studies.

7.3.1 Nutrients and Organic Enrichment

Meiofauna play a crucial role in the decomposition of detritus, in nutrient cycling, and in energy flow (Schratzberger and Ingels 2018). Hence, they are good indicators of biodeposition effects (Mazzola et al. 2000; Mirto et al. 2002, 2012; Vezzulli et al. 2008; Grego et al. 2009). Effects of fish farms and sewage discharges on meiofauna, for example, depend on the culturing method (Mirto et al. 2000; Mahmoudi et al. 2008; Netto and Valgas 2010) and the volume discharged (Bertocci et al. 2019). Interstitial meiofauna are generally more vulnerable to organic enrichment than meiofauna inhabiting mud (Sandulli and De Nicola Giudici 1991; Schratzberger and Warwick 1998b; Mirto et al. 2012) due to alterations in the texture (i.e. occlusion of interstitial spaces by organic matter) and chemistry (i.e. establishment of anoxic conditions) of the substrate. Longer-term effects on meiofauna depend on their response to the accumulation of by-products from bacterial metabolism (i.e. ammonia and hydrogen sulphide) rather than oxygen depletion per se. Nematodes in particular possess numerous behavioural and/or physiological adaptations to prevail in hypoxic or intermittently anoxic conditions (Warwick and Gee 1984; Nicholas et al. 1987; Somerfield et al. 1995; Armenteros et al. 2010; Boufahja et al. 2016; Sapir 2021; Table 7.10; also see Table 7.16 for hypoxia and Chaps. 8 and 11).

Effects on assemblages and their interactions: It is mostly the structure of meiofauna assemblages that is altered by organic enrichment. Changes in total abundance, biomass, diversity, and evenness generally remain weak or inconsistent (Table 7.10).

Table 7.10 Effects of pollution on the fitness, behaviour, composition, and distribution of meiofauna species, populations, and communities

	Nutrients and organic enrichment	Persistent chemical pollutants	Petroleum hydrocarbons
Individual/Species			
Survival	Increased mortality of sulphide-sensitive species, as well as taxa that have a limited ability to move and eventually escape from organically enriched sediments (Warwick and Gee 1984; Nicholas et al. 1987; Schratzberger and Warwick 1998b; Mirto et al. 2002) Survival of slow-moving nematode species, tolerant of low-oxygen concentrations, and with detoxification mechanisms such as the presence of intracellular inclusions of insoluble metal sulphide depositions (e.g. *Sabatieria wieseri*, *Terschellingia longicaudata;* Armenteros et al. 2010) By-products from bacterial metabolism (i.e. ammonia and hydrogen sulphide) are more deleterious for meiofauna survival than organic enrichment or oxygen limitation per se (Schratzberger and Warwick 1998b; Vezzulli et al. 2008; Semprucci et al. 2015)	Survival is generally inversely related to the concentration of contaminants; mixture of contaminants may have synergistic or antagonistic effects on mortality rate (Coull and Chandler 1992; Beyrem et al. 2007) Some species develop different tolerance mechanisms to surve in highly contaminated sediments (Montagna and Li 1997) High mortality of nematodes (approximately 50% decline in total abundance) in response to biocides Irgarol and Diuron (Gallucci et al. 2015)	Survival of harpacticoid *Longipedia americana* nauplii is reduced within 100 m of oil platforms compared to greater distance (Carr et al. 1996) A benthic ecotype vulnerability–resilience matrix classifies nematodes as having high resilience and low vulnerability and harpacticoid copepods as having low resilience and high vulnerability (Schwing et al. 2020) At a total polycyclic aromatic hydrocarbon (PAH) concentration of 4.0 mg/kg (ppm), the probability of effects on meiofauna is less than 20% and more than 80% at concentrations greater than 25 mg/kg (Balthis et al. 2017) The oligochaete *Marionina subterranean* is resistant to up to 1000 ppm crude oil, but toxicity increases in mixtures with dispersants (Giere 1980)

(continued)

Table 7.10 (continued)

	Nutrients and organic enrichment	Persistent chemical pollutants	Petroleum hydrocarbons
Growth	Nematode species with a short life cycle (egg to adult) and rapid embryonic development prevail in organically enriched sediments (Schratzberger and Warwick 1998b; Singh and Ingole 2011)	Metals reduce moulting success of nematodes (Coull and Chandler 1992)	Mean nematode body length is similar in 800 m methane seep and comparison sites (Sommer et al. 2007) Production efficiency of deposit-feeding nematodes is approximately 30%, but decreases to < 15% within 50–100 m from oil platforms (Montagna and Li 1997)
Fecundity	Females of opportunistic nematode species *Daptonema normandicum*, collected near a sewage outlet, can produce their first batch of eggs (approximately 8–10 eggs) after 23 days in the laboratory, and the complete embryonic development in approximately 72 h is consistent with the short life cycle and rapid embryonic development of r-strategists (Singh and Ingole 2011)	Contaminant mixtures have a greater effect on the development rate of harpacticoid copepods than single contaminants, while the development of nematode species seems to be less affected, especially in the first two juvenile stages (D'Agostino and Finney 1974; Lira et al. 2011), although overall juvenile nematodes are more sensitive to contamination than adults (Schratzberger et al. 2002b; Lira et al. 2011)	Number of eggs produced by the polychaete *Dinophilus gyrociliatus* is reduced twofold within 100 m of oil platforms compared to beyond (Carr et al. 1996) Reproduction of the oligochaete *Lumbricillus lineatus* is resistant to oil plus dispersant over the short-term, but reduced over longer periods (Giere and Hauschildt 1979) The harpacticoid copepod *Nitocra lacustris* exposed to phenanthrene has 26% less adult survival, 33% less surviving offspring per female, and 54% less haplotype diversity relative to control cultures (Street et al. 1998)

(continued)

Table 7.10 (continued)

	Nutrients and organic enrichment	Persistent chemical pollutants	Petroleum hydrocarbons
Behaviour/ Species interaction	Feeding peaks are influenced by functional responses to food availability (Buffan-Dubau and Carman 2000) Nematodes that are able to utilise a wide range of trophic resources increase below fish farms (i.e. non-selective deposit and epistrate feeders; Mirto et al. 2002) Trophic diversity of nematodes is altered in polluted areas (Warwick and Clarke 1998)	Food availability and heavy metal concentrations play important roles in influencing nematode trophic structure (Gambi et al. 2020) Although deposit-feeding nematode species are generally less affected by contamination, their production efficiency may be reduced (Boufahja and Semprucci 2015) Epigrowth-feeding nematodes are relatively unaffected by tributyltin (TBT) contamination, probably because they feed more selectively by scraping food off surfaces, piercing it and sucking out the content, thus reducing the probability of ingesting whole TBT-paint particles (Schratzberger et al. 2002b) Scavenging nematodes including oncholaimids, and epistrate-feeding cyatholaimids and chromadorids dominate in contaminated sediments (Schratzberger et al. 2002b; Boufahja and Semprucci 2015; Semprucci et al. 2015; Gambi et al. 2020)	No difference in nematode feeding rates on bacteria or microalgae are detected between an 18 m oil seep and comparison sites (Montagna et al. 1995) Nematode biological traits and polycyclic aromatic hydrocarbon (PAH) concentrations are correlated in sediments near and far from a refinery in a bay in Brazil; traits associated with an opportunistic life strategy are most common in sediments with the highest polycyclic aromatic hydrocarbon (PAH) concentrations (Egres et al. 2019)
Population			
Recruitment/ Immigration/ Emigration	Many harpacticoid copepod species settle as adults around/under fish farms, and hence the copepodites-to-adults ratio is higher and nearly constant in control areas (Guerrini et al. 1998; Dal Zotto et al. 2016) Epibenthic nematode species migrate temporarily in search for more oxygenated substrates (Sandulli and De Nicola Giudici 1991; Dal Zotto et al. 2016)	Some opportunistic nematode species migrate vertically to occupy available niches rapidly; *Oncholaimus*, *Sabatieria* and *Daptonema* species can also withstand starvation, so their activity is less impaired in contaminated sediments (Boufahja and Semprucci 2015) Epibenthic or semipelagic nematode species stay at the surface of contaminated sediments to avoid harm (Lampadariou et al. 1997)	Populations of five harpacticoid species (*Cletodes* sp., *Enhydrosoma pericoense*, *Normanella brevispina*, *Robertsonia* sp., *Tachidiella* sp.) less than 50 m from oil platforms have 33% less haplotype diversity than populations over 3 km from platforms at 100 m depth (Street and Montagna 1996; Lee et al. 2003) Populations of the harpacticoid copepod *Bathycletopsyllus* sp. at 1100 m depth have less haplotype diversity near (500 m) oil platforms than far (10–20 km) from platforms (Gregg et al. 2010)

(continued)

Table 7.10 (continued)

	Nutrients and organic enrichment	Persistent chemical pollutants	Petroleum hydrocarbons
Community			
Abundance/ Biomass	Total meiofauna abundance may either increase or decrease in response to organic enrichment, while negligible variations in total meiofauna biomass are generally documented (e.g. La Rosa et al. 2001; Mirto et al. 2010; Dal Zotto et al. 2016)	Meiofauna abundance generally decreases as contaminant concentrations increase (Coull and Chandler 1992), whereas biomass remains largely unaltered (Gambi et al. 2020)	Nematode abundance in oil seeps is either increased or slightly decreased, the proportion of harpacticoid copepods and their numbers are reduced (Montagna et al. 1989; Sommer et al. 2007) Harpacticoid copepod abundance is more reduced 100 m from oil platforms than nematode abundance, proportion of nematodes increases closer to the platform (Montagna and Harper 1996), following Deepwater Horizon (Schwing et al. 2020; Reuscher et al. 2020), and after an oil spill near a well head (Montagna et al. 2013) due to the increase of opportunistic nematode species (Baguley et al. 2015) Synthetic-based drilling mud discharge reduces meiofauna density by approximately 15% (Netto et al. 2009) The presence of marine snow in laboratory microcosms leads to increased copepod abundance regardless of oil concentration, nematode abundance declines at higher oil concentrations regardless of the presence of marine snow (Rohal et al. 2020) Total biomass in oil seeps is either increased (Montagna et al. 1989) or decreased (Sommer et al. 2007), nematode biomass increases nearly twofold (Montagna et al. 1989); nematode biomass decreases fourfold within 100 m of oil platforms (Montagna and Harper 1996)

(continued)

Table 7.10 (continued)

	Nutrients and organic enrichment	Persistent chemical pollutants	Petroleum hydrocarbons
Structure/ Diversity	Following organic enrichment, the number of species (Grego et al. 2009; Mirto et al. 2010; Netto and Valgas 2010) and diversity (Mirto et al. 2002; Austen and Widdicombe 2006; Mahmoudi et al. 2008; Netto and Valgas 2010) generally decrease; evenness decreases in few cases but remains largely unaltered (Vezzulli et al. 2008; Mirto et al. 2002; Mirto et al. 2010) Nematode diversity and richness in organically enriched sand decline more notably than in organically enriched mud (Schratzberger and Warwick 1998b) An 'opportunistic cage assemblage' and 'control assemblage' are detectable up to 20–25 m away from fish farms (Vezzulli et al. 2008; Grego et al. 2009; Dal Zotto et al. 2016) Organically enriched sediments worldwide are characterised by the occurrence of the same tolerant nematode genera (*Sabateria* spp., *Terschellingia* spp.; Somerfield et al. 2003; Armenteros et al. 2010; Semprucci et al. 2015) The maturity index (MI) of nematode communities under fish farms is reduced whereas there is no change in response to sewage discharge (Mirto et al. 2002 Fraschetti et al. 2006; Armenteros et al. 2010; Netto and Valgas 2010) Nematode species in organically enriched areas are more closely related and functionally similar to each other than those found in unimpacted areas (Clarke and Warwick 1998; Warwick and Clarke 1998)	A general reduction of the number of species is detectable as levels of contamination increase (Coull and Chandler 1992; Balsamo et al. 2012; Gambi et al. 2020); diversity of endobenthic nematodes is closely related to the level of contaminant concentrations in sediments (Somerfield et al. 1994; Austen and Somerfield 1997; Armenteros et al. 2010) Evenness of meiofauna communities is variable in contaminated microcosms (Beyrem et al. 2007; Beyrem et al. 2011) Pollution-tolerant nematode species and genera proliferate in contaminated sediments (e.g. *Ptycholaimellus*, *Sabatieria*, *Molgolaimus*, *Axonolaimus*, *Oncholaimus*), whereas pollution-sensitive ones decline (e.g. *Tripyloides, Desmodora*) or disappear (e.g. *Richtersia, Desmoscolex*; Somerfield et al. 1994, 1995; Balsamo et al. 2012; Gambi et al. 2020) Contaminant effects may be masked or reduced in organically enriched sediments; species from polluted sites are less sensitive to additional pollutants than those from unpolluted sites (Armenteros et al. 2010) Generally, the maturity index (MI) of nematode communities is inversely related to contaminant concentrations although the occurrence of pollution-resistant nematode species in contaminated sediments may maintain relatively high values of MI in some cases (Losi et al. 2013; Gambi et al. 2020) Nematode communities in metal-contaminated sediments are more tolerant to metals than communities in less contaminated sediment (Millward and Grant 1995)	Meiofauna diversity and evenness decrease within 145 km of an oil spill, five months after the spill occurred (Baguley et al. 2015); evenness is negatively correlated with Deepwater Horizon (DWH) contaminants, as is species richness and diversity (Reuscher et al. 2020); diversity remains low post-DWH (Schwing et al. 2020) Nematode taxonomic distinctness and diversity are low in a 20 m oil seep with five families comprising 75% of the total abundance (Gobin et al. 2012) Nematode and harpacticoid copepod diversity is reduced by 10–16% within 100 m of oil platforms (Montagna and Harper 1996); assemblages up to 1000 m distance from platforms have a more homogeneous spatial distribution, increased trophic diversity of deposit feeders, and higher numbers of opportunistic species (Fraschetti et al. 2016) Synthetic-based drilling mud discharge reduces nematode diversity by approximately 30% (Netto et al. 2009)

Especially distinct in nematode assemblages, these structural changes result from the replacement of sensitive species by cosmopolitan and tolerant species (Mirto et al. 2002; Vezzulli et al. 2008; Netto and Valgas 2010). As nematodes and kinorhynchs exhibited species-specific responses to organic enrichment arising from aquaculture, they have been proposed as indicators for fish farm disturbance (Vezzulli et al. 2008; Grego et al. 2009; Dal Zotto et al. 2016; Netto and Valgas 2010). Changes in nematode community structure are accompanied by dominance shifts in trophic guilds: from detritivores, as microbial biomass increases due to decomposition processes, to epistrate feeders tolerant of increasing concentrations of toxic by-products from the breakdown of organic matter (Semprucci et al. 2015). Oncholaimid nematodes have been found to establish dense aggregations in organically enriched sediments (Lorenzen et al. 1987; Moore and Bett 1989; Somerfield et al. 1995; Moore and Somerfield 1997; Warwick and Robinson 2000). The highly localised distribution of these aggregations within enrichment hotspots, which sometimes lack other fauna, may partly be a result of their ability to take up dissolved organic matter directly from the environment (Chia and Warwick 1969; Lopez et al. 1979). Under less polluted conditions, the attributes that contribute to the dominance of oncholaimids in organically enriched sediments may comprise a physiological cost rather than a competitive advantage because of the trade-offs between the ability to exploit resources in environments that few other organisms can tolerate, and the metabolic costs associated with that exploitation.

7.3.2 *Persistent Chemical Pollutants*

Many persistent pollutants, incorporated into sediments by absorption and ion exchange, reach concentrations much higher than those in the water column (Binning and Baird 2001; Dalto et al. 2006; Liu et al. 2015). Particulates are taken up by meiofauna but biological and ecological processes involved in the ingestion and accumulation of pollutants are poorly understood (Balsamo et al. 2012). Uptake occurs via the body surface (through cuticular mucous secretions in nematodes or adsorption to the exoskeleton in harpacticoid copepods) or via the digestive tract following ingestion with food. Nematodes can sense metals and avoid them by ceasing to feed (Ekschmitt and Korthals 2006). Once in the body, pollutants may be eliminated or stored in cells or tissues depending on the organism's metabolism (Howell 1982, 1983; van Damme et al. 1984; Millward 1996; Schratzberger et al. 2002b). Meiofauna living in heavily polluted sediments generally have higher concentrations of metals (between two and eighteen times) in their tissue than meiofauna from unpolluted sediments (Coull and Chandler 1992). Acute and sublethal metal toxicity depends on the type of metal, temperature, salinity, and food (Liu et al. 2015). Many of the physiological responses of nematodes to toxic substances, such as avoidance or induction of detoxification, removal or sequestration pathways are unspecific, and the development of co-tolerance, whereby organisms acquire resistance to numerous pollutants simultaneously (Ekschmitt and Korthals 2006), is probably widespread (see Sect. 7.7). In the most severe circumstances, however, pollution may cause direct mortality and lead to effects on recolonisation and recruitment dynamics.

Adaptive strategies: The effects of biocides such as tributyltin (TBT) on nematode assemblages are generally less pronounced than those of heavy metals (Austen and McEvoy 1997), and nematode responses to single contaminants differ from those to contaminant mixtures, reflecting synergistic and antagonistic effects on the species' mortalities (Beyrem et al. 2007; see Sect. 7.7 and Balsamo et al. 2012 for review). In general, meiofauna respond to persistent chemical pollutants via various adaptive pathways:

- *Adaptation to physico-chemical factors.* Estuarine assemblages are less sensitive than those from sublittoral environments of similar granulometry (Austen and McEvoy 1997; Austen and Somerfield 1997; Semprucci et al. 2014; Sahraeian et al. 2020), and mud-dwelling communities more tolerant than those inhabiting sand (Austen et al. 1994). The former is likely a result of the adaptation of estuarine meiofauna to fluctuating environmental conditions; the latter is most likely due to the binding of metals with the finer particulates, thus reducing their bioavailability (Table 7.9).
- *Physiological mechanisms of tolerance and detoxification* (Millward and Grant 1995; Gambi et al. 2020; Table 7.10). Heavy metals and TBT interfere with cellular and biochemical functions and disrupt physiological and reproductive systems. Egg production of harpacticoid copepods in TBT-contaminated sediments is reduced or ceases (van Damme et al. 1984), and the proportion of juvenile nematodes declines (Schratzberger et al. 2002b). Growth and larval development of some harpacticoid copepod species are inhibited in metal-contaminated sediments, especially when mixtures of metals are present.
- *Autecological changes leading to a prevalence of species with life styles that reduce exposure to pollutants* (van Damme et al. 1984; Somerfield et al. 1994; Lampadariou et al. 1997; Boufahja and Semprucci 2015)*, and/or life history characteristics that allow them to proliferate rapidly in polluted sediments* (Schratzberger et al. 2002b). Subsurface dwellers, such as epistrate and deposit-feeding nematodes, are likely to develop tolerance in response to an accumulation of unexploited resources because fewer macrofauna and meiofauna taxa are generally present in polluted sediments (Schratzberger et al. 2002b; Losi et al. 2013; Gambi et al. 2020). However, some exceptions occur in areas characterised by long-term contamination (Montagna and Li 1997; Gambi et al. 2020; see Sect. 7.7).
- *Synecological changes leading to the dominance of tolerant and opportunistic species.* Highest levels of contamination generally result in decreased meiofauna abundance and diversity (e.g. Millward and Grant 1995; Austen and McEvoy 1997; Austen and Somerfield 1997; Hedfi et al. 2007), despite some exceptions (e.g. Coull and Chandler 1992; Gambi et al. 2020), whereas evenness trends are more variable (Beyrem et al. 2007, 2011). The taxonomic and functional breadth of meiofauna assemblages is reduced in polluted sediments due to the progressive decline of sensitive, and proliferation of tolerant and opportunistic, species.

- *Genetic changes, associated with a genetically inherited increase in tolerance* (Table 7.10) *following exposure to contaminants.* This microevolution can buffer, partially, the effects of contamination in populations. Extremely high metal concentrations lead to the selection of locally adapted pollution-tolerant meiofauna populations. The evolution of heavy-metal resistance occurs within a few generations in some nematode species. Consequently, nematodes from metal-polluted sites are often less sensitive to contamination than those from uncontaminated sites (Howell 1982; Millward and Grant 1995; Austen and Somerfield 1997).
- *Trophic shifts*. Pollution can potentially modify the nature of intra- and interspecific interactions (Warwick and Clarke 1998), further altering community structure indirectly. Uptake of metals by meiofauna may have potential implications for the flux of contaminants from the sediment into the food web (Fichet et al. 1999). Metal (copper) and pesticide (atrazine) contamination, for example, affect diatom biomass (i.e. diet quantity) and lipid (i.e. diet quality) production, altering the energy flow to harpacticoid copepods, the diatoms' main meiofaunal grazers (Mensens et al. 2018). Importantly, contaminant-induced shifts in diatom community structure (resulting from species-specific tolerances) affect the energy flow to their copepod grazers before changes in diet quality may be detected.

7.3.3 Petroleum Hydrocarbons

Effects of oil pollution on meiofauna are complex, because hydrocarbons from both natural and anthropogenic sources are not only ubiquitous within marine ecosystems but also structurally and chemically divergent. In recent decades, oil spills from tanker accidents polluting the sea and shallow shores have been the prevailing threat to marine flora and fauna. Improving safety regulations continue to reduce this threat. However, sophisticated technologies allow oil to be drilled from open water platforms in both coastal and deep-sea environments. Hence, accidents at deep-water operations present a novel threat to sensitive deep-sea benthos. The Deepwater Horizon (DWH) well blowout in the Gulf of Mexico in 2010 led to the discharge of oil and gas under high pressure at 1500 m water depth. It involved the traditional shore-bound surface spill with the novel deep-ocean persistence of intrusions of finely dispersed oil, gas, and dispersants. The formation of marine snow, incorporation of oil, and subsequent gravitational settling to the seafloor were significant pathways for the distribution and fate of oil. Effects on deep-sea meiofauna, however, are poorly understood, due to gaps in baseline information on their communities, their functioning, and their ecotoxicological vulnerability, as well as the challenging sampling conditions. Meiofauna are strongly affected by particular organic carbon fluxes in shelf, slope, and basin habitats (Baguley et al. 2006), so that the deposition of oil in the form of marine oiled snow was particularly destructive to meiofauna communities (Montagna et al. 2020). Thus, deep-sea habitats appear to be especially vulnerable to oil spills because they are affected by deposition, and recover slowly (Montagna and Girard 2020; Rohal et al. 2020).

Effects on species and their interactions: The effects of oil spills and offshore oil and gas exploration on meiobenthos have been well-documented. General trends, ranging from individuals to populations and their communities, are summarised in Table 7.10:

- *At the species level*, concentrations of PAHs as low as 4.0 mg kg^{-1} (ppm) can be toxic to meiofauna (Balthis et al. 2017). Growth and productivity of harpacticoid copepod, polychaete, and nematode species decrease near oil platforms (Carr et al. 1996; Montagna and Li 1997), but toxicity is probably due to heavy metals from drilling because oil concentrations are generally low. The survival rate of harpacticoid copepod nauplii is reduced during oil spills (Street et al. 1998). Oil spills are often treated with dispersants. Dispersants themselves can be toxic to microbes (Montagna and Arismendez 2020) and harpacticoids (Lee et al. 2013), and may increase toxicity by making the water-soluble fraction of the oil more bioavailable (Giere and Hauschildt 1979; Giere 1980).
- *At the population level*, habitat partitioning near oil and gas infrastructure appears widespread in harpacticoid copepods in shallow (Street and Montagna 1996; Lee et al. 2003) and deeper water (Gregg et al. 2010). In both cases, genetic diversity is reduced near platforms, suggesting population subdivision (Street and Montagna 1996; Street et al. 1998). This could be due to the low dispersal potential of harpacticoid copepods because most species brood eggs that then hatch into a benthic naupliar stage.
- *At the community level*, diversity and evenness decrease near offshore platforms (Montagna and Harper 1996; Netto et al. 2009), and during oil spills (Montagna et al. 2013; Baguley et al. 2015; Reuscher et al. 2020). Nematode abundance sometimes increases during oil spills (Montagna et al. 2013), but it typically decreases around offshore platforms (Montagna and Harper 1996; Netto et al. 2009), as does biomass (Montagna and Harper 1996).
- *At the ecosystem level,* environmental persistence, bioaccumulation, and trophic transfer of PAHs in aquatic food webs are of particular interest. A relationship between trophic cascades and pollution effects was demonstrated for nematodes in diesel-contaminated laboratory sediments (Fleeger et al. 2006a). Increased nematode abundance in polluted sediments constituted a bottom-up effect stimulated by diesel-induced increases in diatom abundance. Depressed nematode abundance in the presence of a small, burying goby in oil treatments suggested that the presence of the goby decreased diatom abundance, thereby reducing the likelihood of a trophic cascade in joint diesel-goby treatments.

During oil spills, nematodes appear to have high resilience and low vulnerability, and harpacticoid copepods have low resilience and high vulnerability (Schwing et al. 2020). It is common for the abundance of harpacticoid copepods to decrease and numbers of nematodes to increase (Montagna et al. 2013). These are similar to the responses to organic enrichment (see Sect. 7.3.1), probably because oil is organic matter that is a reduced form of carbon. But oil is toxic as well, so the increase in nematodes has been referred to as the ‘enrichment versus toxicity paradox’ (Spies et al. 1988), suggesting that meiobenthic populations respond to low concentrations of oil in the same way they would respond to other organic matter.

Recovery from oil pollution: Coastal interstitial meiofauna in sandy sediments can recover within a year after an oil spill (Giere 1979). Shallow saltmarsh meiofauna can recover from oil spills within 6.5 years, depending on the recovery of the vegetated foundation species habitat and benthic microalgae (Fleeger et al. 2019). After the DWH oil spill, nematode diversity and functional traits recovered within 12 months in polluted intertidal coastal and bay sediments hit by the upwelling oil (Brannock et al. 2020). Habitat complexity is typically greater in shallower habitats than in the deep sea, so meiofauna diversity, abundance, or biomass can be greater in shallow waters, but they also recover more quickly there than in deeper environments. Faunal abundance generally recovers more quickly than diversity; the latter can remain low even after several decades (Reuscher et al. 2017; Gambi et al. 2020). Rohal et al. (2020) estimated that it could take the area impacted by the DWH spill between 50 and 100 years to recover via natural sedimentation processes that would bury the oil spread at the surface of the bottom sediment. Many studies around oil platforms point towards protracted recovery times. In addition to oil, drill cuttings and drill muds as well as heavy metals are discharged, which can all be toxic to meiofauna (Gee et al. 1992; Netto et al. 2010). Recovery in deep-sea habitats in particular may take years to decades (Montagna et al. 2002).

7.3.4 Resilience to Pollution

Recovery of polluted ecosystems is one of the primary goals of environmental legislation but there are few formerly polluted marine areas in the world with a nearly-complete recovery (Borja et al. 2010). Recovery trajectories of meiofauna are poorly known and are generally inferred by extrapolation from resistance in experimental exposures. This, however, remains challenging because ecological processes and interactions must be understood before experiments in laboratory micro- or mesocosms can be related reliably to natural conditions (Mayer-Pinto et al. 2010). Furthermore, the type and intensity of pollution, the nature of the receiving assemblage and the spatio-temporal scale at which recovery is assessed (i.e. single sites may not capture regional recovery; see Sect. 7.7), all impede inferences regarding potential resistance and resilience of meiofauna to pollution.

The drivers of meiofauna community resilience to pollution are diverse, including habitat characteristics (Bejarano and Michel 2016), the availability and composition of pollutants, biotic controls such as species-specific tolerance (see Sects. 7.3.2 and 7.7), life history characteristics and lifestyles (Sundelin and Elmgren 1991), and biotic interactions including feeding, competition, and predation. Therefore, meiofauna recovery from pollution is highly variable but can be relatively rapid, especially when associated changes in sediment granulometry are limited (La Rosa et al. 2001; Mirto et al. 2002; Netto and Valgas 2010).

What form should future pollution studies take? Given the extreme levels of pollution within sediments in many of the studies reviewed (Table 7.10), it is perhaps surprising that any meiofauna survive at all. Some heavily polluted sediments support high meiofauna densities, albeit often with reduced diversity. While physiological and community responses to pollutants have been investigated in many studies (Table 7.10), little is known about the pollution tolerance or resilience of many meiofauna taxa. Furthermore, it is currently unclear whether sediment-processing undertaken by meiofauna (and their interactions with other fauna) could explain the burial of pollutants. Some evidence suggests that biodiverse and functionally important seabed habitats act as pollutant sinks, with burrowing fauna contributing to this process via well-understood benthic-pelagic pathways. However, the contribution of meiofauna to these ecosystem-wide processes is unknown (Schratzberger and Ingels 2018). After several decades of intensive pollution studies of sublethal effects in the laboratory, progress with identifying field effects is less convincing. The balance of future effort between laboratory studies and field ecology should therefore be tipped heavily in favour of the latter.

7.4 Invaders Among Locals: Response of Meiofauna to the Introduction of Invasive Species

General aspects: Globalisation of trade and mobility has facilitated human-mediated movements of species from one region to another. Introduced species, also called non-indigenous species (NIS), are those arriving in a region beyond their native range due to direct or indirect human intervention. If a species survives, escapes, and begins reproducing without direct human intervention, it becomes established, and eventually invasive if it spreads widely and causes measurable environmental, economic, or human health effects (Table 7.11). Approximately 10–50% of introduced species become established permanently, and approximately the same proportion of these, once established, becomes invasive, depending on the species in question and the region of introduction. Invasive species have notable and long-lasting effects on regions and are now recognised as one of the major drivers of biodiversity change globally (Keller et al. 2011). Coastal estuarine and marine systems are among the most heavily invaded systems in the world (Grosholz 2002). Europe alone contains over 300 aquatic invasive species that cause ecological or economic effects (Vilà et al. 2010).

Non-indigenous and invasive species can affect native species through direct biotic interactions such as competition for food, space, and other resources, and/or predation, thereby changing flows of energy or biomass (David et al. 2017). Some non-indigenous and invasive species are ecosystem engineers, which create, remove,

Table 7.11 Disturbance characteristics of the introduction of invasive species (Vitousek et al. 1997; Reise et al. 2006; Molnar et al. 2008; Williams and Grosholz 2008; Keller et al. 2011; Corriero et al. 2015; Tricario et al. 2016)

Disturbance characteristic	Introduction of invasive species
Source	Introduced species have been introduced intentionally or accidentally outside their native range through human activities (e.g. international shipping, aquaculture) and are able to live, spread, and reproduce in the new habitat; they become invasive when causing ecological or economic harm
Attributes (see Table 7.2)	Include viruses and bacteria to fungi, plants, and animals; more than half of all non-native species are benthic invertebrates, followed by macroalgae
	At least one invasive species has been recorded in 84% of the world's 232 marine ecoregions; levels of invasion are highest in temperate regions of Europe, North America, and Australia and are increasing due to shipping, aquaculture trade, etc
	In some regions, invasions are becoming more frequent; some introduced species may quickly become invasive over large areas whereas others become widespread only after a lag of decades or more

modify, reconfigure, or redistribute habitats by altering their physical or chemical properties for native species (Katsanevakis et al. 2014). Autogenic engineers (e.g. some invertebrates, macroalgae, and seagrasses) provide and alter habitat with their physical structure, thereby offering new habitat, shelter, and food resources for native species. Allogenic engineers (e.g. some burrowing macrofauna) transform their surroundings through their activity and thus alter biogeochemical cycles and resources for native species (Reise 2002). Some (meiofaunal) species associate with the biogenic structures created by non-indigenous and invasive ecosystem engineers and can occupy the environment only when these species are present (Table 7.12).

Table 7.12 Effects of invasive species on the quality, quantity, complexity, and heterogeneity of meiofauna habitat (Crooks 2002; Hendriks et al. 2010; Haram et al. 2020)

Habitat property	Introduction of non-indigenous and invasive species
Physical	Introduction of habitat-forming species may provide protection from exposure to predators, resuspension, environmental conditions, and change the textural characteristics of the seafloor
Chemical	Changes in availability of organic matter pools derived from and/or trapped by non-indigenous species are possible; burrowing activity of invasive species transports oxygen from the surface to deeper layers and modifies biogeochemical cycles
Heterogeneity	Invasive species change the physical structure of the ecosystem itself, thereby increasing or decreasing habitat heterogeneity and altering flows of energy; invasion of seafloor can result in the generation of more microenvironments

Intra- and interspecific interactions between native and invading species comprise both negative (competitive) and positive (facilitative) components (Stachowicz 2001). These may affect the spatial distribution of meiofauna as well as their density, diversity, and species composition (Table 7.13). A common conclusion of many studies therefore is that meiofauna distributions are context-dependent. Effects vary according to the extent to which invasive species create environments that differ from those to which the resident meiofauna is adapted, the life habits of the invader and the resident meiofauna, the magnitude of invasion, and the time since invasion. Many meiofauna studies report positive relationships between the heterogeneity of the habitat and the diversity and abundance of its inhabiting meiofauna (see Ólafsson 2003 for review; macroalgae: Hicks 1980; Warwick 1977; Gee and Warwick 1994; Hull 1997; Arroyo et al. 2006; Da Rocha et al. 2006; Frame et al. 2007; seagrass: De Troch et al. 2001; Fonseca et al. 2011; polychaete tubes: Tita et al. 2000; burrowing crustaceans: Koller et al. 2006; Pillay and Branch 2011; Citadin et al. 2016). Morphological and physiological differences between native and invasive autogenic and allogenic ecosystem engineers affect patterns of meiofauna communities (Table 7.13).

Effects of algae and plant invasions: Even though differences in meiofauna diversity are often weak and inconsistent between native and non-native ecosystem engineers (Austen et al. 2003; Table 7.13), different ecosystem engineers may support distinct meiofauna assemblages (Veiga et al. 2016). This is particularly true for autogenic ecosystem engineers such as macroalgae (Somerfield and Jeal 1995, 1996). A combination of differently structured algal species results in a greater diversity of meiofauna than a monoculture creating homogenised microhabitats (Best et al. 2014; Katsanevakis et al. 2014). Invasive macroalgae including *Sargassum* pose a threat to benthic ecosystems because of their ability to reduce native algal growth and become a monoculture (Britton-Simmons 2004). Diversity in algal morphology is necessary to support a more diverse assemblage of meiofauna, which, in turn, support a more diverse group of species at higher trophic levels (Richardson and Stephens 2014).

At local scales, changes in meiofauna diversity resulting from habitat modifications induced by invasive macroalgae and seagrass species seems to be rather inconsistent (Chen et al. 2007; Gallucci et al. 2012; Pusceddu et al. 2016). However, at larger scales, diversity increases by favouring species that are absent from both vegetated and unvegetated native environments (Gallucci et al. 2012). Lower species richness of sediment-dwelling meiofauna associated with native macroalgae and seagrass is generally related to an advanced stage of ecological succession and indicative of a climax community that comprises fewer, but well-adapted, species (Mateu-Vicens et al. 2010). Higher species richness and diversity recorded from sediments associated with invasive ecosystem engineers probably result from the creation of new microhabitats with different seasonal patterns available for colonisation of opportunistic species or species characteristic of other habitats (Table 7.13).

Selective feeding by meiofauna on different food types can diminish, and in some instances eliminate, competition within a particular habitat. This, for example,

Table 7.13 Effects of invasive species on the fitness, behaviour, composition, and distribution of meiofauna species, populations, and communities

	Changes in sediment resuspension and textural characteristics of the seafloor	Changes in availability of organic pools and biogeochemical cycles	Changes in physical habitat structure and heterogeneity*
Individual/Species			
Survival	Increases in nematodes, foraminifera, and harpacticoid copepods are correlated with sand and algal turf, rather than algal biomass (Gibbons and Griffiths 1986)	Invasive algal turfs trap sediment that is otherwise absent, which provides food and habitat for turf-inhabiting meiofauna (Smith et al. 2014)	Vegetated and biogenic habitats generated by invasive species host an abundant associated meiofauna, distinct from nearby bare sediments; differences in community structure between habitats are often due to variation in relative abundance of common species (primarily small mobile generalists), suggesting that recruitment and survival of some of these generalists differ between native and invaded habitat (Gibbons and Griffiths 1986; Smith et al. 2014)
Growth	Mean body length of nematodes colonising thalassinidean shrimp burrow walls is significantly lower than in ambient sediment and the juvenile-to-adult ratio is significantly higher, indicating rapid reproduction (Koller et al. 2006)		
Fecundity	Reproductive capacity is higher in alga-dwelling harpacticoid copepod species than in interstitial species, longevity, and egg maturation rates of phytal and level-bottom species are comparable (Hicks 1977b)	Nematode species with high reproductive rates and short generation times tend to colonise lower blades of kelp that are the most heavily encrusted with epiphytes (Trotter and Webster 1984) Nematode species with low maturity index (MI) dominate in *Spartina*-invaded compared to native mangroves (Fu et al. 2017)	Sediments in native *Posidonia* meadows are characterised by flat, encrusting, long life-span foraminiferan species whereas in invasive *Caulerpa* habitat, temporarily motile, shorter life-span species tend to dominate (Mateu-Vicens et al. 2010)

(continued)

Table 7.13 (continued)

	Changes in sediment resuspension and textural characteristics of the seafloor	Changes in availability of organic pools and biogeochemical cycles	Changes in physical habitat structure and heterogeneity*
Behaviour/Species interaction		Nematode species feed actively on epibiota of kelp to which they are preferentially attracted and these preferences are not season-specific (Trotter and Webster 1984) Burrowing activity of an invasive polychaete facilitates the vertical penetration of nematode species that are able to utilise additional food sources deeper in the sediment (Urban-Malinga et al. 2013) Long and slender nematode species with a body shape that facilitates the absorption of oxygen and migration between sediment layers proliferate in anoxic sediments of invasive *Caulerpa* meadows (Gallucci et al. 2012)	Foraminifera assemblages in sediments associated with native *Caulerpa* and *Posidonia* comprise fewer well-adapted species than sediments associated with invasive *Caulerpa*; lower species richness is related to an advanced stage of ecological succession as *Posidonia* meadows are indicative of a climax community (Mateu-Vicens et al. 2010)

(continued)

Table 7.13 (continued)

	Changes in sediment resuspension and textural characteristics of the seafloor	Changes in availability of organic pools and biogeochemical cycles	Changes in physical habitat structure and heterogeneity*
Population			
Recruitment/Immigration/Emigration	Population density maxima of alga-dwelling nematode (Warwick 1977; Trotter and Webster 1984) and harpacticoid copepod (Hicks 1977a, b) species occur at different times throughout the year and relate to food availability or differing physiological responses to food and temperature which can influence reproductive activity of constituent species Meiofauna actively move into distinct habitat patches surrounding animal burrows; nematode numbers are threefold and foraminiferan numbers twofold elevated in thalassinidean shrimp burrow walls containing oxidised, highly consolidated, poorly sorted sediment enriched with silt and clay, and small particles of macrophyte debris (Koller et al. 2006) Alga-dwelling harpacticoid copepods are seasonally separated (distinct cycles of population density attain maxima at different times) and spatially segregated into those inhabiting fronds and sediments, respectively; partitioning decreases competition for available habitat resources during times of high population densities (Hicks 1977b); spatial segregation is also common for meiofauna near animal tubes and burrows (Urban-Malinga et al. 2013)		

(continued)

Table 7.13 (continued)

	Changes in sediment resuspension and textural characteristics of the seafloor	Changes in availability of organic pools and biogeochemical cycles	Changes in physical habitat structure and heterogeneity*
Community			
Abundance/Biomass	Total meiofauna abundance and biomass do not vary between native unvegetated sediments and *Caulerpa*-invaded sediments (Pusceddu et al. 2016) Abundance of harpacticoid copepods is increased on artificial structures colonised with invasive tunicates (Cordell et al. 2013)	*Caulerpa* invasion of soft sediments increases meiofauna abundance via increased microhabitat complexity (Sandulli et al. 2004)	Abundance of harpacticoid copepods, ostracods, and isopods increases in sediments colonised with non-native macroalgae (Smith et al. 2014) A generally positive relationship exists between the heterogeneity of physical and biogenic habitat and the abundance and diversity of meiofauna that they support (general overview: Ólafsson 2003; macroalgae: Hicks 1980; Warwick 1977; Gee and Warwick 1994; Hull 1997; Arroyo et al. 2006; Da Rocha et al. 2006; Frame et al. 2007; seagrasses: De Troch et al. 2001; Fonseca et al. 2011; polychaete tubes: Tita et al. 2000; burrowing crustaceans: Koller et al. 2006; Pillay and Branch 2011; Citadin et al. 2016). However, studies of meiofaunal distributions within mangrove sediments tend to highlight the importance of generalised intertidal and estuarine environmental gradients known to influence their distributions everywhere (e.g. tidal height, salinity, oxygen availability, sediment properties) rather than mangrove trees (Nagelkerken et al. 2008)

(continued)

Table 7.13 (continued)

	Changes in sediment resuspension and textural characteristics of the seafloor	Changes in availability of organic pools and biogeochemical cycles	Changes in physical habitat structure and heterogeneity*
Structure/Diversity	Changes in nematode diversity and species richness resulting from habitat modifications induced by invasive macroalgae and seagrass species are inconsistent at local scales (Chen et al. 2007; Gallucci et al. 2012; Pusceddu et al. 2016); at larger scales, invasive macroalgae promote an overall increase in nematode diversity by favouring species that are absent from both vegetated and unvegetated native environments (Gallucci et al. 2012) Sediment assemblages of Foraminifera in areas dominated by invasive *Caulerpa* are more diverse than those associated with native *Caulerpa* and *Posidonia* due to the presence of more opportunistic and generalist species (Mateu-Vicens et al. 2010); effects on nematode assemblages are negligible although compositional turnover between invaded sediments is higher than between non-invaded vegetated and unvegetated sediments, suggesting replacement of nematode species in response to *Caulerpa* invasion (Pusceddu et al. 2016) Unique genera and communities in animal burrows increase compared to ambient uncolonised sediment (Koller et al. 2006), and on different macroalgae in the rocky intertidal (Somerfield and Jeal 1995; Somerfield and Jeal 1996; Frame et al. 2007) and soft-bottom subtidal (Pusceddu et al. 2016) compared to unvegetated habitat Nematode trophic diversity is lower in *Spartina*-invaded habitat than in native seagrass meadows (Chen et al. 2007) but no difference exists between native and *Spartina*-invaded mangroves (Fu et al. 2017)		
	A non-native macroalgae facilitates meiofauna by forming a novel turf habitat in the upper intertidal zone where turfs are uncommon naturally; algal turf can increase habitat complexity, trap sediment, and maintain moisture during low tide which likely benefits meiofauna and macroalgae by providing food, habitat, or refuge from desiccation stress (Smith et al. 2014)	*Caulerpa* invasion of soft sediments decreases diversity of meiobenthic crustaceans (ostracods, amphipods, isopods, tanaids, cumaceans; Sandulli et al. 2004) and some nematode species (Gallucci et al. 2012) sensitive to hypoxia resulting from algal decay Nematode species richness and diversity are reduced in mangroves invaded by *Spartina* compared to native mangroves due to the creation of physico-chemical habitat conditions (e.g. reductions in sedimentary carbon and nitrogen content) that are unfavourable for the majority of nematodes (Fu et al. 2017)	Meiofauna abundance and class diversity (driven by increased evenness) are higher on invasive *Sargassum* than on some native macroalgae (Richardson and Stephens 2014) Diversity and richness of harpacticoid copepods are increased in sediment patches colonised by non-native macroalgae (Smith et al. 2014) No differences exist in epibiotic meiofauna taxon richness between native and invasive (*Sargassum, Asparagopsis*) macroalgae (Warwick 1977; Richardson and Stephens 2014) Invasive *Sargassum* harbours more meiofauna taxa than less structurally complex native macroalgae (Veiga et al. 2016); meiofaunal richness in polycultures of native macroalgae does not differ from that of monocultures of similar morphology, leading to strong effects of algal identity (Best et al. 2014)

* For relevant literature see also Table 7.7 (column entitled ‘Changes in the heterogeneity and topography of the seafloor’)

enables co-habitation of various harpacticoid copepod, ostracod, and nematode species in a small area, such as on algal or seagrass blades (e.g. Hicks 1977a, b; Trotter and Webster 1984; Frame et al. 2007; De Troch et al. 2001, 2008). Local effects on endobenthic meiofauna tend to be more heterogeneous, facilitating some functional groups and species, and impeding others. Varying rates and pathways of decaying invasive algae and seagrass can modify nutrient cycling in estuarine wetlands (Gallucci et al. 2012) and mangroves (Fu et al. 2017). This then leads to the proliferation of those nematode species with specific physiological, morphological, and behavioural adaptations to survive under these specific physico-chemical conditions. Macroalgal detritus can contribute to meiofauna diets (Queirós et al. 2019). However, it needs to be clarified whether the trophic ecology of meiofauna allows exploitation of fresh organic matter derived from, and/or detritus trapped by, invasive macroalgae as a primary resource (Chen et al. 2007). There is some indication that organic pools derived from an invader's biomass are not easily exploited as a primary resource by meiofauna (Pusceddu et al. 2016).

Effects of macrofauna invasions: Settlement and growth within macrofauna burrows may be challenging for meiofauna because bioturbators constantly change their burrows. Burrow-wall meiofauna counters this either by high growth rates (as illustrated by high juvenile-to-adult ratios) and/or by having high locomotive ability (as is often the case in small-sized, slender species; Table 7.13). Studies of nematodes inhabiting sediments inside and adjacent to burrows of native and invasive ecosystem engineers provide an additional perspective to trophic interactions. Microhabitats generated by thalassinidean shrimps, for example, attract nematode genera that are able to benefit from the specific nutritional and physico-chemical sediment characteristics inside the burrows (Koller et al. 2006). Likewise, the burrowing activity of the invasive polychaete *Marenzelleria* spp. was found to transport oxygen from the surface to deeper sediment layers, thereby creating new niches in the micro-oxic environment near its burrows. This, in turn, facilitates the vertical penetration of some nematode species that are able to utilise additional food sources deeper in the sediment (Urban-Malinga et al. 2013).

Ecosystem level effects: Cascading effects of invasive engineers are likely to alter processes and functions: (i) when the invader appears in a habitat where comparable structural forms are absent, thereby modifying flows and associated physico-chemical habitat conditions (e.g. plant and/or animal invasion of unvegetated or uncolonised native sediment, respectively); and/or (ii) when the invader introduces large quantities of novel food sources (e.g. detritus) that are used by a specific suite of meiofauna species (Table 7.13). For example, a decline in the trophic diversity of nematode genera in *Spartina*-invaded seagrass meadows suggests simplification of benthic food webs and compromisation of trophic redundancy in meiofauna communities (Chen et al. 2007). Despite frequently increased alpha-diversity in invaded habitats, these nematode assemblages may therefore be functionally more vulnerable to further invasions, as functional (trophic) complexity has been reduced compared to native habitat (Fridley et al. 2007).

Few studies compare the effects of invasive species on meiofauna communities comprising several species (Beisner et al. 2006). At small spatial scales, invasive species may facilitate the colonisation and settlement of new meiofauna species resulting in positive relationships between native and invasive species richness (Table 7.13). Within the same trophic level, marine invaders often have negative effects on biodiversity, but positive effects on the biodiversity of higher trophic levels (Thomsen et al. 2014). As illustrated by studies with epibiotic meiofauna, contrasting effects are manifested through community-wide antagonism (e.g. competition and consumption) versus facilitation (e.g. habitat and food provisioning) interactions (Table 7.13).

How are entire communities affected by species invasions? Currently, knowledge of meiofauna is largely based on evidence from short-term, small-scale studies (Table 7.13). The complexity of species interactions and the variety of both beneficial and adverse effects associated with an invasive species makes meiofauna-mediated ecosystem consequences difficult to establish. Hence, the simple presence of invasive species is insufficient to assess the magnitude of their effects, which will generally vary across their distributional range. Furthermore, effects vary temporally, as there is a dynamic interaction between the population of invasive species and meiofauna. Significant time-lags can occur between the introduction of a non-native species and its subsequent effects on meiofauna, or the magnitude of effects can change over time.

Are invasion effects long-lasting or even irreversible? Studies with macrofauna revealed significant and multi-annual effects after eradication of invasive *Spartina* (Reynolds et al. 2017). The absence of above-ground *Spartina* structures may, over time, affect the reproduction and survivorship of epibiotic (meio)fauna by removing important egg-laying habitat and food resources (Table 7.13). The slower breakdown of below-ground biomass consisting of roots and rhizomes would dictate the equally slow transition of the benthic food web dominated by sub-surface detritivores to a pre-invasion community. This process may be most expressed in hypoxic or anoxic sediments where anaerobic decomposition dominates, as has been shown for heavily fished sediments (Table 7.7).

The persistence of meiofauna in invaded habitats may be considered a consequence of their favourable life history characteristics that allow them to respond rapidly to the patchy microhabitats generated by invaders. Although invasion may lead to local population losses, species with niches better suited to the new environmental conditions often compensate for species lost. Compared to macrofauna, for meiofauna their small size and high turnover rates may represent valuable compensatory mechanisms that lead to the widespread replacement of habitat-specific ecological specialists by more broadly-adapted ecological generalists and opportunists.

7.5 Living in a Hot, Sour, Breathless, and Disturbed Ocean: Response of Meiofauna to Climate Change

General aspects: The atmospheric concentration of carbon dioxide (CO_2) has been rising since the 1750s to a current value of more than 400 ppm (NOAA[1]). CO_2 and other 'greenhouse' gases absorb the Sun's heat, much of which is taken up by the world's oceans. Increasing global average temperatures drive a number of related climate-change phenomena (Table 7.14; Shukla et al. 2019), including a decrease in the ability of water to hold oxygen. The extent of hypoxic zones has increased significantly over the past five decades (Rabalais et al. 2010). The ocean has also taken up about 30% of CO_2 released into the atmosphere, decreasing ocean pH, and fundamentally changing ocean carbonate chemistry in all ocean regions (Hoegh-Guldberg and Bruno 2010; Brondizio et al. 2019), particularly in cooler, high latitude waters (Sahade et al. 2015). Ocean warming, acidification, deoxygenation, and ice loss are expected to be irreversible on time scales relevant to human societies and ecosystems (Shukla et al. 2019).

Most investigations of the response of seafloor biota to climate change focus on warming, with fewer studies of the effects of changing oxygen, wave climate, precipitation (especially in coastal waters), or ocean acidification (Poloczanska et al. 2016). Meta-analyses across diverse species and ecosystems have so far linked climate change to decreased ocean productivity, altered food web dynamics, reduced abundance of thermally sensitive calcifying habitat-forming species, shifting species distributions, and a greater incidence of disease, among other effects (Table 7.15; Hoegh-Guldberg and Bruno 2010).

The detection and attribution of meiofauna responses to climate change are challenging given the idiosyncratic responses of species and populations (De Mesel et al. 2006; Table 7.16). Many responses are defined, at least in part, by interactions with other organisms and food sources, and there is uncertainty in climatic trends at regional or local scales (Hansen et al. 2016). The picture is further complicated by the interaction of climate change with natural environmental dynamics and other anthropogenic disturbances at regional and local scales (see Sects. 7.2–7.4; Halpern et al. 2008).

Effects of rising temperatures in the ocean: As ectotherms, meiofauna regulate their body temperature by exchanging heat with their surroundings. Their physiological performance, and hence distribution, depends on the range and extremes of temperatures that they experience throughout their life cycle (Giere 2009; Schratzberger and Somerfield 2020). Rising temperatures can shorten generation times and increase fecundity and food assimilation of individual nematode species up to a maximum, which is usually a few degrees below a species' upper temperature limit (Gerlach and Schrage 1971; Hopper et al. 1973; Warwick 1981; Moens and Vincx 1999, 2000). Across shallow-water temperate and tropical habitats, meiofauna abundance generally decreases with both elevated constant and fluctuating temperatures (Table 7.16;

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[1] https://www.climate.gov/news-features/understanding-climate/climate-change-atmospheric-carbon-dioxide

Table 7.14 Disturbance characteristics of climate change (Häder et al. 2015; Sahade et al. 2015; Shukla et al. 2019; Johnson and Lyman 2020; Tsai et al. 2020; Ingels et al. 2021)

Disturbance characteristic	Climate change
Source	Increasing emissions (predominantly human-caused) and subsequent atmospheric warming owing to the greenhouse gas effect is causing numerous primary and secondary effects across habitats
Attributes (see Table 7.2)	***Warming*** (0.73–2.58 °C by 2100 compared to recent past) is projected to continue gradually; average temperatures will increase across habitats ***Cooling*** is predicted for 1–3% of areas that have lost heat through changed circulation patterns ***Glacier and ice-shelf melt, calving, and collapse*** will open new areas; larger areas will be exposed to increased temperatures and sedimentation; increased and faster glacial melt in areas where ice-shelves have retreated or collapsed, and discharge will affect local ecosystems ***Decrease in sea ice extent and thickness*** is altering marine primary production in the Arctic and disrupts sympagic organisms reliant on sea ice as habitat ***Salinisation and freshening*** are variable and challenging to predict in terms of frequency, intensity, and magnitude ***Changes in UV exposure*** may affect biogeochemistry, nutrient cycles, primary production, and organism health ***Extreme events*** (physical, meteorological) are likely to increase owing to rising sea levels, iceberg scouring from increased ice shelf and glacial calving, and discharge ***Acidification*** is projected to increase; a decrease in water pH compared to recent past of between 0.065 and 0.315 is predicted by 2100 ***Changes in water circulation and currents*** will include reduced shallow-to-deep-water exchange owing to increased stratification ***Decline in net primary production*** of 4–11% is predicted by 2081–2100 relative to 2006–2015 ***Decline in dissolved oxygen*** is predicted, with 0.6–3.9% change by 2100 compared to recent past, depending on ocean circulation patterns (including upwelling) and currents

Gingold et al. 2013; Meadows et al. 2015; Mevenkamp et al. 2018; Vafeiadou et al. 2018).

Like all organisms, meiofauna are constrained to exist within physiologically prescribed thermal windows (Widdicombe and Somerfield 2012). At the edges of this thermal window their performance decreases with respect to activity, growth, reproduction, and fecundity (Table 7.16). Biological interactions (e.g. predation, competition) determine which species are able to persist at the edges of the thermal window. Changes in seawater temperature not only alter the performance of resident meiofauna species, but also change competitive interactions among them. De Meester et al. (2015) and Vafeiadou et al. (2018), for example, demonstrated that changes in fitness of nematode species in response to elevated temperature can alter their relative competitiveness, thereby affecting interactions between co-existing and

Table 7.15 Effects of climate change on the quality, quantity, complexity, and heterogeneity of meiofauna habitat (Snelgrove et al. 2018; Shukla et al. 2019)

Habitat property	Climate change
Physical	Heat absorbed by the ocean alters the physical environment (habitat degradation, current/hydrodynamic changes, etc.); changes to circulation and current patterns, ice melt, glacial discharge, scouring and calving may alter sedimentation and disturbance regimes on the seafloor; increasing frequency of extreme events, flooding and increased wave height will cause increased physical disturbance; newly-open areas, following decreasing sea ice coverage and ice shelf demise, will be subject to surface production and potentially bioturbation
Chemical	Warming alters the physico-chemical conditions on and in the seafloor, including oxygenation (i.e. reduction of oxygen availability and penetration in the sediments), carbonate chemistry (i.e. ocean acidification, pH, and alkalinity), atmospheric changes alter light intensity (i.e. UV radiation); salinity changes are likely following ice melt and increased river flow
Heterogeneity	Climate change-induced changes in faunal communities alter bioturbation regimes, thereby affecting biogeochemical processes including the redistribution of particles, organic matter, water and solutes; introduction or loss of ecosystem engineers can change 3D habitat complexity, thereby affecting hydrodynamic and biogeochemical processes; changing sea ice dynamics can increase habitat heterogeneity and aid generation of more microenvironments

competing species. Such shifts in interactions, rather than a differential temperature tolerance alone, trigger changes in abundance of temperature-tolerant and temperature-sensitive species. The latter was demonstrated by Danovaro et al. (2004) who used a decadal dataset of nematodes in the deep Eastern Mediterranean Sea to test direct effects of temperature changes in situ, but also the indirect effects that such changes have on the organic inputs to the deep sea and on related benthic trophodynamics. An abrupt decline in temperature of about 0.4 °C resulted in concomitant changes in nematode abundance and diversity, suggesting that small fluctuations in temperature can have profound consequences for meiofauna communities.

Additional alterations of the physico-chemical environment induced by climate change, such as physical disturbance, hypercapnia, hypoxia, and salinity change, alter the thermal window of meiofauna organisms and therefore affect their susceptibility to temperature changes and extreme temperature events. The interaction of two or more variables at or near tolerance limits produces complex effects on meiofauna (Table 7.16). Densities of a few opportunistic nematode species in tropical subtidal communities, for example, increased when the interactive effects of elevated temperature and reduced pH were tested in combination (Lee et al. 2017). Consistently-observed shifts in dominance patterns of meiofaunal nematode species reflect differences in species-specific physiological tolerances to changes in temperature and pH (Mevenkamp et al. 2018) and shifts in species interactions (Ingels et al. 2018).

Effects of ocean acidification: Meiofauna assemblages comprise both non-calcifying and calcifying taxa. While calcifying taxa generally exhibit more negative responses to hypercapnia than non-calcifying ones (Kroeker et al. 2010), physiological and metabolic functions common to both, such as reproduction and growth, energy production, and protein synthesis, are vulnerable to changes in pH (Vézina and Hoegh-Guldberg 2008; Widdicombe and Spicer 2008). Morphological and physiological effects of experimental hypercapnia on meiofauna have been recorded (Table 7.16). Short-term exposure of calcareous foraminifera to low-pH treatments, for example, leads to reduced survival, growth, and calcification of some species. Sublethal effects, including morphological changes to the test surface and feeding structures are likely to result in longer-term alterations of feeding efficiency and thus long-term ecological competitiveness, energy transfer within the benthic food web, and total production of calcium carbonate (McIntyre-Wressnig et al. 2013; Guaman-Guevara et al. 2019). Calcareous foraminifera in surficial sediments are particularly sensitive (Ricketts et al. 2009).

Sublethal effects of experimentally reduced pH and increased pCO_2 have also been demonstrated for intertidal harpacticoid copepods (Fitzer et al. 2012; Sarmento et al. 2017). Malformations increase whereas developmental time, fecundity, and body length decrease in response to (substantially) reduced pH, suggesting that harpacticoid copepods preferentially re-allocate resources towards maintaining reproductive output at the expense of somatic growth. Physiological effects of low pH on meiofauna remain poorly documented. Alterations to the redox system and an up-regulation of stress-related genes have been shown for harpacticoid copepods (Lee et al. 2019) with nauplii generally more sensitive than adults (Oh et al. 2017). A recent study with the nematode *Caenorhabditis elegans* provided first insights into the effects of declining pH on regulatory mechanisms (Cong et al. 2020). As pH declines, transcriptome genes responsible for cuticle synthesis and structural integrity, and xenobiotic metabolism, are upregulated, presumably to protect against toxic substances likely associated with decreasing pH in the environment. Similarly, drastic pH reductions associated with sequestering CO_2 in liquid form on the deep seafloor have pervasive, and sometimes lethal effects on meiofauna species and their populations (Carman et al. 2004; Fleeger et al. 2006b, 2010; Thistle et al. 2006).

Investigations carried out in shelf seas, in contrast, suggest that meiofauna will be relatively resistant to pH changes akin to a more gradually changing climate (Table 7.16). In situ, shifts in meiofauna community structure are more subtle, and less driven by physiological intolerance to low pH than by the indirect effects of acidification. The latter include changes to habitat type and structure, and shifts in species interactions resulting from, for example, release from predation and altered quantity and type of food available (Garrard et al. 2014; Ravaglioli et al. 2019). Ecosystem engineers mediate the response of meiofauna to ocean warming and acidification. The replacement of coral reefs by algae (Hoegh-Guldberg et al. 2007), for example, can result in the development of meiofauna communities on dead corals, akin to meiofauna colonist communities observed in response to coral loss in trawled areas (Table 7.7). Furthermore, reduced burrowing activity of sea urchins with decreasing pH affects soft-bottom nematodes by limiting the facilitating effects of bioturbation on their assemblages (Dashfield et al. 2008; Table 7.7).

Table 7.16 Effects of climate change on the fitness, behaviour, composition, and distribution of meiofauna species, populations, and communities

	Changes in average temperature and temperature regimes on the seafloor	Changes in carbonate chemistry of the seafloor (acidification and hypercapnia)	Changes in physico-chemical characteristics of the seafloor (hypoxia and salinity)	Physical disturbance of the seafloor (ice melt, glacial discharge, calving, scouring)
Individual/Species				
Survival	Foraminifera and harpacticoid copepods are more sensitive to elevated temperatures than nematodes; e.g. large benthic foraminifera hosting endosymbiotic algae experience symbiont or pigment loss (bleaching) at elevated temperatures (Talge and Hallock 2003; Schmidt et al. 2011) Some studies report the disappearance of certain taxa (harpacticoid copepods and nauplii, gastrotrichs; Mevenkamp et al. 2018), whereas other studies show limited to no effects on meiofauna taxa (especially nematodes; Ingels et al. 2018)	Short-term exposure to increased CO_2 levels may result in reduced survival, growth, and calcification of some foraminifera species (Guaman-Guevara et al. 2019; McIntyre-Wressnig et al. 2013) and reduced survival of harpacticoid copepods, especially nauplii (Oh et al. 2017) Mixed responses are reported for meiofauna to predicted pH changes, with some meiofauna taxa and species disappearing, others increasing (Mevenkamp et al. 2018) or showing limited change (Lee et al. 2017; Ingels et al. 2018)	Harpacticoid copepods are more sensitive to low-oxygen concentrations than nematodes (Hicks and Coull 1983; Josefson and Widbom 1988) Foraminifera in oxygen-depleted sediments are reduced in size and are agglutinated or have thin, porous shells to improve oxygen exchange (Levin 2003; Gooday et al. 2000) Slender harpacticoid copepod species (e.g. Cletodidae) proliferate with increasing duration of anoxia (Grego et al. 2014) Certain meiofauna species are prevalent in hypoxic conditions, while others disappear (Kolesnikova et al. 2014) Mortality of harpacticoid copepods and nematodes increases in response to hypoxia and anoxia (Grego et al. 2014)	Climate-warming-induced loss of sea ice is associated with loss of habitat for sympagic meiofauna and meiobenthos reliant on ice-algal export (Gradinger 1999; Gradinger and Bluhm 2020)

(continued)

Table 7.16 (continued)

	Changes in average temperature and temperature regimes on the seafloor	Changes in carbonate chemistry of the seafloor (acidification and hypercapnia)	Changes in physico-chemical characteristics of the seafloor (hypoxia and salinity)	Physical disturbance of the seafloor (ice melt, glacial discharge, calving, scouring)
Growth	Warming can cause shorter generation times and increased fecundity (and food assimilation) of some nematode species (Gerlach and Schrage 1971; Hopper et al. 1973; Warwick 1981; Moens and Vincx 1999; Moens and Vincx 2000)	Developmental time, fecundity, and body length of intertidal harpacticoid copepods decrease in response to reduced pH/increased pCO_2 and warming (Fitzer et al. 2012; Sarmento et al. 2017; Lee et al. 2019)	Salinity has relatively minor effects on development times, fecundity and metabolic rates of brackish-water, laboratory-reared nematode species but adverse effects on juvenile viability and pre-adult survival are likely at the extremes of the salinity range (Moens and Vincx 1999; Moens and Vincx 2000)	
Fecundity	Some nematodes shift to viviparous reproduction at low temperatures (Gerlach and Schrage 1971)	Fecundity of a harpacticoid copepod species declines in consecutive generations in response to acidification (Fitzer et al. 2012) Nauplii exposed to experimental reduction in pH are more sensitive than adult copepods (Oh et al. 2017)	Juvenile stages of harpacticoid copepods are most sensitive to anoxia; high proportion of gravid females in the surviving adult population aids recovery (Vopel et al. 1998; Grego et al. 2014)	

(continued)

Table 7.16 (continued)

	Changes in average temperature and temperature regimes on the seafloor	Changes in carbonate chemistry of the seafloor (acidification and hypercapnia)	Changes in physico-chemical characteristics of the seafloor (hypoxia and salinity)	Physical disturbance of the seafloor (ice melt, glacial discharge, calving, scouring)
Behaviour/Species interaction	Increased temperature (studied in isolation or coupled with reduced pH) can reduce the fitness and activity of some meiofauna species and functional groups, alter their relative competitiveness, and affect interactions between co-existing and competing species (Danovaro et al. 2004; De Meester et al. 2015; Ingels et al. 2018; Mevenkamp et al. 2018; Vafeiadou et al. 2018; Deldicq et al. 2021)	Nematode abundance decreases in acidified experimental treatments, probably because of reduced facilitating effects of sea urchin bioturbation, but effects on meiofauna species richness and diversity are negligible (Dashfield et al. 2008)	Short-term hypoxia has negligible effects on nematode feeding activity (Taheri et al. 2017)	

(continued)

Table 7.16 (continued)

	Changes in average temperature and temperature regimes on the seafloor	Changes in carbonate chemistry of the seafloor (acidification and hypercapnia)	Changes in physico-chemical characteristics of the seafloor (hypoxia and salinity)	Physical disturbance of the seafloor (ice melt, glacial discharge, calving, scouring)
Population				
Recruitment/Immigration/Emigration	Meiofauna biomass increases under elevated temperature regimes as a result of increased recruitment of temporary meiofauna (polychaetes; Alsterberg et al. 2011) Temperature cooling of the deep Eastern Mediterranean Sea between 1992 and 1994 leads to the proliferation of scavenging and predatory nematodes and immigration of cold-adapted Atlantic species (Danovaro et al. 2004)			The nematode genus *Microlaimus* rapidly colonises newly created habitat following glacial retreat (Pasotti et al. 2015b)

(continued)

Table 7.16 (continued)

	Changes in average temperature and temperature regimes on the seafloor	Changes in carbonate chemistry of the seafloor (acidification and hypercapnia)	Changes in physico-chemical characteristics of the seafloor (hypoxia and salinity)	Physical disturbance of the seafloor (ice melt, glacial discharge, calving, scouring)
Community				
Abundance/Biomass	Across shallow temperate and tropical habitats, meiofauna abundance declines with elevated constant and fluctuating temperature (Gingold et al. 2013; Meadows et al. 2015; Mevenkamp et al. 2018; Vafeiadou et al. 2018), including harpacticoid copepods and copepodites (warming combined with low pH), harpacticoid copepods and ostracods (top-down trophic effect; Jochum et al. 2012) Some studies report very limited or no effects of warming on meiofauna abundance or biomass (Alsterberg et al. 2011; Lee et al. 2017; Ingels et al. 2018) but nematode density and meiofaunal polychaete biomass may increase because of release from macrofauna predation and competition (Meadows et al. 2015) Cooling may cause nematode abundance to decline in the Eastern Mediterranean deep sea (Danovaro et al. 2004)	Abundance of nematodes, ostracods, turbellarians and tardigrades increases and numbers of harpacticoid nauplii decrease in low-pH experimental treatments (Sarmento et al. 2017); nematode abundance increases in response to low pH coupled with elevated temperature (Hale et al. 2011) Meiofauna and nematode abundance decline following increased pCO_2 (Meadows et al. 2015; Widdicombe et al. 2009)	Foraminifera and nematodes persist in sediments devoid of oxygen when larger macrofauna is absent (Levin 2003; Rabalais et al. 2010) In oxygen minimum zones, nematode abundance is driven by the availability of food rather than the availability of oxygen (Cook et al. 2000); nematode abundance increases in response to oxygen limitation due to the combined consequence of reduced competition for food and meiofaunal tolerance to low oxygen levels (Neira et al. 2001; Neira et al. 2018)	Meiofauna biomass and production increase in the early stages following glacier retreat when poor nutritional conditions of the sediment are coupled with high sedimentation rates owing to release from macrofaunal predation and competition (Górska and Włodarska-Kowalczuk 2017) Dense Shelf Water Cascading causes a decline in meiofauna abundance and diversity but recovery is rapid (Pusceddu et al. 2013) Climate change is predicted to cause global reduction in meiofauna biomass (Jones et al. 2014) Sea level rise, and resultant increased number of reflective beaches, may lead to reduced meiofauna abundance and biomass (Yamanaka et al. 2010) Bottom-up climate change effects of increased nutrients (linked to flooding) may enhance biomass and diversity of grazing meiofauna (Jochum et al. 2012)

(continued)

Table 7.16 (continued)

	Changes in average temperature and temperature regimes on the seafloor	Changes in carbonate chemistry of the seafloor (acidification and hypercapnia)	Changes in physico-chemical characteristics of the seafloor (hypoxia and salinity)	Physical disturbance of the seafloor (ice melt, glacial discharge, calving, scouring)
Structure/Diversity	Nematode functional diversity and species evenness may decrease, and taxonomic diversity increase, in response to cooling in the Eastern Mediterranean deep sea (Danovaro et al. 2004) Warming in temperate shallow waters may cause nematode species diversity, evenness, and maturity index (MI) to decline but trophic diversity to increase (Meadows et al. 2015); opportunistic nematode species may increase in warmer acidified tropical subtidal waters (Lee et al. 2017) Nematode species loss in response to warming is a result of selective removal of large predators and omnivores (Gingold et al. 2013)	Different harpacticoid copepod species may increase or decrease under low-pH conditions (Sarmento et al. 2017) Subtle shifts in meiofauna community structure in shelf seas are primarily driven by indirect effects of acidification including changes in habitat type and structure, release from predation, and altered quantity and type of food (Garrard et al. 2014; Ravaglioli et al. 2019) Drastic pH reduction associated with sequestering CO_2 on the deep-sea floor results in increased mortality, decreased richness, and altered behaviour of harpacticoid copepods and nematodes (Carman et al. 2004; Fleeger et al. 2006a; Fleeger et al. 2010; Thistle et al. 2006); mortality and species losses are particularly high for sensitive calcareous Foraminifera in surficial sediments close to the CO_2 injection site (Ricketts et al. 2009) Nematode species diversity and evenness are reduced after 20-week exposure to different levels of acidification; relative abundance of dominant nematode species is altered but community changes are less pronounced than for macrofauna and are weaker in mud than in sand (Widdicombe et al. 2009)	Decreased species diversity of Foraminifera is coupled with shifts in species composition (i.e. dominance of oxygen-tolerant species) under low-oxygen conditions (Gooday et al. 2000) Density and species richness of harpacticoid copepods decline from normoxic to anoxic conditions (Grego et al. 2014); diversity of harpacticoid copepod assemblages decreases in hypoxic zones (Neira et al. 2018) Diversity of nematode assemblages decreases after a hypoxic event in the Baltic (Van Colen et al. 2009)	Scouring of icebergs reduces nematode densities and diversity (Lee et al. 2001a, b) Nematode communities in recently ice-free areas are dominated by opportunistic species (Hauquier et al. 2011; Raes et al. 2010)

Effects of oxygen decrease: Short-term exposure to hypoxia causes mortality in some meiofauna and inhibits growth and reproduction. Experimental evidence has been confirmed by studies of spatial distribution in relation to natural gradients of oxygen content (Tables 7.7 and 7.16). Meiofauna is generally less affected by hypoxia and anoxia than larger macrofauna (Levin 2003); harpacticoid copepods, and in particular their larvae, are more sensitive than nematodes (Vernberg and Coull 1975; Hicks and Coull 1983; Josefson and Widbom 1988). Some specialised nematodes and oligochaetes tolerate temporary anoxia and sulphide development, and prefer the hypoxic/anoxic transition zone between the surficial and deeper sediment layers. Here, they seem to take advantage of less competition and a rich organic food supply (see Chap. 4; Giere et al. 1991; Ott et al. 1991).

Meiofauna lack respiratory organs and depend on diffusive oxygen uptake. Consequently, slender, worm-shaped species with a higher surface-to-volume ratio gather oxygen most efficiently. Despite these generalities, meiofauna responses to hypoxia appear to be species-specific (Modig and Ólafsson 1998); the diversity of nematodes decreases (Van Colen et al. 2009) and some worm-shaped copepod species tolerate hypoxia (Vopel et al. 1996; Grego et al. 2014). Sensitivity to hypoxia tends to increase with increasing temperature (Josefson and Widbom 1988). Foraminifera generally dominate meiofauna in oxygen-depleted deep-sea sediments. While morphological changes such as reduced size and more porous shells improve oxygen exchange under hypoxic conditions (Levin 2003; Gooday et al. 2000), this increases vulnerability to dissolution in more acidic waters. Under hypoxia, the oxygen required by meiofauna to support energetically costly processes such as feeding, assimilation, and digestion of food, is not met by the ambient oxygen supply. This means that meiofauna species, resistant to ocean warming and acidification, might be adversely affected by elevated temperatures and CO_2 when concurrently exposed to hypoxia (Tomasetti et al. 2018).

Secondary ecosystem effects of global warming – the loss of sea ice: Ice-shelf and glacial retreat or collapse lead to more frequent iceberg scouring, freshwater input, and higher sediment loads (Ingels et al. 2021). Although Somerfield et al. (2006) found little evidence for a specialised meiofauna in unconsolidated and nutrient-poor sediments close to a glacier front, meiofauna are members of the sympagic food web inside polar ice (see Chap. 9; Gradinger and Bluhm 2020). In areas where sea ice is persistent, a significant part of sympagic production is exported to the seafloor (Gradinger 1999; Gradinger and Bluhm 2020). Under ongoing climate change, the loss of sea ice, and hence habitat, will affect sympagic meiofauna and meiobenthos reliant on algal export.

Meiofauna rapidly colonise newly created habitat following glacier retreat (Table 7.16). In the early stages, when poor nutritional conditions of the sediment are coupled with high sedimentation rates, macrofaunal biomass is reduced and meiofaunal biomass and production are increased, in part due to release from macrofaunal predation and competition (Górska and Włodarska-Kowalczuk 2017). Gradual increases in primary production and subsequent benthic food influx increase differentiation among trophic niches for more abundant meiofauna (Murray and Pudsey

2004; Pasotti et al. 2015a). Coupled with timings of ice release, nematode communities of low density and low evenness gradually transition to denser, more diverse communities (Raes et al. 2010; Rose et al. 2015). The capacity of some nematode species to colonise new habitat depends on their tolerance of increasing glacial sediment input as glaciers melt, rather than increased iceberg disturbance (Lee et al. 2001a; Pasotti et al. 2015b; Vause et al. 2019).

Iceberg scouring can remove over 95% of the nematode assemblage and reduce diversity (Lee et al. 2001a, 2001b). Recovery from scouring can occur within weeks and without signs of community succession, suggesting the nematode fauna is relatively well-adapted to frequent disturbance. However, in recently ice-free areas, colonisation can lead to community succession with dense communities of opportunistic species occupying scoured areas, which were previously populated by low-abundance, low-diversity assemblages characteristic of sub-ice-shelf conditions (Hauquier et al. 2011; Raes et al. 2010).

Effects on food webs: Meiofauna community responses to climate change integrate direct effects on physiology and function, and indirect effects from altered intensity of ecological constraints (e.g. food availability and variability, predation, competition; Hale et al. 2011), including interactions between microbes, meiofauna, and macrofauna. It is uncertain whether predicted ocean temperature and acidification scenarios will significantly affect meiofauna mortality per se, especially in environments that are regularly exposed to high variability in environmental conditions such as intertidal systems (Table 7.16). Changes in the structural and functional composition of meiofauna communities, however, are likely. To simulate warming in a temperate subtidal bay, Jochum et al. (2012) reduced the body size of the top predator (shore crab *Carcinus maenas*) and amplified nutrient enrichment. A trophic cascade emerged whereby meiofauna-grazing gobies were released from predation by (smaller) crabs, resulting in reduced meiofauna abundance. Under nutrient enrichment, microalgae, the main food source of the dominant meiofauna, could flourish and increased meiofauna biomass and diversity (Jochum et al. 2012), suggesting that pervasive consequences of warming in marine ecosystems include trophic cascades that affect entire food webs.

Meiobenthos and the time factor in climate change: Alterations of environmental conditions by climate change occur over time scales of tens to hundreds of years, encompassing hundreds of thousands of meiofauna generations. The long-term survival of meiofauna is therefore more likely to be determined by their ability to adapt rather than the ability of individuals to persist. Heat stress causes body size reduction in marine species (Piazza et al. 2020), and large animals have higher nutritional needs compared to smaller organisms, and often more specific habitat requirements. Expansion of warmer, more acidic, oxygen-depleted waters is therefore predicted to increase the relative importance of meiofauna in biogeochemical cycling relative to larger taxa (Rabalais et al. 2010; Sweetman et al. 2017). Meiofauna from habitats regularly exposed to highly variable levels of temperature or CO_2, or to low levels of oxygen, are more likely to possess the physiological and ecological adaptations necessary to persist in climate-change-induced, variable environmental conditions than meiofauna from areas with more stable conditions, such as the polar ocean basins, deep sea, or well-oxygenated sands (Table 7.15). In some experiments, climate change effects on meiofauna populations were masked by the dominant influence of sediment granulometry (Gingold et al. 2013; Ingels et al. 2018). If, however, sediment structure begins to shift in response to a warmer, more acidic ocean, changes in meiofauna would be expected. Most effects of climate change are influenced by the meiofauna habitat. Effects of anoxia, for example, are more pronounced in vegetated habitat than in bare sediment. This is due to the increased amount of decaying organic matter, deterioration of sediment chemical composition, and reduction in habitat heterogeneity. Meiofaunal recovery proceeds more slowly in complex habitats, as heterogeneity needs to be restored to facilitate meiofauna settlement, and this can be a lengthy process (Guerrini et al. 1998; Van Colen et al. 2009).

Responses of meiofauna to climate change and associated complex ecological interactions are hard to quantify, although meiofauna appear more resilient to climate change within ranges predicted for the next century than macro- and megafauna (Table 7.16). Under climate change conditions where larger benthos becomes sparse or absent, meiofauna often thrive owing to reduced grazing and predation, and decreasing competition for food resources.

7.6 Scale Matters: Observing the Response of Meiofauna to Anthropogenic Disturbances

The presence of different types of anthropogenic disturbance across marine ecosystems, their occurrence and interconnectedness at a wide range of spatial and temporal scales, and their continuity across all levels of biological organisation are the essence of their importance (Fig. 7.2). Understanding their effects on meiofauna means understanding how man-induced environmental changes at local, regional, and global scales affect individuals, impose selective pressures upon their populations, and alter assemblages. There is, therefore, no single scale at which meiofauna responses should be studied. Rather, the challenge is to bridge across very different spatial and temporal scales, from one cubic centimetre of sediment to ecosystem, or indeed global, scales, while reconciling ecological and evolutionary temporal scales (Chave 2013), as well as the heterogeneity of those scales (Ellis and Schneider 2008).

The scales at which meiofauna responses are observed and tested are critical. Our literature review in preceding sections exemplifies the rather artificial separation into small-scale laboratory studies, addressing the disturbance responses primarily of meiofauna species and populations, and larger-scale in situ investigations addressing the responses of meiofauna communities within the wider ecosystem. This research divide is not unique to meiofauna studies but seems common in benthic ecology (Ellis and Schneider 2008).

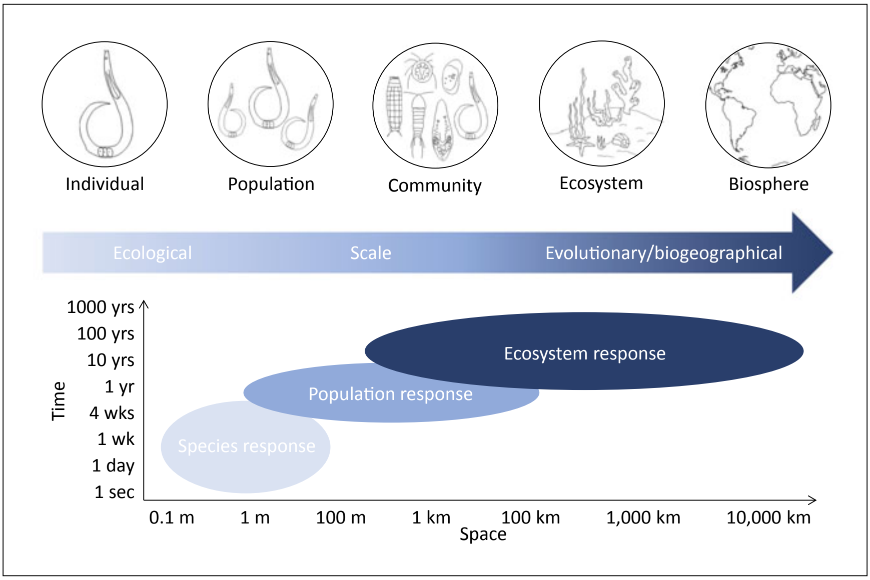

Fig. 7.2 Spatial and temporal scales at which meiofauna individuals, their populations, their communities, and entire ecosystems respond to anthropogenic disturbances (adapted from Van Goethem and Van Zandem 2019). See text for details

'Study windows' are usually constrained by practicalities and costs associated with collecting meiofauna and other relevant environmental and faunal data. Meiofauna studies reviewed here rely heavily on experimental approaches that inevitably limit the spatial and temporal scales that can be investigated. Assessing wider ecosystem effects of anthropogenic disturbances, and the roles that meiofauna play, must also consider large-scale patterns in the distributions of populations and communities (Ellis and Schneider 2008). The relevant processes underlying these are primarily large in scale and/or infrequent, and thus challenging to identify, track and investigate.

When attempting to determine the likely effects of climate change on meiofauna, concerns exist about the validity of short-term experiments simulating conditions at levels that are unrealistically lower (e.g. pH, oxygen) or higher (e.g. temperature, pCO_2) than those predicted under future climate change scenarios (Widdicombe et al. 2009). However, increasing magnitudes and frequencies of extreme events (e.g. heat waves, winter storms, hypoxic events) render short-term experimental exposures more useful compared to their application to long-term climate change scenarios or other types of chronic anthropogenic disturbance. The often high phenotypic plasticity of meiofauna species, illustrated by their ability to alter their growth rate, physiology or behaviour to better suit the environmental conditions with which they are faced (Schratzberger et al. 2009), can mask the effects of short-term (weeks to months) exposure to elevated temperature, hypercapnia, hypoxia, and salinity changes (Table 7.16). Similar concerns exist regarding testing of acute toxicity of pollutants in the laboratory versus effects of chronic exposure in situ (Table 7.10). Compensatory mechanisms in response to acute anthropogenic disturbance place an energetic burden on the individual, which could be unsustainable in the long-term. The longer-term consequences of the short-term physiological and metabolic responses of meiofauna, or indeed how these responses are manifested under (future) conditions in the field, are currently unknown and a central research challenge.

Many of the reviewed studies highlight the scale dependence of the mechanisms that underlie the resistance and resilience of meiofauna to anthropogenic disturbances. Studies assessing the resilience of meiofauna communities to experimental trawling, for example, revealed the spatial scale of disturbance and the proximity of potential recruits to be important factors that facilitate relatively rapid recovery (Table 7.7). Recovery dynamics in areas disturbed at the scale of a fishing ground differ because reproduction and growth of resistant meiofauna species are the main processes driving observed recovery if immigration from surrounding areas is limited. Initial successional stages involve meiofauna species characterised by rapid dispersal, high reproductive rates, and short generation times, later joined by better resource competitors which, over time, displace the opportunistic species in less frequently fished areas or in areas where fishing results in specific habitat characteristics that benefit particular species. A similar interplay between biotic and abiotic drivers also applies to spatial scales of observation, as revealed in meiofauna studies investigating their response to species invasions (Table 7.13). At small scales where abiotic drivers (e.g. resource availability) of community composition are relatively homogeneous, biotic interactions among meiofauna species and between meiofauna and other benthic components dominate. The significance of biotic interactions generally diminishes as survey area increases.

7.7 Invisible Allies: New Horizons for Future Meiofauna Research

Meiofauna communities are complex, as are their responses to anthropogenic disturbances. The detail matters; meiofauna responses to disturbance are largely nonlinear and context-dependent. The net effects of anthropogenic disturbances on meiofauna species, populations, and communities vary. They depend on the abiotic and biotic context in which the disturbance occurs, on the scales at which meiofauna responses are observed (see Sect. 7.6), and on the extent to which the disturbance creates novel environments that differ from those to which the resident meiofauna is adapted (Fig. 7.3; Hobbs et al. 2009).

The generally weak effects of anthropogenic disturbances on meiofauna community metrics (e.g. abundance, diversity, biomass) mask generally stronger responses of species with physiologies and life histories that either allow or prevent them from thriving under disturbed conditions (Schratzberger and Somerfield 2020; see Sects.

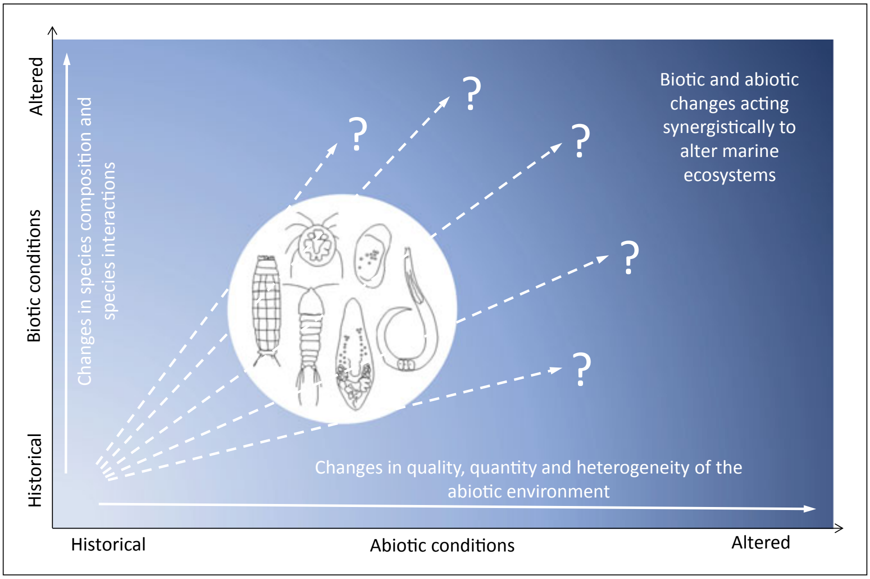

Fig. 7.3 Interactive biotic (species composition, species interactions) and abiotic (quality, quantity, complexity, and heterogeneity of the physico-chemical environment) changes lead to alteration in meiofauna communities (adapted from Hobbs et al. 2009). See text for details

7.2–7.5). Higher meiofauna abundances and numbers of species relative to macro- and megafauna generally enable meiofauna to acclimatise and adapt to environmental change more effectively.

High meiofauna functional diversity means that there may be species that can be lost from some ecosystems without substantial alteration of ecosystem function, as two species can show similarities in the way they feed, reproduce, and move within the habitat (Schratzberger et al. 2007). However, co-existing species probably do not carry out these activities in exactly the same way or at the same time, and the functional significance of these differences is likely to depend on the species and ecosystem in question (Snelgrove 1999). The morphological similarity of many meiofauna species often hides high genetic diversity (Todaro et al. 1996; Warwick and Robinson 2000; Jörger et al. 2012; Kieneke et al. 2012; Derycke et al. 2016). Cryptic species have subtly different environmental preferences and sensitivities to changes in, for example, temperature and salinity, as demonstrated by lineages of cryptic species from an intertidal flat (De Meester et al. 2015). Therefore, sympatric community shifts and local adaptation of genotypes to specific sets of environmental conditions will most likely determine longer-term changes in meiofauna taxonomic and functional diversity in the face of anthropogenic disturbances.

Meiofauna research to date illustrates how far the field has advanced and how well it has assimilated a cross-disciplinary view. It also points to new horizons for future research, pertaining to the following questions (Box 7.2):

Box 7.2. New horizons for meiofauna research

Ecosystem consequences of anthropogenic disturbances

Does the resistance and resilience of meiofauna to anthropogenic disturbances buffer against further ecosystem change?

Research priorities:

- Relationship between species richness, environmental and biotic homogenisation, and species interactions
- Drivers and consequences of changes in the strength and nature of microbe–meiofauna–macrofauna interactions
- Potential of trophic cascades involving meiofauna to alter entire ecosystem productivity and energy transfer

The importance of disturbance history

To what extent do responses of meiofauna to anthropogenic disturbances depend on the history of previous disturbance events?

Research priorities:

- Interactions between disturbance attributes and adaptive traits of dominant and rare meiofauna species
- Effects of disturbance history on the resistance and recovery of meiofauna in response to novel disturbances (including novel pollutants)
- Relative influence of ‘disturbance-induced community tolerance’ and ‘disturbance-induced community sensitivity’ on meiofauna responses to environmental change
- Genetic basis of biotic interactions and local adaptations/phenotypic plasticity of meiofauna species

Interactive effects of multiple disturbances

How do mutually reinforcing or antagonistic interactions between disturbances affect meiofauna?

Research priorities:

- Relative effects of disturbances of the same or different type applied at different frequencies and in different sequences
- Interactive effects of multiple anthropogenic disturbances on meiofauna against a background of climate shifts
- Interactive disturbance effects and tipping points beyond which the long-term viability of meiofauna populations, communities, or ecosystems are compromised

- ***Does the resilience of meiofauna to anthropogenic disturbances buffer against further ecosystem change?***

There is little evidence for the extirpation of meiofauna across anthropogenically disturbed seafloor habitats. The persistence of meiofauna is the combined consequence of their small size, life history characteristics, and their phylogenetically and functionally diverse species pools. These allow meiofauna to respond rapidly to the patchy microhabitats generated by anthropogenic disturbances, as well as to adapt to new environmental conditions on a molecular level more rapidly than larger organisms. Intermediate levels of disturbance often affect larger-sized macrofaunal predators with longer generation times and/or lower fecundity more strongly than their meiofaunal counterparts.

Although responses of meiofauna communities to anthropogenic disturbances are complex, generally severe disturbance leads to dominance of opportunistic species. The widespread replacement of habitat-specific ecological specialists by broadly-adapted ecological generalists and opportunists mixes the taxonomic and functional composition of once disparate biotas, resulting in biotic and functional homogenisation (sensu McKinney and Lockwood 1999; Schratzberger and Somerfield 2020). Some anthropogenic disturbances facilitate novel interactions among meiofauna species and between meiofauna and other benthic organisms. Meiofauna studies investigating the effects of invasive species introductions (Table 7.13), for example, reported both, increasing and declining numbers of meiofauna species. Increased species richness is often the consequence of habitat modification caused by invasive species that facilitate the colonisation of opportunistic meiofauna species or meiofauna species characteristic of other habitats. The number and breadth of these novel species interactions are therefore likely to be limited. This potentially narrows the availability of functional groups of species for renewal and reorganisation and could lead to further ecosystem change (Falk et al. 2019; WWF 2020).

While biotic homogenisation in meiofauna species composition has been recognised as a common consequence of anthropogenic disturbances, less is known about how species relationships change over space and time. There are many more interactions than species, but does biotic homogenisation of species composition lead to homogenisation of species relationships or are changes in species composition decoupled from the dynamics of species relationships? It is likely that the rate at which species interactions respond to anthropogenic disturbances differs from the rate at which species per se, and their populations and communities, respond. Modelling studies in terrestrial habitats suggest that such decoupling can be negative or positive. Consequently, the rate of species loss may be delayed or accelerated depending on the balance of interaction losses (Valiente-Banuet et al. 2015; Li et al. 2018). Understanding the relationship between species richness, biotic homogenisation, and species interactions will help to better estimate the wider ecosystem consequences of anthropogenic disturbances, and the parts meiofauna play.

Despite the proven interdependence between microbe, meiofauna, and macrofauna production (Hunter et al. 2012; Baldrighi and Manini 2015), understanding the drivers of changes in the strength and the structure of their interactions is still limited.

A mesocosm experiment designed to investigate climate-change-induced alterations in an intertidal food web, for example, showed that meiofauna does indeed mediate the effects of increased nutrient input following increased frequency of flooding and agricultural run-off through its trophic interactions with primary producers and higher-level consumers. Although opportunistic meiofauna grazers (copepods and ostracods) benefited in terms of population densities, energy transfer to higher trophic levels was hampered, thereby reducing the overall biomass of the system (Jochum et al. 2012). Future research into the potential of trophic cascades involving meiofauna to alter ecosystem productivity and energy transfer following anthropogenic disturbances would enhance our understanding of the key roles meiofauna will play in future benthic ecosystems.

- ***To what extent do responses of meiofauna to anthropogenic disturbances depend on the history of previous disturbance events?***

The seafloor is subject to natural disturbance regimes that operate across a range of temporal and spatial scales. Natural disturbances have characteristic magnitudes and frequency distributions to which local meiofauna assemblages are adapted, and from which they can recover. Anthropogenic disturbances are often of greater magnitude, higher frequency and/or longer duration. Whereas the effects of severe, acute anthropogenic disturbances are relatively straightforward to establish, it is less clear how moderate, more prolonged levels of anthropogenic disturbance affect meiofauna populations. Studying the latter is particularly important because most marine ecosystems have become mosaics of natural and anthropogenic disturbances.

Although previous sections highlight anthropogenic disturbance as an important influence on meiofauna communities, understanding how the context of previous disturbances influences the ability of communities to respond to novel disturbances is largely missing. Laboratory and in situ studies investigating the response of meiofauna from contrasting habitats to anthropogenic disturbances showed that natural disturbances including fluctuations in physico-chemical parameters (e.g. currents, salinity, temperature, etc.) play a role in the observed shift toward more disturbance-adapted meiofauna communities. The effects of anthropogenic disturbances are minimised if there is close congruence with natural disturbances. For example, shallow-water meiofauna in unconsolidated sediments is generally less adversely affected by bottom-fishing than meiofauna in either structurally complex habitats such as biogenic reefs, or habitats that are relatively undisturbed by natural perturbations such as deep-sea mud (see Sect. 7.2). Sediment movement, erosion, and deposition are natural processes to which benthic organisms are adapted (Hall 1994). Benthic infauna burrow upwards or downwards to maintain an ideal position in the sediment but the rates and magnitudes of bottom-fishing often exceed those of natural occurrences. Understanding how disturbance interacts with the adaptive traits of dominant and rare meiofauna species would provide some clarity about the broader ecosystem consequences of human-induced changes (Fig. 7.3). Differences in meiofauna resistance to, and recovery from, anthropogenic disturbances clearly reflect local disturbance history due to disturbance filtering out ill-adapted species, but where is the limit of tolerance of meiofauna to new environmental conditions and disturbance regimes? Do disturbances function as a catalyst of change?

When species sensitivities to two disturbances are positively correlated, either disturbance eliminates certain species, but leaves more species that are tolerant of the other disturbance than if species sensitivities were unrelated (Fig. 7.4). Therefore, a positive correlation between species sensitivities (i.e. positive species co-tolerance) increases resistance to one disturbance as a result of exposure to the other. Vinebrooke et al. (2004) termed this stress-induced community tolerance, following the ecotoxicological concept of pollution-induced community tolerance where communities that have been chronically exposed to pollutants are relatively less affected by exposure to new pollutants (see Sect. 7.3). Positively correlated species co-tolerances lead to antagonistic disturbance interactions and hence disturbance-induced community tolerance. Conversely, negatively correlated species co-tolerance would result in additive or synergistic disturbance effects and hence in disturbance-induced community sensitivity (Vinebrooke et al. 2004). Evidence to date suggests that previous natural and anthropogenic disturbances strongly influence how vulnerable meiofauna communities are to additional/novel disturbances (also see disturbance interactions in Box 7.2 and below), and so these should be considered when predicting how shifts in disturbance regimes will affect future (meiofauna) community composition.

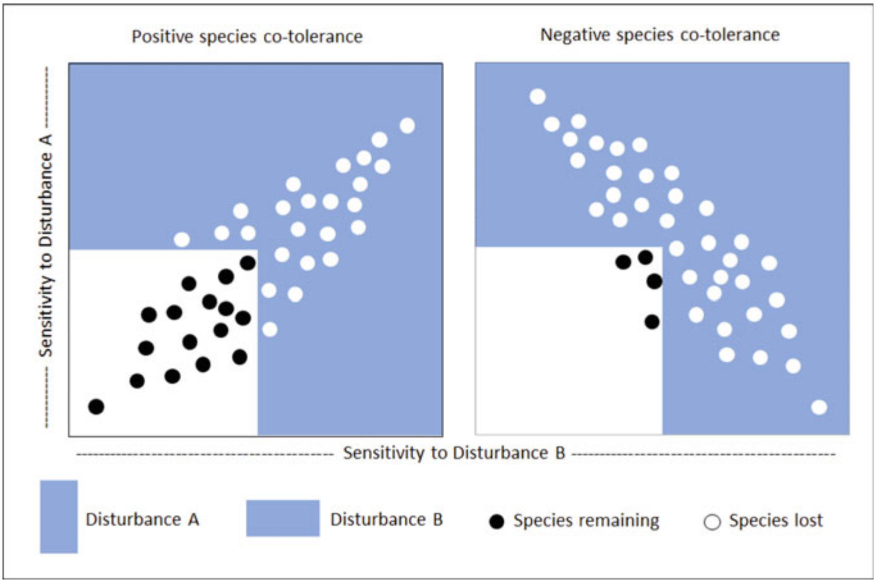

Fig. 7.4 Hypothetical effects of two disturbances (Disturbance A vertical, Disturbance B horizontal) on 40 meiofauna species as influenced by positive co-tolerance (left) and negative co-tolerance (right). The combined effects of Disturbance A and B are reduced when tolerances are positively correlated (i.e. disturbance-induced community tolerance; adapted from Vinebrooke et al. 2004). See text for details

Empirical tests, however, are challenging because the time scale of available historical data constrains the ability to identify drivers of long-term, large-scale changes. In situ changes resulting from anthropogenic disturbances occur well beyond the weeks or months, and square centimetres or metres typical of micro- or mesocosms used to study meiofauna in the laboratory. Natural analogues of experimental treatments replicating oil pollution, for example, such as oil seeps (MacDonald 1998), can provide insights into how organisms respond to the presence of oil, recognising though that there is a great deal of variability in the scales of oil spills (i.e. a few litres spilled during refuelling to millions of litres spilled during a large accident). Also, while human accidents are stochastic, natural oil seepage is more constant. Because oil seeps occur in geological structures where oil can be produced, it is also possible that meiofauna communities in areas where there is hydrocarbon exploration and production could be adapted to the presence of oil and other hydrocarbons such as methane.

Equally, analogues replicating increases in temperature and CO_2, such as hydrothermal and CO_2 vents (Dahms et al. 2018; Foo et al. 2018), provide critical insights into potential longer-term consequences for, and adaptations of, meiofauna to global change. For instance, using shallow-water CO_2 vents in the Mediterranean as a proxy for potential CO_2 leakage (following sub-seafloor CO_2 storage), meiofauna abundance and biomass declined and community composition changed, despite the overall increase of microphytobenthos productivity as a meiofaunal food source (Molari et al. 2018). Similarly, sub-surface marine hydrothermal vent conditions cause effects akin to those expected from various global change scenarios, with retarded growth, chemosynthesis and photosynthesis fuelling biomass, and physiological adaptations owing to exposure to high concentrations of heavy metals, low pH, and elevated temperature (Dahms et al. 2018). Novel genetic and genomic approaches are expected to reveal molecular mechanisms of adaptation of meiofauna to such conditions, and in particular the genetic basis of biotic interactions and local adaptation/phenotypic plasticity of meiofauna species (Schratzberger and Somerfield 2020).

- ***How do mutually reinforcing or antagonistic interactions between disturbances affect meiofauna?***

In situ, meiofauna communities are often exposed to multiple anthropogenic disturbances that can occur either simultaneously or sequentially and, moreover, differ in frequency and intensity. Taken collectively, the multiple anthropogenic disturbances investigated in Sects. 7.2–7.5 interact across scales of space and time (Côté et al. 2016). The recognition that disturbance interactions can lead to unexpected, rapid, and nonlinear change has been growing in recent years (Buma 2015; Halpern et al. 2019). There are now examples from several marine ecosystems on interactive effects of anthropogenic disturbances and climate change (Occhipinti-Ambrogi and Galil 2010; Planque et al. 2010). However, the consequences of disturbance interactions on meiofauna, where known, are not always synergistic or additive, nor necessarily intuitive.

Studies at fishing grounds, for example, indicated that repeated bottom-trawling influences the resilience of meiofauna communities (Table 7.7). Passages of a bottom trawl occurring at short intervals clearly prevent successful recovery of an appropriate portion of the population or assemblage because there is an insufficient proportion of reproducing adults in the population. Largely additive cumulative effects on meiofauna are thus likely and have been demonstrated by empirical studies in the field and the laboratory. Disturbances of the same type occurring at different frequencies could amplify, or attenuate, the effects of individually occurring disturbances, but there are as yet few empirical studies that have quantified potential interactive effects of different types of anthropogenic disturbances on meiofauna. For instance, experiments investigating the combined effects of warming and acidification (Table 7.16) recorded decreased meiofauna diversity, owing to increased dominance by few opportunistic species, whereas reduced pH alone did not decrease diversity (Lee et al. 2017). Also, complex interactions between nutrient load and toxicant exposure suggest that non-additive effects (synergetic or antagonistic) on meiofauna may be more common than additive effects (Sundbäck et al. 2010).

Understanding how disturbances interact with each other would provide some clarity about the broader ecosystem consequences of human-induced changes. To what degree is the response of meiofauna to a particular anthropogenic disturbance contingent on the response to other co-occurring disturbances of a different type? What are the consequences of multiple anthropogenic disturbances for meiofauna? It will not be possible to identify the effect of every disturbance interaction on every species' physiology and every community's structure and function because the number of anthropogenic disturbances and their potential interactions are growing rapidly. The ability to predict the nature of interactions between different disturbances thus depends primarily on understanding the underlying processes and mechanisms.

The concept of co-tolerance (Vinebrooke et al. 2004) is again a useful starting point here (also see disturbance history in Box 7.2 and above). When different types of anthropogenic disturbance act on the same physiological or ecological processes, then antagonistic interactions are likely. A common physiological response across meiofauna taxa and disturbance types is energy transfer from growth and reproduction under heavily disturbed conditions to ensure that basic metabolic processes are maintained, leading to reduced rates of growth and development (see Sects. 7.2–7.5). Acclimation to one kind of anthropogenic disturbance may therefore prevent, or at least reduce, damage by another because more vulnerable individuals or species are removed from the community and replaced by more resistant individuals or species. However, when different types of disturbances act on different mechanisms, individuals or species may be equipped to resist one type of disturbance but not another. The latter can increase the susceptibility of the community to the effects of multiple disturbances (Côté et al. 2016).

The co-occurrence of different types of anthropogenic disturbances either in time or space, is likely to have important cumulative effects on meiofauna communities. Improved understanding of how different types of (natural and) anthropogenic disturbances interact would therefore provide key information to aid predictions of their effects on meiofauna resilience (also see meiofauna resilience in Box 7.2 and above), particularly in the context of global change. Identifying dominant, additive or non-additive disturbance effects, as well as tipping points beyond which the long-term viability of meiofauna populations and communities is compromised, is an imperative focus for future meiofauna research.

7.8 Concluding Remarks

With more than 600 million years of evolutionary history (see Chap. 1), and high phylogenetic and phyletic diversity, the ecological success of meiofauna is strongly linked to their ability to survive in contrasting environmental conditions and to proliferate rapidly (Schratzberger et al. 2019). As a consequence, they are ubiquitous in marine benthic systems, from the upper reaches of estuaries to the deepest parts of the ocean, from the poles to the tropics, and from swell-beaten rocks to low-energy deep muds. With such a broad range of meiofaunal potential on which to draw, it seems likely that meiofauna will adapt to, and thrive in, most changes that anthropogenic disturbances are likely to inflict upon them. It is also clear that our understanding of meiofauna ecology is derived from an overwhelming preponderance of spatial (with a small proportion of temporal) studies that compare communities from one place (or time) with others. The scales of these studies, whether in the field or in the laboratory, rarely consider the world as experienced by meiofauna. Meiofauna are small and inhabit a world dominated by viscous forces and chemical gradients (see Chaps. 2 and 3). Disturbances that appear to humans as severe may be practically undetectable to individual meiofauna organisms. On the other hand, some disturbances that may have severe effects on meiofauna may be ignored by human investigators because these disturbances cannot be seen or have not been thought of. Advances in imaging and analytical technology are opening windows through which we may observe the world that meiofauna inhabit, and indeed the meiofauna themselves. It is time for meiofauna research to move beyond spatial comparisons and to pay more attention to the meiofauna themselves and to their world as they perceive and experience it, in order to understand what they do, how they do it, what effects we are having on them, and how their responses to those effects may alter our world in the future.

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Chapter 8
Deep-Sea Meiofauna—A World on Its Own or Deeply Connected?

Jeroen Ingels, Daniel Leduc, Daniela Zeppilli, and Ann Vanreusel

Abstract The deep sea is Earth's most typical environment and meiofauna its most common and arguably its most diverse metazoan inhabitants. They are therefore key in understanding temporal and spatial patterns in biodiversity and biogeography and are major contributors to ecological processes and functions. Meiofauna are integral to deep-sea benthic communities, with numerous links to other benthic organisms and the interstitial environment, the habitat from where they experience life around them. Although many meiofaunal patterns and relations have been identified, limited progress has been made in answering questions as to "why" and "how" these patterns and relations exist or are formed and maintained, and in many cases such knowledge does not exist. In this chapter, we review the knowledge we do have and present interpretations and explanations that bring a better understanding of how meiofauna patterns in the deep sea can be explained in terms of processes and ecological interactions. We applied this approach in four distinct fields of study: trophic interactions; biodiversity and ecosystem function; distribution and diversity patterns; and connectivity patterns. All four illustrate the extent to which meiofauna relate to other biological components and the abiotic environment. Moreover, technological advances and the increase in multidisciplinary approaches (inherent to offshore deep-sea research) show that meiofauna studies are becoming better integrated with other fields of deep-sea research. Meiofauna, therefore, offer an exciting scientific and diverse future of discovery with research operating at the frontiers of deep-sea science.

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8.1 Introduction

The deep sea (generally defined as deeper than 200 m water depth) covers vast expanses of the globe, providing an unimaginable amount of habitat space for microscopic organisms, to the point where it becomes difficult to grasp—at least for one not immersed in the study of meiobenthos. Those tiny animals, the size of a sand grain or smaller, can make a meaningful contribution to ecological processes on such a vast scale. Ubiquity and abundance, two important characteristics of meiofauna worldwide, make these organisms an essential part of deep-sea habitats and ecosystems. They should therefore be seen as central to the study of temporal and spatial patterns in biodiversity and biogeography, as key contributors to ecological processes and functions.

This is in opposition to misguided descriptions of meiofauna as an interesting but non-essential sideshow. Deep-sea meiofauna are, after all, the most common metazoan organisms living in the largest ecosystem on the planet. In other words, they are among the planet's most typical organisms living in the planet's most typical environment. Not only are they connected to deep-sea habitats by the simple fact that the abiotic environment, or environmental envelope, of these habitats provides them with the means to survive, but they are also an integral component of benthic communities. It is therefore not surprising to see links between the meiofauna and their biotic and abiotic surroundings everywhere in the deep sea. However, it behooves us to investigate questions beyond establishing a link and investigate the "why" and "how" of the observed relationships.

From the continental slope, to canyons, seamounts, guyots, abyssal plains, trenches, hydrothermal vents, and seeps, meiofauna are prevalent (Fig. 8.1). Foraminiferans, nematodes, and copepods constitute the most abundant taxa in deep-sea sediments (Zeppilli et al. 2018) and, at depths below 3000 m, meiofauna surpass larger size groups such as macrofauna and demersal fish in terms of total biomass (Rex et al. 2006; Wei et al. 2010). How can this be the case? Oligotrophy and intense natural selection for particle selection and resource exploitation ability have been posited as potential mechanisms for the prevalence of meiofauna in the deep sea and for the diminutive size of macrofaunal taxa in the deep sea (Jumars et al. 1990; Kaariainen and Bett 2006).

Considering the increasing relative abundance and biomass of meiofauna with water depth, we must also consider contributions of meiofauna to ecosystem functions (and ultimately services) in the deep sea. Their dominance over other deep-sea metazoan life forms needs to be explained by ecological processes and mechanisms providing them a competitive advantage. We should therefore also expect meiofauna to make an important contribution to ecosystem function, especially on continental margins, the transition zone from the shallow shelf to the oligotrophic abyssal plains, where much of the essential ecosystem services provided by the deep sea are concentrated [e.g., hydrocarbons, fisheries, and carbon burial (Levin and Dayton 2009; Sarmiento and Gruber 2002)]. However, despite their importance, many deep-sea

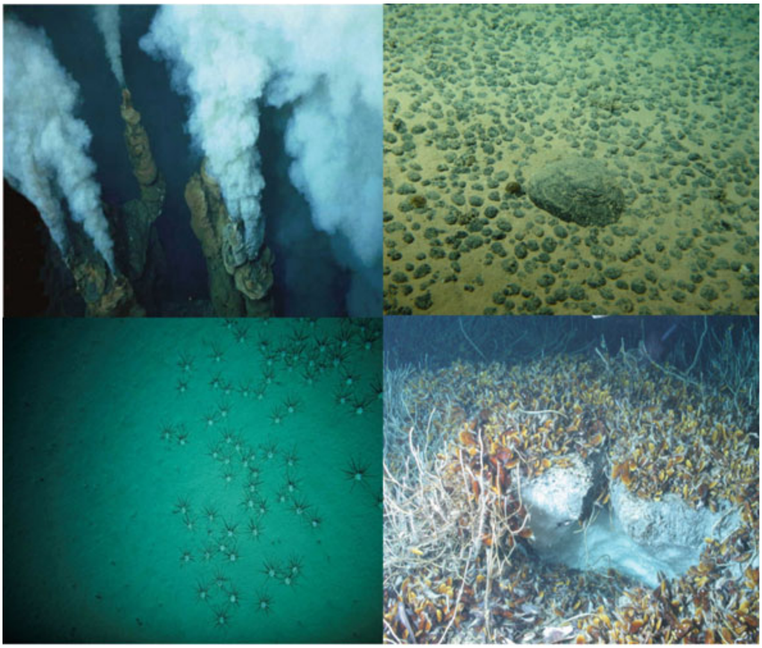

Fig. 8.1 Examples of different deep-sea ecosystems: top left: hydrothermal vent; top right: deep-sea nodules on the abyssal plain; bottom left: canyon (Gulf of Gascogne); and bottom right: REGAB pockmark © Ifremer

ecological processes are still not understood. This lack of knowledge is particularly acute for meiofauna, and most microscopic organisms, including protozoans, bacteria, archaea, and viruses.

In this chapter, we will address advances in our understanding of four broad topics in meiofauna research that illustrate their relation to the deep ocean, the environment they inhabit, and the other biological components they relate to. This is by no means an attempt to review the entirety of available literature, but rather to present in-depth case studies of existing paradigms and ecological questions that merit further investigation and have relevance to the general field of marine ecology:

1. Trophic interactions
2. Biodiversity and ecosystem function
3. Distribution and diversity patterns
4. Connectivity

These four fields of study illustrate how meiofauna species and communities are connected to each other and the world around them. These disciplines have seen substantive increases in understanding in the last decade or so, supported by advances in technology and the tools with which to investigate important scientific questions. These make them ideal study topics to highlight what we currently understand to be frontiers in deep-sea meiofauna research.

8.2 Trophic Interactions of Deep-Sea Meiofauna: "You Are What You Eat" But What Do Deep-Sea Meiofauna Eat?

When staring down a microscope looking at an intact meiofauna sediment sample, one is immediately confronted with the hidden nature and intricacies of interstitial space. Jansson (1971), in his work "The "Umwelt" of the Interstitial Fauna" in the Proceedings of the First International Conference on Meiofauna, describes elegantly the functional environment of meiofauna from their point of view in an attempt to understand better the environmental parameters that drive the behavior and function of the microscopic organisms living between the sediment grains. It is easy to imagine the grain surfaces to be analogous to vast landscapes filled with green hills of micro-algae and meadows of bacteria on which meiofauna may feast (Meadows and Anderson 1966, 1968). It is evident that such an image evokes the necessity of a myriad of ecological connections between meiofauna and other organisms in their immediate surroundings, trophic, or otherwise. Ecological interactions between different meiofauna taxa and between meiofauna and other benthic components have been amply documented for shallow waters, but much less so for the deep sea (Schratzberger and Ingels 2018).

The deep ocean relies almost exclusively on a food supply originating from primary production in surface waters (except for chemosynthetic ecosystems where chemical energy is harnessed as the basis for the food web). Benthic–pelagic coupling, the exchange of energy, mass and nutrients between the water column and seafloor ecosystems, is crucial to deep-sea benthic life (Woolley et al. 2016). This organic matter, produced in surface waters as a result of photosynthetic primary production (phytoplankton), is converted into sinking particles by food web processes (zooplankton, other grazers, microbes), by aggregation and fecal pellet production (Cavan et al. 2015), as well as microbial colonization and growth during sinking (Azam and Malfatti 2007). Once on the seafloor, bacterial activity normally increases, and together with the deposited material, serves as a rich food for protozoans and small metazoans (Gooday 1993; Moodley et al. 2002; Witte et al. 2003a, b).

Meiofauna play a key role in linking detrital and prokaryotic food resources with higher-level consumers, making available energy that may remain unused in their absence, therefore fulfilling an essential ecological role (Schratzberger and Ingels 2018). High metabolic and reproductive rates and high standing stocks of meiofauna in coastal areas and shallow waters imply that meiofauna play an important role in benthic energy transfer. However, what about deep-sea settings? Owing to a lack of direct observations of deep-sea meiofauna life histories and metabolic characteristics, the same trophic linkages have not yet been explicitly documented in deep-sea settings. There, the limited evidence available suggests that meiofaunal energy demand is met through consuming labile and refractory detritus, bacterial resources, or dissolved organic matter (Gontikaki et al. 2011; Guilini et al. 2010; Ingels et al. 2010; Pape et al. 2013c; van Oevelen et al. 2006, 2011a, b;) and potentially other sources [e.g., fungi and protozoa such as foraminifera and ciliates (Bhadury et al. 2011; Majdi et al. 2020)]. However, they also respond to episodic food falls

(Debenham et al. 2004; Soltwedel et al. 2018) and may consume other meiofauna organisms as evidenced by gut-content observations (Fonseca and Gallucci 2008). In addition, stable isotope and fatty acid analyses have shown the capacity of the nematode *Deontostoma tridentum* in deep-sea sediments off New Zealand, to consume a relatively wide range of food sources, spanning three trophic levels, while the species itself is highly nutritious to other predators as shown by elevated poly-unsaturated fatty acid content (Leduc et al. 2015). In some deep-sea habitats, such as canyons, increased numbers of predatory and scavenging nematodes also suggest that preying on small metazoans may be a successful strategy (Ingels et al. 2009; Soetaert and Heip 1995).

Meiofauna have been shown to exploit newly arriving phytodetrital matter in deep-sea settings, which can enhance both meiofauna densities and diversity (Lins et al. 2014; Pape et al. 2013b). Response times vary widely and range from days to weeks (Ingels et al. 2011a; Witte et al. 2003b). In contrast, other studies have shown metazoan meiofauna may in fact fail to exploit and use phytodetritus and associated microorganisms, unlike foraminifera. There is a distinct likelihood that foraminifera are more responsive to food arrival through efficient food-gathering organelles and their ability to raise metabolic activity very rapidly (Gooday 1993; Gooday et al. 1996). Metazoan meiofauna, on the other hand, may be hampered owing to potentially slower growth rates and higher reproductive expense, which puts them at a disadvantage in competitive interactions with foraminifera.

Veit-Köhler et al. (2011) noticed metazoan meiofauna becoming more concentrated at the sediment surface following a phytoplankton bloom deposition event, suggesting either active migration to where fresh phytodetritus had arrived to feed on bacteria and/or more degraded material, or migration to avoid increased respiration and declining oxygen concentration in deeper sediment layers. Further experimental evidence suggests (1) potential passive uptake of bacterial carbon in limited time periods (Guilini et al. 2010); (2) preferential bacterial carbon consumption by meiofauna (Ingels et al. 2010; Pape et al. 2013c); (3) or even dissolved organic matter uptake (Pape et al. 2013c).

Using experimental pulse chase and natural isotopic data in modeling has brought valuable perspectives into the contribution of meiofauna to total organic matter and carbon processing in various deep-sea settings (Gontikaki et al. 2011; van Oevelen et al. 2011a, 2011b). In subarctic conditions (−0.7 °C) in the Faroe–Shetland Channel at about 1000 m water depth, Gontikaki et al. (2011) reported that bacteria dominated carbon flow and respiration in the sediments, but nematodes were responsible for 96% of the refractory detritus uptake, almost entirely covering their energy requirements in this way. This implies an important role for nematodes in phytodetrital carbon turnover. However, only 2% of overall macrofaunal consumption was linked to predation on nematodes (but 35% of that of polychaetes), suggesting limited trophic transfer. In the upper sections of submarine canyons on the other hand, meiofauna can be responsible for over one fifth of carbon remineralization, suggesting high current speeds and sediment resuspension could favor meiofauna communities compared to macrofauna and megafauna (van Oevelen et al. 2011b).

Experiments and in situ observations have demonstrated how surface bloom fallouts and subsequent deep-sea arrival of food sources fuel the benthic food web. However, there is still large uncertainty about the mechanistics of meiofauna responses to this arrival and how selectively they can feed on various resources. Deducting from different buccal or mouth structures, as well as pharyngeal characteristics, some degree of selectivity or competitive advantage must exist if we accept the benefits of evolutionary adaptations to efficient feeding and niche segregation. However, Schuelke et al. (2018), investigating nematode-associated microbiomes in various ocean regions, could not find any relationship between these microbiomes (from the different parts of the nematode's body) and nematode feeding morphology nor nematode taxonomy. This would suggest decoupling of food source identities and nematode taxonomic and functional diversity.

Experimental observations have not yet revealed how meiofauna meet their energetic requirements. How much energy is needed to sustain growth and reproduction? Metabolism rates of meiofauna (and hence also their energy requirements) may be currently overestimated depending on environmental conditions (Braeckman et al. 2013). The apparent lack of uptake of administered food in experiments could be explained (1) by non-selectively feeding on the bulk organic matter already present in the sediments, (2) by very high trophic specialization so that uptake, measured on assemblage or community level would strongly dilute the signal of administered food sources. In addition, the oligotrophic deep-sea floor provides an environment where small metazoans are most of the time exposed to limiting resource conditions, likely responsible for body-shape, behavioral, and metabolic adaptations that enable them to survive long periods without abundant food sources.

An overview of meiofauna diets in the deep sea would be incomplete without considering chemosynthetic food sources. Seeps and associated bacterial mats, pockmarks, etc., often exhibit increased meiofaunal abundance compared to adjacent, phytodetrital-dependent deep-sea environments (Cepeda et al. 2020; Vanreusel et al. 2010, 1997). Deep-sea hydrothermal vents on the other hand exhibit generally low meiofauna standing stock (Vanreusel et al. 2010). Three reasons are evoked why vents are characterized by low meiofauna abundances: (1) unsuitability of hard vent substrates, (2) possibility that quality and quantity of vent food sources can't sustain high standing stocks, and (3) predation and competition with abundant macro-invertebrates (Vanreusel et al. 2010).

Chemosynthetic systems harness chemical energy through bacterial activity, rendering it directly or indirectly (through bacterial lysis) available to heterotrophic meiofaunal consumers or in close association with meiofauna in the form of symbioses such as for the nematode species *Oncholaimus dyvae*, *Parabostrichus bathyalis,* and *Astomonema southwardorum* (Bellec et al. 2018; Tchesunov et al. 2012). This is exemplified in isotopic work on deep-sea nematodes and copepods in or near chemosynthetic systems: thiotrophic and methanotrophic bacteria are likely contributors to their diets (Pape et al. 2011; Van Gaever et al. 2006, 2009).

Intricate, potentially symbiotic, relationships between bacteria and meiofauna (especially nematodes) have long been reported, (see Chap. 4), but in the deep sea, their relevance has only been considered relatively recently (Bellec et al. 2018;

Tchesunov et al. 2012). Evidence is emerging that chemosynthetic and photosynthetically derived heterotrophic pathways are not mutually exclusive, suggesting that a black-and-white approach to resolving deep-sea benthic food webs may be inadequate to assess carbon flows (Ingels et al. 2011b; Tchesunov et al. 2012; Zeppilli et al. 2019).

While meiofauna can feed on a variety of food sources (of photosynthetic or chemosynthetic origin), evidence of higher consumers feeding on meiofauna has been much less documented. Selective predation on meiofauna taxa may occur in shallow waters (Coull 1990; Jochum et al. 2012), and in fresh water where meiofauna are prey to a large number of macroinvertebrates (Ptatscheck and Traunspurger 2020). However, to our knowledge, such data do not exist for the deep sea (e.g., Gontikaki et al. 2011). Experimental results from exclusion studies suggest that megafaunal grazing in the deep sea reduces meiofauna abundance and diversity (Gallucci et al. 2008a). This is likely caused by indirect effects through competition of resources, sediment disturbance, and burrowing of megafauna, rather than through direct grazing; an observation that was also supported in shallow-water experiments under a controlled environment with different megafauna species (Ingels et al. 2014).

So far, studies have attempted to unravel meiofauna diets and nutritional selectivity in various deep-sea habitats of the world's oceans. Different approaches have been used, from field studies on natural lipid biomarkers and stable isotope signatures to enrichment experiments performed ex situ and in situ, supported or not by carbon flow modeling studies. However, out of necessity modeling studies still include assumptions and parameterizations for meiofauna metabolism and physiology that stem from shallow-water investigations and may exclude potentially important food sources such as dissolved organic matter and protozoa.

Moreover, in many deep-sea studies, meiofauna are typically considered as one functional group, thus ignoring the structural and functional diversity found across the many meiofauna taxa. Since meiofauna comprise minute organisms, traditional approaches such as stable isotope analysis require extraction of many individuals to obtain sufficient biomass. Moreover, traditional methods involve destructive manipulation so that individuals are not preserved for further taxonomic analysis. Although new technological developments such as NanoSIM allow for isotope identification on a (sub)cellular level, such techniques are currently still prohibitively expensive or not widely accessible. This normally hampers dietary assessments on the level of genera or species to enhance the resolution of intricate deep-sea food webs.

In the few habitats that are dominated by a few species, these methods are more easily applicable, but for most of the deep sea, where meiofauna are characterized by high diversity and low abundance (i.e., most species are rare, and abundance is relatively low) we must rely on more advanced technology to move forward in this field of study. However, technological advances, progress in microscopy, and novel molecular and isotopic procedures, should bring the elucidation of meiofauna diets and their trophic interactions with other benthic components within reach (Majdi et al. 2020).

8.3 Meiofauna Biodiversity and Ecosystem Function in the Deep Sea

There is still ample scientific debate about the relation between deep-sea meiofauna taxonomic diversity, their functional diversity, and ecosystem function. Functional diversity can be identified as a measure of how diverse functional traits (i.e., traits that bear importance to processes and functions in an ecosystem, such as body size and buccal cavity structure) are within a group of taxa. Ecosystem function, on the other hand, is a term encompassing many different processes operating in an ecosystem, such as nutrient fluxes or secondary productivity. Ecosystem function results from the interaction of organisms with their environment. Although linked, functional diversity and ecosystem function are largely different and influenced by environmental constraints depending on the habitat or ecosystem. This is a topic worthy of intense future study since the relationship "biodiversity–ecosystem function" is central in understanding the role of biodiversity: Which processes and functions within an ecosystem are maintained? How do these processes and functions generate and maintain the services the ecosystem provides, and how does biodiversity contribute to them (Loreau et al. 2001)? The deep sea and meiofauna, in particular, may offer unique insights into our understanding of species interactions, ecosystem functioning, and, thus, implications of biodiversity loss (Loreau 2008).

Several studies have shown that in the deep-sea, meiofaunal structural, or taxonomic diversity can be closely linked to meiofauna functional diversity (often expressed in terms of trophic diversity or life-history characteristics for nematodes) (Danovaro et al. 2008; dos Santos et al. 2020; Gambi et al. 2014; Leduc et al. 2013). Yet, meiofaunal diversity and ecosystem function/efficiency, the latter measured by means of biomass, production, respiration, bacterial processes, or enzyme concentrations, have been found to co-vary either positively or negatively in the deep sea (Danovaro et al. 2008; Leduc et al. 2013; Pape et al. 2013a) or not to vary at all (Pape et al. 2013a).

Leduc et al. (2013) highlighted the importance of environmental drivers in affecting the biodiversity–ecosystem function relation. They noted that the previously documented exponential relation between nematode diversity and ecosystem function [sensu Danovaro et al. (2008)] appears to largely break down beyond a certain diversity. This is potentially owing to increased competition or greater functional redundancy under a given set of environmental constraints, such as available resources or carrying capacity of the habitat or ecosystem. In other words, adding species to an already high-diversity assemblage will likely not additionally contribute to ecosystem function (Leduc et al. 2013). Loreau (2008) expresses how extraordinary the findings by Danovaro et al. (2008) are, considering that, in general, diversity has a positive but saturating influence on ecosystem function. Generally, a plateau is reached in the biodiversity–ecosystem function relation at high biodiversity levels, and meta-analyses have shown that this paradigm is remarkably consistent across different ecosystem types and trophic levels (Balvanera et al. 2006; Cardinale et al. 2006; Loreau 2008; Worm et al. 2006). Future research into this phenomenon should consider the full range of deep-sea meiofauna diversity in assessing its relationship with deep-sea ecosystem function, and, importantly, move further into investigating the causal mechanisms responsible for that relation (Fig. 8.2). It is possible that characteristics of deep-sea ecosystems such as low disturbance and low food availability somehow promotes facilitation among species, unlike what has been observed in other ecosystems. However, that does not mean that coexistence and facilitation among (nematode) species is a relation that does not eventually saturate.

More broadly, there are many examples of facilitation between different components of deep-sea benthic communities. A few cases in point are as follows:

(1) facilitative meiofauna–bacteria relationships; whereby bacteria serve as nutrition for meiofauna (symbiotic or otherwise) and are stimulated for growth when grazed upon by meiofauna;
(2) bioturbation activities by macrofauna (and large meiofauna) and sediment disturbance by megafauna species enhance biogeochemical cycling and nutrient exchange, or may redistribute food sources to consumers (Levin et al. 2001; Lohrer et al. 2004);
(3) deep-sea species such as large xenophyophorans (megafauna-sized foraminifera) may cause enhanced microbial activity, while itself processing dissolved organic matter and acting as particle traps as do other structure-forming organisms, thereby enhancing sedimentary food-source retention and promoting meiofaunal abundance and diversity (Levin and Gooday 1992);
(4) positive relationships between meiofauna and macrofauna taxonomic and functional diversity (including feeding morphology, predator richness, and bioturbation potential) (Baldrighi and Manini 2015).

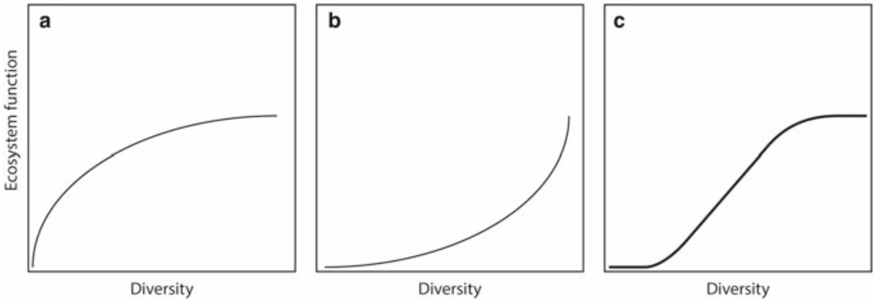

Fig. 8.2 Three different types of relationships between ecosystem function and diversity have been used to explain observed patterns in the deep sea. **a** Saturation: as diversity increases, ecosystem function increases, but only to a certain point where the relationship becomes saturated and increases in diversity do not increase ecosystem function, possibly because of competitive processes or functional redundancy. This relationship has been observed in most ecosystems (Loreau 2008). **b** Exponential (unsaturated) relationship: as suggested by Danovaro et al. (2008), an exponential relationship between diversity and ecosystem function suggests facilitation between biological components, where diversity increases only lead to increased ecosystem functioning. **c** Combined exponential–saturation relationship: The diversity–ecosystem function relationship starts exponentially but eventually saturates due to functional redundancy (Leduc et al. 2013)

These are just four examples of how the relation between biodiversity and ecosystem function in the deep sea may be characterized by enhanced facilitative interactions to maintain important ecosystem processes and functions involving meiofauna. Theoretically, these examples could also occur in shallow-water benthos, but it can be argued that such facilitative relationships have a better chance of developing and being sustained in the deep sea. Deep-sea sediments seem to generally have a more even distribution of individuals, faster accumulation of species with individuals, and often a higher proportion of singletons in a given sample compared to their shallow-water counterparts (Snelgrove and Smith 2002). This suggests species populations in deep-sea sediments are smaller than in shallow waters, but also distributed over larger areas, allowing increased habitat and resource space that may attenuate intense competition processes and promote facilitation. In more dynamic shallow-water environments, facilitative relationships may break down more quickly. Perhaps it is not surprising that increased niche space, as found in the deep sea, in addition to habitat patchiness (caused by biotic activity and abiotic regimes) plus intermediate levels of disturbance allows for the smaller meiofauna to become more dominant than larger organisms, and more diverse and successful, especially below 3000 m water depth, as previously noted.

8.4 Distribution and Diversity of Deep-Sea Meiofauna: Local to Global Scale Patterns

Standing stocks—Food availability [i.e., particulate organic carbon (POC) flux to the seafloor] is the main factor influencing the abundance and biomass of deep-sea meiofauna, explaining not only bathymetric patterns but also geographical variation among and within ocean basins. On a global scale, the highest biomass is found in areas with coastal upwelling (e.g., continental margins), and the lowest biomass is found in central abyssal plains of major ocean basins (Wei et al. 2010). The bathymetric decline of benthic standing stocks is not equal across different size classes; meiofaunal abundance and biomass decrease more slowly with depth than macro- and megafauna, resulting in the dominance of meiofaunal-sized organisms below 3000 m depth. Indeed, the reduction in average animal body size with depth is among the best established macro-ecological patterns in the deep sea (Rex et al. 2006; Thiel 1975). This pattern is thought to originate from the effect of food limitation, which disproportionately affects the ability of large species with a high energy demand to maintain populations above a critical threshold required for reproduction (Thiel 1975). Although the meiofauna-dominated seafloor below 3000 m depth is characterized by low benthic standing stocks relative to coastal, shelf and slope environments, it accounts for more than half of global benthic biomass due to its large surface area (Wei et al. 2010). The oceans' deepest ecosystems therefore play a critical role in global biogeochemical cycles (see Chap. 2) despite the paucity of large fauna.

Species richness and diversity patterns—As Rex and Etter (2010, p. 25) noted, '[benthic] standing stock is the culmination of pelagic–benthic coupling, (…) and is the most directly relevant measure of ecological and evolutionary opportunity in the deep sea'. Given the importance of POC flux in determining deep-sea meiofaunal standing stocks, it is perhaps not surprising that food availability (i.e., chemical energy) has emerged as the main driver of deep-sea meiofauna species richness, in addition to standing stocks (Mokievsky et al. 2007; Soltwedel 2000). This contrasts with coastal marine environments where thermal energy has a dominant role in determining species richness (Yasuhara and Danovaro 2016).

The relationship between productivity and local species richness in the deep sea generally takes a unimodal shape, at least when the full range of productivities is considered. In studies confined to a relatively narrow range of productivities, the unimodal curve can be skewed to the right or left or can show positive or negative relationships with productivity (Rex and Etter 2010). The unimodal relationship was demonstrated for deep-sea nematodes by using biomass as a proxy of productivity (Leduc et al. 2012b) and the relationship also seems to hold in newly studied deep-sea systems (e.g., Dos Santos et al. 2020). Because this relationship persists at both regional and global scales, the mechanisms involved are likely to be of an ecological rather than an evolutionary nature. The ascending limb of the unimodal curve may be the result of higher proportions of rare (Preston 1962) and specialized species (Evans et al. 2006), whereas the descending limb may result from increased competitive exclusion (Grime 1973; Rosenzweig and Abramsky 1993), temporal variability in productivity (Chown and Gaston 1999), or environmental stress (e.g., hypoxia; Levin and Gage 1998). Gray (2002) suggested that the role of productivity lies primarily in setting the upper limit of species diversity, with other factors such as disturbance and habitat heterogeneity (e.g., grain size diversity; Leduc et al. 2012b) influencing the realized diversity at a given location.

The richness of infauna also decreases with distance to the nearest landmass (Woolley et al. 2016). Although it is difficult to disentangle the effects of water depth (i.e., POC flux) and distance from landmass, it is possible that the transport of propagules (Rex et al. 2005), land-derived organic matter (Leduc et al. 2020) and sediment particles of various sizes and mineralogy (Cerrano et al. 1999) have an impact on deep-sea meiofaunal diversity. The fact that meiofauna lack pelagic larval stages and still have abyssal populations of relatively high density means they are more likely to be self-sustaining. Passive dispersal of meiofaunal adults may be more widespread than once thought (see Sect. 8.5 on connectivity and dispersal), and source-sink processes could be influencing deep-sea meiofaunal diversity patterns in low productivity areas.

As seen for standing stocks, meiofaunal diversity is less sensitive to the declines in productivity than that of larger fauna, as might be expected from meiofauna's smaller body size and energy requirements. Relative to shallow water environments, local species richness of meiofauna in bathyal and abyssal environments is often elevated perhaps reflecting not only lower rates of competitive exclusion due to lower overall productivity, but also lower levels of physical disturbance, and/or lower likelihood of species extinction due to wider species distribution ranges in the vast deep-sea environments (Rex and Etter 2010; Zeppilli et al. 2018).

Data on nematode species richness obtained from across the full range of ocean depths (200–11,000 m), from across the Pacific Ocean and including data from Tonga, Kermadec, and Mariana trenches show a trend of decreasing species richness with depth (Fig. 8.3; $P < 0.0001$, $R^2 = 0.49$). A closer look at the data, however, shows that there is no significant relationship between depth and nematode species richness within each of the 200–6000 and > 6000 m depth ranges ($P > 0.1$). The overall decrease across the full ocean depth range is therefore due to lower species richness values in hadal trenches (mean ES(51) = 16) relative to slope and abyssal environments (mean ES(51) = 33).

Although at a glance these data suggest that species richness does not respond to depth-related environmental gradients in slope and abyssal environments, it seems more likely that the lack of trend reflects wide variation in bathymetric environmental gradients across different locations in the Pacific Ocean. The apparently sudden twofold decrease in nematode species richness observed as we cross the abyssal–hadal trench boundary at ca. 5500–6000 m depth (Fig. 8.3) indicates that habitat-related factors are limiting species richness in the oceans' deepest environment.

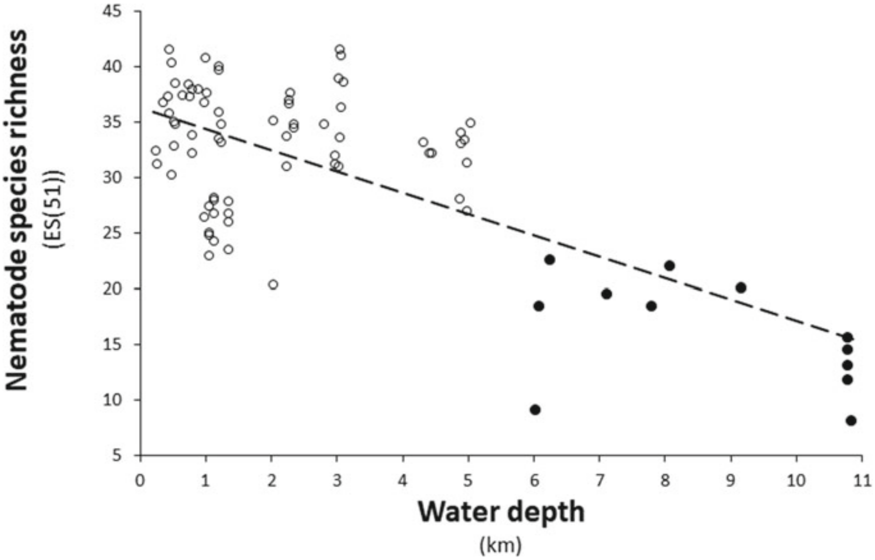

Fig. 8.3 Nematode species richness (ES(51)) from 200 to 11,000 m depth in the Pacific Ocean. The dotted line indicates a significant negative correlation with depth ($P < 0.0001$, $R^2 = 0.49$) across the full depth range; however, there is no relationship with depth within each of the 200–6000 (empty circles, mean species richness = 33) and >6000 m depth ranges (filled circles, mean species richness = 16). Note the paucity of data below 3000 m depth. (Data from Danovaro et al. 2008; Danovaro et al. 2002; Frank Wenzhöfer, unpublished; Guilini et al. 2012; Lambshead et al. 2002; Leduc et al. 2010b; Leduc and Rowden 2018; Leduc et al. 2012a; Leduc et al. 2016; Miljutin et al. 2010; Miljutin et al. 2011)

Relative to abyssal plains, the limited extent of hadal trench environments as well as their recent geological formation and isolation likely limit the size of the species pool available for colonization. The greater frequency of physical disturbance induced by turbidity flows in hadal trenches is also likely to limit local species richness. These findings are not irreconcilable with the unimodal model relationship between nematode species richness and productivity since habitat-related factors may affect the general decline of available energy with increasing water depth. Also, food input may be considered a disturbance at levels consistent with high organic loads. To expand our understanding of these patterns, more data on species richness from the full range of ocean depths (200–11,000 m) should be obtained. Our knowledge has so far been hampered by the limited amount of data available for abyssal plains (ca. 4000–6000 m) and hadal trenches (>6000 m) in particular.

Species richness from local to regional and global scales—Meiofauna species number estimates in the deep sea is still fodder for rich debate. Lambshead (1993) noted that local diversity of deep-sea nematodes is roughly the same as that of polychaetes (which typically dominate macrofaunal species richness and abundance), but that nematode abundance is one order of magnitude higher. He concluded that both local and global nematode diversity should therefore be about one order of magnitude greater than macrofaunal diversity. It has since been shown that when all meiofaunal individuals from a site are identified (as opposed to the common practice of estimating species richness based on relatively small subsamples) local nematode and harpacticoid species richness is indeed much greater than polychaete species richness. Perhaps the best illustration of this comes from a study conducted at an abyssal site in the Angola basin, where a total of 600 harpacticoid copepod species were identified based on the identification of 1804 adult specimens, with over half of species represented by a single specimen (George 2014). Extrapolating this order of magnitude difference between meiofaunal and macrofaunal species richness at the global scale, however, relies on the potentially flawed assumption that meiofaunal species turnover is also high.

Based on a dataset from the equatorial central Pacific Ocean, Lambshead and Boucher (2003) later showed that his estimate of nematode species globally had to be revised down because “similar patches with similar species are duplicated over large areas resulting in a more modest regional diversity.”

In other words, while local diversity is high, turnover diversity and hence regional/global diversity are lower than previously assumed. This pattern of very high local species richness but limited spatial turnover was also demonstrated in a study where the identification of 1850 nematode specimens from a single bathyal site on Chatham Rise, New Zealand continental margin, revealed 247 morphospecies, which represents about a third of all 775 morphospecies species identified from the entire Chatham Rise (Leduc et al. 2010a, 2012a).

The assumption of high turnover diversity in deep-sea meiofauna communities followed from the premise that meiofauna have limited dispersal capabilities and therefore restricted geographical distributions. However, the dispersal potential of meiofauna may have been underestimated, at least in shallow-water environments where processes such as zoochory, rafting, drifting, and anthropogenic vectors can disperse meiofaunal organisms across vast distances (Ptatscheck and Traunspurger 2020). On the other hand, the presence of cryptic species complexes suggests that morphospecies distributions may hide true species distributions, resulting in high turnover diversity that can only be detected through molecular analysis. Although the nature and extent of transport mechanisms are less clear in the deep sea, some molecular data provide support for widely distributed deep-sea nematode species (Bik et al. 2010; see next Sect. 8.5 "Connectivity and dispersal").

Of great interest in determining local to global diversity patterns of meiofauna is the notion that biogeographic distribution patterns of species are likely driven by the size of the organism in the context of the ubiquity model of global distribution. Azovsky et al. (2020) demonstrated how body size is the "master trait" that shapes global biogeographic patterns of marine micro- and meiofauna. The smallest of organisms, such as flagellates, tend to show low endemicity, high regional but low global diversity, and relatively little sign of dispersal limitation. Larger organisms within the size range investigated, such as harpacticoid copepods, on the other hand are posited to have higher endemicity and more restricted global distributions caused by dispersal limitation. These findings support the idea that body size is shaping global biogeographical patterns toward higher predictability and greater dispersal limitation for larger organisms (Azovsky et al. 2020).

Scalability of drivers and mechanisms of diversity distributions—While the size of the organisms seems important in shaping diversity patterns, the scales at which environmental variables operate and drive communities in the deep sea may vary substantially. A meta-analysis of deep-sea meiofaunal studies (Rosli et al. 2018) has shown that most of the variability in communities occurs at the largest (100–10,000 km) and smallest spatial scales (0.001–0.1 m), while the effect of intermediate scales (0.1 m–100 km) is usually less pronounced. At the small scale, gradients in meiofaunal communities are primarily linked with vertical gradients in food and oxygen availability into the sediments (see also Ingels and Vanreusel 2013). However, at the scale of ocean basins, evolutionary/geological history, dispersal barriers, and environmental variables such as surface productivity may all act to increase variability. Although studies have shown that some meiofaunal species can have distributions spanning several 1000s of km within an ocean basin (Ingels et al. 2006; Lambshead and Boucher 2003; Vermeeren et al. 2004), minimal overlap in species distributions across basins has also been observed (Fonseca et al. 2007; Ingels et al. 2006).

The causes behind the high local species richness of meiofauna in some parts of the deep sea are not yet fully understood. While we know that the relatively low levels of productivity in the deep sea should slow down rates of competitive exclusion, thus promoting species coexistence, we have very little information on the nature and extent of competitive interactions and niche segregation among meiofaunal species. The limited information that is available shows high levels of horizontal heterogeneity in meiofaunal communities at the centimeter scale, with the size of patches varying from less than 4–64 cm^2 depending on the mobility of different taxa (e.g., nematodes vs copepods and small sedentary nematode species vs large and mobile nematode species) (Gallucci et al. 2008b). Therefore, if we assume that competitive exclusion takes place among meiofauna, we could expect that a greater number of species can coexist in a given area of sediments when species sizes decrease, which could partly explain the high species richness in the deep sea relative to shallow-water environments. Microhabitat heterogeneity resulting from steep vertical gradients in food availability, oxygen and sulfide concentrations as well as particle size diversity, and biogenic structures are also likely to play an important role.

It has been shown that closely related, cryptic meiofaunal species can differ markedly in their competitive abilities, response to environmental stressors, and trophic preferences despite having almost identical morphologies (De Meester et al. 2012, 2015). This indicates that a considerable degree of niche segregation may be occurring, which would facilitate species coexistence. While it will be difficult to investigate niche segregation among deep-sea species, predictions based on species size and mobility could be tested using existing data sets.

Major challenges, which have prevented further investigations of deep-sea species distributions, particularly at ocean basin and global scales, include the time-consuming nature of species identifications, the paucity of taxonomic expertise, the large number of species (many of which are undescribed), and the limited geographical extent of most deep-sea investigations. Although methodologies such as environmental DNA have been touted as potential solutions to this problem, sequence libraries remain far from complete and most sequence data obtained from deep-sea sediment samples cannot be assigned to species (Laroche et al. 2020). Taxonomists working on deep-sea meiofaunal taxa should therefore give sequence data in their species descriptions a high priority so to maximize the uptake of their research among the wider scientific community.

8.5 Connectivity, Dispersal, and Origins of Deep-Sea Meiofauna

The knowledge on population connectivity for deep-sea meiofauna taxa is limited in general. While meiofauna are relatively abundant in the deep sea, most meiofaunal species are rare, with a distinct lack of abundant, dominant species. This results in high species richness in deep-sea assemblages. The exceptions to this impediment may be presented by foraminifera, copepods, and nematodes, which can reach abundances sufficient for such studies. Furthermore, deep-sea meiofauna have a tendency for dwarfism, which is an additional hampering factor for widespread connectivity studies on bathyal, abyssal, and of course hadal meiofauna species.

Despite the fact that the deep seafloor comprises the largest contiguous biotope on Earth, deep-sea populations of benthic species are in general fragmented with evidence of cryptic speciation (Taylor and Roterman 2017). Benthic species from sediments show in general a more restricted dispersal compared to species from hard substrate, demersal, or pelagic habitats. Obviously species with pelagic and/or feeding (planktotrophic) larvae are more dispersive than other larval types (Baco et al. 2016). There is controversy as to the importance of geography versus bathymetry as a barrier for gene flow (Havermans et al. 2013; Zardus et al. 2006). Most studies seem to support the notion that vertical divergence between deep-sea populations is more pronounced than horizontal divergence over similar scales (reviewed in Taylor and Roterman 2017). The mechanisms responsible for this pattern are not clear at present but could relate to differences in currents and oceanographic patterns. This is not just of scientific relevance: Growing interest in deep-sea resources makes connectivity research critical for understanding the mechanisms that regulate population sizes and its function in the context of spatial management and mitigation of recovery from anthropogenic disturbance.

In contrast to the majority of macrobenthic species, connectivity in meiofauna taxa is not achieved through planktonic larval stages, and the dispersal processes are still a major gap in our understanding. Nematodes carry and/or lay eggs, while harpacticoid copepods have naupliar larvae but are still mainly restricted to a benthic lifestyle [despite documented emergence patterns of copepods, see Thistle et al. (2007)]. Also, other meiofauna taxa tend to lack life stages with pelagic dispersal capacities. While some shallow-water species exhibit a relatively wide geographic distribution, especially for opportunistic taxa (Bhadury et al. 2008; Sahraean et al. 2017), evidence is growing, based on an increasing number of molecular-based studies, that so-called cosmopolitan species are part of species complexes with a high degree of cryptic speciation (Bhadury et al. 2008; Cerca et al. 2018; Derycke et al. 2007, 2005; Sahraean et al. 2017). While these cases demonstrate a “hidden diversity” in shallow waters, for the deep sea, information is scant so far. Hauquier et al. (2019) demonstrated that gene flow and cryptic speciation can be very different among nematode species on the deep Antarctic shelf (300–500 m) depending on whether the species is a surface dwelling or deep burrowing species, with the latter showing lower gene flow. There are still many questions surrounding our understanding of meiofauna distributions and dispersal, especially in the deep sea. It seems that the meiofauna paradox is not so much a paradox, but rather a paradigm fed by a lack of understanding and underestimation of true species diversity and dispersal mechanisms (Cerca et al. 2018; Ptatscheck and Traunspurger 2020).

It is little understood to what extent the underestimation of species diversity and dispersal mechanisms holds for deep-sea meiofauna. Here, no major environmental drivers or obvious dispersal barriers are present, except for depth, certain topographies, water mass characteristics, and surface productivity. According to a study by Bik et al. (2010), Enoplids, an important nematode order, are not represented by endemic deep-sea lineages nor do their populations cluster according to bathymetry or geography. The study provides evidence for several cosmopolitan marine species at least at a trans-Atlantic scale. Moreover, Lecroq et al. (2009) and Pawlowski et al. (2007) found a wide bathymetric and geographic distribution of benthic foraminifera species in the deep sea. In contrast to shallow-water benthic foraminiferans, the common species *Epistominella exigua* showed a remarkably high genetic similarity between Arctic, Atlantic, Pacific, and Antarctic populations, implying a true cosmopolitan distribution (Lecroq et al. 2009). Pawlowski et al. (2007), on the other hand, discovered very limited genetic differentiation between Arctic and Antarctic specimens of two species (*E. exigua*, *Cibicides wuellerstorfi*), suggesting huge metapopulations for these species extending from pole to pole across vast bathymetric ranges (1351–4975 m, 573–4407 m, respectively). They also found genetically similar specimens of the same species in the North Atlantic Ocean, suggesting distributions of the species beyond the Arctic and Antarctic.

It is also remarkable that non-chemosynthetic meiofauna taxa dominate deep-sea cold seeps or hydrothermal vents, in contrast with what has been observed for macrofauna and megafauna (Vanreusel et al. 2010; Zeppilli et al. 2018). Several studies have shown that meiofaunal species recorded from chemosynthetic environments are also distributed across proximate and distant habitats, suggesting that populations close to these chemosynthetic systems can be the result of a continuous colonization from adjacent areas (Gollner et al. 2015 and references therein; Zeppilli et al. 2018). A study by Gollner et al. (2016) based on the analysis of mitochondrial DNA of nine dirivultid copepod species occurring at hydrothermal vents in different ocean basins suggests wide dispersal capacity for all species. Despite different geological settings and wide geographic distances, the vents were occupied by these same species indicating high population expansion and high connectivity of these copepod populations with great dispersal capacity.

On the other hand, natural disturbance events (such as volcanic eruptions) at these ephemeral and harsh environments may prevent settlement and successful arrivals. They may even wipe out entire populations, thereby affecting realized rates of dispersal of these hydrothermal species. The authors put forward various reasons for the overall, large-scale genetic exchange between populations:

(1) ocean current regimes may favor dispersal of these copepods since they have lecitotrophic nauplii and feeding copepodites that have been observed in the water column above vents;
(2) intermediate habitats between vents may be used as stepping stones, since vent copepods have been observed up to 1 km away from active vents; and
(3) the potential of biological traits such as lecitotrophy and directed migration during current entrainment may support successful dispersal (Gollner et al., 2016).

Very little is known about the evolutionary origins of deep-sea meiofaunal taxa. Most nematode genera are globally distributed, and most are found both in shallow and deep-sea settings, although some genera occur mostly (e.g., *Acantholaimus*) or exclusively (e.g., *Bathyeurystomina, Manganonema, Thelonema, Cricohalalaimus*) in the deep sea. Some recently discovered genera are so far only known from hadal trench environments (>6000 m, e.g., *Lamyronema, Maragnopsia*). Relative to macrofauna, little is known about the depth distribution of meiofaunal species. So far, forty-eight nematode species are known to have a depth range over 2000 m, and half a dozen have a depth range exceeding 4000 m (Miljutin et al. 2010), which suggests that species ranges for nematodes may be wider than for macrofaunal species.

On the other hand, phylogenetic analyses of deep-sea and shallow-water nematodes suggest repeated and recent interchanges between the deep-sea and intertidal zone and provide evidence for multiple, independent invasions of both deep-sea and shallow-water habitats (Bik et al. 2010). This supports the suggestion of Holterman et al. (2008) that habitat transitions are frequent and common in this taxon. Apart from generally smaller body size, there is no evidence for morphological adaptations specific to deep-sea meiofaunal taxa, although it seems likely that physiological and enzymatic adaptations have developed (Zeppilli et al. 2018).

Given the low abundances and high species richness of meiofauna taxa in the deep sea, our knowledge on species distribution and population connectivity is growing only slowly. To solve questions related to the dispersal, radiative adaptation, and genetic diversity of deep-sea meiofauna, high-throughput sequencing such as genome scanning approaches, metagenomics or metatranscriptomics is very important (Cerca et al. 2018). A metabarcoding approach applied at a wide geographic scale in the NE Pacific abyss provided some insights regarding the distribution of deep-sea nematodes and the tentative mechanisms defining their community structure (Macheriotou et al. 2020). From a phylogenetic perspective, nematode assemblages from the abyssal plains in the Pacific Clarion Clipperton Fracture Zone were characterized by high relatedness.

But factors controlling phylogenetic structuring, or the relative dominance thereof, remain mostly unknown and can differ between genera. Areas located at a few hundreds to thousands of km distance showed a high degree of rarity represented by a large proportion of unique single DNA sequences recovered from a high-throughput molecular analysis (~85% of the entire sequence assemblage). These unique Amplicon Sequence Variants (ASV) have a higher degree of re-usability, reproducibility, and comprehensiveness, and are increasingly replacing Operational Taxonomic Units (OTU) as the standard unit of marker-gene analysis: They can be based on single nucleotide changes instead of a cluster analysis using fixed dissimilarity thresholds (Callahan et al. 2017). However, interpretation of distributional isolation or connectivity between geographical areas, based on ASV's units, remains, as yet, problematical.

8.6 Conclusions, Thoughts, and Future Perspectives

We attempted to address a common theme that is often discussed in deep-sea meiofauna research: How connected are meiofauna in the deep sea? We used four different topics to illustrate the advances in these research frontiers:

- trophic interactions,
- biodiversity and ecosystem function,
- distribution and diversity patterns, and
- connectivity.

In the field of **deep-sea trophic ecology**, it is obvious that meiofauna is inherently linked to the dominant food source—marine snow, and the remnants and microbes that travel to great depths to feed the benthos. Meiofauna respond to these fluxes of particulate rain coming down. However, it is also becoming clearer that in the deep sea, meiofauna are not exclusively reliant on phytodetrital food sources, but that they can acquire energy from microbial and chemosynthetic sources through consumption or symbiosis. Innovative modeling approaches together with stable isotope information (from natural data or experiments whereby food sources are labeled) have brought a better understanding of energetic pathways and carbon cycling and what role meiofauna plays in them. So far, habitat characteristics and their respective environmental conditions seem to affect to a great degree how food webs function and how much energy is transferred through the meiofaunal component to higher trophic levels. However, our understanding of dietary and metabolic mechanisms for meiofauna species is still limited, exacerbated by the complexity of obtaining in situ data. In addition, the observation that many meiofauna exhibit dietary plasticity and the fact that their energetic requirements are not met based on our current understanding of meiofauna metabolisms and food availability lays open a field of study that is certainly worth pursuing. Research into food selectivity and the energetic mechanisms used by meiofauna to cope with the general oligotrophy in the deep sea will give us a better idea of how meiofauna contribute to overall functioning of the deep seafloor and give much-needed insights into the adaptation of deep-sea organisms in general to the deep sea.

In recent years, insights into meiofauna **biodiversity and ecosystem function** patterns have drastically increased as more data from different deep-sea habitats that may cover larger swaths of seafloor become available. Also here, the connection between meiofauna, their environment, and other organisms is essential in shaping the observed patterns. This is particularly the case when assessing ecosystem function using microbial activity and biomass/production, or biogeochemical processes such as nutrient consumption and cycling. The paradigms associated with the idea that facilitative interactions may play a very important role, and according to some, cause an exponential relationship between meiofauna biodiversity and ecosystem function, must receive further attention in future studies. As more data from full water-depth spectra become available, a more complete picture of this relationship should become more apparent (e.g., Fig. 8.3).

Distribution and diversity patterns are perhaps the best-studied topics in deep-sea meiofauna research. Small-to large-scale studies, ranging from a very specific sampling area to sometimes global-scale assessments, have shown that meiofauna communities respond to environmental conditions in relatively predictable ways. However, new genetic information and insight into cryptic species have demonstrated that distribution patterns of deep-sea meiofauna species that are based on morphological identifications alone are smaller than originally thought. In other cases, globally distributed meiofauna species in the deep sea have been confirmed by molecular studies. Questions as to why distributions of different meiofauna species can differ so drastically have not been answered satisfactorily, but recent insights into body-size distributions suggest that being small may positively influence large-scale dispersal and distribution ranges. Further study into why meiofauna diversity is high in the deep sea is also needed. Ecological theory has been used to explain diversity patterns to a great extent, but our understanding of speciation and niche differentiation for meiofauna in the deep sea does not seem entirely consistent with resource ecology as used for larger organisms such as macrofauna and megafauna.

In the field of **meiofauna connectivity** research in the deep sea, great advances have been made in the past few years. Yet, the contrast between species that have wide distributions and high gene flow between distant locations, and species that have very limited distributions remains unexplained. Rarity seems to be the norm in the deep sea, with low abundance of many unique DNA sequences in any particular area, but some species do not answer to that paradigm. The evolution and origin of deep-sea meiofauna are relatively unstudied, but some studies suggest that repeated exchange between shallow waters and the deep sea lie at the cause for the large depth ranges observed for some meiofauna species. Morphological adaptations to living in the deep sea (apart from perhaps smaller body size as a consequence of oligotrophy) have not been posited, but it is likely that molecular or enzymatic adaptations exist that allow successful exploitation of the unique challenges the deep sea and its various habitats pose.

Concluding, it emerges that it is not particularly useful to make a distinction between marine benthic ecology and deep-sea benthic ecology. This distinction would contribute to the perception of the deep sea as a disconnected and atypical ecosystem not relevant to society (Jamieson et al. 2020). Deep-sea benthic ecology really is just benthic ecology since the deep sea comprises over 98% of the oceans' depth range and most of the seabed surface.

Likewise, the study of deep-sea meiofauna is not some esoteric pursuit focusing on organisms that are tiny, strange, difficult to study, and ecologically irrelevant. On the contrary, meiofauna are a dominant component of benthic ecosystems and although there is still much to learn, our knowledge has increased dramatically owing to hundreds of deep-sea meiofauna studies covering thousands of sites sampled across the globe since the pioneering work of Wigley and McIntyre (1964).

Despite the progress, however, many questions about meiofauna in the deep sea remain. It is not surprising that also the diversity of topics being studied in this field seems to increase. Advances in technology and large integrative projects, often involving multiple nations, are improving access to the deep sea and therefore also access to meiofauna samples or ship time to conduct experiments. Advances in analytical procedures, notably in molecular science, with ever-decreasing sequencing costs and increasing resolution and reliability, help to generate vast amounts of new, previously inaccessible information. The multidisciplinary nature of the research is another notable advance. Many studies take advantage of diverse fields of study such as oceanography, modeling approaches, microbiology, geology, and biogeochemistry, to answer questions on the meiofauna patterns we observe: How do meiofauna organisms live and function in the largest, and therefore most characterizing environment on Earth—the deep sea?

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Chapter 9
Polar Meiofauna—Antipoles or Parallels?

Jeroen Ingels, Christiane Hasemann, Thomas Soltwedel, and Ann Vanreusel

Abstract At opposite ends of our world lie the poles. In the North, the Arctic, an ocean surrounded by coasts; in the South, the Antarctic continent surrounded by an ocean that separates it from the nearest landmasses. At first glance, the poles could not be more dissimilar owing to their contrasting location, geography, and tectonic and evolutionary history. The amplitude and types of ice cover, though differing between the poles, are influenced by the same climatic, atmospheric, and hydrodynamic processes that affect the entire Earth. Freshwater influx into their coastal areas too—beyond the effects of glaciological changes and dynamics such as glacier melt and increasing meltwater discharges—is different: in contrast to the Arctic, the Antarctic continent and sub-Antarctic islands lack major rivers. However, their latitudinal range and low temperatures, ice shelves, icebergs, sea ice, impacts from tidewater and land-based glaciers, significant seasonal variation in light intensity and, hence, primary productivity, offer parallel environments for organisms that have adapted to such conditions. Although we know much about the similarities and differences from an environmental perspective, there are still many unknowns about how benthic communities, especially the meiobenthos, from both regions compare. In this chapter, we provide an overview of the contrasts and parallels between Arctic and Antarctic meiobenthos and place it into context of their extreme habitats. Following a brief account of Arctic and Antarctic evolution and the historical study of their faunas, we (i) compare how extreme polar conditions affect meiofauna across four main habitats: polar coastal areas and fjords, continental shelves and ice shelves, the deep sea, and sea ice, and we (ii) discuss the implications of climate change on meiofauna in these habitats. Reflecting on (i) and (ii) allowed us to identify frontiers for

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future research of polar meiofauna, which we put forward in the concluding sections of this chapter.

9.1 An Old Continent and a Young Ocean—How Different or Similar Are the Poles?

"Old" continent. The Antarctic is separated from other continents by at least 1000 km and surrounded by some of the deepest and coldest seas in the world. In Palaeozoic times, the Antarctic was part of Gondwana, but continental drift in the Early Jurassic eventually separated an Antarctic continent from South America by a deep-water passage 23–32 million years ago (Lawver et al. 2014; Thomson 2004). Significant cooling of the Southern Ocean can be traced back to about 40 million years ago (Clarke and Crame 1992). Separation continued, opening the Drake Passage, leading to the appearance of the Antarctic Circumpolar Current (west to east) between 22 and 17 million years ago and the development of a separate Antarctic fauna, including meiobenthos (Crame 1999, 2014; Knox 2006). Along the northern border of the Antarctic Circumpolar Current, the cold Antarctic waters mix with the warmer sub-Antarctic waters forming the Antarctic Convergence (41–61° S). This maritime Polar Front, together with steep temperature and productivity gradients, the long period of isolation, and the occurrence of succeeding glacial and interglacial periods drove evolution and has led to distinct patterns in diversity and biogeography, with endemism on different taxonomic levels being a common phenomenon in Antarctic waters.

However, despite its depth, the Antarctic shelf has seen significant numbers of major and minor glacial advances in the last 2.6 million years, and up until about 11.7 thousand years ago, affecting benthic fauna. The origin and evolution of Antarctic benthos has therefore intrigued scientists for a long time and several hypotheses have been put forward. It may represent a relict autochthonous fauna, or consist of (i) eurybathic species derived from adjacent deep-water basins, (ii) abyssal species and sub-Antarctic species of predominantly northern origin, or (iii) species of Magellanic origin which have migrated to Antarctica via the Scotia Arc and vice versa (Knox 2006).

"Young" Ocean. With three million years, the Arctic ocean is a relatively young ecosystem that is regulated to a large extent by sea-ice cover (Clarke and Crame 2010; Grebmeier and Barry 1991). Hence, the period in which fauna has had the opportunity to generate distinct biogeographic and diversity patterns has been much more limited and shaped by recent glacial and interglacial processes. The Arctic seas comprise the waters over the continental margin of numerous adjacent shelves as well as the Barents and Bering Seas (Piepenburg 2005). Currently, the Arctic seas are characterized by very low, but relatively constant, water temperatures, and long-lasting seasonal ice cover. However, these seas were under the influence of temperate climate conditions throughout the Miocene (ca. 23 to 5 million years ago). Until then, the Arctic Ocean was largely ice-free and was connected with the Pacific and Atlantic oceans. The drastic decrease in sea temperatures started approximately four million years ago and intensified at the beginning of the Pleistocene (about 1.8 million years ago); a period that was characterized by alternations of cold glacial and warm interglacial climate conditions. The sea-level changes between these alternations caused the Arctic shelf areas to dry up or become covered by glaciers in the glacial intervals. In interglacial periods, the last of which started around 13,000 years ago, the environment was recolonized. These fluctuating processes, including massively destructive ice sheet incursions and subsequent recolonizations from relict populations, have shaped the evolutionary history of the contemporary Arctic fauna (Clarke 2003; Clarke and Crame 2010).

9.2 Brief Historical Perspective on Polar Meiobenthic Research

In the last few decades, a wealth of information has been obtained from meiobenthic studies in the Arctic and Antarctic regions, but polar meiobenthic research is not limited to the late twentieth and twenty-first centuries. The earliest Antarctic expeditions that yielded meiofauna information date back to the late nineteenth and early twentieth centuries, the Heroic Age of Antarctic Exploration (1897–1922). About 17 expeditions generated a vast number of samples and data, many of which served extensive taxonomic treatises. However, quantitative comparisons were challenging owing to the different sampling techniques and the explorative nature of sampling. Sampling was not necessarily based on detailed spatial sampling strategies or driven by ecological hypotheses, but rather determined by discovery and documentation as main purposes. For instance, the first Antarctic scientific expedition "Expedition Antarctique Belge 1897–1899"[1] resulted in many scientific reports on meiobenthic taxa,[2] including Nematoda (De Man), Copepoda (Giesbrecht), Ostracoda (Müller), Tanaidacea (Monod), and Turbellaria (Böhmig). Apart from continuing taxonomic treatises, a hiatus followed until late in the second half of the twentieth century, when interest renewed nationally and internationally, leading to multiple sampling efforts and expeditions. These were mostly associated with the development of multidisciplinary research programmes at research stations or based on deep-sea expeditions, with mainly international consortia using large research vessels capable of breaching annual sea ice to access various regions of the Southern Ocean. Forty-two countries operate seasonal and year-round research stations in the Antarctic with most of them having direct access to the coastline. Only a few stations were established prior to

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[1] The Belgian Antarctic Expedition under the command of A. de Gerlache de Gomery – Summary Report of the Voyage of the Belgica in 1897–1898-1899; digitally available at https://core.ac.uk/download/pdf/80828963.pdf

[2] The data and scientific reports from the Belgian Antarctic Expedition (1897–1899) are digitally available via http://www.vliz.be/en/imis?dasid=4228&doiid=68.

the 1940s, followed by a substantial post-second world war expansion. Ecological research only became more prevalent much later, with several studies appearing in the 1980s and 1990s when the drive to advance ecological knowledge of the environment from an ecosystem perspective took hold. To the best of our knowledge, early ecological papers on Antarctic meiofauna started to be published in the 1980s, intensified in the 1990s and became more prevalent in the twenty-first century.

Similar to the situation in the Antarctic, scientific interest in the Arctic has increased dramatically since the 1980s (Dayton 1990; Dayton et al. 1994; Piepenburg 2005), and is now seeing a veritable revival, owing to the reduced annual ice cover as a consequence of climate change, the opening up of the Arctic Ocean, and the subsequent economic and ecological consequences. This has been resulting in numerous larger national and international research projects and programmes. Ecological meiobenthic studies in the Arctic may well outnumber equivalent studies in the Antarctic (Table 9.1 for deep-sea studies). Perhaps even lesser known is the fact that the Arctic seas off Russia and Siberia had been extensively explored throughout the twentieth century, but the resulting—mostly Russian—publications remained relatively inaccessible to the international community until English translations of these works were published in the 1960s and 1970s, whereas more recently, taxonomic and ecological studies of meiofauna from Eurasian-Arctic areas are mostly available in international journals.

9.3 Meiofauna Along Polar Seascapes—From Coasts to Shelf and the Deep Sea, Including Sympagic Ecology

How are the extreme polar conditions affecting meiofauna? We will address four main habitats: subtidal meiofauna from sheltered bays and fjords connected with glaciers, continental shelf meiofauna and communities associated with ice shelves, sympagic meiofauna, and deep-sea meiofauna. We will look for parallels and contrast between polar regions (Table 9.2).

9.3.1 Polar Coastal Areas and Fjords

Despite the differences in geological history, polar coastlines share several geomorphological features such as the numerous sheltered bays and fjords, but also the exposed coarse-grained sandy and gravel-dominated beaches (Fogg 1998). Polar and subpolar coasts are largely protected from strong wave activity by the development of sea ice and a shore-fast ice-foot in winter, as well as ice shelves where they occur. However, polar coasts experience strong erosional forces from the seasonal freeze and melt cycle of sea ice and when wave activity forces sea ice to scour the

Table 9.1 Meiofauna studies in Arctic and Antarctic regions > 200 m water depth

Region	Sampling dates	Water depth range (m)	Metazoan abundances	References
Northern polar regions (north of 75° N)				
SE Beaufort Sea, 70–72° N	October/November 2003; June–August 2004	250–530	23–3386	Bessière et al. (2007)
Eastern Greenland, Greenland Abyssal Plain, 75° N	October/November 1965	250–2250	550–1470	Thiel (1975)
E Greenland slope, 75° N	July 2000	656–3033	71–209*	Fonseca and Soltwedel (2007)*
Chukchi Sea slope, 75–77° N	September 2010	393–2300	235–628	Lin et al. (2014)
S Fram Strait, 76–77° N	August 1975	3208–3709	186–1068	Dinet (1979)
W and E Fram Strait, 76°N, 79° N	August 2006	~2000	242–2001	Fonseca and Soltwedel (2009), Fonseca et al. (2010)
Cross Arctic Section, 76–90° N	September 1991, July/August 1994	540–4273	28–639	Vanreusel et al. (2000), Renaud et al. (2006)*
W Novosibirskiye Island, Nansen Basin, 77–79° N	September 1993	1935–3237	418–700	Vanaverbeke et al. (1997)
E Fram Strait, 79° N	Summer 2000–2014	1280–5500	148–3409	Hoste et al. (2007); Gallucci et al. (2008a, b, 2009), Guilini et al. (2011)*, Hasemann and Soltwedel (2011), Hasemann et al. (2013, 2020), Soltwedel et al. (2013, 2017, 2020), Gorska et al. (2014, 2017)
E Greenland slope, 79° N	July 2018	1056–2558	83–245	Hoffmann et al. (2018)

(continued)

Table 9.1 (continued)

Region	Sampling dates	Water depth range (m)	Metazoan abundances	References
Kara Sea, 79–80° N	September 2015	241–335	378–1519	Portnova and Polukhin (2018), Garlitska et al. (2019)
Yermak Plateau, 80–82° N	July/August 1999	744–3020	175–568	Schewe and Soltwedel (2003)
Cross Arctic Section, 80–88° N	August/September 1991	258–4427	2–211	Kröncke et al. (2000)
Yermak Plateau, 81–82° N	1997, 1999, 2003, 2006	635–1232	136–601	Soltwedel et al. (2009)
Yermak Plateau, 81–83° N	July 1997	481–4268	220–3955	Soltwedel et al. (2000)
NE Svalbard, Nansen Basin, 81–82° N	July 1980	342–3920	342–1330	Pfannkuche and Thiel (1987)
Central Arctic, Alpha Ridge, Lomonosov Ridge, 84–88° N	July 1998	1270–3170	29–94	Schewe (2001)
Central Arctic, 84–90° N	July–September 1996	864–4187	68–247	Schewe and Soltwedel (1999)
Molloy Deep, 79° N	1997, 1999, 2000, 2001	5416–5589	935–1295	Soltwedel et al. (2003)
Southern polar regions (south of 60° S)				
W Antarctica, Drake Passage, 60–62° S	January/February 2002	2274–5194	75–2731	Gutzmann et al. (2004)
Weddell Sea, 61° S	April 2003	307	3409	Ingels et al. (2006)
Drake Passage, Weddell Sea, 62–64° S	January–March 2015	437–518	3049 -7196	Hauquier et al. (2015)
King Haakon VII Sea, 62–70° S	December 2007, January 2008	1935–5323	704–1193	Lins et al. (2014), Guilini et al. (2013)*
Weddell Sea, 63–64° S	February–April 2002	4541–4995	317–678*	Sebastian et al. (2007*)
E Antarctic Peninsula, Weddell Sea, 65° S	March 2002, December 2006, January 2007	242–4068	381–1792	Rose et al. (2015)

(continued)

Table 9.1 (continued)

Region	Sampling dates	Water depth range (m)	Metazoan abundances	References
E Antarctic Peninsula, Larsen B Area, Cold Seep, 65° S	January 2007, March 2011	818–820	2220–4205	Hauquier et al. (2011, 2016)*
Lazarev Sea, 66–71° S	January 1982	227–3580	111–2977	Parulekar et al. (1983)
Ross Sea, Scott and Admiralty seamounts, 67–75° S	March 2008	849–3543	236–7023*	Leduc et al. (2012)*
E Antarctica, Prydz Bay, 69° S	February/March 2006	525–722	120–320	Ingole and Singh (2010)
Weddell Sea, Kapp Norvegia, 71–72° S	January–March 1989	211–2080	815–5122	Vanhove et al. (1995, 1999)*
Ross Sea, 72–74° S	November–January 1994	432–587	192–1191	Fabiano and Danovaro (1999)
Weddell Sea, Halley Bay, 74–75° S	January–March 1989	339–1958	792–3119	Herman and Dahms (1992)

*only nematode data

shores. The short summers are mainly dominated by wave and sea-ice erosion at high latitudes and by wave activity at lower latitudes (Hansen et al. 2014).

Polar fjords. Most of the Arctic fjord research on meiofauna has been conducted around the Svalbard archipelago (mainly Spitsbergen). In the Antarctic, studies are limited to a few areas close to research stations. The few meiofauna studies that document coastal Antarctic fjord meiofauna have predominantly focussed on Potter Cove, a shallow bay under the influence of the Fourcade Glacier and Admiralty Bay, both on King George Island (Mayer 2000; Pasotti et al. 2012, 2014, 2015a, b; Veit-Köhler 2005, 2008). Potter Cove sediments contain rich meiofauna assemblages (18 phyla/orders), with nematodes dominating the metazoan fraction (90–95% abundance (Veit-Köhler 2005)), and peak meiofaunal densities of 1.5×10^6 ind. m^{-2}, despite the high disturbance levels in the bay (compared to Andvord Bay on the Western Antarctic Peninsula (WAP) for instance). Likewise, Martel Inlet on King George Island exhibited very high meiofauna densities (3.5–4.1×10^6 ind. m^{-2}), mainly driven by sedimentary features and food availability (de Skowronski and Corbisier 2002).

Food input and food reserves, even in winter, do not seem limiting for meiofauna (Pasotti et al. 2014), a pattern that may be related to the food bank hypothesis. This hypothesis, originally developed for the shelf systems along the Western Antarctic Peninsula (Mincks et al. 2005), postulates that phytodetrital material deposited from

Table 9.2 Summary information on the main environmental influences for the different polar habitats, and characteristics of their meiobenthic standing stocks (densities/biomass), community structure, diversity, and trophic complexity when information was available in literature

	Arctic				Antarctic			
	Coastal areas and fjords	Continental shelves	Sea ice	Deep sea	Coastal areas and fjords	Continental shelves	Sea ice	Deep sea
Main environmental influences	Sediment structure, often coarse sediments. Protection from strong wave activity by sea ice, ice-foot, ice shelves where they occur, but strong erosional forces from seasonal ice. Terrestrial influx from rivers and glacial discharge. Inner-outer fjord gradients owing to glacial effects, sedimentation, and freshwater input. Strong seasonal signal owing to ice cycles, terrestrial influx, and high seasonal marine food input	Possible terrestrial and freshwater influence from nearshore. Complex hydrodynamic, topographical, and ice influences, leading to increased heterogeneity on the seafloor. Strong seasonal influences related to ice cycles on the fringe of the Arctic Ocean, but perennial ice in the central area with stabile environment (not considering climate change induced ice melt)	3D matrix of the brine channels in the ice provides habitat, influenced by seasonal melt, and freeze of the ice	Ice-coverage, water depth, oxygen concentrations, water temperature, sediment type, near-bottom currents all influence the benthic communities in the Arctic deep sea. Benthic communities are strongly coupled to seasonal surface production and ice cycles, especially around the ice margin	Coarse sediments or fine in depositional (often in the middle basin) areas. Sedimentation may be more moderate than in the Arctic. Protection from strong wave activity by sea ice, ice-foot, ice shelves where they occur. Strong erosional forces from seasonal ice and glacial discharges (ice scouring). Terrestrial influx from glacial discharge and basal scouring. Inner-outer fjord gradients owing to glacial effects, sedimentation. High habitat heterogeneity owing to mix of soft sediments and drop stones, and high spatio-temporal variability in surface production. Hypoxia may occur owing to high POC flux in temperate fjords	Freshwater influence from nearshore owing to glacial melt and discharge, seasonal in many areas. Compared to Arctic, Antarctic shelves are deeper and seem less sensitive to seasonal food input when not covered by ice shelves; exploitation of food sources seems to be more gradual (i.e. foodbank hypothesis). Strong influence of ice shelves, precluding food provision to the benthos from above; only advective food supply sustains the benthic communities	3D matrix of the brine channels in the ice provides habitat, influenced by seasonal melt, and freeze of the ice	Ice-coverage, water depth, oxygen concentrations, water temperature, sediment type, near-bottom currents

(continued)

Table 9.2 (continued)

	Arctic				Antarctic			
	Coastal areas and fjords	Continental shelves	Sea ice	Deep sea	Coastal areas and fjords	Continental shelves	Sea ice	Deep sea
Meiobenthic standing stocks	Can be high despite relatively high disturbance levels in some areas, but generally lower than at lower latitudes at similar depths, unless in sheltered intertidal areas. Communities do not seem food-limited, resulting from high POC fluxes (i.e. no seasonal response to food influx). Glacial disturbance in inner bays and fjords may reduce standing stocks, especially in ice-prone areas	Low under ice shelves but high on open shelf. Distinct gradient influenced by terrestrial influx (low standing stocks at shallow depths) and surface water productivity (high standing stocks at mid-shelf depths as a result of high-productivity surface blooms). Highly heterogeneous owing to spatial and hydrodynamic variability, and linked to terrestrial sources	Can be very high, representing a significant biomass reservoir; mostly meiofauna tolerant to freezing. Habitat offers feeding grounds, nursery, and shelter from predators	Variable, following bathymetric gradient (cf. Figure 9.2 and9.3). Lower densities in the Central Arctic, with perennial ice precluding surface production influx to the deep seafloor	Very high despite relatively high disturbance levels in some areas; often higher than in comparable Arctic systems, but generally lower than at lower latitudes at similar depths unless in sheltered intertidal areas. Communities do not seem food-limited, resulting from high POC fluxes. Glacial disturbance in inner bays and fjords may reduce standing stocks, especially in ice-prone areas	Low under ice shelves owing to food poverty but high on open shelf; subject to slow recolonization after ice-shelf retreat or collapse. Evidence of food banks resulting from high surface water productivity, decoupling benthic standing stocks from seasonal influx	Can be very high, representing a significant biomass reservoir; mostly meiofauna tolerant to freezing. Habitat offers feeding grounds, nursery, and shelter from predators	Variable, following bathymetric gradient which may be stronger than in the Arctic (cf. Figure 9.2 and 9.3)

(continued)

Table 9.2 (continued)

	Arctic				Antarctic			
	Coastal areas and fjords	Continental shelves	Sea ice	Deep sea	Coastal areas and fjords	Continental shelves	Sea ice	Deep sea
Meiobenthic community structure, diversity, trophic complexity	High rates of sedimentation may lead to burial disturbance, reduced food availability, loss of habitat heterogeneity, and hence low diversity towards the inner-parts of fjords and nearshore. However, high spatial and temporal heterogeneity may increase diversity in fjord basins. Low trophic complexity possible owing to increased disturbance nearshore but high in basin and outer fjord owing to habitat and resource heterogeneity. Low diversity in ice-prone areas	Very low diversity/high dominance under ice shelf, high on open shelf	Relatively diverse considering the ecosystem (2–8 higher taxa). dominated by ciliates, copepods/nauplii	High diversity, high evenness	High rates of sedimentation may lead to burial disturbance, reduced food availability, loss of habitat heterogeneity, and hence low diversity towards the inner-parts of fjords and nearshore. However, high spatial and temporal heterogeneity may increase diversity in fjord basins. Low trophic complexity possible owing to increased disturbance nearshore but high in basin and outer fjord owing to habitat and resource heterogeneity. Low diversity in ice-prone areas	Very low diversity/high dominance under ice shelf, high on open shelf. Opportunists colonizing areas which have been ice-free (time scale: years)	Relatively diverse considering the ecosystem; dominated by Foraminifera, copepods/nauplii and turbellarians. Turbellarians dominate biomass. No rotifers or nematodes, which is in contrast with the Arctic	High diversity, high evenness

the summer bloom provides a sustained source of food for benthic detritivores during winter months, when organic matter flux from the water column is extremely low.

On King George Island, the retreat of Fourcade Glacier has resulted in meiofauna dominating benthic colonization following glacial melting (Pasotti et al. 2015a). Glacial-related disturbance may enhance trophic diversity, most likely by allowing continuous, rapid recolonization by diverse meiofauna (Pasotti et al. 2015b). Results from stable-isotope tracer experiments suggested that different meiofauna can feed selectively on the different food sources available, and that their trophic plasticity allows them to exploit high Particulate Organic Carbon (POC) fluxes in this fjord-like ecosystem (Pasotti et al. 2012). Meiobenthic abundance and biomass are frequently positively correlated with POC flux, especially in low-current, fine-sediment habitats similar to the WAP fjord basins and the open WAP shelf (de Skowronski and Corbisier 2002; Lins et al. 2014). Greater POC flux enhances food availability and carrying capacity for benthic detritivores in general, supporting also greater meiobenthic community abundance and biomass (Rex et al. 2006; Soltwedel 2000; Wei et al. 2010). High rates of terrigenous sedimentation may also alter the enhancing effects of high POC flux by diluting food for detritivores and causing physiological stress through burial (Lohrer et al. 2006; Norkko et al. 2002; Wlodarska-Kowalczuk et al. 2005).

In general, the steep environmental gradients created by sedimentation processes and freshwater input are reflected in the benthos. From the open water towards the inner part of a fjord, water depth and oceanographic conditions decrease while glacier effects increase, reducing abundance, biomass, and diversity of meiofauna taxa in the same way as for macrofauna. Patterns of decreasing density, biomass, and biodiversity of meiofauna towards the active glacier have been observed in different fjords on Svalbard (Kongsfjorden (79° N) (Jima et al. 2021; Kotwicki et al. 2004); Adventfjorden (78° N) (Pawłowska et al. 2011; Włodarska-Kowalczuk et al. 2007, 2016); Hornsund Fjord (77° N) (Grzelak and Kotwicki 2012). The inner fjords close to the glacier show low faunal abundance and biomass, independent of water depth due to sedimentation of inorganic particles and sediment instability. Both nematodes and copepods seem to be affected, resulting in low densities or occasionally even absence of these taxa. Despite the intense disturbance, no specialized nematode assemblage has been reported in the area with strongest deposition of sediment (Somerfield et al. 2006). The combined survey of meio- and macrobenthic communities in several of these studies showed a similar sensitivity to sediment instabilities and physical disturbance caused by high sedimentation (Włodarska-Kowalczuk et al. 2007). This has also been demonstrated for the meiofauna (Giere 2009) and its dominant components, the Nematoda (Leduc et al. 2012; Moens et al. 2013; Schratzberger et al. 2009) and Copepoda (Guidi-Guilvard et al. 2009, 2014; Hicks 1984; Hicks and Coull 1983) (for more details see Chap. 7 on effects, patterns and processes of disturbances on meiofauna). Biodiversity patterns in Arctic subpolar fjords are consistent with general ecological predictions; high rates of terrigenous sedimentation (> 2 cm year^{-1}) cause intense burial disturbance, reduction of food availability (through food dilution), and loss of habitat heterogeneity, yielding low species diversity and trophic complexity in inner-middle fjords, with biodiversity increasing down fjord to the open shelf (Renaud et al. 2007; Syvitski et al. 1989; Wlodarska-Kowalczuk et al. 2005). Meiofauna abundance increases with increasing distance from the source of disturbance caused by tidal glaciers (Grzelak and Kotwicki 2012) and a clear environmental gradient owing to glacial disturbance effects is reflected in distinct meiofauna communities along Arctic fjords axes (Grzelak and Kotwicki 2012; Kotwicki et al. 2004; Somerfield et al. 2006).

While the same processes are at play in **Antarctic fjords**, preliminary data and ecological theory suggest that here biodiversity forcing—particularly along the WAP—differs from that in the Arctic:

- Terrigenous sedimentation rates appear to be more moderate in the middle basins of WAP fjords; with for instance, 0.03–0.2 cm year^{-1} in the middle Andvord Bay basin (Kennicutt et al. 2014; Powell and Domack 1995),
- Elevated productivity in the fjords is likely to offset moderate sedimentation stress (Huston 1994)
- The middle-outer basins of WAP fjords are likely to contain high habitat heterogeneity resulting from juxtaposition of soft sediments and drop stones, and high spatio-temporal variability in trophic resources resulting from seasonal phytoplankton blooms, krill falls, and whale faeces, and the cascade of macroalgal detritus as well as the spatio-temporal trophic processes that influence the distribution of these food sources when they descend to the seafloor (Ingels et al. 2021).
- Hypoxia/anoxia resulting from very high POC flux and/or limited bottom water exchange reduces metazoan standing crop and body size in many benthic habitats, including temperate fjords (Dias et al. 2002; Levin et al. 2009; Middelburg and Levin 2009; Pearson and Rosenberg 1978). Although low oxygen levels and reducing sedimentary conditions may not affect the standing stock of the nematodes to the same extent as other meiofauna, nematode community structure and biodiversity are altered and despite rapid colonization by certain species, recovery may be a lengthy process (Austen and Wibdom 1991; Cook et al. 2000; Hua et al. 2006; Josefson and Widbom 1988; Levin 2003).

It is clear that habitat heterogeneity and processes such as disturbance, production, and trophic interactions all work in concert on different spatial and temporal scales in fjord ecosystems, which leads to a complex picture of observable patterns in meiobenthic communities. All of these sources of heterogeneity may enhance meiofaunal taxon diversity and trophic complexity in fjord basins and will affect meiofaunal contributions to ecosystem processes (Ingels and Vanreusel 2013; Levin and Dayton 2009; Snider et al. 1984; Vanreusel et al. 2010).

Remarkable—although similar as for macrofauna—is the absence of a response in Arctic subtidal meiofauna to a marked seasonality in pelagic phytodetritus fluxes. Włodarska-Kowalczuk et al. (2016) suggested that the presence of organic matter reserves in sediments is large enough to sustain the detritus feeders on a year-round basis, in parallel with the food bank hypothesis formulated for Antarctic shelf sediments (see above; Mincks et al. 2005). Variations in meiobenthic population density and structure seem to be regulated by input and availability of organic matter and less so by water temperature. The absence of a "winter decline" in densities supports the idea that food is not limiting in the Antarctic coastal areas.

The densities of meiofauna taxa can be significantly higher in Antarctic than in Arctic subtidal areas (de Skowronski and Corbisier 2002). Occasionally, densities up to 18,000 ind. 10 cm^{-2} have been recorded (Vanhove et al. 2000), while in the Arctic, the maxima recorded so far lie below 4000 ind. 10 cm^{-2} (Table 9.3). However, a high spatial variability in Antarctic areas is characteristic too (Stark et al. 2017, 2020), similar as for Arctic fjords in relation to glacier impacts, but very much dependent on the local conditions. The comprehensive study by Stark et al. (2020) on the meiofauna (focussing on nematodes and copepods at locations around Casey station, East Antarctica, and comparing other Antarctic meiobenthos studies) suggested that within the Antarctic region, differences in primary productivity, sea ice, and temperature define the meiobenthic differences observed, and encompass significant spatial variability in nearshore environments. Here, the colder and more ice-prone area around Casey station in East Antarctica resulted also in lower abundances and diversity compared to those of the Antarctic Peninsula region.

Coarse sediment beaches—like elsewhere in the world—do not seem to be a suitable habitat for meiofauna taxa (Włodarska-Kowalczuk et al. 1998), except for Turbellaria which can occasionally be found as the dominant taxon (Kotwicki et al. 2005; Urban-Malinga et al. 2005). Kotwicki et al. (2005) studied latitudinal patterns in meiofauna biodiversity in sandy littoral beaches and found that both the Arctic and Antarctic beaches exhibited much depressed densities compared to temperate, subtropic and tropic areas. In addition, and most relevant for our considerations here, they documented that the meiofauna communities from the Arctic and Antarctic were in fact more similar to each other than to communities from lower latitudes, suggesting similar polar environmental conditions could result in similar communities (at least at higher taxon level).

While diversity was low at higher taxon level in the above studies, others suggest that Antarctic diversity is likely underestimated (Fonseca et al. 2017). In addition, the more sheltered **intertidal areas** show meiofaunal densities and diversities similar to those in temperate areas (Bick and Arlt 2005). This refers particularly to the subsurface layers where meiofauna densities appear to be higher than at the surface (Urban-Malinga et al. 2005). In Arctic eulittoral areas, with their large salinity fluctuations, diversity was reduced with juvenile oligochaetes (enchytraeids) dominating. The Antarctic intertidal is even less studied. The expected poverty in biodiversity and the lack of tidal sandy beaches has kept scientific interest low. However, as deposition zones for macroalgae and resting places for birds and mammals, some beaches are expected to receive a high organic load and may be very suitable habitat for meiofauna.

Table 9.3 Nematode studies in Arctic and Antarctic regions > 200 m water depth

Region	Sampling date	Water depth range (m)	Nematode density (ind./10 cm^2)	Nematode diversity	Dominant genera	Reference
Northern polar regions (North of 70°)						
Haakon Mosby Mud Volcano, 72° N	June/July 2003	1255–1885	N/A	4–65 ($EG_{(600)}$)	*Halomonhystera, Microlaimus, Metalinhomoeus, Aponema, Dichromadora, Sabatieria, Molgolaimus, Metalinhomoeus, Dichromadora*	Van Gaever et al. (2006, 2009, 2010)
E Greenland slope, 75° N	July 2000	656–3033	~71–209*	0–2.8 ($H_{(loge)}$)	*Thalassomonhystera, Acantholaimus*	Fonseca and Soltwedel (2007)
Cross Arctic Section, 76–90° N	September 1991, July/August 1994	540–4273	1991: 51–1100 1994: 0.3–2367	1991: 50 genera in total (23–29 genera per station) 1994: 111 genera in total (16–52 genera per station)	*Monhystera, Acantholaimus, Daptonema, Campylaimus, Amphimonhystrella, Halalaimus, Aegialoalaimus, Sphaerolaimus, Leptolaimus, Metalinhomoeus*	Vanreusel et al. (2000)

(continued)

Table 9.3 (continued)

Region	Sampling date	Water depth range (m)	Nematode density (ind./10 cm^2)	Nematode diversity	Dominant genera	Reference
W-Novosibirskiye Island, Nansen Basin, 77–79° N	September 1993	230–3237	361–2133	95 genera in total, 30–56 (N0)	*Chromadora, Halalamius Leptolaimus, Metalinhomoeus, Monhystera*	Vanaverbeke et al. (1997)
E Fram Strait, 79° N	Summer 2000–2014	1280–5500	315–3091[1], 920–1703[2], 407–1406[3], 1223[4], 1467 (m.v.)[5], 1494–2884[6], 1477 (m.v.)[7], 1035 (m.v.)[8], 134–3093[9], 237–2054[10]	8–12 ($EG_{(30)}$) 8–24 ($EG_{(50)}$) 16 $EG_{(51)}$) 18–30 $EG_{(100)}$) 30–59 $ES_{(100)}$)	*Monhystrella, Tricoma, Acantholaimus, Halalaimus, Desmoscolex, Microlaimus, Thalassomonhystera, Daptonema, Leptolaimus, Sabatieria, Leptolaimus, Theristus*	Hoste et al. (2007)[1], Gallucci et al. (2008b)[2], 2009)[3], Guilini et al. (2011)[4], Hasemann and Soltwedel (2011)[5], Hasemann et al. (2013[6], 2020)[7], Soltwedel et al. (2013[8], 2020)[9], Grzelak et al. (2017)[10]
Amerasin Basin, 79°–87° N Eurasin Basin, 84°–90° N Lomonosov Ridge, 87°–88° N	1991/1994	1000–3475 3844–4273 1020–2150	N/A (1615 in total)	20 ($EG_{(125)}$) 17 ($EG_{(125)}$) 20 ($EG_{(125)}$)	*N/A*	Renaud et al. (2006)

(continued)

Table 9.3 (continued)

Region	Sampling date	Water depth range (m)	Nematode density (ind./10 cm^2)	Nematode diversity	Dominant genera	Reference
Southern polar regions (south of 60°S)						
King Haakon VII Sea, 62–70° S	December 2007, January 2008	1943–5323	2007: 833 2008: 1102	29–39 (EG$_{(100)}$)	*Desmoscolex, Acantholaimus, Tricoma, Halalaimus, Actinonema, Desmodora, Microlaimus, Chromadorina, Paramesacanthion, Sabatieria, Dichromadora*	Guilini et al. (2013)
Wedell Sea, 63° S Drake Passage, 62° S	January–March, 2013	475–517 488–497	5532 2751	26 (EG$_{(200)}$) 33–35 (EG$_{(200)}$)	*Microlaimus, Linhomoeus, Daptonema, Sabatieria, Halalaimus Terschellingia*	Hauquier et al. (2015)
Weddell Sea, 63–64° S	February–April 2002	4541–4871	~ 300–700 (m.v.)*	22–32 (N0)	*Thalassomonhystera, Microlaimus, Acantholaimus, Theristus, Halalaimus Southerniella, Chromadorita*	Sebastian et al. (2007)

(continued)

Table 9.3 (continued)

Region	Sampling date	Water depth range (m)	Nematode density (ind./10 cm^2)	Nematode diversity	Dominant genera	Reference
E Antarctic Peninsula, Larsen A/B Area, (S, N, W), 65° S E Antarctic Peninsula, Larsen B Area, Cold Seep, 65° S E Antarctic Peninsula, Kapp Norvegia, 65° S E Antarctic Peninsula, Halley Bay, 65° S E Antarctic Peninsula, Drake Paasage, 65° S	January 2007	819–820	2107–4125 (data only for Larsen B Area available)	8–18 ($EG_{(51)}$) 5 ($EG_{(51)}$) 24 ($EG_{(51)}$) 26 ($EG_{(51)}$) 18 ($EG_{(51)}$)	*Halomonhystera, Ethmolaimidae gen. nov., Theristus, Daptonema*	Hauquier et al. (2011)
E Antarctic Peninsula, Larsen B Area, South 65° S E Antarctic Peninsula, Larsen B Area, West 65° S	March 2011	405–422 275–288	2548 4832	24 ($EG_{(200)}$) 6 ($EG_{(200)}$)	*Microlaimus, Monhystrella, Halomonhystera, Chromadorita, Leptolaimus, Dichromadora*	Hauquier et al. (2016)

(continued)

Table 9.3 (continued)

Region	Sampling date	Water depth range (m)	Nematode density (ind./10 cm^2)	Nematode diversity	Dominant genera	Reference
E Antarctica, Prydz Bay, 69° S	February/March 2006	525–722	109–245	2.07–2.23 (H’)	*Paralinhomoeus, Sabatieria, Axonolaimus, Terschellingia, Araeolaimus, Sphaerolaimus, Daptonema, Siphonolaimus, Theristus, Chromadorella, Halalaimus*	Ingole and Singh (2010)
Ross Sea, 74° S	March 2008	849	7023	22 ($ES_{(51)}$)	*Monhysteridae, Sabatieria,*	Leduc et al. (2012)
Ross Sea, 72° S		1604	777	30 ($ES_{(51)}$)		
near Admirality Sea mount, 66°		3403	338	34 ($ES_{(51)}$)		
near Scott Sea mount, 67°		3245–3543	236–450	20–31 ($ES_{(51)}$)		

Nematode diversity as estimated number of genera/species per number of individuals ($EG_{(n)}/ES_{(n)}$), Hill numbers (N0) and Shannon–Wiener index (H'). m.v. = mean value. * = no information in the text, values are taken from figures

9.3.2 Polar Continental Shelves and Ice Shelves

In recent decades, a major driver of benthic research on Antarctic shelves has been the retreat and collapse of ice shelves (Ingels et al. 2021). Most Antarctic ice shelves have covered the continental shelves for thousands of years, impoverishing the benthic communities by exclusion of local primary productivity and export of detrital food sources to the sea floor. However, some studies have documented life underneath ice shelves, including meiofauna (Ingels et al. 2021 and references therein). For instance,

- Pawlowski et al. (2005) documented meiobenthos from underneath the Ross Ice Shelf 450 km away from the open sea, including nematodes, polychaetes, oligochaetes, sipunculids, molluscs, and cumaceans (all passing through a 0.5 mm sieve and retained on a 125 μm mesh sieve). One litre of sediment contained 16 foraminifera morphotypes and 18 unique phylotypes.
- Studies at boreholes through the McMurdo, Armery, and Filchner-Ronne ice shelves (Griffiths et al. 2021; Kim 2019; Riddle et al. 2007) have documented sessile, filter feeding communities, and suspension feeders underneath the ice 16–80 km, 100 km, and 625–1500 km away from the nearest source of primary production, respectively (Griffiths et al. 2021; Kim 2019; Riddle et al. 2007). This suggests that advection of food fuels the benthos underneath ice shelves and challenges the contention that resources are so limited that benthic life diminishes with increasing distance away from open water and further underneath ice shelves.
- A benthic sampling campaign in Larsen A and B (ice shelves at the Antarctic Peninsula; ice-free since 1995 and 2002, respectively) revealed sub-ice communities characterized by low densities and low diversity (Raes et al. 2010). Opportunistic nematode species dominated, suggesting that they took advantage of the increased food supply in the sediments, while other species were absent. Nematode diversity was elevated at locations that had been ice-free for 12 years, but densities were still low and dominance of opportunistic species high, suggesting that those meiofauna communities represented a later stage of succession. The composition of the meiofauna still showed some minor differences with offshore shelf communities, when the area was revisited by Hauquier et al. (2016). From the same study, a revisited inner station nine years after ice-shelf collapse still showed a species-poor community dominated by monhysterids that represented 94% of all nematodes. However, densities had increased nearly tenfold between 2007 and 2011. This confirms the slow colonization by species other than monhysterids, which seemed the only taxon that could take advantage of the available food supply resulting in strongly elevated densities. Rose et al. (2015) reported that meiofauna communities that were no longer underneath an ice shelf, still showed more resemblance with communities from the oligotrophic deep Weddell Sea than with shelf sites that had been receiving surface input for a longer period of time (see also Ingels et al. 2021).

Ecological research suggests that the strong seasonality of productive waters overlying continental shelf environments in the Antarctic does not necessarily result in seasonal patterns of sedimentary labile organic material and microbial biomass (Mincks et al. 2005). Composition of macrofauna communities seems to confirm this, with the year-round presence of small juveniles suggesting continuous recruitment albeit with periodic enhancement coinciding with resource enrichment from seasonal bloom events (Mincks and Smith 2007). In addition, trophic analyses suggest inertia in benthic-pelagic coupling on the Antarctic shelf, with sediments integrating long-term variability in receiving seasonal surface water input (Mincks et al. 2008).

These observations have been captured in the food bank hypothesis (see above; Mincks et al. 2005) and have been confirmed for meiofauna (particularly nematodes and copepods) at Antarctic shelf depths by Veit-Köhler et al. (2018). Cold conditions could enhance the persistence of food resources on the Antarctic deep-shelf, but climate change will likely drastically change these standing-stock-enhancing food conditions and alter pelagic-benthic coupling (Veit-Köhler et al. 2018).

In the Arctic, distinct gradients in sedimentary food sources are observed along the continental shelf depth gradient (McMahon et al. 2021). The Canadian Beaufort Sea is characterized by an organic carbon reservoir fed by terrestrial nutrients fuelling surface water production and under ice primary production. Terrestrial factors dominating shallow shelf sites limited meiofaunal populations, while benthic production at deep sites was limited by low levels of labile organic matter. At mid-shelf depths, however, peak densities of diatoms and dinoflagellates corresponded with higher meiofaunal abundance (McMahon et al. 2021). These observations indicate the importance of terrestrial versus marine input in shelf benthic systems, as well as the highly variable spatial distributions of meiofauna communities in the Arctic compared to the Antarctic.

High spatial variability in Arctic shelf sediments has also been observed in the Northeast Chukchi and Beaufort Seas when considering nematode genus composition (Mincks et al. 2021) and for meiofauna in general along a depth gradient that included the Barents Sea shelf and slope (Oleszczuk et al. 2021). While the quality and quantity of sedimentary organic matter sources drove broad spatial and bathymetric gradients in nematode communities, local patchiness as observed in nematode genus differences within the various sampling areas were mainly driven by grain size, and possibly related to complex hydrographic patterns and disturbance events (Mincks et al. 2021). Interestingly, the distribution patterns of the dominant nematode genus *Sabatieria* in Mincks et al.'s (2005) samples suggest a potential relation with high organic loading and limited oxygen availability in Arctic areas under the influence of large river systems. Further, in the Beaufort Sea, Bessière et al. (2007) reported large numerical variability in meiofauna communities (2.3×10^5 to 5×10^6 ind. m^{-2}) as well as spatially and seasonally changing dominance of different taxa). This suggests the presence of meiofauna communities that are responsive to changing environmental conditions and not representative of a continuously available food reservoir as proposed for Antarctic shelf sediments. Moreover, significant relationships found between sediment-bound photopigments and various meiofauna taxa point to sediment phytodetritus as main food source for the meiofauna. Also carbon-based grazing models suggest that meiofauna in Arctic shelf sediments may be significant and responsive consumers of phytodetrital material (Bessière et al. 2007).

9.3.3 Sea Ice and Sympagic Meiofauna

Sympagic meiofauna spend all or part of their life cycle in the ice, living mainly in the brine cavities within the sea-ice matrix. Most organisms live near the bottom of the sea ice in close contact with the pelagic and benthic sub-ice environment. A surprisingly large amount of information on sympagic systems of the Arctic has been gathered since the 1980s—see review by Bluhm et al. (2018). However, large gaps in knowledge on Antarctic sympagic fauna remain and present a promising ecological and physiological research frontier.

This fauna must be environmentally adaptable considering the dynamics of sea-ice and the seasonal advance and retreat of this special habitat. It has been shown that copepods in particular are tolerant to the extreme conditions. They withstand freezing for short periods of time and reproduce several times per year unaffected by winter conditions (Ehrlich et al. 2020). Nematodes and rotifers are also successful ice-inhabitants—evidenced by their pan-Arctic distribution associated with ice—owing to their ability to produce resting stages (Bluhm et al. 2018). The brine channel network and ice-water interface provide habitable space that can serve as a feeding ground, nursery for juveniles, and offer shelter from predators, so that meiofauna can be abundant (10–10,000 s of individuals per cubic metre of ice; (Bluhm et al. 2018; Schnack-Schiel et al. 2001)). Numerous eggs and juveniles of different taxa (nematodes, polychaetes, harpacticoids) are observed regularly, suggesting that ice may have a sheltering nursery function for sympagic species (Gradinger and Bluhm 2020; Marquardt et al. 2011; Nozais et al. 2001).

Sea ice of the Weddell Sea was dominated by foraminifera (75% of total meiofauna abundance) and by turbellarians in terms of total biomass (45%; Schnack-Schiel et al. 2001). Meiofauna was concentrated in the lowest parts of the sea ice, especially in winter and autumn, whereas in summer time, meiofauna occurred much higher up in the ice matrix (Schnack-Schiel et al. 2001). The most recent comprehensive study of sympagic meiofauna was conducted by Ehrlich et al. (2020), covering numerous stations in a large area north of Svalbard and sampling organisms both inside the ice as underneath the ice: diverse assemblages with more than 17,000 ind. m^{-2} were reported. Ciliates dominated the assemblages (46%), followed by copepod nauplii (29%) and harpacticoid copepods (20%).

Pelagic and benthic meiofaunal communities and sympagic assemblages are closely connected but information about the dynamics of exchange between these habitats in ice-covered regions is limited. To our knowledge only Leasi et al. (2020) specifically assessed meiofauna communities from all three habitats (pelagic, benthic, and ice) and investigated potential exchange between them across different seasons:

- Community patterns were distinct between habitats, even though the sedimentary environment was less than 5 m underneath the ice, but with notable shifts across habitats with changing seasons.
- Winter ice communities showed taxonomic similarities with spring benthic communities, and winter benthic communities were more similar to spring ice communities. These patterns were a result of the interaction between strong environmental selection and organisms' seasonal preference for particular habitats as well as life-history strategies.
- The exchange of taxa apparently occurred in April, around the peak of the algal bloom, suggesting that seasonality has an important role in the appearance and distribution of meiofauna in these habitats.
- Some taxa may be able to withstand the reduction or disappearance of ice by migrating and settling in either the pelagic or the benthic habitat. While these taxa may be able to withstand the habitat dynamics, other taxa are heavily dependent on the sea ice and the seasonal food sources may be at risk of disappearing because of climate change.

The present lack of detailed taxonomic resolution in many studies hampers conclusions regarding species-specific distribution patterns, although analyses of some species data suggest that broad species distribution ranges may be common. This is entirely plausible considering the pan-Arctic drift patterns of pack ice and consequentially high potential for connectivity and exchange (Bluhm et al. 2017). In a meta-analysis of sympagic meiofauna communities in the Arctic, Bluhm et al. (2018) reported that, across the Arctic ice cover, essentially the same sea-ice meiofauna higher taxa occur. Even comparisons between Arctic and Antarctic sympagic fauna did not indicate drastic differences, at least at higher taxonomic levels (Gradinger, 1999). Only rotifers and nematodes were restricted to the Arctic. Hence, comparisons between the Arctic and Antarctic sympagic fauna do not indicate substantial differences (at higher taxonomic levels).

Biomass transport with ice floes in the form of sympagic fauna (for instance amphipods) can be significant. About 80×10^3 t C year^{-1} of biomass has been estimated to be transported by ice floes to southern marginal seas from the Arctic (Hop and Pavlova 2008) and this can represent a substantial part of the total ice-derived particulate organic carbon (Gradinger and Bluhm 2020). Moreover, in some areas of the Arctic marginal ice zone, sinking material can be dominated by ice-algal matter fuelling benthic systems (Tamelander et al. 2008). Hence, climate-induced reductions of sympagic biomass may have consequences for the ice-associated food webs and the outfall to benthic systems underneath the ice.

Meiofaunal ingestion rates of ice algae can vary between seasons. Therefore, consumption of other food sources by sympagic meiofauna such as bacteria or dissolved organic matter seems plausible as suggested by isotope data (Gradinger and Bluhm 2020). Despite the close relationship between sympagic meiofauna and sea-ice algae, meiofauna grazing rates are generally lower than ice-algal production, implying sympagic meiofauna is not food-limited and most of the ice-algal production is available for consumption by pelagic and benthic organisms (Gradinger 1999, 2001).

9.3.4 Polar Deep Seas

9.3.4.1 Sampling for Meiofauna in Polar Deep Seas

Meiofauna research in polar deep-sea regions has seen much progress over the last decades, but the overall number of publications and sharing of resulting data remains low compared to meiofauna studies from other deep-sea regions. Meiofauna research in deep Arctic regions started in the late 1960s (Paul and Menzies 1974), while studies on deep-sea meiofauna in Antarctica started only in the early 1980s (Parulekar et al. 1983). Our literature review reveals 33 publications on Arctic deep-sea meiofauna (including those focussing exclusively on nematode assemblages), but only 16 from deep-sea regions off the Antarctic continent (Table 9.1).

Arctic and Antarctic deep-sea ecosystems differ in both the amplitude and nature of their ice-cover. Although generally decreasing in extension and thickness over the last decades, large parts in the central Arctic Ocean still hold (thicker) multi-year ice with small variations in extension (Cavalieri et al. 2003). The ice extending over the deep Antarctic Ocean is thinner and seasonally more variable that that in the Arctic (Comiso and Nishio 2008). These differences have fundamental effects on the primary production in both oceanographic regions, and subsequently on the settling of particulate organic matter to the deep seafloor, which represents the major food source for deep-sea benthic communities.

Without standardized techniques for sampling, sorting and biomass determination, comparison of meiofauna data from the literature poses a significant challenge (Rosli et al. 2018; Soltwedel 2000). For instance, investigators of polar deep-sea meiofauna have used multiple corers (26 studies), box corers (8 studies), Reineck grabs (1 study), and a Niemistö corer (1 study). All these differences in the sampling methods and sample processing affect the meiofauna data that have been produced so far. In addition, the limitations in spatial and temporal coverage of polar deep-sea meiofauna data remain limited (Fig. 9.1, Table 9.4). Thus, the following comparisons of deep-sea meiofauna stocks in the Arctic and Antarctic should be considered with caution.

Compared to the deep Arctic Ocean, vast regional meiofauna data gaps exist in the deep Southern Ocean.

9.3.4.2 Meiofauna Composition and Standing Stocks in Polar Deep Seas

Meiobenthic standing stocks in polar regions decrease with increasing water depth and distance from the coast because the energy content of settling organic matter

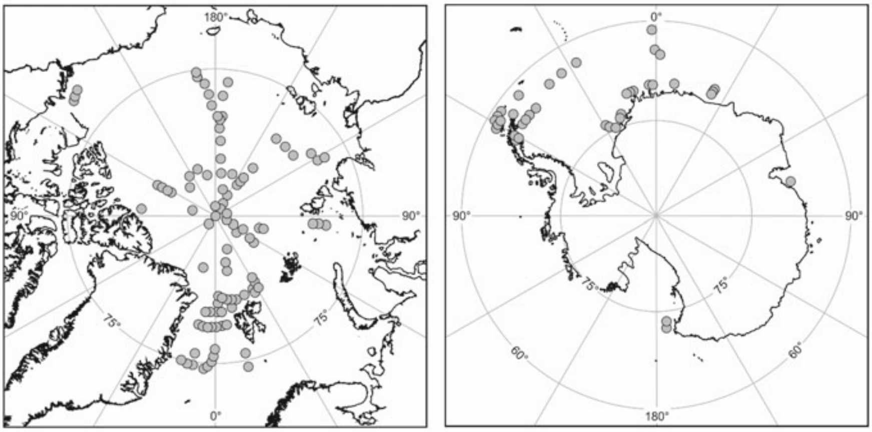

Fig. 9.1 Sampling locations for polar deep-sea meiofauna (> 200 m water depth) in the Arctic (left) and Antarctic (right). For details of data points arising from a total of 35 publications see Table 9.4

Table 9.4 Distribution of data points arising from 35 studies in the deep Arctic and deep Antarctic (for study locations see Fig. 9.1)

	Deep Arctic	Deep Antarctic
No. of data points	237	54
Geographic limit	Southernmost limit at 75° N*	Northernmost limit at 60° S
Distribution of data points	Two thirds of the data points are from the Fram Strait (Dinet 1979; Fonseca and Soltwedel 2007, 2009; Gorska et al. 2014; Grzelak et al. 2017; Hoffmann et al. 2018; Hoste et al. 2007; Soltwedel et al. 2003, 2020; Thiel 1975), including Yermak Plateau (Schewe and Soltwedel 2003; Soltwedel et al. 2003, 2009) All other data points cover Arctic cross-sections (Kroncke et al. 2000; Vanreusel et al. 2000), transects across the Gakkel, Lomonosov, and Alpha Ridges (Schewe 2001; Schewe and Soltwedel 1999), the Nansen Basin slope (Pfannkuche and Thiel 1987; Vanaverbeke et al. 1997), and slope transects in the SE Beaufort, Chukchi, and Kara Seas (Bessière et al. 2007; Garlitska et al. 2019; Lin et al. 2014; Portnova and Polukhin 2018)	Data points come almost exclusively from the Scotia, Weddell, and King Haakon VII seas between approx. 60°W and 30° E (Gutzmann et al. 2004; Hauquier et al. 2011; 2015; Herman and Dahms 1992; Ingels et al. 2006; Lins et al. 2014; Parulekar et al. 1983; Rose et al. 2015; Sebastian et al. 2007; Vanhove et al. 1995) Additional information comes from a few sites in the Cooperation and Ross Seas (70° E and 175° E, respectively) (Fabiano and Danovaro 1999; Ingole and Singh 2010)

*except SE Beaufort Sea with deep stations at 70–72° N generally decreases during degradation processes within the water column. Interestingly, meiofauna depth gradients in the peripheral Arctic and in Antarctic regions were almost identical (Fig. 9.2), with overall only slightly higher meiofauna densities in water depths between 200 and approx. 2000 m in southern polar regions. Data from the central Arctic Ocean with its perennial ice cover revealed overall significantly lower meiofauna densities, however, with a similar rate of decrease in the number of individuals with increasing water depth.

Higher taxon composition and standing stocks. There were no higher taxa restricted to either northern or southern polar regions. Total meiofauna densities in the deep Arctic Ocean range between 2 and 3955 ind. 10 cm^{-2}, while in the deep Antarctic Ocean, meiofauna numbers vary from 111 to 7196 ind. 10 cm^{-2} (Table 9.3). The proportion of single higher taxa within the meiofauna community could only be determined from nine studies in the North and four studies in the South. Nematodes usually dominate the polar deep-sea metazoan meiofauna with an average share of 91.0% in the Arctic deep sea (range: 65.9–99.1%) and 89.9% (range: 56.8–97.2%) in the deep Antarctic Ocean. Copepods (including nauplii) were second dominant with a mean relative abundance of 6.5% (range: 0–27.9%) in the deep Arctic and 5.3% (range: 1.0–34.9%) in the Antarctic Ocean. All other taxa made up 2.6% in the North and 5.0% in the South. Other taxa than Nematoda showed a stronger

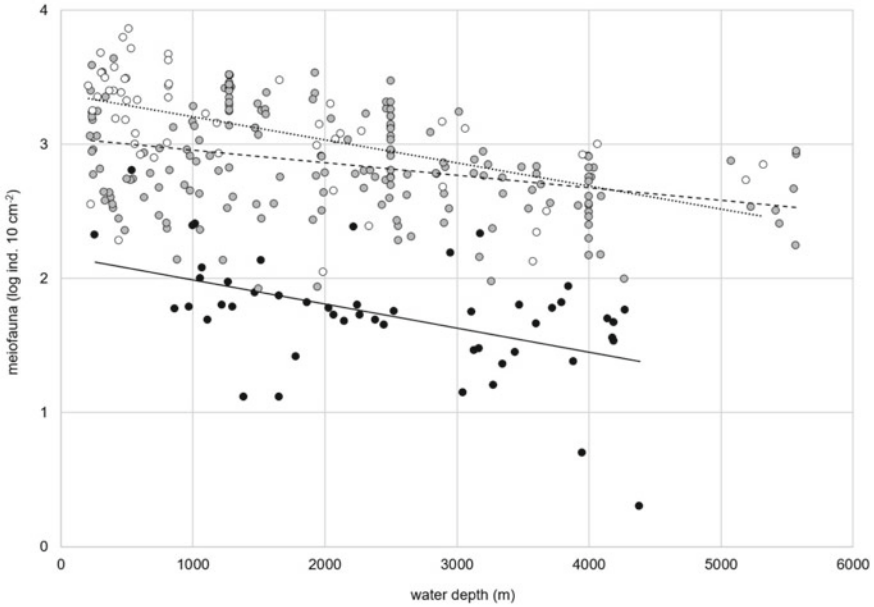

Fig. 9.2 Meiofauna densities in polar deep-sea regions (> 200 m water depth); data points/regression lines: black circle/straight line—central Arctic Ocean (n = 50), grey circle/hyphenated line—peripheral Arctic Ocean (n = 187), circle/dotted line—Antarctic Ocean (n = 54)

decline in relative abundance with increasing water depth in the Arctic, compared to the deep Antarctic Ocean. However, it is uncertain whether these differences truly reflect fundamental ecological differences or are the result of the low number of data points in Antarctic studies (29 data points, compared to 165 data points from Arctic studies).

Nematode standing stocks. In both hemispheres, gradients of nematode densities along increasing water depth generally resembled results for the total meiofauna (Fig. 9.2). However, the proportion of nematodes from the total meiofauna in Antarctic regions exhibited a slightly stronger decrease with increasing water depth, compared to those in the Arctic. Total nematode biomass followed the same trend with decreasing values along the bathymetric gradient in both the Arctic and Antarctic Ocean. In contrast, individual nematode biomass (data derived by dividing total nematode biomasses by the number of nematodes per site) showed no trend over the entire bathymetric range from 200 m down to > 5000 m water depth in peripheral Arctic and Antarctic regions. Udalov et al. (2005) generated a similar result when analysing a global set of nematode biomass data and concluded that this finding might reflect that individual nematode biomass is not just a function of food availability but also of other environmental characteristics, e.g. sediment grain size distribution or biogeochemical gradients. Mean individual nematode biomasses in the central, permanently ice-covered Arctic Ocean, however, showed clearly decreasing values with increasing water depth, implying that, here, nematodes on average decrease in size with increasing water depth.

Nematode composition and diversity. Like deep-sea areas worldwide, few families and genera dominate Arctic and Antarctic meiofauna (Table 9.3). Species diversity within some nematode genera was studied on Antarctic shelves and slopes (De Mesel et al. 2006; Fonseca et al. 2006; Ingels et al. 2006; Vermeeren et al. 2004), reporting high local and regional species diversity (Brandt et al. 2007). The highest number of co-existing species within the same genus was found for *Acantholaimus*, with 29 species recognized in only one sample (Brandt et al. 2007; De Mesel et al. 2006).

Studies in the deep Arctic Ocean that identified nematodes to genus or species level have been performed in the western Greenland Sea, the eastern Fram Strait, the Laptev Sea, and in the deep central Arctic, recording between 70 and 640 (putative) species, and between 29 and 180 genera (Table 9.3).

In the Antarctic, studies of nematode genera and species found between 94 and 137 genera in total, but Leduc et al. (2012) reported a species richness $ES_{(51)}$ between 20 and 34 species (water depths between 500 and 3500 m).

Although a vast number of Arctic and Antarctic deep-sea nematode species probably remains undiscovered due to chronic under-sampling, and despite the lack of specialists, we can generally state that deep-sea nematode communities are characterized by high alpha species diversity, where most species are represented by only few specimens; hence, a high evenness is typical (Miljutin et al. 2010 and citations therein; Vanaverbeke et al. 1997).

9.3.4.3 Food Availability—An Important Driver of Polar Deep-Sea Meiofauna

Food supply has been proven to structure benthic communities and several indices have been used to estimate flux rates of settling organic matter to the seafloor. For instance, concentrations of sediment-bound pigments, chloroplastic pigment equivalents (CPE), which comprise the bulk of intact chlorophyll *a* and its derivatives, were introduced as an indicator of food/energy availability from primary production in sea surface layers (Thiel 1978) and have been applied in numerous studies to explain spatial and temporal variations in benthic standing stocks. In the deep Arctic and Antarctic Oceans, a total of 14 meiofauna studies (one in the central Arctic, 10 in the peripheral Arctic, three in Antarctica) have provided information on the sedimentary pigment inventory. The analysis of meiofauna numbers and pigment concentrations from these studies (183 data points) reveals a statistically significant correlative relationship (Fig. 9.3), which is indicative of a close pelagic-benthic coupling. However, the large variation in the data suggests that their relationship is complex, and likely influenced by various other abiotic factors (e.g. pressure, water temperature, oxygen concentrations, sediment characteristics), in conjunction with biological processes in the water column (i.e. the degradation of organic matter in the pelagic food web), and interactions with other faunal groups (e.g. competition, predation).

Recognizing food availability in quantity and quality as a decisive factor for meiobenthic densities and the community composition, one should assume that regional differences at broader spatial scales exist. In polar regions, the marginal ice zone (MIZ) appears to be a region of enhanced primary production and subsequently increased input of particulate organic matter to the deep seafloor. Along a bathymetric transect of stations on the East Greenland continental margin crossing the MIZ off Greenland, Fonseca and Soltwedel (2007) found clear evidence for the impact of locally enhanced food availability on deep-sea meiobenthic communities. The amount of phytodetritial material was approximately threefold higher in sediments underneath the ice-edge and ice-free regions, compared to the shallower, but ice-covered stations of the transect. The increased amount of phytodetritus at these stations not only enhanced bacterial activities, but also meiofauna abundance and diversity (number of nematodes species).

Despite the traditional bathymetric decline of meiobenthic standing stocks, unusually high meiofauna densities and biomasses can occasionally be found at deep abyssal and hadal depths in polar regions. At about 5500 m water depth in the Molloy Deep (Fram Strait), Soltwedel et al. (2003) found metazoan meiofauna numbers in the range of 935–1295 ind. 10 cm^{-2}, similar to numbers recorded at 2500 m water depth off Svalbard. In Antarctica, Lins et al. (2014) reported a nematode biomass of 11.75 μg dry weight at 5323 m water depth in the Kong Haakon VII Sea, which is similar to the nematode biomass found at 1943 m water depth on the nearby slope off Dronning Maud Land (12.45 μg dry weight). Topographic settings and special hydrographic conditions are most likely responsible for the increased food

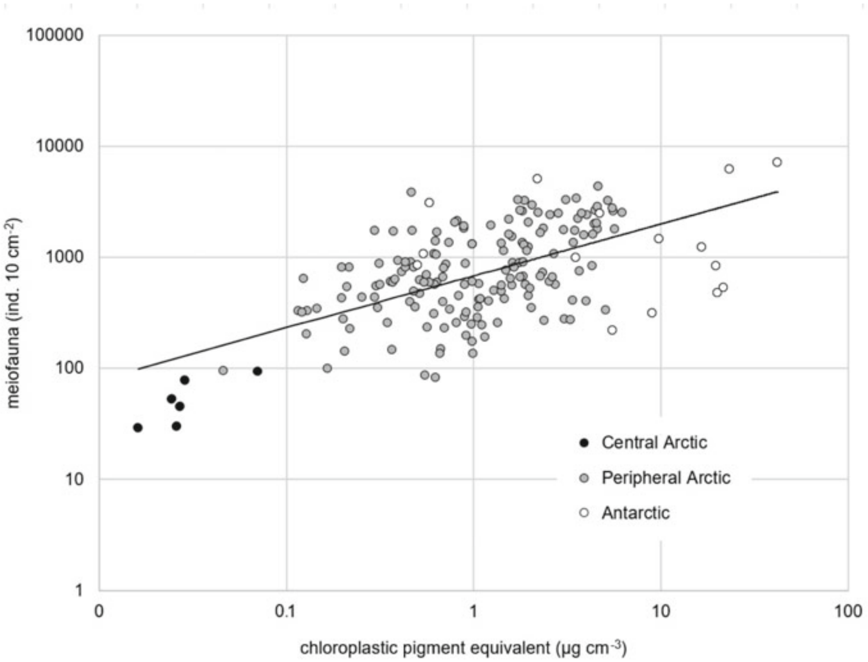

Fig. 9.3 Correlation between sediment-bound chloroplastic pigment equivalents (CPE) and meiofauna densities in the polar deep sea; double-logarithmic display; regression line for the entire data set

availability at some very deep sites which promotes increased meiobenthic standing stocks at these deep sites.

The decisive influence of food availability on meiobenthic assemblages (see above) is also visible in those polar regions that episodically face profound changes in the ice cover: the collapses of the Larsen A and B ice shelves at the eastern coast of the Antarctic Peninsula in 1995 and 2002 more or less instantly transformed an oligotrophic sub-ice ecosystem to a productive shelf ecosystem. Based on a comparison of meiobenthic diversity and composition (higher taxa) of Larsen continental shelf stations and deep stations in the adjacent Western Weddell Sea, Rose et al. (2015) could show that the food limitation in the shelf regime at times of ice-shelf coverage resulted in meiobenthic communities similar to those in the nearby deep sea.

9.4 Polar Meiofauna and Climate Change—Observations, Conclusions, Prognoses

As much as the polar regions of our globe differ, their ecosystems are both affected by climate change, which is altering the extent and dynamics of the cryosphere rapidly (Meredith et al. 2019). Global warming, mainly resulting from continued anthropogenic emissions, causes the loss of ice, ocean acidification, and changes other ocean conditions that alter patterns of primary production and subsequently benthic-pelagic coupling (Meredith et al. 2019). Much of the polar ocean ecosystem is modulated by ice dynamics and the associated biology and ecology of organisms (including ice-associated or sympagic communities). Climate change is therefore highly likely to cause profound and far-reaching consequences such as changing organic matter quality and quantity, and biological transformations of carbon and nutrient pools. Despite increased understanding of benthic meiofaunal communities in polar regions, it is currently not entirely clear how biodiversity of meiofauna will respond to climate change at varying scales of space and time (but see Ingels et al. 2012, 2021; Zeppilli et al. 2015), and what the resultant effects on the functioning of polar ecosystems may be. However, below we briefly summarize some findings that may shed some light on expected changes. For an overview on changing meiofauna in response to climate change, we also refer to Chap. 7, where the matter is discussed more generally in the context of disturbance effects.

While both polar oceans have continued to warm in recent years, the Arctic is suffering greatest and most rapid sea-ice loss (Yadav et al. 2020). In the Antarctic, climate change effects are mainly occurring along the Antarctic Peninsula, but are much less obvious in other Antarctic regions (Meredith et al. 2019; Meredith and King 2005; Turner et al. 2013; Turner et al. 2005). It is predicted that Arctic sea ice will disappear entirely in summer by 2040 (Serreze and Stroeve 2015), which will impact benthic organisms that are reliant on the surface productivity and sympagic production associated with sea ice. Potential effects can be deducted from the meiofauna standing stock data from the Central Arctic with perennial ice cover (Figs. 9.2 and 9.3). Densities there are much lower than in the peripheral Arctic Ocean and the Antarctic Southern Ocean owing to the severely limiting food supply to the benthos. While there is still a water depth gradient observable in the central Arctic Ocean, CPE values are orders of magnitude lower compared to the peripheral Arctic Ocean and the Antarctic, resulting in much lower densities (Fig. 9.3). The opening up of the Central Arctic Ocean will lead to increased food resources becoming available to the meiobenthos, potentially leading to colonization dynamics and shifts in standing stocks as observed in the Antarctic where ice shelves have retreated or collapsed. These changes will affect shelf depths as well as the polar deep seas. The shift from an ice-covered and cold ocean to an ice-free and warmer ocean will have severe impacts through altered algal abundance and composition (Nöthig et al. 2015), which will affect zooplankton community structure (Chiba et al. 2015) and subsequently the flux of particulate organic matter to the seafloor (Tamelander et al. 2017). Here, the changing quantity and quality of this matter will impact benthic communities

(Campanyà-Llovet et al. 2017; Jones et al. 2014; Kortsch et al. 2012)—including the polar meiofauna.

In shallow polar waters, meiobenthic dynamics in response to climate change may be more complex as the vicinity of land results in closer interaction with glacial effects such as terrestrial discharge, freshwater inflow, iceberg scouring, and drop stone incidences, which will inevitably bring significant changes to coastal ecosystems (Ingels et al. 2021; Rogers et al. 2020). In the sheltered bay on King George Island, meiofauna seems to respond differently from micro- and macrofauna to climate change effects such as glacier retreat with different functional traits responding in a different way to newly ice-free areas (Pasotti et al. 2014). Similar evidence from temperate environments suggests that species are feeding partly (but not necessarily selectively) on bacteria or microalgae. The specific roles of meiofauna in food web ecology have not yet been defined clearly, but current evidence suggests that meiofauna may exploit new conditions and available habitats very rapidly and benefit in the short term from climate-induced glacial changes in shallow waters (Pasotti et al. 2012). On the other hand, increased warming will initially lead to increased iceberg scouring, a physical disturbance which can remove more than 90% of the fauna (Lee et al. 2001a, b). However, this major physical disturbance is also assumed to lay at the origin of the high-latitude benthic biodiversity including the meiofauna (Peck et al. 1999). Over the longer term, as ice continues to retreat and diminish, iceberg presence, scouring, and the prevalence of drop stones (which can increase habitat heterogeneity) are expected to decrease. A similar scenario is expected in the Arctic, where latitudinal and time-series studies of Arctic fjords (Kędra et al. 2010; Syvitski et al. 1989) suggest that climate warming and glacial retreat will eventually reduce glacial disturbance in these fjords, yielding increased productivity and meiobenthic biomass and diversity.

With the strong decline in sea-ice cover over the past five decades, it seems very likely that sympagic fauna will lose significant habitat or disappear altogether (Bluhm et al. 2017), with ramifications for sympagic-pelagic-benthic coupling (Søreide et al. 2013) and pelagic and benthic food webs supported by ice algae and sympagic fauna. Potential shifts may have been observed already. Ehrlich et al. (2020) documented more diverse but less abundant assemblages underneath the ice compared to in the ice matrix in the Arctic, with 32 taxa belonging to eight phyla. However, nematodes and flatworms were not found, an observation supported by previous extensive work in the Arctic (Bluhm et al. 2018). Climate-driven sea-ice shifts may be behind this contrast, because the now-dominant first-year pack ice tends to form further offshore and harbour more pelagic-sympagic species compared to the multi-year land-fast ice or pack-ice formed on the shallow shelves that harbour more benthic-sympagic taxa (Ehrlich et al. 2020). This was confirmed by backtracking satellite data to investigate the origins of the ice floes that had been studied: the shift from a system dominated by multi-year ice with established sympagic communities to a system dominated by annual ice and hence yearly recolonization of new ice mass seems to favour sympagic fauna of pelagic origins. Kramer et al. (2011) supported a similar conclusion by comparing sympagic meiofauna from the perennially ice-covered western Weddell Sea and the seasonally ice-covered southern Indian Ocean: Perennial ice seems to be important for the establishment of abundant and diverse meiofaunal ice communities and as the climate continues to warm and the ice retreats further these communities are likely to impoverish as a result.

9.5 Gaps, Directions, and Methods in Polar Meiofauna Research

Ice coverage and harsh weather conditions in winter times generally impede the accessibility of polar regions. Although meiofauna studies in the Arctic and Antarctic Oceans have steadily increased over the last decades, it is not surprising that most sampling campaigns, whether at sea or from coastal research stations, are carried out in the northern and southern hemisphere's respective summer months. Hence, information about seasonal variations in meiobenthic communities is largely missing. This is especially the case for deeper waters or shallow waters far removed from research stations.

Since polar regions are generally only accessible by means of expensive modern infrastructure and instrumentation, multi-year time-series studies of Arctic and Antarctic marine ecosystems are very sparse, even near research stations where some long-term programmes do not necessarily include data on meiobenthos since the expertise may not be generally available or studies focussing on or including meiobenthos were of shorter duration—a few years at most (e.g. Signy, LTER Palmer, Rothera in the Antarctic, Svalbard in the Arctic). Therefore, essential research questions such as "how does polar meiofauna survive the dark season and the greatly reduced, altered or perhaps completely suppressed food input; and what are their community dynamics under such conditions?" remain unanswered for the time being and present a scientific frontier in polar meiobenthic research.

9.5.1 Future Field Work

Next generation mobile autonomous sampling devices, able to work for at least one year on the deep seafloor, can overcome some of the challenges mentioned above. A few vehicles which can move on the seabed, so-called benthic crawlers, already exist (e.g. the Benthic Rover at the US Monterey Bay Aquarium Research Institute, MBARI, as well as TRAMPER and NOMAD at the German Alfred-Wegener-Institute, AWI) (Lemburg et al. 2018; McGill et al. 2007; Wenzhöfer et al. 2016). However, devices that sample benthos routinely (in situ sampling and preserving sediment cores at defined local and temporal intervals for retrieval months later) are still under development. Notwithstanding, long-term exploration is required for assessing the roles that polar ecosystems will play in future of benthic ecosystems under progressing climate change conditions. At the moment, multi-year time series of Arctic and Antarctic marine ecosystems are still in their infancy.

There is, however, one exception: The Arctic Long-Term Ecological Research (LTER) observatory HAUSGARTEN in the Fram Strait between Greenland and Svalbard so far remains the only monitoring location with long-lasting and automated scientific work sea (Soltwedel et al. 2005, 2016). The HAUSGARTEN observatory (about 79° N, 04° E, ~2500 m water depth) was established in 1999 to detect and track the effects of large-scale environmental changes on the marine ecosystem in the transition zone between the northern North Atlantic and the central Arctic Ocean. Repeated sampling both in the water column and at the seafloor during yearly expeditions in summer months was complemented by continuous year-round sampling and sensing using autonomous instruments on anchored and mobile devices.

Unique time-series studies at HAUSGARTEN include regular meiofauna sampling campaigns along a depth transect with nine stations between 1280 and 5500 m water depth. Despite the inter-annual variability in meiofauna densities at all sites, 15 years of continuous sampling showed generally declining meiofauna numbers. This decline was most pronounced at the shallowest station and diminished towards deeper sites (Soltwedel et al. 2020)—a remarkable result that would not have been observed with sporadic sampling only. This finding emphasizes the importance of long-term data with sufficient temporal resolution.

9.5.2 Future Experimental Work

Rather late in the history of meiofauna research have experimental studies tried to address specific, physiological or biochemical questions (see Giere 2019). Experimental studies with polar marine meiofauna, especially controlled field experimentation and experiments conducted during deep-sea expeditions are no exception—they present rare, time-consuming, and costly endeavours. For example, ship-board lab experiments with ^{13}C-labelled food sources (e.g. bacteria, algae) were carried out only relatively recently to study food preferences of Arctic and Antarctic deep-sea nematodes (Guilini et al. 2010; Ingels et al. 2010), and a limited number of innovative experiments have been carried out in and near Potter Cove on King George Island in the Antarctic (Pasotti et al. 2012, 2014, 2015a, b; Veit-Köhler et al. 2008; Wiencke et al. 2008) as well as Casey station, one of the Australian Antarctic Research Stations in the East Antarctic (Stark et al. 2017).

To reduce artefacts in ship-borne experiments with deep-sea organisms, similar experiments were also conducted in situ, e.g. in experimental approaches at the deep seafloor of the Arctic LTER observatory HAUSGARTEN (Braeckman et al. 2018; Guilini et al. 2011). Other in situ experiments with deep-sea meiofauna (and special focus on nematode communities) at the HAUSGARTEN observatory studied the exclusion of larger benthic organisms to reduce predation pressure (Gallucci et al. 2008a), the increase of near-bottom currents (Soltwedel et al. 2013), and local effects of large food-falls (Soltwedel et al. 2018). All these deep-sea experiments depend on expensive modern instrumentation, i.e. free-falling devices (Bottom-Lander) and Remotely Operated Vehicles (ROV) for manipulation at the deep seafloor or continuous access to Antarctic research stations which have experimental facilities. Hence, although urgently needed, future experimental work on polar meiofauna, especially experiments simulating scenarios in changing environmental settings, will most probably continue to be conducted to a limited extent only.

9.5.3 Tracking Ecosystem Change in Polar Regions

Perhaps most poignant in this context is the fact that the poles, once considered the most pristine environments on Earth, are apparently undergoing the most rapid and significant impacts by climate change. Despite increased efforts, our attempts to achieve a complete baseline of [meiofauna] biodiversity data in the Arctic and Antarctic will likely fail as we continue to progress through the Anthropocene. "Future climate-induced changes in the polar oceans, sea ice, snow, and permafrost will drive habitat and biome shifts, with associated changes in the ranges and abundance of ecologically important species " (Meredith et al. 2019). Any study aiming at documenting species, communities, and their biology and ecology in the light of changing environmental conditions must consider the reality that polar regions are changing very fast, and that any establishment of a current baseline is a relative one.

Bringing to light the need for investigating dynamic baselines also highlights the importance of assessing biodiversity, underpinned by robust morphological and molecular species identification. Many meiobenthic species from polar regions, particularly the deep sea, remain undocumented. Increased efforts to document species diversity are necessary if we are to establish a record against which to measure anthropogenic change. The same predicament can be argued for our understanding of processes and functions of meiobenthos in polar regions. Information on the roles that meiobenthos play in the functioning and biogeochemistry of polar sedimentary environments, typically very different habitats compared to sediments from lower latitudes, temperate, subtropical and tropical regions, is very limited.

9.5.4 Adaptations to 'Extreme' Polar Environments

Meiofauna have adapted to extreme polar conditions and thus represent meaningful model organisms for (eco)physiological, behavioural, developmental, and (epi)genetic studies. The complex traits that characterize adaptations to polar environments is unexplored for marine meiofauna (but relatively well known for Antarctic terrestrial nematodes, see for instance works by David A. Wharton), yet could provide many answers to pressing questions related to how organisms can survive and persist in extreme conditions, with implications for our understanding of biological theory (see Chap. 11 for more details on meiofauna research in extreme environments).

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Chapter 10
Cave Meiofauna—Models for Ecology and Evolution

Alejandro Martínez

Abstract Caves can be used as model systems for developing and understanding evolutionary and ecological theory. Yet, most scientists have paid little attention to cave meiofaunal communities, thereby potentially underestimating subterranean biodiversity. To date, meiofauna has been recorded in only 2026 caves, totalling 31% of caves for which information on aquatic fauna is available around the world. However, these records primarily originate from Europe and the Western Mediterranean and focus on target species, rather than on describing entire communities. Of the 1856 meiofaunal species recorded in caves, 699 might be regarded as restricted to subterranean habitats. Most of those species belong to Arthropoda, with Copepoda the richest species group, both in terms of the number of species recorded and the number of taxa restricted to the subterranean world. Different models have been proposed to explain the origin of meiofaunal cave lineages, but testing them is hampered by the lack of phylogenetic information for most taxa. Although the current lack of diversity data renders studies at a community level challenging, studies to date suggest that cave meiofauna might play a central role in carbon cycling and crucially affect the composition of the groundwater in inland and coastal aquifers. The fundamental ecosystem services that aquifers provide and the pivotal role groundwater discharge attains in the chemical balance of the ocean offer new horizons for future research on cave meiofauna. Cave meiofauna might affect our everyday life much more than we have so far imagined.

10.1 Introduction

Caves are defined as voids in the rock matrix large enough to allow the penetration of a human being. They are generally dark, extremely humid, and poor in organic matter (Poulson and White 1969; Mammola 2019). Furthermore, most caves harbour vertical pits and narrow passages (MacNeil and Brcic 2017), or even

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flooded passageways whose exploration demands cave diving training (Exley 1986). Although humans may perceive cave exploration as *extremely challenging,* this does not mean that the cave environment within caves is *extreme* for the many organisms that complete their life cycles belowground (Mammola 2020). The anthropocentric view of caves as *extreme* and *unique* environments tends to overlook the roles caves have as ecological, spatial, and temporal subsets of their surrounding environments (Mammola 2019), and hence their utility for understanding general problems in ecology and evolution (Poulson and White 1969; Mammola and Martínez 2020; Mammola et al. 2020a, b, c). Indeed, many scholars have regarded caves as island-like environments due to their discrete nature and their younger age compared to nearby surface habitats (Dawson 2016). Caves around the world offer multiple repetitions of comparable processes. Yet, in contrast to islands, caves harbour distinct and stable ecological conditions compared to those found in their surroundings; they represent well-defined, comparable ecological filters for potential colonizers (Culver 1970; Fattorini et al. 2016).

Over the last decade, most scientists studying caves as eco-evolutionary models have focused on relatively large animals (e.g. Moldovan et al. 2018). In contrast, little attention has been paid to the ubiquitous meiofaunal communities that inhabit cave environments (Table 10.1; Zeppilli et al. 2018). This is unfortunate because meiofauna include representatives of most described animal phyla, allowing scholars to address general eco-evolutionary questions without the confounding effect of the phylogeny (Giere 2009; Schmidt-Rhaesa 2020). Meiofauna are also a numerically important component of most ecosystems on Earth (Creer et al. 2010), and therefore, by neglecting small organisms in caves, bioespeleologists might be overlooking many of the species occurring in those subterranean habitats (Kennedy and Jacoby 1999). Interestingly, microscopic animals do not seem to conform with some of the general macroecological patterns, insofar as many microscopic species are ubiquitous and do respond differently to environmental parameters compared to larger species (Fontaneto 2011). Therefore, cave meiofauna might also represent useful tools to test lineage-specific questions even for those scholars interested in macroecological problems (Table 10.1).

Beyond summarizing our knowledge on the often disregarded cave meiofauna, this chapter is focusing on the potential use of those organisms to address general questions in ecology and evolution. The data presented are compiled from "Stygofauna Mundi", a public database that gathers and shares all available information on subterranean and interstitial aquatic environments of the world, including caves (Botosaneanu 1986; Martínez et al. 2018). This chapter covers all types of caves (see Box 10.1): caves directly connected to the ocean (hereafter 'marine caves'), caves reaching phreatic saline coastal groundwaters ('anchialine caves'), and inland caves harbouring different types of freshwater bodies, such as phreatic or percolation pools, rivers, or springs ('freshwater caves'). The term meiofauna is used to refer to the fraction of organisms retained on a 63-μm mesh and passing through a 1000-μm mesh, so it often includes animals visible to the naked human eye (see Box 10.1).

Table 10.1 Summary of the problems preventing a wider use of meiofauna cave animals as models for ecology and evolution, in relation to the "eight knowledge shortfalls" (Hortal et al. 2015)

Shortfall	Problems associated to cave meiofauna
Linnaean (species identity)	Lack of taxonomists for many cave and meiofaunal groups (Moldovan et al. 2018; Appeltans et al. 2012)
	Old or insufficiently detailed species descriptions (Viets 1937; Riedl 1959)
	A lack of reliable estimation of diversity (Zagmajster et al. 2018)
	A high prevalence of cryptic species (Delic et al. 2017b; Fontaneto et al. 2015)
	A bias favouring studies on large cave animals (Zagmajster et al. 2010) or hard-bodied meiofaunal groups (Curini-Galletti et al. 2012)
Wallacean (species distribution)	Geographically biased studies (Zagmajster et al. 2018; Fontaneto et al. 2012)
	Variable ranges of endemism, from species geographically very restricted (Iannella et al. 2020; Martínez et al. 2019), to nearly cosmopolitan taxa (Fontaneto 2011)
	A high prevalence of cryptic species, due to conservative morphologies or lack of conspicuous morphological characters (Delic et al. 2017a; Mills et al. 2017; Worsaae et al. 2021a, b)
	Absence of open-access database for cave species (Gibert et al. 2004)
Darwinian (species evolutionary histories)	Unknown relationships between subterranean-surface species (Juan et al. 2010) and meiofaunal-macrofaunal species (Laumer et al. 2015)
	A high range of variation in diversification patterns across different lineages (Juan et al. 2010)
	Difficulty in dating diversification events and distinguishing amongst diversification mechanisms (Morvan et al. 2013; Tiley et al. 2020)
Raunkiaeran (species ecological functions)	A lack of functional traits allowing predictions of the effects of impacts on ecosystem level (Zeppilli et al. 2015; Ho 2020)
	A lack of knowledge on life cycles in most species because of difficulties in monitoring species' populations in their habitats (Mammola et al. 2020b)

(continued)

Table 10.1 (continued)

Shortfall	Problems associated to cave meiofauna
	A lack of biological traits predicting potentials to disperse and colonize new habitats, such as presence of larvae or resistance forms (Kano and Kase 2004; Fontaneto 2019)
Prestonian (species abundances)	Limited quantitative ecological studies (Ape et al. 2015; Riera et al. 2018; Mammola et al. 2020a)
	A lack of reliable estimations because of biological or habitat impediments (de Faria et al. 2018; Mammola et al. 2020a, b, c)
	A lack of reliable estimations because of difficulties of species identification (Fontaneto et al. 2015; Mammola et al. 2020b)
	An intrinsic bias of most available methods because of low or patchy population densities (Studinski 2005)
Eltonian (biological interaction)	A lack of knowledge on the ecological networks that help unravel the mechanisms promoting and maintaining subterranean biodiversity (Mammola 2019; Bellisario et al. 2021)
	A lack of network analyses to calculate the resilience of subterranean environments to anthropogenic perturbations (Saccò et al. 2020)
	A lack of studies on the impact of different carbon sources on subterranean ecosystems (Brankovits et al. 2017; Saccò et al. 2019)
Hutchinsonian (species abiotic tolerance)	Small populations are difficult to assess and most are unsuitable for field experiments (Magagnini 1982; Mammola et al. 2020a, b, c)
	Breeding species for experimental purposes is mostly challenging (Mammola et al. 2020a, b, c)

Supporting references based on cave and meiofaunal studies are reported separately (adapted from and inspired by Fonseca et al. 2018; Mammola et al. 2019)

Box 10.1: Glossary

A range of terms and definitions as used in the scientific literature on cave meiofauna (see Martínez and Mammola 2021 for a broader discussion on terminology). The definitions adopted here are as follows:

Cave is any void large enough to allow human exploration. I considered as caves also sinkholes, fissures, and large cracks that reach groundwater through more or less extensive fissures, even if those do not allow human exploration (e.g. Dahlak crack, the *grietas* from Galapagos, and many Mexican cenotes). I subdivided caves into three categories:

> ***Marine caves*** are voids that can be entered from the open ocean by an average-size swimmer or diver. They are often affected by tidal or current-driven inflows of marine water. They might be extensive enough to reach the coastal aquifer (e.g. Caye Chapel Cave in Belize). Although some of those caves are often considered as anchialine, I didn't include this distinction here
>
> ***Anchialine caves*** are voids that open inland and reach saline groundwater of marine origin, but whose passages have not been found connected with the sea. They might be tidally influenced, but always experience a delay in relation to the tides in the sea
>
> ***Freshwater caves*** are voids that open above sea level and contain non-haline waters of any origin, including groundwater, rivers, or percolation. A few oligohaline caves containing saline waters without marine origin and opening very far from the ocean are also included in this category (e.g. Kaptar-Khana cave in Turkmenistan)

Meiofauna organisms retained on a 63-µm mesh and passing through a 1000-µm-sized mesh. These include animals not visible by the naked eye but also some animals that are such as primarily interstitial lineages of annelids (e.g.) and platyhelminths (e.g. Proseriata), as well as certain crustaceans (e.g. *Trogloleleupia*, *Deeveya*)

Subterranean meiofauna is a category that I have tailored for the purposes of this chapter, departing from the criteria introduced in the World Register of Cave Species (Gerovasileiou et al. 2016). I consider as *subterranean meiofauna* all species traditionally seen as stygobitic (i.e. exclusive to groundwater), together with those that have never been recorded outside caves.

10.2 An Overview on Cave Meiofauna

10.2.1 *Regional Aspects*

The data presented here originate from 2026 caves across the world, including 1577 freshwater caves, 119 marine caves, and 250 anchialine caves (see Box 10.1). This represents only 31% of the total 6482 caves investigated for aquatic fauna (Martínez et al. 2018). The relatively low proportion partly reflects cave scientists' preference to study macrofauna over meiofauna (Fig. 10.1). Amongst scientific articles on cave meiofauna, most have focused on freshwater caves (Vandel 1965; Iliffe 1981), whereas research in marine and anchialine cave habitats started later, in parallel with the development of cave diving technologies (Bozanic 1997).

Geographically, most research on cave meiofauna has focused on Europe and a large proportion of the data on cave meiofauna has been collected from Western Europe and the Balkans, particularly from Italy, Spain, France, Slovenia, Rumania, and Bulgaria (Fig. 10.2). These countries have also reported the highest number of cave-exclusive meiofaunal species. In America, most records come from the Eastern

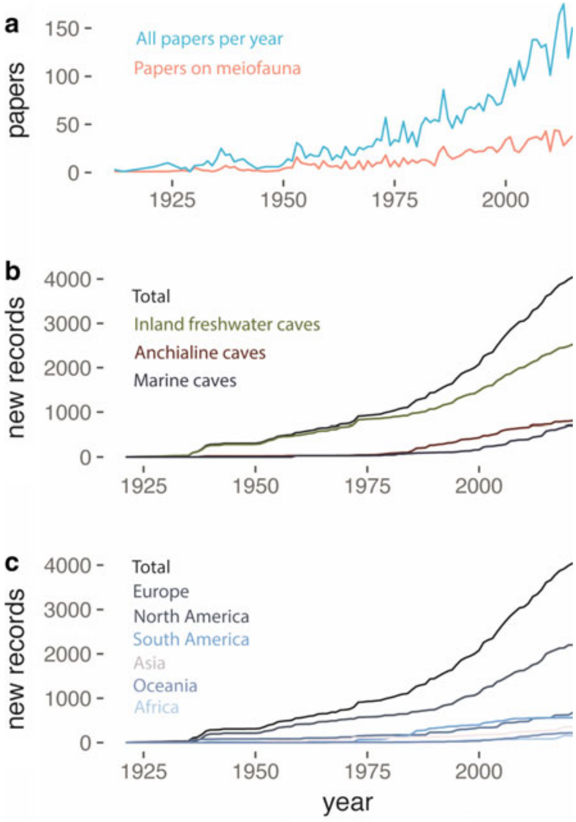
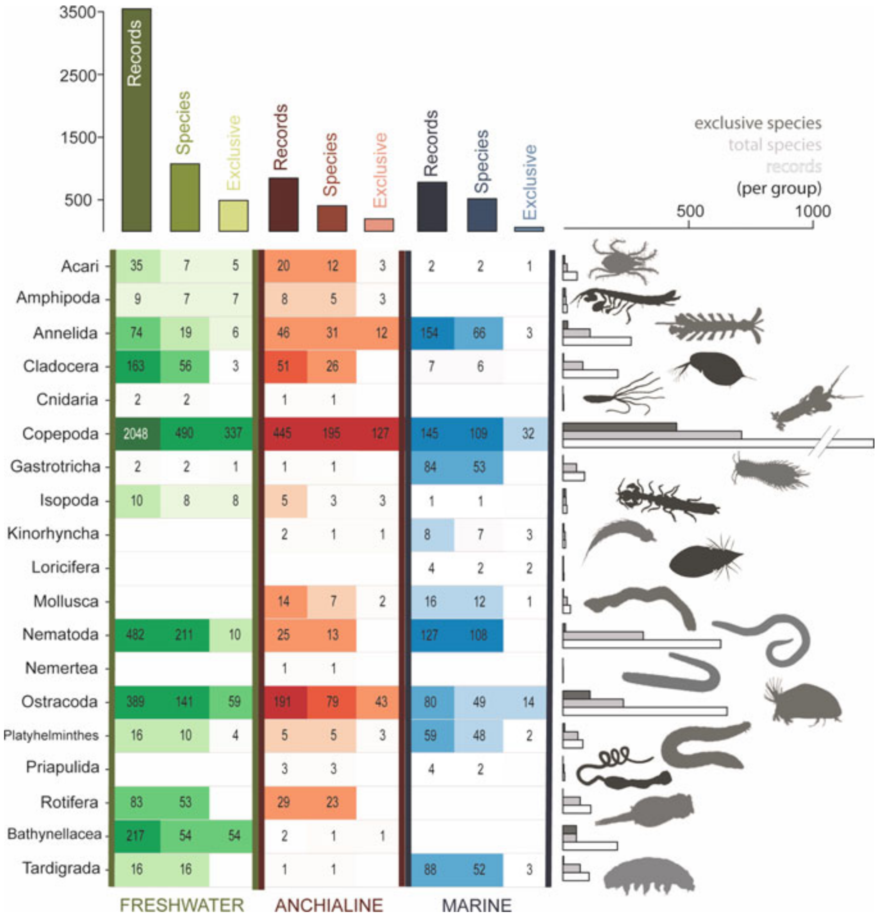


Fig. 10.1 Bibliographic trends in cave meiofauna research. **a** Number of papers published per year on cave aquatic species compared to cave meiofaunal species. **b** Number of new records of cave meiofauna species published annually at the three different types of caves discussed in this chapter (see Box 10.1). **c** Number of new cave records published annually in each continent. See text for further explanations

USA, the Mexican States of Yucatan and Quintana Roo, and Cuba. Other well-investigated regions include Thailand, Vietnam, Western Australia, and the Canary Islands. This geographic pattern parallels our general knowledge of subterranean aquatic macrofauna (Botosaneanu 1986; Zagmajster et al. 2018). Particularly in North America, very few meiofaunal species are known despite the long tradition of subterranean studies in this area (Culver et al. 2000).

Marine caves have been better investigated in the Western Mediterranean (Gerovasileiou and Voultsiadou 2014), the Macaronesia archipelagos (Freitas et al. 2019), and the Bahamas (Juberthie and Iliffe 1994; Kornicker et al. 2002), followed



	FRESHWATER Records	FRESHWATER Species	FRESHWATER Exclusive	ANCHIALINE Records	ANCHIALINE Species	ANCHIALINE Exclusive	MARINE Records	MARINE Species	MARINE Exclusive
Acari	35	7	5	20	12	3	2	2	1
Amphipoda	9	7	7	8	5	3			
Annelida	74	19	6	46	31	12	154	66	3
Cladocera	163	56	3	51	26		7	6	
Cnidaria	2	2		1	1				
Copepoda	2048	490	337	445	195	127	145	109	32
Gastrotricha	2	2	1	1	1		84	53	
Isopoda	10	8	8	5	3	3	1	1	
Kinorhyncha				2	1	1	8	7	3
Loricifera							4	2	2
Mollusca				14	7	2	16	12	1
Nematoda	482	211	10	25	13		127	108	
Nemertea				1	1				
Ostracoda	389	141	59	191	79	43	80	49	14
Platyhelminthes	16	10	4	5	5	3	59	48	2
Priapulida				3	3		4	2	
Rotifera	83	53		29	23				
Bathynellacea	217	54	54	2	1	1			
Tardigrada	16	16		1	1		88	52	3

Fig. 10.2 Meiofauna diversity in various cave habitats. The upper bars represent the total number of records, species, and subterranean-exclusive species found in each habitat. The numbers within the table correspond to the diversity of each of the groups. The grey bars on the right hand side are proportional to the total number of species per group (see Table 10.2). Note that when the same species has been reported in two different habitats, it is only counted once in the total

Table 10.2 Summary of the diversity of the groups discussed in this chapter

	Total species	Total meiofaunal species	Total subterranean species	Cave meiofauna species	Cave-exclusive meiofauna species
Phylum Cnidaria	> 12,000	93	1	**2**	**0**
Spiralia					
Phylum Annelida	> 23,000	425	119	**109**	**19**
Phylum Gastrotricha	800	789	1	**55**	**1**
Phylum Mollusca	> 85,000	500	358	**17**	**2**
Phylum Nemertea	1200	34	2	**1**	**0**
Phylum Platyhelminthes	3000*	1700	45	**60**	**7**
Phylum Rotifera	1500	1500	0	**69**	**0**
Phylum Gnathosthomulida	100	100	0	**(2)**	**0**
Ecdysozoa					
Phylum Kinorhyncha	350	314	4	**9**	**4**
Phylum Loricifera	31	31	2	**2**	**2**
Phylum Priapulida	21	13	10	**4**	**0**
Phylum Nematoda	20,000	4870**	29	**323**	**10**
Phylum Tardigrada	> 1200	> 1200	3	**69**	**3**
Phylum Arthropoda					
*** Class Ostracoda	6600	4700	310	**243**	**109**
*** Class Copepoda	11,300	6514	985	**718**	**457**
*** Class Branchiopoda	800	700	8	**80**	**3**
*** Superorder Syncarida	250	250	250	**54**	**54**
*** Order Amphipoda	9900	60	1181	**12**	**10**
*** Order Isopoda	13,500	343	1000	**12**	**11**

(continued)

Table 10.2 (continued)

	Total species	Total meiofaunal species	Total subterranean species	Cave meiofauna species	Cave-exclusive meiofauna species
*** Family Halacaridae	1200	1184	20	**17**	**7**

Number of total and meiofaunal species in each group estimated from several sources. Total subterranean species, cave species, and cave-exclusive species extracted from Stygofauna Mundi. Columns: “total”, approximate number of species; “total meiofauna”, estimation of the number meiofaunal species in the group; “total subterranean”, estimation of the species recorded in subterranean habitats; “cave meiofauna”, meiofaunal species reported in caves; “cave-exclusive meiofauna”, number of meiofaunal species restricted from cave habitats (see Box 10.1)
Notes: *Platyhelminthes correspond only to free-living species; **Nematoda only account for marine meiobenthic species; Gnathostomulida are shown in parenthesis to indicate no reports have been identify to species. *Sources* (Schmidt-Rhaesa 2020; WoRMS Editorial Board 2022)

by the Eastern Mediterranean (Bitner and Gerovasileiou 2021), the Black Sea (Ereskovsky et al. 2015), the Caribbean (Huys and Iliffe 1998), Bermuda (Iliffe 1981; Bartsch and Iliffe 1985), and few archipelagos in the Indopacific, such as the Maldives (Ape et al. 2015), Ryukyu Islands (Fujimoto and Miyazaki 2013; Yamasaki 2016; Jimi et al. 2020), Palau (Boxshall and Iliffe 1990; Fosshagen et al. 2001), and Easter Island (Whatley and Jones 1999).

Within each region, the quality of information available for different caves is rather heterogeneous. The few studies attempting to describe entire meiofaunal communities have highlighted a rich diversity in few marine and anchialine caves: in the Indopacific (Sørensen et al. 2000; Boesgaard and Kristensen 2001; Sandulli et al. 2006; Heiner et al. 2009; Jørgensen et al. 2014), the Mediterranean (Palacin and Masalles 1986; Todaro et al. 2006; Curini-Galletti et al. 2012; Janssen et al. 2013; Ape et al. 2015), and the Canary Islands (Riera et al. 2018; Martínez 2019). These studies have primarily focused on the interstitial fauna associated with sediments, and only few have paid attention to the communities in the water column (Moscatello and Belmonte 2007; Martínez et al. 2019). There are fewer studies describing entire meiofaunal communities in freshwater caves, and these have mostly focused on few hard-bodied meiofaunal groups, such as nematodes (Altherr 1938, 1971; Andrássy 1959, 1973) and copepods (Pearse and Wilson 1938; Brancelj 1987). In context with planktonic communities inhabiting the cenotes in Yucatán Peninsula, numerous rotifers, copepods, and ostracods have been found in entrance environments, but only rarely in the dark sections of these cave systems (Moravec et al. 1995b, a; Suárez-Morales et al. 2004; Vasquez-Yeomans 2005; Quiroz-Vázquez 2012).

10.2.2 *Taxonomic Composition of Cave Meiofauna: Which Animals Are Found in Caves?*

At present, most cave meiofaunal species belong to Arthropoda (1136 species), Nematoda (323 species), and Annelida (109 species, 19 exclusive); followed by Rotifera and Tardigrada (69 species each), Platyhelminthes (60 species), and Gastrotricha (55 species). Mollusca (17 species) and the Scalidophora phyla (9 Kinorhyncha, 4 Priapulida, and 2 Loricifera) are represented by fewer species, whereas Cnidaria and Nemertea are only known by two and a single species, respectively (Table 10.2). The number of subterranean-exclusive species varies greatly within each group. For example, all species of cave Loricifera might be considered so far as cave-exclusive (Heiner et al. 2009; but see below), in contrast to all species of Cnidaria, Nemertea, Rotifera, and Priapulida, which have also been found elsewhere. Annelida, Arthropoda, Gastrotricha, Mollusca, and Platyhelminthes present a variable percentage of cave-exclusive species (Table 10.2). Some of those so far cave-exclusive species might be recorded elsewhere in the future, specially when belonging to poorly studied groups, such as Loricifera.

The richness of meiofaunal arthropods in caves is unsurprising because arthropods also represent major components of meiofaunal communities elsewhere (Giere 2009). Amongst cave meiofaunal arthropods, cave Copepoda consist of 794 species, 64% of which are exclusively subterranean (Galassi et al. 2009; Mercado-Salas and Martínez 2022; George et al. 2021). Ostracoda is second in number of species with 243 species (109 of them stygobitic), followed by Bathynellacea (54 species, all stygobitic), Branchiopoda (80 species, only 3 stygobitic), and Halacaridae (17 species, 7 stygobitic). Cave meiofaunal Amphipoda and Isopoda are represented by 12 cave-exclusive meiofaunal species, although those numbers might vary greatly depending on which groups within these two taxa are considered as meiofaunal (Higgins and Thiel 1988). In fact, Amphipoda and Isopoda are amongst the most species-rich groups in groundwater and are also very diverse in marine caves (Navarro-Barranco et al. 2015; Borko et al. 2021). The low diversity of cave nematodes is somewhat surprising and likely reflects sampling bias. Published reports suggest that nematodes are ubiquitous across different cave microhabitats, such as guano deposits, soils (Du Preez et al. 2017), and underwater sediments (Ape et al. 2015; Riera et al. 2018; Pérez-García et al. 2018). More investigations are necessary to fully understand the ecological significance of nematodes in caves compared to the crucial roles they play in surface environments (Altherr 1938; Muschiol and Traunspurger 2007; Traunspurger 2021).

The distribution of meiofauna sampling records and species also differs amongst different types of caves (Fig. 10.3). However the larger number of records in freshwater caves might reflect the greater attention they have received historically; differences in taxonomic composition are most likely linked to the ecological processes exerted by each type of habitat as well as the evolutionary history and phylogenetic affinities of the different colonizing cave lineages.

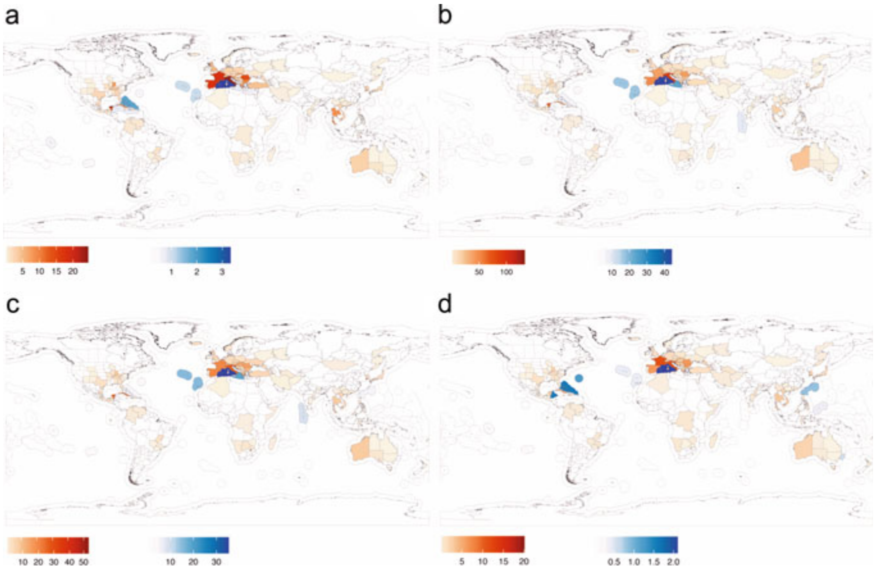


Fig. 10.3 Geographic distribution of cave meiofaunal species across the world. Anchialine and inland freshwater caves are represented according to the biogeographic units defined by the Biodiversity Information Standards of the Taxonomic Database Working Group (www.tdwg.com). The records from marine caves are represented in marine provinces (Spalding et al. 2007). Numbers are normalized to the area of each polygon. **a** Number of caves with recorded meiofaunal species or genera. **b** Number of records of meiofaunal species or genera in caves. **c** Number of meiofaunal species recorded in caves. **d** Number of meiofaunal subterranean-exclusive species recorded in caves. Source: Stygofauna Mundi (Martínez et al. 2018)

The number of meiofauna species known in each cave group is probably underestimated (Table 10.1). Recent cave surveys have highlighted a large diversity of undescribed meiofaunal species (Pérez-García et al. 2018; Gonzalez et al. 2020), even in regions or individual caves with a long tradition of meiofaunal studies (see Curini-Galletti et al. 2012; Martínez et al. 2019). Meta-barcoding surveys might help to estimate diversity more efficiently in those areas (Hoffman et al. 2018), but integrative taxonomic studies and molecular analyses will be necessary to reveal, and formally describe, the presumably high number of species within those habitats that are still to be collected and described (Jugovic et al. 2012; Bilandžija et al. 2013). Our poor knowledge of the meiofauna in many areas with caves might artificially inflate the number of cave-exclusive species, unless research in caves is complemented by inventories of the regional surface diversity (Martínez et al. 2019).

10.2.3 Distribution Patterns of Cave Meiofauna: Different from Other Subterranean Organisms?

Although global patterns of cave meiofauna distribution often mirror sampling biases, in some areas, our better knowledge allows us to discern certain regional distribution patterns (Zagmajster et al. 2018). For example, 11–15% of freshwater European species are restricted to groundwater, and some orders, families, and genera of Crustacea are only known from those habitats (Galassi and Stoch 2010). Indeed, the distribution patterns of European groundwater fauna have been analysed at different spatial scales (Rouch 1988; Marmonier et al. 1993; Fiasca et al. 2014; Galassi et al. 2017), revealing a relatively high percentage of rare species in groundwater communities and emphasizing the challenge of obtaining robust knowledge of the distribution of most groundwater taxa (Castellarini et al. 2007; Dole-Olivier et al. 2009; Stoch and Galassi 2010). The fact that many species are currently considered being rare suggests that higher sampling effort is needed to fully capture the diversity of these areas. If larger species are rare, smaller species may be even more so, given that many meiofaunal groups are very elusive in surface environments (e.g. the case of *Lobatocerebrum* Rieger 1980).

Amongst European taxonomic groups, the distribution patterns of groundwater copepods have been particularly well investigated. Several hotspots can be defined by their species richness, as well as by high levels of endemicity, phylogenetic rarity, and habitat specificity (Iannella et al. 2020, 2021). More characteristics described for groundwater animals in Europe remain to be tested for cave meiofauna. These include the general reduction in species number contrasting to the increase in their distribution ranges towards northern latitudes. The marked differences in species composition across European regions also need further scrutiny. Do they depend on the large proportion of short-range endemic species (Stoch and Galassi 2010; Zagmajster et al. 2014, 2018)?

Marine caves generally harbour more species than their inland counterparts, and marine cave species tend to exhibit wider distributional ranges (Gerovasileiou and Bianchi 2021). This has been shown for the Mediterranean, where various caves were found inhabited by the same pool of macrofaunal species with few locally endemic species (Gerovasileiou and Voultsiadou 2014). A similar pattern seems valid for the decapod fauna across the Indopacific when comparing caves and other anchialine habitats (Holthuis 1963). For small organisms, the presence of corresponding distribution patterns remains to be investigated.

10.2.4 What Do We Know About the Phylogenetic Position of Cave Meiofaunal Species?

Many species now regarded as cave-exclusive might just be waiting to be discovered in non-cave environments. These discoveries are more likely to happen in areas poorly investigated for meiofauna, i.e. most of the world, but not only, as we have already learned from research in Europe and the Canary Islands (Pascual et al. 1996; Schmidt-Rhaesa et al. 2013; Andrássy 1971; Todaro and Thomas 2003). Robust phylogenetic information on putatively endemic cave species is important not only as a tool for tackling ecological questions from an evolutionary perspective, but also as an essential source of scientific evidence underpinning the identification of priority areas for species conservation, selecting model organisms, etc. (Mammola et al. 2020b; Mammola and Martínez 2020; Wynne et al. 2021). Formal phylogenies are missing for most meiofauna cave groups (Table 10.1; see Chap. 1). However, the Linnaean classification of many groups, based on detailed comparative morphology (e.g. Huys and Boxshall 1991), allows us to use it as a proxy of the phylogenetic position of key species (see Iannella et al. 2020).

Amongst all phyla with cave meiofaunal representatives, Arthropoda comprise the greatest number of subterranean-exclusive genera, families, and even orders and classes (Yager 1981; Bowman et al. 1985; Huys 1988b; Fosshagen et al. 2001; Iliffe and Kornicker 2009). The copepod order Gelyelloida is only known from groundwater (although not yet found in caves; Huys 1988b), and about half of the described species in the order Platicopioida and Misophrioida are restricted to anchialine and marine caves (Huys 1988a; Boxshall et al. 2014; Gonzalez et al. 2020; Mercado-Salas and Martínez 2022; Fig. 10.4). Subterranean-exclusive families and genera are also common amongst the orders Cyclopoida, Calanoida (Fig. 10.4), and Harpacticoida, at times characterized by plesiomorphic characters, and therefore, representing basally splitting branches within each of those orders (Boxshall and Huys 1992).

Three subterranean-exclusive families of Halocyprida (Ostracoda) are restricted to anchialine caves (Kornicker and Iliffe 1985, 1989, 1995; Fig. 10.4), and many more families and genera are scattered amongst Podocopida, occurring both in saline and freshwater aquifers (Maddocks 1991, 2005; Karanovic and Pesce 2001; Karanovic 2007, 2012). Cave meiofaunal Amphipoda and Isopoda include the interstitial families Ingolfiellidae and Microcerberidae (Vonk 2003; Fig. 10.4), the former with several freshwater cave species across South Africa and Namibia and worth being reviewed with modern methods (Barnard 1967; Griffiths 1989; but see Box 10.1). Bathynellaceans are all restricted to fresh groundwater (Camacho and García-Valdecasas 2008). Cave Halacaridae represent another very interesting group, often neglected by the recent literature (Bartsch 2006). Four marine species are known from anchialine caves in Bermuda (Bartsch and Iliffe 1985), two monotypic genera seem restricted to caves (Walter 1931; Viets 1937), and most freshwater members of *Soldanellonyx, Lobohalacarus, Porolohmanella,* and *Porohalacarus* are interstitial or subterranean (Bartsch 2006). Since Halacaridae disperse poorly and present well-defined adaptations to different types of substrate (see Martínez et al. 2021), halacarid *mites* represent interesting models for subterranean biogeography (e.g. Notenboom 1991; Rubio-López et al. 2022).

Other than arthropods, many cave-exclusive annelids have been described in recent years (Martínez et al. 2013; Gonzalez et al. 2017). Amongst meiofaunal cave species (Núñez et al. 1997, 2009; Martínez et al. 2017; Jimi et al. 2020), members of Nerillidae are particularly interesting because they have apparently colonized caves

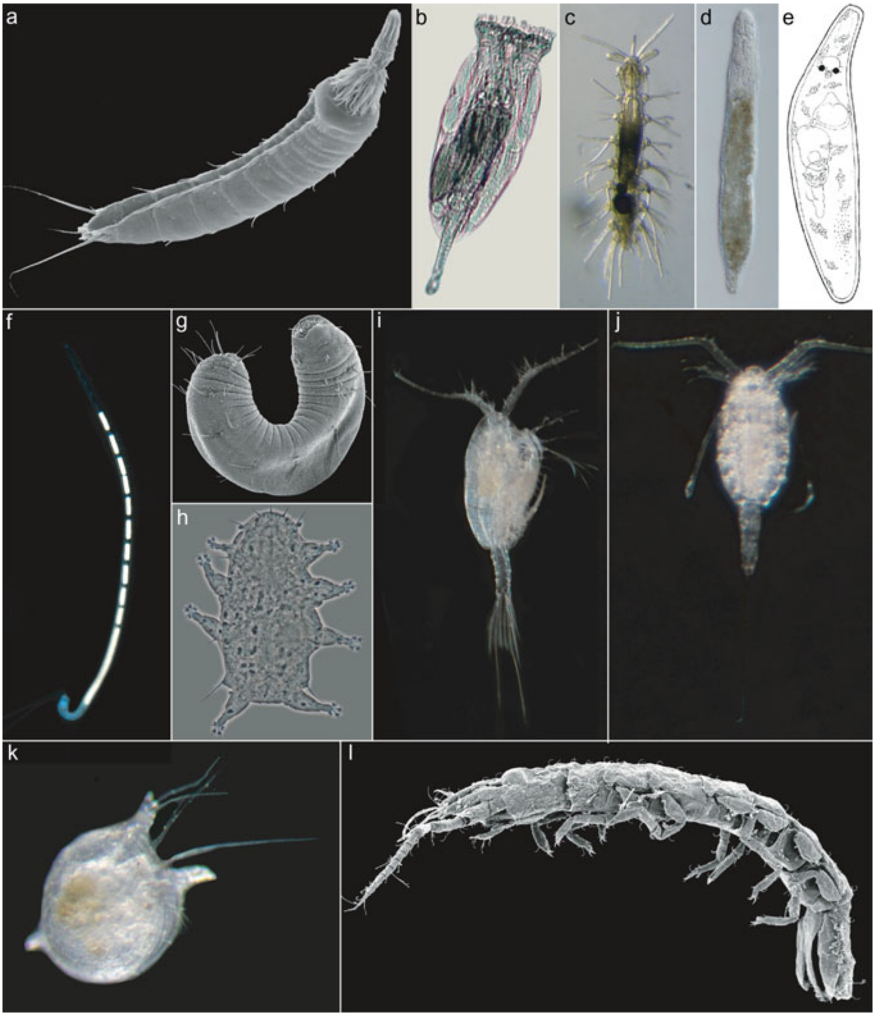


Fig. 10.4 Cave meiofauna species. **a** Kinorhyncha. *Ryuguderes imajimae,* cave-exclusive genera from Japan (H. Yamasaki). **b** Rotifera. *Testudinella* sp., Morske jame u Kravljačici (Kornati, Croatia) (D. Fontaneto). **c** Annelida. *Leptonerilla diatomeophaga*, Los Jameos del Agua (Lanzarote, Canary Islands). **d** Platyhelminthes, *Stenostumum* sp., percolation pond in Grotta degli Stretti (Toscana, Italy) (A. Martínez & U. Jondelius). **e** Platyhelminthes. *Tyrrheniella sigillata,* exclusive from Grotta del Tuffo-Tuffo (Gulf of Napoli, Italy). **f** Annelida. *Megadrilus pelagicus,* Túnel de la Atlántida (Lanzarote, Canary Islands). **g** Annelida. *Fauveliopsis jameoaquensis*, Los Jameos del Agua (Lanzarote, Canary Islands). **h** Tardigrada. *Cyaegharctus kitamurai,* Daidokutsu marine cave (Iejima, Okinawa). **i** Copepoda, Calanoida. *Exumella* n. sp., Túnel de la Atlántida (Lanzarote, Canary Islands). **j** Copepoda, Misophrioida *Palpophria aestheta,* cave-exclusive misophrioid family Palpophriidae, Túnel de la Atlántida (Lanzarote, Canary Islands). **k** Ostracoda, *Danielopolina orghidani,* Casimba El Brinco (Matanza, Cuba) (A. Martínez & B. Gonzalez). **l** Isopoda, Lepicharontidae gen. sp. 1. *Montaña de Arena* (Túnel de la Atlantida, Lanzarote; Bradford-Grieve et al. 2014)

multiple times, including the anchialine ecological radiation of the genus *Speleonerilla* (Worsaae et al. 2019a, b)*,* the numerous marine cave species in *Leptonerilla* (Núñez et al. 1997; but note Martínez et al. 2021; Fig. 10.4) and the monotypic *Nipponerilla* (Worsaae et al. 2009, 2021b). Interestingly, the nerillid *Troglochaetus beranecki* has been recorded from both, freshwater caves and hyporheic environments in Europe and North America, most likely representing a species complex (Andrássy 1956; Pennak 1971; Särkkä 1998).

Kinorhyncha, Loricifera, Platyhelminthes, and Tardigrada include few, but phylogenetically interesting cave species (see Chap. 1). Kinorhyncha include the Japanese endemic cave-exclusive genus *Ryuguderes* (Yamasaki 2016; Fig. 10.4), as well as cave species in Japan, Mexico, and the Canary Islands belonging to marine genera (Sánchez and Martínez 2019; Yamasaki et al. 2020). Loriciferans comprise two cave-exclusive species (Heiner et al. 2009), including *Austroloricus oculatus,* one of the few loriciferans known with pigmented eyes (Bang-Berthelsen et al. 2013). Amongst the few cave platyhelminths found in marine and anchialine caves in Lanzarote and the Mediterranean (Gobert et al. 2019), *Tyrrheniella sigillata* (Riedl 1959; Fig. 10.4) is particularly interesting because it presents spicules resembling those found in interstitial Rhodopeomorpha (Mollusca). It might therefore represent either an interesting case of evolutionary convergence or a misidentification. Tardigrada are known from three cave-exclusive genera in French and Japanese marine caves (Villora-Moreno 1996; Fujimoto and Miyazaki 2013; Fujimoto 2015; Fig. 10.4). In contrast, we know very few cave-exclusive nematodes, all of which are restricted to freshwater and terrestrial environments and belong to otherwise epigean groups. No cave-exclusive Nemertea, Priapulida, and Rotifera are known so far (Andrássy 1971; Schmidt-Rhaesa et al. 2013; Fontaneto pers. comm.; Fig. 10.4). Gnathostomulida found in caves have never been investigated in detail (Martínez et al. 2019), and all cave Acoela and Nemertodermatida might be rather considered as belonging to macrofauna (Riedl 1959; Curini-Galletti et al. 2012).

The presence of cave-exclusive lineage scattered across the animal tree of life suggests that subterranean habitats might have played an important role in the evolution of several animal groups at different geological times. On the one hand, cave meiofauna seem to be crucial to understand the morphological evolution of many animal lineages, insofar as many cave meiofaunal species retain ancestral characters, and potentially represent basally splitting branches in relatively deep metazoan lineages (Galassi et al. 2009; Mercado-Salas and Martínez 2022). More recent cave lineages present conspicuous adaptations to survive in caves that might help to better understand morphological plasticity, particularly in groups with comparatively simple morphologies (Martínez et al. 2017; Worsaae et al. 2019a). This even relates to many of those meiofaunal lineages that are poorly understood and sometimes only known from their relatively old original descriptions (e.g. Viets 1937; Riedl 1959). The status of many of these highly elusive, yet fascinating, cave species might remain uncertain for many more years.

10.2.5 Evolutionary Origin of Cave Meiofauna: What Do We Know About the Processes Leading to the Origin of Cave Meiofauna?

Inferring evolutionary processes is challenging (see Chap. 1), as it requires robust phylogenies as well as accurate morphological, ecological, and distributional data for the target group. However, for most cave meiofaunal lineages, information is sparse and fragmented. Given that the origin of cave fauna is at the core of biospeleological literature, this chapter would be incomplete without summarizing some of the most popular theories (Juan et al. 2010). The hypotheses discussed here are rather heterogeneous insofar as some of them address the origin of cave species from a hypothetical non-cave ancestor (Iliffe 1986; Notenboom 1991; Boutin and Coineau 2012), whereas others focus on how the species might have diversified from an *already* subterranean ancestor (Hart et al. 1985; Danielopol et al. 1994). However, models within both groups can be discussed together since they mostly differ regarding the relative importance attributed to vicariant versus dispersal processes (Culver et al. 2009). After the historical tendency to progressively abandon vicariant models and rather favour the role of active colonization and dispersal, it appears, as molecular phylogenies have demonstrated, that the origin of cave faunas is more complex than any single model predicts (Koenemann et al. 2007; Juan et al. 2010; Botello et al. 2012; Page et al. 2016). However, as simplified as these hypotheses might seem, they have inspired generations of cave biologists and still remain powerful sources for novel research questions (Iliffe and Kornicker 2009).

Many explanatory hypotheses for the origin of cave fauna have relied on tectonics to explain the current disjunct distribution of many cave lineages. Ancient Tethyan vicariance, for example, has been invoked to explain such patterns in several lineages restricted to anchialine caves across continents (Koenemann et al. 2007, 2009; Bracken et al. 2010). This hypothesis remains popular, although it cannot explain the presence of some of these groups in relatively young oceanic islands (Bowman and Iliffe 1986; Koenemann et al. 2009). Recent phylogenetic tests have consistently yielded some degree of dispersal to explain the distribution of all those so-called Tethyan anchialine groups (Jurado-Rivera et al. 2017; Page et al. 2016; Koenemann et al. 2007). Amongst meiofauna, Tethyan-related vicariance has been proposed for thaumatocyprid ostracods (Iglikowska and Boxshall 2013, Fig. 10.4) and is plausible for cave nerillids distributed across the Atlantic Ocean (Worsaae et al. 2019a). Another type of tectonic vicariance, associated with the fragmentation of Gondwana, has been proven of importance for subterranean Milyeringidae gobiform fish (Chakrabarty et al. 2012), and, amongst cave meiofauna, has been suggested for bathynellaceans (Schminke 1972). On the other hand, an alternative dispersal through fluvial networks seems more plausible for those crustaceans (Camacho and García-Valdecasas 2008).

Vicariant events associated with sea level changes have provided another set of explanatory hypotheses, particularly in the Mediterranean, where several transgression-regression events have been registered after the Triassic (Notenboom

1991). Marine transgressions have been invoked mostly for freshwater subterranean species with a marked marine affinity, yet without extant surface relatives in freshwater, such as ingolfiellids, microcerberids, and harpacticoids (Coineau 1994; Boutin and Coineau 2012; Coineau et al. 2013; Iannella et al. 2020; Fig. 10.4). Those models propose that originally littoral marine ancestors actively colonized and adapted to littoral cave sediments, to become thereafter stranded by the regression of the Tethys, thus, passively forced to colonize fresh groundwater (Riedl 1966; Notenboom 1991; Boutin 1994; Holsinger 1994). A more cataclysmic variant of these models has invoked the Messinian salinity crisis as an event triggering vicariance to explain the origin of cave calanoids without interstitial ancestors and living in saline waters (Carola and Razouls 1996). For Australian stygobitic species with a freshwater affinity, a similar model based on aridification has been proposed (Humphreys 2000).

A deep-sea origin, involving dispersal and niche conservatism, has been proposed for species associated with saline coastal aquifers and otherwise belonging to lineages restricted to the ocean depths (Fuchs 1894; Racovitza 1907). The hypothesis has been explicitly tested for macrofaunal annelids (Martínez et al. 2013; Gonzalez et al. 2018) and suggested for fish (Cohen and McCosker 1998; Springer and Johnson 2015) and crustaceans (Van der Ham 2003; Álvarez et al. 2004; Mejía-Ortiz et al. 2017). This putative deep-sea origin has been framed under the so-called darkness syndrome (Danielopol et al. 1996), suggesting that the ecological similarity between certain deep-sea and cave environments might have favoured similar faunas in both habitats. Animals would have been able to disperse between both environments through the crevicular surface present in the oceanic crust (Hart et al. 1985). Amongst meiofaunal organisms, morphological phylogenies have suggested a deep-sea affinity for misophrioid copepods and thaumatocyprid ostracods (Boxshall and Jaume 1999; Danielopol and Humphreys 2005; but see Jaume et al. 2000; Boxshall and Jaume 2000). They have also been suggested for annelids (Worsaae and Rouse 2009; Núñez et al. 1997; Jimi et al. 2020), tardigrades (Villora-Moreno 1996; Fujimoto et al. 2017; Fig. 10.4), and some basally branching lineages of calanoid, cyclopoid, and harpacticoid copepods (Mercado-Salas and Martínez 2022, Fig. 10.4).

Finally, there are a few models that involve both active colonization and ecological shifts. The so-called zonation model proposes a progressive adaptation to subterranean environments through the ecological gradients offered by caves that open into the sea and penetrate deeply into the aquifer (see Yager 2013). The model, first proposed for freshwater cave species with marine ancestors living on oceanic islands (Iliffe 1986), states that marine ancestors of today's cave-exclusive species might have progressively entered extensive cave systems, slowly adapting to the decreasing concentration of dissolved oxygen and particulate organic matter found in many caves (Fichez 1991). This model was formulated for atyid shrimps of the genus *Typhlatya* (Iliffe 1986; Ballou et al. 2021), and applies well to cave mysids (Bowman 1985; Meyer-Rochow and Juberthie-Jupeau 1987). Amongst meiofaunal groups, it has been proposed for cave calanoids of the family Epacteriscidae and Stephidae (Fosshagen et al. 2001; Gottstein et al. 2007; Kršinić 2015). The alternative interstitial shift model applies to meiofaunal lineages that have secondarily colonized the water column of anchialine caves from marine interstitial ancestors. That model was first proposed for the suspension feeding protodrilid *Megadrilus pelagicus* and later for the nerillid genus *Speleonerilla* (Martínez et al. 2017; Worsaae et al. 2019a; Fig. 10.4). Those animals present highly modified morphologies, including a secondary development of long palps and ciliary structures used to drift or swim in the water column. This conspicuous morphological change might be favoured by the shift from interstitial deposit feeding to suspension feeding strategies in the water column in those caves systems. The colonization of the water column is favoured by the lack of porous sediments in most caves and the richer trophic resources in the water column (Fichez 1991; Brankovits et al. 2017). Indeed, the water column of any anchialine caves is dominated by suspension feeders, including various groups of copepods, ostracods, amphipods, and thermosbaenaceans. However, many of those animals are hyperbenthic outside caves (Jaume et al. 2000).

10.3 An Overview of Cave Meiofaunal Communities

We are far from understanding the functioning of cave communities, insofar as we know very little about the factors affecting the abundance of different species or their functional roles, ranges of tolerance, and their inter- and intraspecific interactions (Table 10.1; also see Moldovan et al. 2018).

Cave meiofaunal communities consist of seemingly distantly related taxa, and are characterized by high taxonomic and phylogenetic diversity. Endemism, on the other hand, varies a lot depending on the taxonomic group and the type of cave habitat: copepods and annelids exhibit a higher proportion of geographically restricted species compared to nematodes (Stoch and Galassi 2010; Martínez et al. 2016; Du Preez et al. 2015, 2017), and inland freshwater caves have more endemic species than those directly connected to the sea (Gerovasileiou and Voultsidou 2014).

Abundances of macrofaunal species are generally lower in caves than in surrounding environments (Mammola et al. 2020b). However, the study of macrofauna has revealed exceptions amongst certain functional groups. For example, sessile fauna might exhibit higher abundance (and a larger number of species) in the twilight zone of marine caves than in other marine environments (Gerovasileiou and Bianchi 2021). The abundance and richness in marine caves seem to be as high as in the surrounding environments, and more dependent on the sediment granulometry than on other environmental parameters (Palacin and Masalles 1986; Riera et al. 2018). In contrast, some anchialine and freshwater caves harbour clearly impoverished meiofaunal benthic communities (Pérez-García et al. 2018), but this might be linked to the presence of poorly oxygenated muddy sediments in many anchialine cave systems (Fig. 10.5). This conclusion is corroborated by data from anchialine caves where coarse sediments are present. Here meiofauna abundance and richness are higher (Martínez and Gonzalez 2018).

The distribution of meiofauna within a single cave depends on the presence and nature of sediments (Martínez et al. 2019) and the quantity and quality of trophic resources (Altherr 1938; English and EdytaBlyth 2003; Du Preez et al.

Fig. 10.5 Cave environments relevant for cave meiofauna. **a** Montaña de Arena (Túnel de la Atlantida, Lanzarote, Canary Islands) (J. Heinerth). **b** Entrance of an anchialine cave in Matanzas (Cuba). **c** Alphonse Dean Marine Blue Hole (Long Island, Bahamas) (T. Thomsen). **d** Percolation freshwater in a water mine in Lanzarote (David Brankovits). **e** Stratified water column in a Bahamian inland blue hole (T. Thomsen). **f** Volcanic scoria and sediments in Túnel de la Atlantida, Lanzarote. **g** Diatoms in the twilight zone of Los Jameos del Agua (Lanzarote). **h** Fine muddy sediments and guano in Conch Bar cave (Turks and Caicos Islands, Caribbean). Concentration of organic matter settling from the water column and facilitated by the lack of turbulence and large predators

2015). Cave sections enriched by the excrements of larger animals (bats, birds, or even *Bonellia viridis,* see Brito et al. 2009, Fig. 10.5), illuminated entrance zones, sulphuric springs, or patches of coarse sand generally harbour higher abundances and a larger percentage of epigean species compared to regions of dark anchialine cave systems. The latter are poorer in species but richer in cave-adapted lineages (Martínez et al. 2009). Nevertheless, nematodes can occur in resource-poor cave sections (Andrássy 1965). Nematode populations of otherwise epigean species might even play a central role in isolated cave ecosystems, often coexisting with more specialized forms (Altherr 1938, 1971; Schroeder et al. 2010; Muschiol et al. 2015; Du Preez et al. 2017).

Caves might represent useful systems to understand the interplay between biotic and abiotic parameters structuring biological communities (Mammola and Isaia 2018). In stable environments, biotic factors have a strong effect on structuring meiofauna communities (Giere 2009). Most caves, however, harbour steep gradients of light, organic matter availability, and often salinity and temperature, favouring an increase in numbers of more specialized species from the entrance zone towards the inner reaches. Valid for macrofauna, similar gradients have been found in meiobenthic cave copepods (Janssen et al. 2013). However, these gradients disappear in studies with a coarser taxonomic resolution (Palacin and Masalles 1986; Riera et al. 2018).

The subterranean environment has a notable ecological filtering effect on potential colonizers, resulting in functionally and taxonomically distinct communities whose composition is often deviating from those at the surface. There is some evidence that this might also be the case for meiofaunal communities in some cave environments. A good example might be anchialine systems, which are dominated by suspension feeders, some of which exhibit secondary adaptations to this feeding mode (Martínez et al. 2009, 2017).

Very little is known about cave trophic interactions, even amongst large animals (Chávez-Solís et al. 2020). Studies in terrestrial caves suggest that the richness and abundance of detritivores might act as a regulating factor for the entire cave community through a bottom-up control mechanism which is strongly dependent on external energy inputs. These inputs, in turn, limit the abundance and diversity of predators (see Mammola and Isaia 2018 for an overview). Given that many meiofaunal species are detritivores, research on meiofaunal distribution and richness points at mechanisms regulating interactions with larger organisms and perhaps even at the factors regulating carbon cycling in those systems (Brankovits et al. 2021). Similar to other detritus-based food webs, the most important interspecific interactions amongst cave fauna are competition and predation (Mammola 2019). However, the relevance of competition might vary depending on the type and nature of the trophic input (Vandel 1965). Furthermore, primary producers, occurring at the entrance zone of caves, may locally attain trophic significance, as chemolithotrophic bacteria which can become extremely abundant at discontinuity layers between different water bodies (e.g. influx of springs or waters enriched by certain minerals (Jones et al. 2008; Brankovits et al. 2017; Brad et al. 2021)).

10.4 Emerging from the Dark: New Horizons for the Study of Cave Meiofauna

For us, inhabiting the above-ground world, caves are full of surprises (Mammola 2020). Even a short visit or dive into a cave would reveal animals with conspicuous adaptations (Martínez et al. 2017; Worsaae et al. 2019a, b), and foreign taxa not seen in the outside world (Iliffe and Kornicker 2009). Organisms belonging to new species are not rare (Martínez et al. 2019; Gonzalez et al. 2020) often exhibiting narrow distribution ranges (Galassi and Stoch 2010). Describing these results of evolution is worthwhile but using them to explore general eco-evolutionary questions might seem, as yet, unrealistic given our current limitations related to:

- *Logistic constraints associated with collecting and describing cave meiofauna:* We are far from a complete inventory of subterranean faunal diversity, especially that of meiofauna, in most regions of the world (Curini-Galletti et al. 2012; Zagmajster et al. 2018). Rectifying existing sampling is challenging, given the biological and habitat impediments associated with collecting and describing cave fauna (Mammola et al. 2020a, b, c), and meiofauna in particular (Fonseca et al. 2018) (Table 10.1).
- *Geographically fragmented information on cave meiofauna*: Indeed, we know nothing about cave meiofauna from large areas of the world, and from others, the available information remains largely fragmented. This problem, which affects even the most basic description of cave meiofaunal communities (i.e. species identity and distribution), limits our capacity to understand the evolutionary history of individual cave species, their traits, and their tolerance ranges, as well as their abundances and interactions within different cave assemblages (Hortal et al. 2015). Unfortunately, the lack of taxonomic information for many important meiofaunal groups implies that this situation will not be alleviated within the near future.

If, however, we focus our efforts wisely, the study of a single cave lineage might tell us a lot about general ecological and evolutionary processes. Selecting some scientifically and logistically suitable caves for detailed, longer-term research will provide deeper insights into critical unknown aspects of cave meiofauna than dispersed sampling efforts in various new caves and countries.

Studies on selected cave species may be crucial to understanding the evolution and biogeography of major animal lineages and their morphological plasticity compared to larger-sized animals. Promising topics of interest include.

- Evolution of meiofauna under cave conditions—Identify those species that can render particularly deep insights of evolutionary processes (e.g. some Copepoda, Annelida, Nematoda, see Chap. 1)
- Structural, functional, and behavioural adaptations and plasticity—Compare and contrast cave and non-cave counterparts of meiobenthic or macrobenthic size to understand the selective demands put on cavernicolous life.

- Biogeography—Since plate tectonics and marine transitions seem to have particularly affected cave meiofauna, the study of targeted cave meiofaunal species might provide novel insights into the biogeography of microscopic animals in comparison with their non-cave counterpart (Fontaneto 2011).
- Ecological adaptations to cave conditions—Design and apply experimental approaches (e.g. "cave laboratories") that allow testing of various factors (including food spectra, role of bacteria in biofilms, light conditions, temperature, variations in salinity, etc.) on cave meiofauna populations and communities and their intra- and interspecific interactions with microbes and macrofauna.
- Mediation of wider ecosystem processes and provision of ecosystem services—Identify key cave meiofaunal activities (e.g. bioturbation, feeding) that regulate processes beyond the subterranean environment and potentially affect the provision of associated ecosystem services.

Within caves, meiofauna might play a central role in carbon cycling comparable to that in the outside world (Bonaglia et al. 2014). Thus, communities of small organisms might crucially affect the composition of the groundwater in inland and coastal aquifers (Saccò et al. 2019, 2022). Considering the fundamental ecosystem services that aquifers provide to humans, and the crucial role groundwater discharge attains in the chemical balance of the ocean (Luijendijk et al. 2020), cave micro- and meiofauna might affect our everyday life much more than we have so far imagined.

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Chapter 11
Meiofauna—Adapted to Life at the Limits

Jeroen Ingels, Daniela Zeppilli, and Olav Giere

Abstract Meiofauna are ubiquitous members of aquatic ecosystems worldwide. Some of them can thrive under boundary conditions that are challenging to most other organisms. The discovery of well-adapted meiobenthic communities under extreme environments (e.g., sub-glacial sediments or deep in the Earth's crust) has opened new insights into life under limiting conditions, insights relevant not only with respect to distributional and physiological aspects, but also of potential importance in research on venturous exobiological and medical frontiers. Although meiofauna do not have pelagic dispersal stages and, therefore, are directly exposed to the limiting environment of their immediate habitat, representatives from various taxa can survive environmental conditions often fatal to all other fauna. Typical 'extremophiles' belong to the abundant and diverse group of nematodes, but also, tardigrades, rotifers, loriciferans, kinorhynchs, and the protozoan foraminiferans (especially in polar regions). In addition, some can modulate their metabolism by temporarily switching to an 'alternate life' where they can 'escape in time' (Jönsson 2005). This extraordinary potential explains why they became preferred objects for biochemical, physiological, medical, and even exobiological studies. Natural extremes have always occurred, but under the present conditions of climate change, the frequency of extreme environmental challenges is increasing and represents a planetary threat. Therefore, understanding pertinent adaptations can provide vital information on how organisms may

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survive stressful challenges such as acidification, lack of oxygen, and rising temperatures. Thus, research on the biology, ecology, and physiology, including genetic studies, of these exotic meiobenthic taxa is gaining importance. As diversified as the taxonomic affiliations of extremophiles are their adaptive patterns that have evolved under hostile life conditions. The variety of pathways leading to their survival, including a temporary metabolic suspension or 'dormancy' (see Table 11.1), points to independent routes that have evolved repeatedly over evolutionary time. Pertinent studies may even shed light on their evolutionary diversification and their phylogenetic relationship (see Chap. 1). Since, in addition to nematodes, many specific studies are on tardigrades and rotifers, their life under extreme conditions, mostly in freshwater and desiccating terrestrial habitats, is also considered in this chapter.

11.1 Extreme Environments and Meiofauna

Environments near the limits of 'normal life' cover wide areas of the Earth's surface. However, our perspective of normal and extreme environments differs from those of meiofauna, particularly in the marine realm. From our perspective, the oceanic realm is still a rather inaccessible, if not hostile world, where the inhabitants, especially those in oceanic depths, remain 'foreign'. Can we really transfer our understanding of 'extreme' or 'limiting survival' to marine meiofauna, since these ubiquitous organisms seem well adapted to sometimes the most inhospitable conditions? How then can 'extreme' conditions for meiofauna be assessed in an objective way and how should we appraise what is stressful or identify the conditions that constrain them? There are several information sources that allow us to build this knowledge:

- From previous research data under exceptional environmental conditions,
- From studies testing comparable factors/conditions in more easily accessible areas, or
- From experimental analyses in the laboratory.

Environmental limitations may cause stress or even death for organisms, so these threshold conditions can be measured, compared, and evaluated. Criteria for stress under defined conditions can be derived from death rates higher than usual, from abnormal physiological, developmental/ontogenic, or reproductive pathways, or from diminishing protective adaptations or responses. These can distinguish 'extreme' from 'normal' and, thus, objectify our data (see, e.g., high content of certain stabilizers in hadal fish, Yancey et al. 2014). Assessment of these required differentiations and objectifications is challenging, but also important to advance our understanding of life on Earth—a major research frontier. To paraphrase and simplify: an environment may be considered extreme 'if one or more of the physical or chemical variables are near the limits of what is known to be tolerable by most known life forms' (Zeppilli et al. 2018).

In studying extreme environmental conditions, a remarkable potential and variety of adaptations have been revealed (Møbjerg et al. 2011; Poli et al. 2017; Rebecchi et al. 2020), together with insights into the evolution and diversification of life (Martin et al. 2008; McMullin et al. 2007). In extreme environments, one or several physical or chemical variables are near the limit of what is known from other animals and habitats, or from experiments, to be tolerable by most life forms (e.g., extremely high or low temperatures, pressure, oxygen or salt concentrations, or toxic compounds, see Fig. 11.1). Also, extreme variability may characterize these habitats (Amils et al. 2007; Ellis-Evans and Walter 2008; Rothschild and Mancinelli 2001). In the marine realm, extreme environments are often associated with ephemeral and unstable ecosystems (e.g., seasonal flood plains, food-falls, volcanic areas). In other cases, conditions may remain relatively stable, yet are extreme in their range and become hostile to the metabolism of most organisms (e.g., anoxic basins, abyssal plains, deep hypersaline anoxic basins). Both types of biotopes can host various, sometimes endemic, and well-adapted, meiofaunal species with high resistance to extreme environmental conditions and hence high persistence in such biotopes.

In marine extreme ecosystems, e.g., in hypersaline areas, anoxic basins, polar ice floes or desiccating muds, and hydrothermal vents, three meiofauna groups often dominate: foraminiferans, nematodes, and copepods. Specific meiofauna are also

Fig. 11.1 Examples of extreme environments (from left to right): shallow-water hydrothermal vent (Secca delle Fumose, Mediterranean Sea), deep-sea hydrothermal vent (East Pacific Rise, Copyright IFREMER), deep-sea pockmark (REGAB, Copyright IFREMER), and deep-sea brine pool (Cheops mud volcano, Nile Deep-Sea Fan, MEDECO Cruise 2007, Copyright IFREMER)

found in desiccation-prone, often amphibious freshwater habitats where conditions only intermittently allow for an active life, e.g., in ephemeral lakes or seasonal rivers during draught periods, in frozen polar ponds, in uppermost tidal shores, or in thin water films covering exposed grains and plants (e.g., kinorhynchs in mangroves, nematodes and rotifers in polar ponds or within brine channels of ice, tardigrades in mosses). For marine ecosystems, the biodiversity and ecology of ‘extreme’ meiobenthic specialists were the main topic in a review by Zeppilli et al. (2018). For nematodes, tardigrades, and rotifers living in freshwater and moist terrestrial habitats, Rebecchi et al. (2020) emphasize the physiological processes involved in adaptation. The basic prerequisite for all adaptive pathways to persist in extreme environments is an effective osmoregulatory potential, e.g., salt-, water-, and thermoregulation (Wright and Newall 1980; Wharton 2007). When conditions become limiting for ‘normal’ life, it is ‘dormancy’ that can considerably expand the range of survival. Dormancy warrants a ‘dual existence’ with an active phase where habitat conditions (e.g., water content) remain in the normal range and a dormant phase (where active life is reversibly suspended, e.g., extreme frost with no liquid water present). The predominant modes of dormancy, cryptobiosis, and diapause are further differentiated (see Table 11.1).

While cryptobiosis is under environmental control (adverse life conditions) and may become repeatedly triggered and quickly reversed, diapause, especially encystment or production of resting eggs, is strongly regulated by endogenous stimuli and often restricted to set developmental (cyclomorphotic) phases. Among cryptobiotic meiobenthos, anhydrobiosis (osmobiosis) and cryobiosis are encountered most

Table 11.1 Modes of dormancy occurring among meiofauna classified (based on Rebecchi et al. 2020) (Original)

DORMANCY—any form of resting stage in stressful environments
Cryptobiosis (‘anabiosis, quiescence’) (also ‘hidden life’, under exogenous control, occurs in all life stages from eggs to adults, may get quickly reversed by external stimuli)
e.g., anhydrobiosis—maintenance of a reduced form of life under extreme desiccation, the most common and best investigated form of stress resistance
e.g., osmobiosis—maintenance of a reduced for of life under extreme salinities
e.g., cryobiosis—maintenance of a reduced form of life under extreme cold
e.g., anoxybiosis—maintenance of a reduced form of life under anoxic conditions (with hypoxybiosis—maintenance under extremely low oxygen concentrations)
Diapause (complete suspension of growth and development, triggered by endogenous and exogenous stimuli, with far-reaching morphological changes)
Encystment—encapsulation of organism in sheltering exuvia of cuticle (‘Russian doll principle’, known from limnetic tardigrades, but also from the marine *Echiniscoides*; typical also for many rotifer taxa)
Resting eggs—Among meiofauna mostly restricted to monogonont rotifers, usually developing at certain developmental phases only, extremely resistant to all kinds of stressors, often serving as mode of distribution

frequently; anoxybiosis is restricted to habitats with reduced or even absent oxygen supply. Some freshwater nematodes, tardigrades, and rotifers can include into their life cycle a metabolic diapause as a reversible phase of extreme tolerance (for details, see Rebecchi et al. 2020).

The most widespread survival strategy under extreme conditions is the capacity to regulate the composition and water content of body fluids. Highly efficient osmoregulation mechanisms are fundamental for survival of meiofauna organisms under both extreme salinity and temperature conditions and determine their life in polar ice (see Chap. 9), in brackish and hypersaline waters as well as in desiccation-prone habitats. However, pertinent functional studies and physiological measurements remain scarce. Most investigations are based on reporting meiofaunal composition and distribution, while studies reporting on ecophysiological or biochemical processes often involve macrofauna only.

The presence of meiofauna living in the sympagic channel system of sea ice has been well described (Ehrlich et al. 2020; Gradinger 2001; Gradinger and Bluhm 2020; Schnack-Schiel et al. 2001) with nematodes, turbellarians, rotifers, and harpacticoids dominating. However, the pathways of maintaining an efficient osmoregulation for survival under these extreme conditions are often based on analogous studies of the accompanying macrobenthic Arctic amphipods. These have been found to adapt by maintaining high concentrations of inorganic ions and specific amino acids in their hemolymph when salinity drops to 5 PSU (Aarset 1991). The diverse meiofauna thriving in the brine channels of ice floes prevent the formation of ice crystals in their bodies by special hemolymph 'antifreeze' proteins (for details, see Sect. 11.6).

11.2 'Toughest Animals on Earth' (Erdmann and Kaczmarek 2017)

Knowledge on the mechanisms involved in facilitating 'life at the limits' can be gained by focusing on three meiobenthic taxa: nematodes, ecologically the most successful and often dominant phylum, rotifers and tardigrades. The latter, although less dominant, are bizarre and famous for their successful excursions into outer space (Figs. 11.2 and 11.3) although nematodes have also been used in space missions under experimental conditions.[1] All these phyla are well known for their ability to cope with desiccation, extremes of temperature, hypersalinity, etc. First, we examine in more detail the ubiquitous nematodes, and then, we will provide more details on arguably the hardiest of meiobenthic organisms, the (freshwater) tardigrades and rotifers.

In Antarctic dry valleys, where extreme conditions provide the bare minimum for sustaining life, the top level of the terrestrial, 'ephemerally aquatic' soil food chain is represented by nematodes (Wharton 2003). Perhaps even more astonishing

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[1] https://theconversation.com/all-you-need-to-know-about-the-space-travelling-nematode-a-worm-like-no-other-47949.

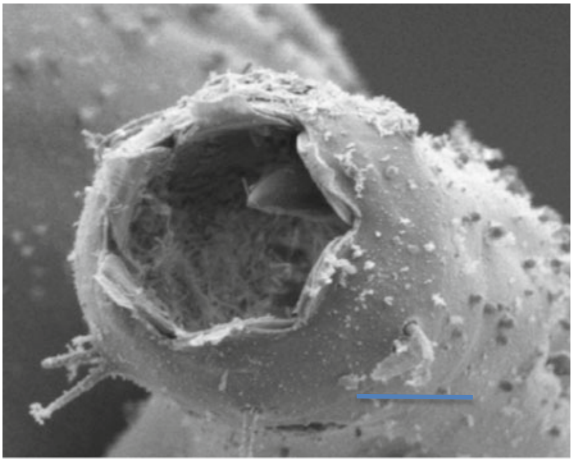

Fig. 11.2 Nematode *Oncholaimus dyvae*, buccal cavity. Species living at deep-sea hydrothermal vents and feeding on bacterial mats (scale bar: 10 µm) (Copyright: IFREMER)

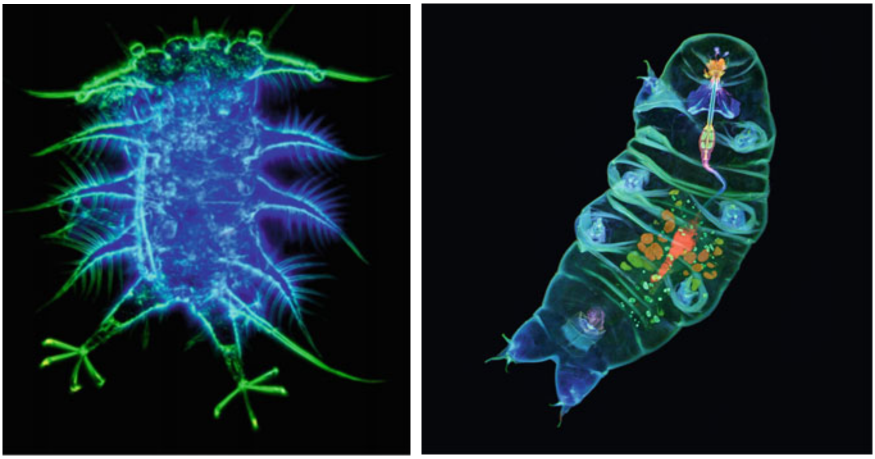

Fig. 11.3 Immuno-fluorescence photographs of two tardigrade species. Left—*Neostygarctus oceanopolis,* particularly abundant on deep-sea seamounts (total length incl. toes: 250 µm) (Copyrights IFREMER); right—*Hypsibius exemplaris,* common in freshwater ponds and lakes, known as a 'laboratory species' (total length 220 µm) (Copyrights Tagide deCarvalho, USA)

are reports of nematode specimens that, according to Shatilovich et al. (2018), were revived from permafrost soils frozen in prehistoric times. Another astounding example of viability under extreme conditions is the finding of nematodes (*Halicephalobus mephisto*) in rocks of the Earth's crust in km-deep fracture water up to 12,000 years old (Borgonie et al. 2011). In marine oxygen minimum zones, areas in the world's oceans characterized by very low oxygen (<0.5 ml/L), nematodes dominate (up to 99.9%) the benthic realm with macrofauna and other meiofauna being absent (Neira et al. 2018, 2001; Veit-Köhler et al. 2009).

As for tardigrades and rotifers, their extreme potential of cryptobiosis (anhydrobiosis, cryobiosis, anoxybiosis) was reviewed by Rebecchi et al. (2020), and tardigrades, suppositioned as the 'toughest animals on Earth', are now of global interest to astrobiologists because of their high resistance to conditions akin to the challenges encountered in space (Erdman and Kaczmarek 2017).

11.3 Why Are Nematodes so Successful Under Extreme Conditions?

Nematodes have been reported from every habitat, from the bottom of the deepest sea to the top of the highest mountains, and from arid deserts to the deep Earth's crust. A recent paper elegantly proposes that the unique combination of five nematode characteristics may explain their successful adaptation to extreme habitats (Sapir 2021).

These can be summarized as follows:

(i) Simple body plan (cylindrical with no appendages),
(ii) Adaptation to low concentrations of oxygen,
(iii) Minimal dietary requirements,
(iv) Various strategies for suspended animation,
(v) Pre-adaptation and tolerance across different stressors.

Freshwater and marine environments offer conditions in which nematodes have shown exceptional aptitude to thrive, dominate, and outcompete other metazoans. However, many of these environments expose nematodes to most variable and even hostile conditions, such as high pressure, extreme temperatures, osmotic/ionic stress, hypoxia, methane and carbon dioxide release, and other chemical stressors. Some may survive for months in liquid nitrogen; others may live in vinegar, glue, or even in soaked beer mats. What these all have in common, however, to sustain life with active metabolic processes, is that they require some moisture. Only in the status of 'diapause', a number of species can survive for months or years as dry 'aggregations' until water re-enters their environment and revives them from the desiccated state (Kitazume et al. 2018).

Nematodes, lacking circulatory or respiratory systems and appendages, are structurally a simple life form, with a rather invariant body plan, comprised of about 1000 cells in the adult stage (e.g., *Caenorhabditis elegans*, Sulston and Horvitz 1977). Their body is dominated by the alimentary and reproductive systems and mechano- and chemosensory receptors (e.g., setae, amphids). The anatomical simplicity contrasts with their functional efficiency, evolutionary diversification, and capacity adaptation. Nematodes exhibit complexity in many other ways, (i) morphologically (body sizes from hundreds of micrometers to >6 m), (ii) life cycles (from parthenogenesis to complex parasitic cycles or alternating sex strategies), and (iii) their ecology (Blaxter 2011). In addition, they possess many metabolic and developmental processes and specializations that allow them the physiological adaptability to withstand stress and adverse conditions (Lee 2010; Tahseen 2012). The key for this enormous diversification despite anatomical simplicity seems to be a complex mechano- and chemosensory system allowing them to respond to a wide range of environmental stimuli (Lee 2010). Numerous developmental, physiological, and biochemical adaptations, allowing nematodes to survive under extreme conditions (Wharton 2003, 2004, 2007), triggered investigation of the underlying processes and genetic origins (Perry and Wharton 2011).

Nematodes can be dated back using trace fossils to the Cambrian period at least (see Chap. 1). Hence, the evolutionary age of nematodes provides considerable time for adapting to the diversity of (marine) ecosystems. A study using nucleotide diversity confirmed that free-living nematodes conquered land before most other metazoans did (Rota-Stabelli et al. 2013), allowing time for adaptations to extreme environmental conditions to develop. In addition, the generational turnover of nematodes is fast: Life cycles between three days and several months (although in marine nematodes usually not exceeding a few weeks, see Gerlach and Schrage 1971; Tietjen and Lee 1972) allow them, with modifiable genetic material, to adapt or change relatively rapidly when subjected to selective pressures. Successful habitat transitions between marine, freshwater, and terrestrial ecosystems could be the basis for the extensive diversification of nematodes (Holterman et al. 2019). Hence, it is probable that different adaptations and life strategies have evolved independently and repeatedly also within each of the three main nematode clades Chromadoria, Enoplia, and Dorylaimia (Blaxter 2011; De Ley 2006; De Ley and Blaxter 2002).

A deeper understanding into the survival mechanisms that make nematodes so successful may provide important information on how organisms may respond and adapt to increased impacts in the Anthropocene, and, even, bring some insight in the potential of life in extreme conditions outside our Planet's biosphere.

11.4 Adaptive Responses of Nematodes to Extreme Environments

Survival abilities include morphological adaptations, behavioral changes (migration, dispersal, phoresis, aggregation, swarming, coiling, etc.), or resistance-adaptive measures that are often linked to metabolic processes (Wharton 2002, 2007). Adaptations such as maximizing body surface/volume ratio, increasing body length, and protective cuticle structures (providing protection to pollutants and other chemical stressors) may be considered as general and widespread pre-adaptations in nematodes (see Soetaert et al. 2002; Sapir 2021). However, among nematode groups, they seem to vary. The relatively impermeable cuticle of diplogasterids and rhabditids, for instance, makes them more tolerant to pollutants, while a more permeable cuticle in actinolaimids renders them more susceptible to pollutants (Bongers 1999).

On the genetic level, a pre-adaptation seems to be the basis for the extreme chemical resistance, both in an extremophile *Anuanema* species from the arsenic-rich, hypersaline Mono Lake and in the ubiquitous *C. elegans*. Possession of a gene known to confer arsenic resistance (Shih et al. 2019) suggests conservation of a nematode trait with pre-adaptive potential in both taxa. Moreover, diverse pheromonal substances called 'ascarosides' are widespread in the phylum Nematoda and can vary in number and concentration depending on the species and their diverse ecologies (Choe et al. 2012). This would suggest that chemotaxis and the associated potential to efficiently sense the chemical environment are features that facilitate survival in challenging conditions.

While juvenile and adult nematodes are morphologically similar, the adaptive physiology of their various life stages is highly diverse (Wharton 2012). Adaptations to cope with unfavorable environmental conditions can often be linked to nematode life cycles, to their inherent ontogenies, and 'timing mechanisms' of development and growth. This includes their ability to reduce or suspend movement, metabolic activity, growth, and development. For example, a classic response to unfavorable environmental conditions, the onset of cryptobiosis or quiescence, occurs as a temporary metabolic slow-down in numerous extremophile nematodes (Rebecchi et al. 2020). Normal development and growth are resumed as soon as favorable conditions return. In other cases, nematodes can counteract conditions that would be normally lethal in a stage of developmental suspension or 'diapause' (see Table 11.2). Here, under severe or prolonged environmental stress and/or at certain phases in their life cycle, they can bring their metabolism to a long-lasting halt, to a stop of growth and even ageing. The metabolic rate may fall below detectable levels and 'appears' to cease (Rebecchi et al. 2020; Wharton 2004).

As shown in Tables 11.1 and 11.2, a variety of environmental stress factors, typically occurring in extreme environments, may trigger quiescence (desiccation, draught and high temperature (anhydrobiosis), low temperature (cryobiosis), osmotic stress (osmobiosis), and low oxygen (anoxybiosis) (Tahseen 2012). In contrast, developmental arrest such as diapause is initiated by certain environmental stressors, but also requires an 'internal' conditioning (e.g., photoperiod and pheromonal stimuli) that may occur at a certain developmental stage (Wharton 2004). The onset of diapause as well as the return to active life requires specific environmental and physiological cues. For example, in response to various types of environmental or nutritional stress in their ontogenesis, some nematodes develop 'resting eggs' and 'dauer larvae' or stay alive as cysts (Bird and Bird 2001; Wharton 2012). This status of diapause can keep the organism alive for years by a structural change of the cuticle, a decrease of permeability and in some cases an additional protection through encapsulation in the previous molts (Evans et al. 1976). When conditions improve, the nematode reverts to its normal metabolism. This has been shown by Shatilovich et al. (2018) who reactivated specimens of the nematode *Panagrolaimus detritophagus* found in permafrost-frozen cores thousands of years old.

Table 11.2 Categories of nematode responses and adaptations to extreme conditions (Original)

Categories	Characteristics and types
Morphology	Cuticle (permeable or non-permeable) Sheaths Eggshell Structural integrity Body shape (miniaturization, filiform habitus to maximize surface-volume ratios in hypoxic environments)
Behavior	Aggregation, clumping, swarming, individual or group movement, synchronous behavior, coiling Migration over short (mm) to long (1000 s kms) distances depending on the dispersal ability (limited active, wider range passive) and the spatial influence of the stressor Migration can, aside limited active moving away from the stressor, also be in the form of phoresis and epibiosis Can be triggered by chemotaxis using amphids or other sensory organs (setae, eye spots)
Resilience and capacity adaptations	**Timing mechanisms and survival**
	Diapause (obligatory/facultative), developmental arrest
	Quiescence, cryptobiosis, anabiosis (anhydrobiosis, cryobiosis, osmobiosis, anoxybiosis)
	Dauer stages (pheromones/chemosensory induced)
	Slowing or arrested development and growth (hypobiosis)
	Infective stages
	Resistance adaptation
	Reduced metabolism, stupor, coma
	Specific proteins and enzymes (e.g., trehalose, Desc47, COR, LEA, and interactions) Detoxification (metals, sulfides, assimilation, and locking away in vacuoles) **Symbioses** External and internal symbionts Detoxification and food supply

11.4.1 Prevalent Stressors for Nematodes

The well-documented persistence of nematodes in all kinds of environments is based on a variety of adaptations that enable their survival under harmful or lethal conditions and explains their ubiquitous occurrence. For a consideration of their extreme adaptive potential, a selected variety of limiting physical and chemical stressors is depicted in Fig. 11.4.

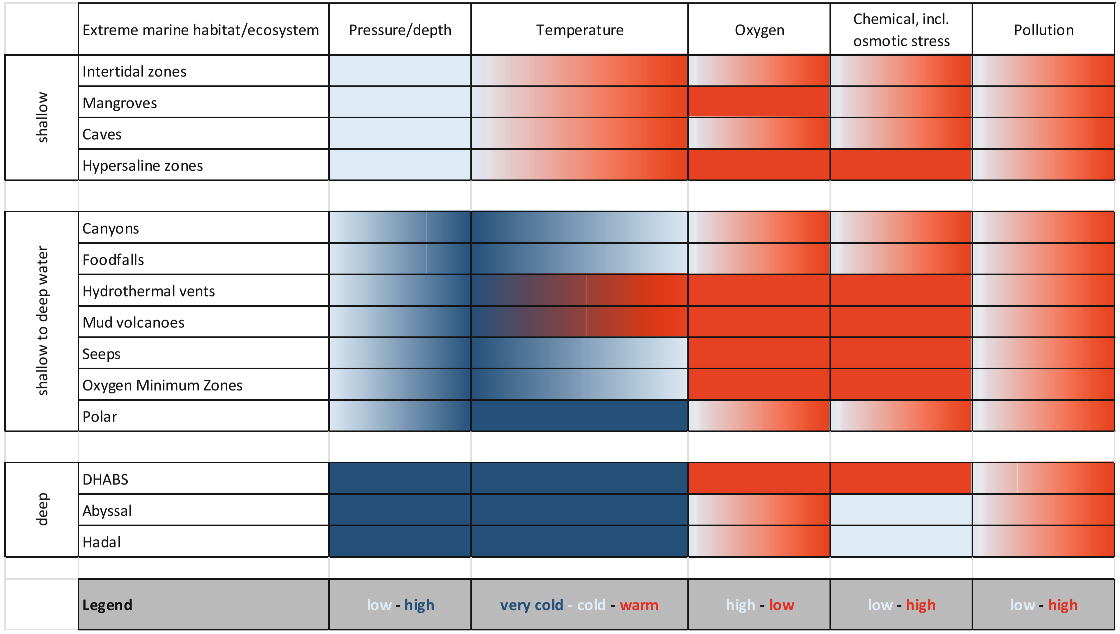

Fig. 11.4 Stressors frequently encountered by nematodes in different coastal and marine habitats (vertically arranged by water depth in three groups). Pressure/depth according to water depth. Temperature: generally very cold (<0 °C) in deep-water and polar regions; cold to warm in shallow habitats; high temperatures compared to surrounding waters at hydrothermal vents and mud volcanoes; seeps can be slightly warmer than surrounding waters; otherwise relative to water depth and influence from hydrodynamic processes. Oxygen: Most habitats can experience low levels of oxygen, generally lower in mangroves, very low/anoxic in hypersaline zones, DHABS (deep hypersaline anoxic basins), and centers of vents, mud volcanoes, seeps, and oxygen minimum zones. Generally high in polar regions but can be low in areas affected by sedimentation and higher organism oxygen demand. Chemical stressors (e.g., ocean acidification, vent fluids, etc.) can be high in most habitats; abyssal and hadal depths are generally less affected (unless for specific seafloor features). In the Anthropocene, no habitat seems impervious to pollution (Original)

11.4.1.1 Oxygen

The worldwide increase of areas where hypoxia or anoxia and sulfides prevail is prompting intensive research on the oxygen metabolism of organisms. The frequent occurrence of nematodes in various oxygen-deficient and/or hydrogen sulfide-rich biotopes is resulting in increasing information about adaptive modes specifically related to oxygen stress, more than for most other stressors (Wetzel et al. 2001). Structural and biological (life-history) aspects are followed by ecological and physiological data that can explain the extreme stress potential of nematodes.

The aerobic metabolism of nematodes, which lack respiratory and circulatory organs, depends on the diffusion of ambient oxygen into the tissues (Lee 2010; Lee and Atkinson 1976). The developing diffusion gradient transports oxygen into the pseudocoelomic fluids and the central gut. Therefore, a notable morphological adaptation is the extremely slender body of nematodes, maximizing surface-volume ratio and enabling efficient uptake of oxygen through the cuticle into the peripherally located muscles and nerves. As shown by *Terschellingia* spp., these adaptations are particularly expressed in nematodes from deeper sediment layers, often occurring under hypoxic, thiobiotic conditions near the redox-discontinuity layer (Steyaert et al. 2007). The role of viscous epidermal sulfur inclusions found in the epidermis of some thiobiotic nematodes (Thiermann et al. 2000; Vincx 1987) is, as yet, unclear, since pathways of their effective and regular removal have so far not been found.

In addition to structural adaptations, numerous ecological adaptations help to understand how nematodes are responding to low-oxygen/high-sulfide conditions. Due to the limited oxygen penetration into marine and freshwater muds, hypoxia and anoxia occur widely, yet nematodes are regularly found under these conditions. In marine oxygen minimum zones (<0.5 ml/L), for instance, nematodes dominate benthic communities (Neira et al. 2001; Veit-Köhler et al. 2009). Within these nematode communities, many species are present under oxygen limitations, but distinct differences between species do occur (Cook et al. 2000; Gambi et al. 2009; Levin 2003; Neira et al. 2013). The specialists among them, with their extreme tolerance to low-oxygen and high-sulfide conditions, have ecological advantages: They can populate the competition-reduced layers using the rich (bacterial) food supply around the oxic/anoxic interface, the ‘discontinuity layer’ (Jensen 1986, 1987a; Losi et al. 2013; Soetaert et al. 2002, 2009; Zeppilli et al. 2018). In experiments with short-term hypoxia, several nematode species may show resistance without differences in community structure or diversity compared to normoxic conditions. However, under long-term exposure (up to 305 days of anoxia), distinct species-specific responses and mortality can occur, and survival may be community-dependent (Taheri et al. 2014). Community recovery after severe oxygen limitation can take between 30 and 90 days after the return of normoxia (Steyaert et al. 2007; Taheri et al. 2015), indicating a relatively rapid response to ameliorating conditions. *Sabatieria* is one of those genera with high densities in anoxic and strongly reduced muddy sediments. *Sabatieria pulchra* for instance is often found as the single remaining species in deeper sediment layers near the redox discontinuity, but suffers mortality when exposed to more severe oxygen limitation (Steyaert et al. 2007).

One remarkable pathway to adapt to low-oxic or anoxic as well as sulfidic conditions is found in the nematode genera *Eubostrichus*, *Stilbonema,* and *Astomonema*: They developed obligate symbioses with bacteria. Ultrastructural evidence, stable isotope values, and molecular data have shown that these gutless nematodes and their interacting bacterial partners are capable of oxidizing toxic sulfide compounds and can provide the hosts with food (for details, see Chap. 4 and (Giere et al. 1995; Musat et al. 2007; Ott et al. 1982, 1991, 2004a, b; Tchesunov 2013; Tchesunov et al. 2012)).

Much less well-understood is the non-symbiotic *Theristus anoxybioticus.* As indicated by its species name, this marine nematode is regularly found in anoxic and sulfidic layers. In choice experiments, its juveniles even preferred staying in hypoxic or anoxic conditions (Jensen 1995). Here, they survived for more than two weeks in anoxic sediments. However, when exposed to oxygenated water, they died within half an hour.

Some species that can thrive in low-oxygen sediments show specific life-history adaptations. Under severely hypoxic conditions, some of these species reduce their movements and enter a state of 'suspended animation' (Kitazume et al. 2018), effectively switching to anaerobic metabolic pathways (Atkinson 1980). Or they can enter a temporary cryptobiotic state (anoxybiosis, see above). By reducing growth during metabolic inertia or during low-oxygen conditions, nematodes have even been found to extend life spans of individuals and persistence of populations (Van Voorhies and Ward 2000; Cooper Jr and Van Gundy 1970). A perhaps less spectacular but notable example is the occurrence of ovovivipary in some nematode species such as *Geomonhystera disjuncta* (Van Gaever et al. 2006) and *Metachromadora vivipara* (Steyaert et al. 2007). Hatching of juveniles within the adult body is thought to increase the survival rate and successful development of their brood in anoxic and sulfidic environments. This reproductive mode likely allows gravid females to escape toxic environments before releasing the juveniles.

The numerous examples where nematodes were found exposed to anoxia and high hydrogen sulfide levels have sparked detailed research on the oxygen metabolism of organisms. A central question remains: 'Which physiological adaptations enable (some) nematodes to live under these variable and hostile conditions?' While the preferred oxygen concentrations may differ among species and developmental stages, many nematodes require surprisingly low oxygen tensions, even when active. Nematodes respond to hypoxia or anoxia by using up their glycogen reserves to exhaustion (and death) or by obtaining alternative energy and retaining a cryptobiotic, non-metabolizing state until conditions improve (Gaugler and Bilgrami 2004). The presence of hemoglobin may support tolerance of relatively low O_2 tensions (Weber and Vinogradov 2001). The hemoglobins contained in some nematodes have a high affinity for oxygen and can attain an oxygen-carrying or oxygen-storing capacity (Atkinson 1980; Lee and Atkinson 1976).

The oxyhemoglobins of many nematodes become deoxygenated under anaerobic conditions and re-oxygenate when traces of oxygen become available again. The marine mud-feeder *Enoplus brevis* has high hemoglobin concentrations in its esophagus, a strategy, which allows oxygen storage and release when needed. Thus, it can live consistently exposed to extremely low oxygen tensions and shows higher feeding rates than its hemoglobin-lacking congener, *E. communis* (Atkinson 1977, 1980; Ellenby and Smith 1966b). Hemoglobin concentrations under low-oxygen conditions can vary significantly between species and in different body regions, with some species requiring readily available oxygen in certain body tissues (Ellenby and Smith 1966a, b) (an insect-parasitic nematode even alternates between aerobic and anaerobic metabolism) (Shih et al. 1996).

For most free-living nematode species (except for *C. elegans,* see Baumeister et al. 2021; Horsman et al. 2019; Ng et al. 2020), the physiological pathways involved in these adaptations to stressful low oxygen concentrations remain little understood for now. In summary, the widespread ability of nematodes to cope with oxygen-deficient or even anoxic conditions is based on an array of structural, ecological, life-history, and physiological adaptations not found, or at least not as well-studied, in other meiobenthic taxa (Bryant et al. 1983; Schiemer and Duncan 1974).

11.4.1.2 Hydrogen Sulfide

A high tolerance to extremely toxic hydrogen sulfide is found in many animals inhabiting the sea floor around hydrothermal vents. Here, nematodes such as *Oncholaimus* spp. seem adapted to sulfide-rich and iron-rich habitats, facilitated by their specific symbiotic internal and external bacteria (Zeppilli et al. 2018; Bellec et al. 2020). In *Oncholaimus campylocercoides*, secretion of sulfur-containing droplets, when exposed to hydrogen sulfide, presumably reduces the toxic effect of hydrogen sulfide (Thiermann et al. 2000). Also, other species of *Oncholaimus* were found to live in large populations in hydrothermal vent sediments rich in sulfur and iron. The nematode *Halomonhystera* exhibits ovoviviparous reproduction in vent sediments as well as in other extreme environments where the concentrations of sulfide and other noxious chemicals are particularly high (Van Gaever et al. 2006; Zeppilli et al. 2015). At physiological concentrations, *C. elegans* even seems to experience protective effects from exogenous H_2S, which even increased lifespan (Topalidou and Miller 2017; Horsman et al. 2019).

11.4.1.3 Temperature, Desiccation, and Osmotic Stress

While most of the deep-sea floor populated by nematodes are characterized by a relatively constant low temperature of ~2 °C, they are exposed to temperatures of up to 50 °C around hot vents. With regards to cold temperatures in polar and sub-polar areas, nematodes regularly tolerate temperatures around 0 °C. At lower temperatures, all processes slow down because kinetic energy becomes reduced, ultimately leading to suspended animation. Extreme freeze tolerance is often linked to anhydrobiotic processes (see below). Extremes of frost may provoke stupor or even complete and long-lasting diapause if no essential damages occurred.

In all poikilotherms, also in nematodes, the metabolism is dependent on temperature, since temperature affects the maintenance and stability of molecular processes and fluidity in many biological structures, (e.g., enzymes and lipid bilayer membranes). Therefore, prevalence of nematodes in biotopes with extreme temperatures (from deep frost to near boiling water) requires regulative processes structuring molecular, physiological, behavioral, and reproductive pathways (Gaugler and Bilgrami 2004; Wharton 2007; Atkinson 1980; Moens and Vincx 2000).

Cold Tolerance

Strategies mainly found in nematodes (Lee 2010; Wharton 2003, 2004; Rebecchi et al. 2020, see also corresponding data in tardigrades):

(1) **Tolerance of freezing**, where animals can withstand ice formation in their bodies and/or maintain the body fluids in a liquid phase even at temperatures below the melting point. Some extreme freezing-tolerant Antarctic and Arctic nematode species (e.g., *Plectus antarcticus*, *Scottnema lindsayae*, *Chiloplacus* sp.) can either complete their entire life cycle at low temperatures or are able to maintain faster development and higher reproductive rates at lower temperatures compared to most other nematodes (Caldwell 1981; Overhoff et al. 1993; Procter 1984). Freezing tolerance has been demonstrated in several species of Antarctic nematodes (Wharton and Block 1997), with for instance *Plectus murrayi* (Timm 1971) being able to survive extreme desiccation and freezing conditions (Adhikari et al. 2009).

(2) **Avoidance of freezing** by supercooling effects. In supercooling, the body fluids remain liquid below their nominal freezing point, so that lethal freezing is avoided. In supercooling (investigated mainly in parasitic nematodes), external ice formation can provide a sheltering layer in the cuticle ('inoculative freezing'). Thus, the species can avoid freezing of its internal tissues, but it will die once these themselves freeze (Wharton 2007). In addition, the well-documented production of cryoprotective compounds (trehalose, glycerol, polyhydric alcohols) can enhance supercooling abilities (Ash and Atkinson 1982, 1983; Behm 1997; Jagdale and Grewal 2003; Wharton 2004). Temperature thresholds at which supercooling is triggered in several species were found to vary with season (Pickup 1990) indicating temporal changes in their metabolic status.

(3) **Anhydrobiosis** is an extreme status of complete desiccation where the animals lose all features characteristic of a living organism. In this drastic status of non-detectable metabolism, the animals, not alive and not dead either, can survive frost without the risk of freezing. Without any internal water present, nematodes have been found to survive for years (Lee 2010; Wharton 2002, 2004) and even for millennia (Shatilovich et al. 2018). Several species of free-living nematodes can survive periods of anhydrobiosis by desiccation (see below) (Wharton 2002, 2004, 2007).

Heat Tolerance

Heat can have destructive effects on molecules and cells and interrupt central body functions. Protein denaturation, caused by high temperatures, often leads to subsequent loss (reversible or irreversible) of associated functions (Hochachka and Somero 1984; Tahseen 2012). Several species have been reported to occur in hot springs at temperatures around 40 °C (Abebe et al. 2001; Ocaña 1991a, b), and even surviving up to 92 °C water. In shallow-water hydrothermal vents, nematodes occurred at sites close to the geyser point, at temperatures around 80 °C (Zeppilli and Danovaro 2009). At a deep-sea hydrothermal vent along the Mid-Atlantic Ridge, meiofauna represented at least 50% of the total vent fauna diversity and meiofaunal communities were dominated by generalist nematodes (Zeppilli et al. 2018; Baldrighi et al. 2020). In some cases, however, nematodes can thrive in hydrothermal vent systems owing to their symbiotic associations with prokaryotes (see Sect. 11.4).

Desiccation

A general prerequisite of desiccation-tolerant nematodes is lowered permeability of their cuticle (Gaugler and Bilgrami 2004) and tissues becoming condensed and packed together (Bird and Buttrose 1974) to maintain structural integrity in the anhydrobiotic status. A common response to ambient drought is reduction in nematode movements mainly caused by a lack of a water film (Wharton 2004). Another physical response is coil formation requiring the coordinated contraction of all muscles on one side of the body. Coiling minimizes the exposed surface of the cuticle, thus reducing water loss (Gaugler and Bilgrami 2004). Certain nematode species tend to congregate, forming lumps of ‘nematode wool’ that protect the innermost specimens.

Beside these structural/behavioral adaptations, metabolic changes during nematode desiccation have been observed. Desiccation leads to a decrease of glycogen and lipid levels and an important increase of protective agents (‘bioprotectants’) such as trehalose and glycerol as well as certain proteins (Rebecchi et al. 2020). Trehalose has been found to replace internally bound water, thus stabilizing membranes and protecting cells during dehydration (Crowe et al. 1984; Womersley 1981). In combination with some desiccation-induced proteins, it forms a glassy matrix (‘bioglass’), which prevents desiccation-induced damages (Browne et al. 2002; Solomon et al. 2000).

In the desiccated phase of ‘suspended life’, the organisms can be biostable for months or years. For example, limnic nematodes such as *Actinolaimus hintoni* and *Dorylaimus keilini* can survive several months of drought in temporary ponds in Nigeria (Lee 1961), provided that water loss proceeds gradually. Dehydration proceeding too fast would usually kill most nematode species. Some ‘fast-desiccation strategists’ (e.g., *Plectus* sp., *Panagrolaimus* sp. and *Dytilenchus* sp.) are able to survive immediate exposure to 0% Relative Humidity (Lee 2010; Perry 1999; Wharton 2002).

When water re-enters the body surface of desiccated nematodes, these physiological ‘dehydration processes’ become reversed. The animals become rehydrated and return back to normal activity after a lag phase of hours/days between immersion and regaining normal activity (Gaugler and Bilgrami 2004; Lee 2010; Wharton 2007).

Osmotic Stress

Most nematodes have no specialized excretory systems, and (nitrogenous) wastes are released directly across the body wall. Most of them, especially the marine species, are osmo-conformers: Their internal osmotic concentration more or less follows in parallel to changing external osmotic concentrations (Willmer et al. 2009). However, especially in coastal habitats, littoral nematodes are subjected to varying intermittent or even longer-term phases of dehydration and rehydration. Some of these nematode species effectively osmoregulate due to the presence of specific excretory cells or glands. Cuticular permeability and intestinal water removal can also play a role in nematode osmoregulation and reduction of osmotic stress (Lee 2010; Wright and Newall 1980). When exposed to hyperosmotic environmental conditions, these 'osmobiotic' nematodes experience saltwater entering their bodies. Excretion of salts can lower the osmotic gradient (Oglesby 1981). In brackish, hypo-osmotic conditions, nematodes experience water loss (Lee 2010). One example is *Enoplus brevis*, which is able to regulate its volume and adapt to unstable environment such as salt marshes and estuaries (Wharton 2004, 2007). The Antarctic nematode *Panagrolaimus davidi* maintains its higher internal osmotic concentration above the environmental level by effectively acting as hyperosmotic regulator (Wharton 2010).

11.4.1.4 Pressure

Marine nematodes, surprisingly numerous in hadal ecosystems (Zeppilli et al. 2018), seem naturally adapted to high hydrostatic pressure. However, nematode genera reported from hadal trenches are also found in a wide range of other deep-sea and shallow-water ecosystems, probably indicating that only minor adaptations are required for their survival under extreme water pressure (Gambi et al. 2003; Kitahashi et al. 2012, 2013; Tietjen 1989). Conversely, marine nematodes may survive rapid decompression: *Oncholaimus dyvae*, retrieved from water depth of 1700 m in hydrothermal vents of the Mid-Atlantic Ridge, not only survived hauling up, but remained alive in laboratory conditions for up to 4 months and juveniles showed normal growth at atmospheric pressure. Other oncholaimid species stayed alive for up to 48 h after retrieving them from 5000 m water depth (Zeppilli, unpublished).

11.4.1.5 *CO_2 and pH*

In times of rapid global climate change, aquatic as well as terrestrial animals and ecosystems have to cope with rising CO_2 concentrations. A large spectrum of nematode behavioral responses to CO_2 has been described, emphasizing the fundamental role of CO_2 in nematode life (Banerjee and Hallem 2019 and references therein). In both marine and terrestrial nematodes, high CO_2 levels may provoke different behavioral and physiological responses (signals for food, predators, pathogens, or conspecifics, see Banerjee and Hallem 2019; Carrillo and Hallem 2015). Free-living nematodes (*Acrobeloides* sp.) isolated from a volcanic vent could survive in the laboratory for five days at full CO_2-saturation, even at extremely low oxygen content (Pilz and Hohberg 2015; Pilz et al. 2017). Concerning acidification, pH seems not to be a decisive factor for most aquatic nematodes (Gaugler and Bilgrami 2004).

Some species even favour CO_2 enrichment (Hale et al. 2011; Ingels et al. 2018; Kurihara et al. 2007; Meadows et al. 2015). CO_2 enrichment is involved in food-searching behavior of nematodes: The marine nematode *Adoncholaimus thalassophygas* was attracted to CO_2 enrichment produced by bacteria associated with decomposing carcasses (Riemann and Schrage 1978). In this case, CO_2 acted indirectly by indicating bacteria aggregations that served as the main food. Under natural conditions, *Caenorhabditis elegans* lives in rotting vegetation where O_2 and CO_2 levels are fluctuating (Félix and Braendle 2010; Schulenburg and Félix 2017). In this complex habitat, O_2- and CO_2-sensing pathways are used for orientation and foraging (Bendesky et al. 2011; Juozaityte et al. 2017; Milward et al. 2011). Dauerlarvae of *C. elegans* were attracted to CO_2, probably because this might enhance their chances to find bacterial sources (Banerjee and Hallem 2019). In contrast, starved adults shifted from repulsion to attraction by CO_2 (Rengarajan et al. 2019). However, if well-fed, nematodes avoided high levels of CO_2 (Bretscher et al. 2008; Hallem and Sternberg 2008). Dependent on its nutritional status, *C. elegans* reduced or even stopped pharyngeal pumping when exposed to high concentration of CO_2 (Sharabi et al. 2009). This is in line with other observations on *C. elegans* that the first effect after high CO_2 exposure was an overall decrease in locomotion (Dunsenbery 1985). Exposure to chronically high concentration of CO_2 caused movement deficiencies and serious damages to the muscular morphology (Sharabi et al. 2009). Also, undernourished specimens avoided high levels of CO_2 (Bretscher et al. 2008; Hallem and Sternberg 2008). High concentrations of CO_2 in laboratory experiments can impact the development of nematodes (*C. elegans*): The laying of eggs becomes inhibited at high CO_2 concentrations (Fenk and de Bono 2015). A delay in the development of embryos was also recorded when CO_2 levels were above 9% (Sharabi et al. 2009). The brood size of the freshwater nematode *Panagrellus redivivus* increased in response to an increase in CO_2 concentration (Hansen and Buecher 1970).

However, in general, and judging from experimental evidence mostly using *C. elegans* as model organism, nematodes do not seem adversely affected by realistically increased CO_2 levels. This refers also to marine nematodes (and other marine meiofauna), which seem to be fairly insensitive to the globally increasing CO_2 concentrations and, linked to this, the decrease in pH (Ingels et al. 2018; Kurihara et al. 2007; Gaugler and Bilgrami 2004). Even at concentrations to be expected in the remote future, results from experimental studies indicated limited to no acute effects. However, so far very little research has been conducted that investigates the cost of maintaining metabolism and energy expenditure, as well as behavioral changes that may affect ecological interactions under increased acidification stress in meiofauna organisms.

11.4.1.6 Chemical Stressors

As shown above, chemosensation is fundamental for regulating food availability, reproductive partners, and predation or other dangers. Chemical stressors can be defined as exogenous, environmental compounds. In general, exposure to chemical stressors causes diverse effects ranging from reduction of movements over inactivity to toxicity, which can either end in resistance or death (Kaminsky 2003). This is principally valid for feared notorious and widespread environmental toxins, arsenic, and heavy metals (see also Chap. 7).

Arsenic (As): Environments with high contents of arsenic are usually lethal for most metazoan organisms. However, regarding nematodes, *Auanema* sp. survived concentrations up to 500 times the human lethal dose. This nematode expressed the gene dbt, known to confer arsenic resistance (Shih et al. 2019).

Heavy metals: As shown by the rich literature on pollution, many nematode species, both marine and freshwater, do not seem to be very sensitive to moderate, often even high concentrations of heavy metals, including the marine species *Diplolaimella dievengatensis* and *Halomonhystera disjuncta* (Gyedu-Ababio et al. 1999; Vranken and Heip 1986; Vranken et al. 1991). Some of them were even found to store metals in their subcutaneous tissues (Howell 1983) and gastrointestinal tract (Harvey and Luoma 1985). Marine species can accumulate heavy metals in their mucus (Decho 1990; Jensen 1987b; Riemann and Schrage 1978). The genera *Monhystera* and *Theristus,* dominating in estuarine sites contaminated by various heavy metals, have even been considered as ‘indicators for polluted sediments’ (Gyedu-Ababio et al. 1999).

11.4.2 Interaction Between Stress Factors

In general, studies on nematode adaptations, and their response, to extreme conditions are still based on single-factor systems. However, in nature, nematodes are exposed to more than one stress type at the same time. The relatively few existing multistressor experiments have revealed complex biological interactions. For example, the combined impact of low temperatures and osmotic stress may result in another stress factor, ice crystal formation in the cell liquids (Lee 2010). In addition, desiccation in its extreme form (anhydrobiosis) is mostly integrated in the complex of cryoprotective dehydration. Specialized nematodes can dehydrate because the vapor pressure of water in their tissues exceeds that of the surrounding ice (Smith et al. 2008). The presence of a sheltering ice sheath can be an alternative to prevent inoculative freezing in nematodes (Wharton 2002, 2004).

One of the best studied extremophile nematodes that exhibits cryoprotective dehydration is the Antarctic *Panagrolaimus davidi* (Timm 1971). It is able to withstand freezing temperatures over nine months of the year and exhibits both freeze-avoidance and freeze-tolerance strategies (Gaugler and Bilgrami 2004). *P. davidi* can undergo cryoprotective dehydration and even survive cellular ice crystallization in all its intracellular compartments (Wharton and Brown 1991; Wharton and Ferns 1995). This freezing can occur via the excretory pore while initiating a molting phase at the onset of the freezing process. *P. davidi* is also characterized by a higher (82%) and faster (0.21 s) conversion of body water into ice when compared to other animals (usually hours/days) (Wharton and Ferns 1995; Wharton and Block 1997). Such rapid and simultaneous freezing avoids osmotic stress to occur when different body compartments would freeze at different times. While *P. davidi* produces abundant cryoprotectant trehalose during cold acclimation, a number of genes related to survival are active during freezing and cause production of, among others, the protease *Neprilysin* and various proteins involved in initiating ice formation, in the antioxidant metabolism, and in prevention of ice nucleation (Thorne et al. 2014; Wharton et al. 2005). Further research into the specificity of the genes and the associated processes and products at the molecular level is needed, but first insights indicate that adaptations and tolerances to very low temperatures may be specific and distinct from those that developed as a general response to stressors (Thorne et al. 2017). Within the genus *Panagrolaimus,* there is a continuum of strains, ranging from (i) slow desiccation strategists, through (ii) strains that have a limited ability to survive rapid desiccation, to (iii) strains of fast-desiccation strategists (*P. superbus*) that can readily survive immediate desiccation. The strongly anhydrobiotic strains of *Panagrolaimus* represent one phylogenetic lineage, distinct from the weakly anhydrobiotic strains. The latter are also phylogenetically divergent from each other (Shannon et al. 2005). *Panagrolaimus* can freeze entirely and, once thawed, even reproduce again. Other extreme cases have been documented: The resuscitation of the nematode *Tylenchus polyhypnus*, n.sp., after almost 39 years of dormancy was reported by Steiner and Albin (1946). The first data demonstrating the capability of multicellular organisms for long-term cryobiosis belong to two nematodes *Panagrolaimus* aff. *detritophagus* and *Plectus parvus* isolated and revived from the 40.000-year-old Pleistocene permafrost deposits of the Kolyma River Lowland (Shatilovich et al. 2018).

During anhydrobiosis, nematodes may survive extreme temperatures. However, if simultaneously exposed to stress, e.g., by hostile chemicals, lethal conditions may develop (Barrett 1991). Temperature is also controlling CO_2 perception and tolerance in nematodes (Banerjee and Hallem 2020), and oxygen levels have been found to influence the CO_2 tolerance in nematodes. If accustomed to an environment with low O_2 levels, they avoided increased CO_2 concentrations compared to those living under high O_2 conditions (Carrillo et al. 2013; Kodama-Namba et al. 2013). The hypoxia-inducible factor gene hif-1 suppresses CO_2 protection in nematodes (Bretscher et al. 2008). Nematodes sampled in water rich in natural CO_2 showed a species-specific respiratory ability even under low oxygen levels and high CO_2 concentrations (Pilz et al. 2017).

Longer-term experiments under close-to-natural conditions are another example of how complex and multimodal stress factors usually interact. Petroleum hydrocarbons can illustrate this: As each variety of 'oil' is a complex and continuously changing mixture of toxic hydrocarbons that becomes continuously modified by oxidative decomposition, the specific toxicant responsible for a resulting impact on a specific meiofauna is difficult to identify. As details of this complex are given in

Chap. 7, we give a single example here where nematodes in microcosms with natural sediment have been tested for the effects of diesel oil (Mahmoudi et al. 2005): While most species, even the hardy *Oncholaimus campylocercoides*, became negatively affected, other species, such as *Marylynnia stekhoveni*, increased their populations, even at high oil concentrations. Since noxious effects are never unimodal, the question of how to interpret these effects remains. Was this increase due to higher tolerance or to an increase in bacterial populations in combination with decreasing competition, or both? Therefore, any interpretation of close-to-natural experiments with several (nematode) species remains vague. General conclusions from such experiments are impossible to obtain, and differentiation is needed. Also here, we have to overcome the descriptive level and step to the level of deeper understanding. It is time to leave behind the 'what-phase' and broaden the 'why-horizon'!

11.4.3 A Better Survival with Partners? Nematodes and Their Microbiomes

In many nematodes from extreme habitats, functioning and fitness fundamentally depend on mutualistic microbiomes. While research on obligate symbioses of meiofauna, especially nematodes, with bacteria has reached the biochemical and genomic level and is well documented (Dubilier et al. 2015; Foster et al. 2017; Sogin et al. 2020; see Chap. 4), some bacterial associations of nematodes with a varying degree of interdependence between host and microbial partner shall be described here. One relatively well-documented example is the symbiotic relationship between Oncholaimidae and bacteria, which occur in extreme environments of varying water depth, from polluted harbor muds to deep-sea vents. All of these oncholaimid species possess specific prokaryotic associations, which most likely enhance the survival capacities of nematodes in these extreme environments.

- The anoxic and sulfidic sediments in the harbor of Roscoff (France) are dominated by *Metoncholaimus albidus* representing >90% of the local nematofauna (Bellec et al. 2019). The striking appearance of this species (Fig. 11.5) is due to its conspicuous 'head cover' with ectosymbiotic bacteria (Campylobacterota and Gammaproteobacteria) involved in sulfur metabolism.
- In a shallow-water vent field (Gulf of Naples, Italy), the sediment around a solitary hydrothermal geyser (hydrothermal fluid temperature ~80 °C) is dominated by an undescribed species of *Oncholaimus* with numerous specific bacteria in the intestine involved in sulfur-oxidizing/sulfur-reducing metabolic pathways and bacteria of the iron cycle (Bellec et al. 2020).
- In the hydrothermally active deep-sea vent field of 'Lucky Strike', the nematode *Oncholaimus dyvae* is particularly abundant. *O. dyvae* is associated with sulfur-oxidizing bacteria related to Epsilonproteobacteria and Gammaproteobacteria on its cuticle, in the digestive cavity and in its intestine (Bellec et al. 2018). Indicated by stable isotope ratios, it feeds on and in mats consisting of thiotrophic and methanotrophic bacteria (Zeppilli et al. 2019).

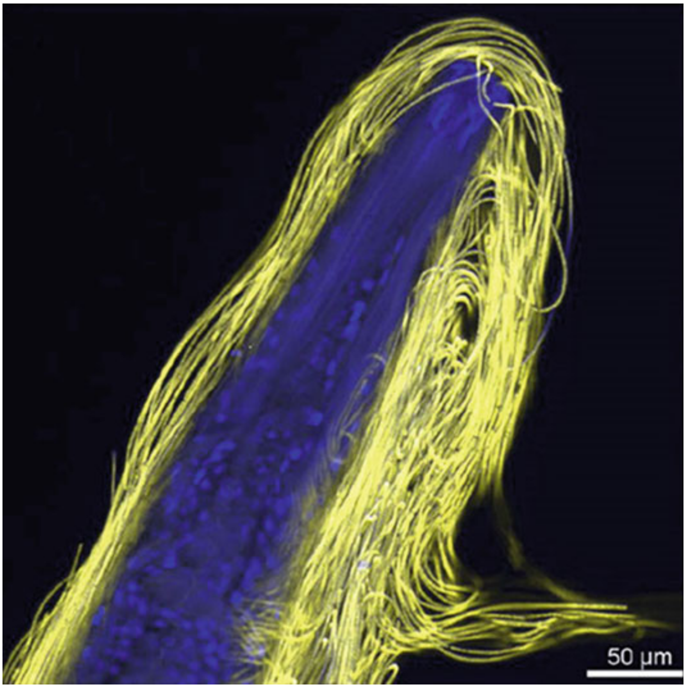

Fig. 11.5 *Metoncholaimus albidus*, with its mantle of filamentous ectosymbionts (Bellec et al. 2019, CCA 4.0; Copyrights IFREMER). In blue: anterior body region; in yellow: dense cover of Eubacteria

A second example worth noting is the Astomonematinae (Monhysterida: Siphonolaimidae), very long and slender nematodes which possess symbiotic bacteria located inside the body (Ott et al. 1982; Giere et al. 1995; Musat et al. 2007). Dependence of Astomonematines on their symbionts is obvious because these nematodes lack a mouth. These nematodes are usually associated with reduced conditions in shallow waters (Ott et al. 1982; Austen et al. 1993). Members of this group have also been recovered from the deep sea (Tchesunov et al. 2012; Ingels et al. 2011). Molecular characterization of the symbionts associated with Astomonematines has shown them to be known sulfur-oxidizing bacteria (Musat et al. 2007).

11.5 Meiofauna Surviving at the Limits

It is not surprising that the group of meiobenthic taxa adapted to extreme environments with various kinds of extreme stress is restricted. Beside the dominating nematodes, presented above, there are primarily Tardigrada to be mentioned here, the most bizarre masters of survival and revival potential. Also, Rotifera from freshwater habitats contain specialized species that can endure environmental extremes. They possess exceptional resistance and adaptations to various kinds of environmental stress, such as draught, frost, and noxious radiation. Less known, though frequently found in extreme marine habitats, are Foraminifera, protozoans which can have a complex calcareous shell. A new physiological dimension of extreme life in free-living multicellular animals has been discovered in Mediterranean sediments (Danovaro et al. 2010): some Loricifera, which lack mitochondria and live under permanently anoxic conditions.

11.5.1 Tardigrada

‘Water bears’ gained worldwide attention in public media because some of them (e.g., *Paramacrobiotus richtersi*, *Milnesium tardigradum*) have survived travels through the vacuum of our orbit during space missions (Jönsson et al. 2008) both in an active and in an anhydrobiotic state. Later experiments showed that under anhydrobiosis they could survive not only temperature extremes near absolute zero, but also solar ultraviolet and ionizing radiation.

From the orbit back to Earth: In lab experiments, tardigrades survived (for varying experimental time periods) -273 °C as well as $+150$ °C, Arctic soil conditions (-80 °C) up to 6 years, extremes of pressure, and high doses of radiation including X-rays. If not restricted to physical extremes, they tolerated high concentrations of hydrogen sulfide, ethanol, and CO_2 (Erdmann and Kaczmarek 2017). However, not all genera and species of tardigrades show this extreme resistance to drying out, and differences can occur even between populations. Many are well adapted to survive the frequent summer droughts; others are more resistant to polluting agents.

One feature is common to all these extreme adaptations, both in tardigrades and in rotifers (see below): Exposure to the stress factor (dryness, cold, heat, chemicals) has to be in physiologically adequate steps. Slowing down unbearable stress increase attenuates impacts of morphological and physiological changes and avoids detrimental effects or shocks too rapid for an adaptive response. But what about the extremes mentioned above? Beside the cryptobiosis already described, many tardigrades (and rotifers as well, see below) developed a specialized form of resistance, encystment in a ‘diapause’, also called ‘suspended life’ (see Table 11.1). This unique adaptation entails a ‘dual existence’ of the animals (Rebecchi et al. 2020).

The start of the complex process towards diapause is a gradual shrinkage, a folding of the body in a specific and coordinated way to reduce the exposed surface area, followed by enclosing the body with several protective internal cuticle layers, and ending in the formation of a shrunken ‘tun’ (see Figs. 11.6 and 11.7), a cyst stage in which movements have ceased and body water becomes reduced by 97%. More strikingly, the body organization changes profoundly: In *Hypsibius exemplaris*, the body cells not only become compacted, but they also secrete a specific (protective) layer and enhance the density of the endoplasmic reticulum while the number of mitochondria is reduced (see Fig. 11.6). The entire epidermal layer has even been observed to detach from the cuticle, which gets wrinkled in a regulated way. While the musculature contracts, hard structures such as pharynx and claws become softened and withdrawn into the trunk (Rebecchi et al. 2020; Richaud et al. 2020). As a tun, the tardigrade can survive extremes such as polar cold or complete dryness for a sufficiently long time to get a chance to return to ‘normal’ conditions again. Several years of dormancy are normal; longer lasting records are debated (see nematodes, this chapter). Hence, the potential of dormancy in all the taxa discussed here has been described as an ‘escape in time’ avoiding hostile periods ‘in loco’ by remaining

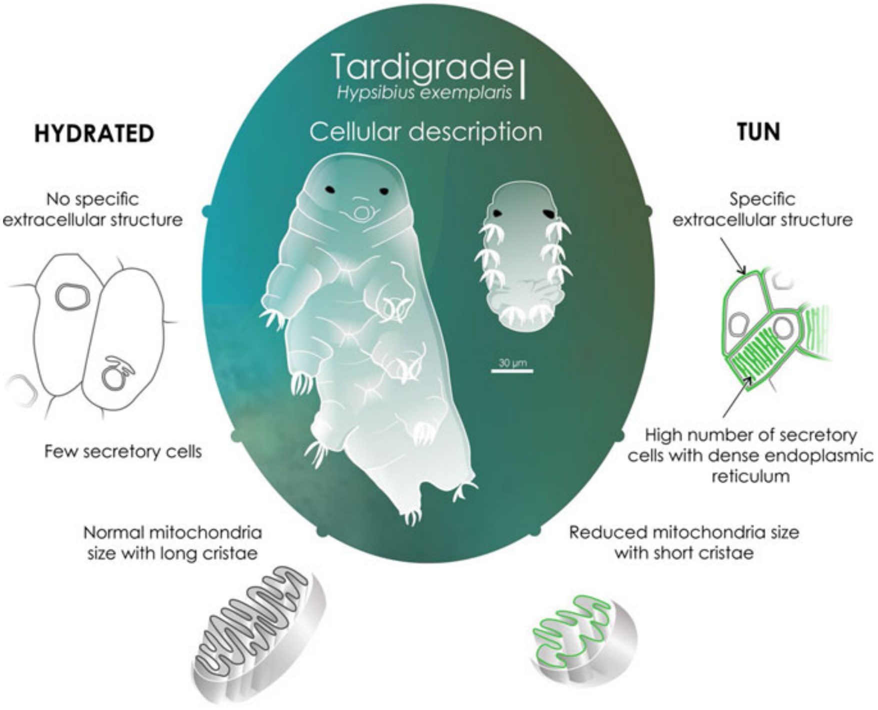

Fig. 11.6 Comparison of cellular reactions in tun and hydrated individuals of *Hypsibius exemplaris* (Copyrights M. Richaud, Montpellier, France; Open Access 2020, https://doi.org/10.1038/s41598-020-61165-1)

stationary without the need of active dispersal (Kaczmarek et al. 2019). Internally, bioprotectant physiological processes accompany all morphological changes. Very relevant is the production of some sugars (disaccharides such as trehalose), but also of specialized proteins (e.g., anti-heat shock, anti-dehydration) and various antioxidants protecting from DNA damage (Rebecchi et al. 2020). In contrast to anhydrobiosis, this suspension of life as a cyst is triggered by a combination of external and internal factors. Similar resting phases may also occur during early development when 'resting eggs' are formed. And yet, despite this complex and extensive conversion of the body structure and tissues, it takes tardigrades only a few hours to days to rehydrate their body and end their diapause. Hence, after repositioning of their pharynx, claws and mouthparts tardigrades can re-start active life again—a structural and physiological 'wonder'.

However, long phases of cryptobiosis and diapause seem to act as physiological stressors. The considerable energetic costs of both anhydrobiosis and diapause can extend to metabolic and molecular damages that need mechanisms of repair with the onset of revival; e.g., expression of DNA-repair molecules becomes enhanced. So, in general, the extreme tolerance and potential survival seem to be an energetic trade-off: Considerable physiological costs and genetic modifications must be weighed up against ecological advantages such as persistence and longevity (see Jönsson 2005). The aspect of longevity is underlined by the fact that in several species capable of dormancy, the process of aging seems to be slowed down or halted (the 'Sleeping Beauty' model). Based on various molecular changes, even the term 'rejuvenation' has been used since some dormant rotifers were waking up with a better fitness than before. However much debated this 'biological wonder' may be, it needs detailed studies from all the groups considered here and preferably on a molecular basis.

11.5.2 Rotifera

Less famous and less in the public spotlight are rotifers, or commonly named wheel animals. Especially, species of the class Bdelloidea have the potential to live at extreme limits, under hostile conditions like those endured by some tardigrades and nematodes. Almost all the adaptations to dormancy described before, anabiosis, diapause, chemical and radiation resistance, and tun formation (see Fig. 11.7), have also been found to occur in these tiny meiobenthic forms living in freshwater and moist terrestrial habitats. Bdelloids have also survived orbital extremes on space excursions; even the extreme longevity over thousands of years, reported for some nematodes (see above), is paralleled by the recent finding of specimens of *Adineta* which were successfully revived from 24,000-year-old permafrost ice (Shmakova et al. 2021). Hence, especially studies on aging and juvenation (see above) are based on findings in bdelloid rotifers.

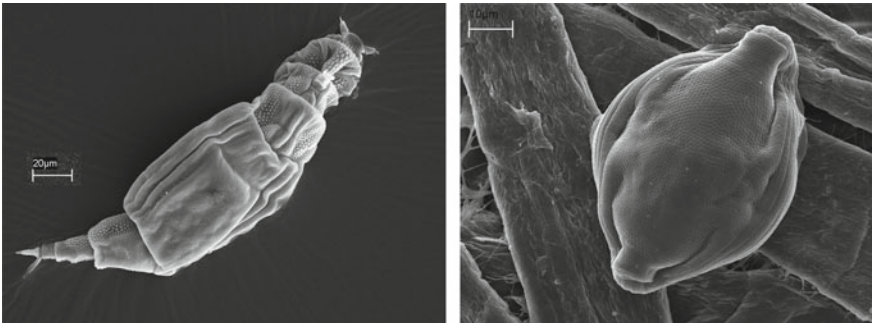

Fig. 11.7 Bdelloid rotifer *Adineta tuberculosa*, left: active phase, right: 'tun stage'. Note different scale (left 20 μm, right 10 μm); courtesy of D. Fontaneto, Italy

However, there are also differences compared to the other 'extreme taxa', and some of them are even unique:

- Bdelloid rotifers can resist hostile conditions at any life stage, but only by cryptobiosis, while the monogonont rotifers can only survive extremes as resting eggs (see Table 11.1).
- Metabolic pathways when entering cryptobiosis differ from those in tardigrades (e.g., no trehalose as protectant).
- For millions of years, so cytogenetic studies suggest, it seems bisexual reproduction is lacking in bdelloid rotifers and only females exist (Welch and Meselson 2000). Hence, reproduction is by parthenogenesis only. This 'asexual' situation invited an entire branch of studies on the evolution and nature of sex.
- Parthenogenesis may enable benthic rotifers to escape limiting conditions. A limited genetic selection and high reproduction rates combined with resistance to adverse conditions may facilitate survival in refugia not available to less-adapted competitors. This combination of features might enable a wide geographical distribution by colonizing regions otherwise hostile to life (see Fontaneto et al. 2008).
- High rates of horizontal transfer of 'foreign genes' have been found in some bdelloid genomes (Gladyshev et al. 2008)—at that time considered unique among free-living metazoans. These genes probably have been incorporated from bacteria, fungi, and plants. Since they mainly code for protective and repair processes, they may enable effective resistance to desiccation by anhydrobiosis.

11.5.3 Foraminifera

The frequent occurrence of Foraminifera in sediments regularly exposed to hypoxia and even anoxia suggests that this protozoan taxon is particularly adapted to oxygen capture (Gooday et al. 2000; Levin 2003). The main adaptation to survive hypoxia/anoxia and colonize areas hostile to most free-living organisms seems to be the ability of nitrate respiration, common in Foraminifera (Koho and Piña-Ochoa, 2012). Additionally, the capacity of many species to exist under minimal oxygen concentrations seems markedly enhanced by frequent presence of bacterial endosymbionts. Some foraminiferans can also sequester chloroplasts or proliferate peroxisomes and mitochondria for a metabolism of oxygen-rich H_2O_2 (Bernhard and Bowser 2008). Some foraminiferans from 600 m water depth retained chloroplasts derived from diatoms they had incorporated (Grzymski et al. 2002). These chloroplasts might enable them to become photosynthetically active and to meet their nitrogen demands by assimilation.

11.5.4 Loricifera

Continuing the series of aberrant metazoans that can exist under unique conditions, we have to emphasize the Loricifera, a meiofauna phylum only discovered in 1983, and later studied in more detail. Some of them (e.g., *Spinoloricus* sp.) have been shown to master most extraordinary and hostile conditions in the deep sea (Danovaro et al. 2010). Aside from their exotic appearance (see Fig. 11.8), these Loriciferans were the first meiobenthic animals that have been proven to persist in permanently hypersaline deep water (Atalante Basin) where molecular oxygen is entirely absent and no other live fauna could be found. In at least one of the *Spinoloricus*-species studied so far, there is a structural feature entailing physiological pathways new to free-living metazoans: presence of hydrogenosome-like structures substituting mitochondria with their ribosomes. Due to this unique loss of the central organelles for oxidative metabolism, new respiratory pathways had to be 'invented': Hydrogenosome-like organelles have hitherto been reported from ciliates living in permanently anaerobic sediments (Müller et al. 2012). Future studies focusing mainly on functional, physiological, and molecular aspects should elucidate the relation between loriciferan and protozoan hydrogenosomes and clarify processes underlying the evolution of these organelles.

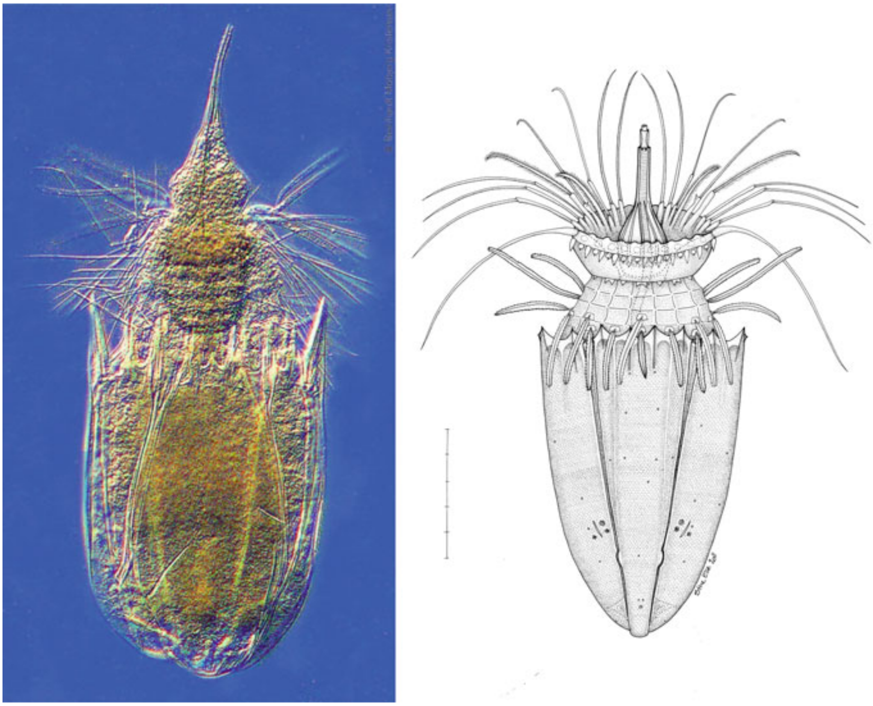

Fig. 11.8 Physiologically extreme Loricifera. Left: *Nanaloricus mysticus* – the first described loriciferan; total width 70 μm (microphotograph of allotype, courtesy R.M. Kristensen). Right: *Spinoloricus cinziae*; scale bar 50 μm (original line-art drawing of holotype by Stine Elle, courtesy R.C. Neves and R.M. Kristensen; see also Neves et al. 2014)

11.6 Advantages of Extremobionts and Why to Study Them? New Horizons and Some Conclusions

It does not lack a certain irony that the hardiest, most numerous, and ubiquitous metazoans belong to the smallest ones—the meiofauna. This may not be accidental. Small animals are usually physically unprotected and cannot readily change their habitat position or forcefully modify their environment. They have to find their niches, have to struggle, and adapt rather than conquer. Through millions of years, they were exposed to new and often extreme conditions. As their adaptive 'solutions', e.g., dormancy or anhydrobiosis, developed independently in different taxa and phyla, under various types of stress and unrelated to geographic distribution, they seem to have evolved in independent phylogenetic, ecological, and physiological lines.

The study of meiofauna living and thriving under what appears to humans extreme and hostile environmental conditions poses several biologically relevant questions for which they have found sometimes incredible answers:

- How to survive in adverse environments with low oxygen, extreme cold or heat, or with devastating droughts? Develop specialized biochemical, physiological, and structural pathways, so that all activities can become suspended in dormancy.
- How to maintain an extremely wide distribution despite minimal mobility? Rely on powerful distributors such as currents, tectonic forces, even air transport, and transport through flora and fauna (see Chap. 6).
- How to compete against powerful and large competitors? Focus on ubiquitous food sources like bacteria and diatoms. Search for refuges without (many) competitors, such as in the polar sympagic systems. Produce high numbers of offspring outweighing their loss rates.

Research on these adaptive frontiers will not only lead to a deeper understanding, but it will also open novel insights pointing to innovating pathways, which may shed light on the diverse, yet hidden world of meiofauna. For over a century we have known about this small world, we have been appreciating its inhabitants as beautiful and exciting, and we have been learning about their successful, hidden life. However, amazement aside, regarding the biological success of these 'meiofauna at the limits' we can envisage many aspects of essential value, highly beneficial to mankind. We can see many novel applications for our own future—an intriguing challenge for biologists.

- Of course, first the eternal quest for rejuvenation reducing the process of aging, even for the secret of life—conservation and stabilization of cells, membranes and proteins, and development of bioprotective molecules,
- Stabilization of various cells including spermato- and oocytes and stable transport of vaccines,
- Research on stress, e.g., from radiation and chemical stressors,
- Understanding and optimizing the phenomenon of biological fitness and health,
- Ecological and evolutionary effects of increasing temperatures and droughts and their implications,
- Potentials of extraterrestrial life. In the phase of 'suspended life' tardigrades, rotifers and nematodes are candidates to bridge planetary distances.

As much as the 'extremophile meiofauna' can fascinate with their amazing capacities and characteristics, we know little about the physiological and molecular pathways involved, but we are certain about one fact: No astounding adaptation, no single molecule or protectant, and no individual pathway of repair alone will be found responsible for these structural and physiological 'wonders' of survival under extreme conditions. It always needs coordinated developments to elaborate these almost unimaginable processes in minute meiobenthic animals, and it will always need our coordinated research effort to understand them. But perhaps most importantly, in doing this we must modestly acknowledge: As much as we may expand our human sphere toward unforeseen limits—the limits of meiofauna in their world are wider.

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Correction to: Meiofauna—Adapted to Life at the Limits

Jeroen Ingels, Daniela Zeppilli, and Olav Giere

Correction to:
Chapter 11 in: O. Giere and M. Schratzberger (eds.), *New Horizons in Meiobenthos Research*, https://doi.org/10.1007/978-3-031-21622-0_11

In the original version of the chapter, the author provided belated correction has been incorporated: In the Chapter 11, figure 11.8 figure caption have been updated. The correction chapter and the book have been updated with the changes.

The updated version of this chapter can be found at
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Correction to: Marine Meiofauna Diversity and Biogeography—Paradigms and Challenges

Ann Vanreusel, Pedro Martínez Arbizu, and Moriaki Yasuhara

Correction to:
Chapter 5 in: O. Giere and M. Schratzberger (eds.), *New Horizons in Meiobenthos Research*, https://doi.org/10.1007/978-3-031-21622-0_5

In the original version of the book, the misspelt co-author name "Moriaki Yauhara" has been changed to read as "Moriaki Yasuhara" in chapter 5. The correction chapter and the book have been updated with the change.

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Concluding Remarks: New Horizons in Meiobenthos Research—Profiles, Patterns and Potentials

Meiobenthology, the microscopic branch of ‘classical’ benthology, is gaining increasing importance and traction through the development of innovative approaches and the application of novel methods. These not only provide new, broader insights into the amazingly diversified morphological structures of meiobenthos and their adaptive potential, but also help to identify new links between the microbial and our visible world.

Following these promising developments, we are, however, under the impression that in recent years, the rapidly growing body of new and detailed research that touches on novel and specialised aspects of meiobenthology has expanded and diversified into numerous, and at times disparate, niches. The diversification is reaching a level where unifying concepts and research lines appear to be dwindling. This risks losing the common perspective, the integrating ‘meiobenthic thread’ that prevents the various interesting facets of relevant research and knowledge from getting lost in diversity. Therefore, an important aim of this book was to provide an updated account of knowledge of meiobenthos on contemporary topics, but doing so from a broad ecosystem perspective. This allowed us to identify new horizons for future scientific research.

Outlining ‘future meiobenthology’, the present book may be seen as part of a triadic complex, based on the monographic textbook ‘Meiobenthology. The Microscopic Motile Fauna of Aquatic Sediments’ (Giere 2009). More recent aspects in meiobenthology that presently prevail (the state of the art) are highlighted in a short reflection entitled ‘Perspectives in Meiobenthology’ (Giere 2019), a booklet that attempts to indicate critical knowledge gaps and to outline perspectives and promising avenues to be pursued in future meiobenthology. The booklet intended to stimulate thoughts by asking: Where to focus future meiofauna research? Both publications are aptly complemented by the recent classification and identification guide edited by Schmidt-Rhaesa (2020).

The present book on new horizons in meiobenthos research, written by leading specialists in the field of meiobenthology, is a compilation of promising new thinking,

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data, methods, and approaches in many relevant fields of meiobenthos research, all driven by the vision of advancing knowledge and understanding of benthic ecosystems. This requires a focus on the 'bigger picture', on the processes and aspects that connect the hidden world of meiobenthos with that of the more conspicuous macroscopic fauna. Why is this important? These faunas are connected by common, general principles that determine the limits and potential of the benthic realm. Stronger connections between the research fields that study these interconnected faunas will undoubtedly open new opportunities to investigate, and better understand, how benthic ecosystems respond to environmental dynamics and global change.

All authors of this treatise worked toward these goals under the aggravating Covid-19 pandemic, alongside their professional duties and private commitments, which made editing this book a challenging undertaking. United by the idea of shaping an exciting, meaningful, and successful future for meiobenthology, this book is the result of our shared passion and determination. The editors and authors hope that the work presented here will direct and influence meiobenthology for some time.

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