

# Chapter 2

## Meiofauna Shaping Biogeochemical Processes



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**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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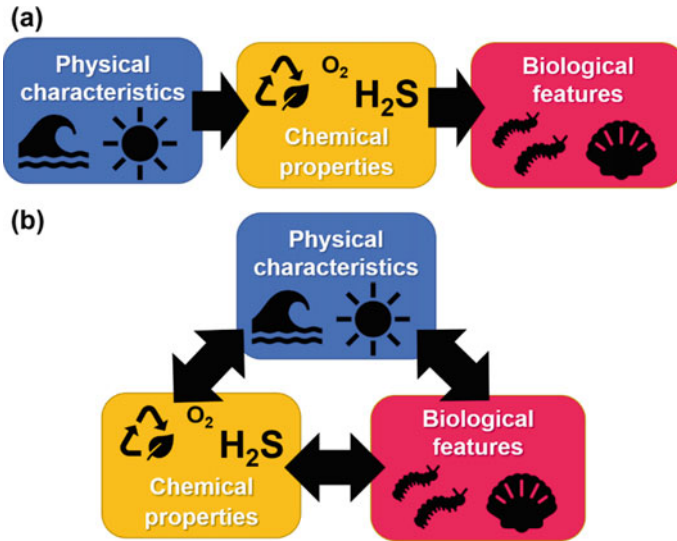
## 2.1 Sediment Biogeochemistry—Of Basic Relevance to Meiobenthos

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 (Bernier 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



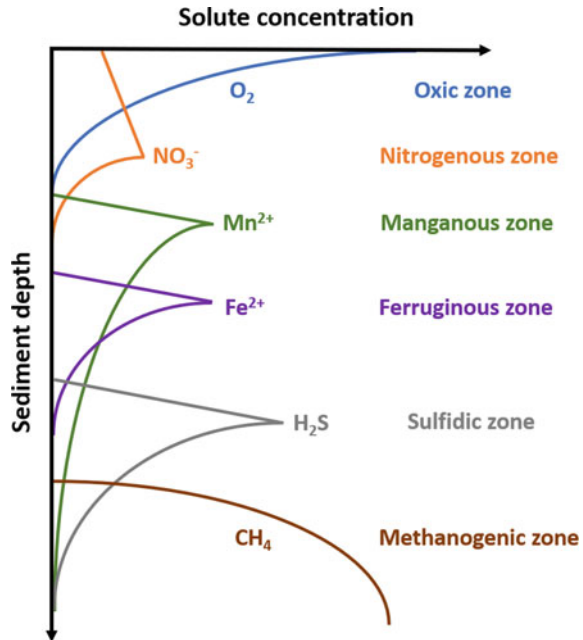
**Fig. 2.1** Diagrammatic comparison of earlier (a) and recent (b) conceptions of benthic interactions in marine research. Original

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  $\text{CO}_2$  and use it to oxidize organic matter into methane ( $\text{CH}_4$ ).

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  $\text{CO}_2$  and  $\text{CH}_4$ , 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  $\text{CO}_2$  and  $\text{CH}_4$  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.

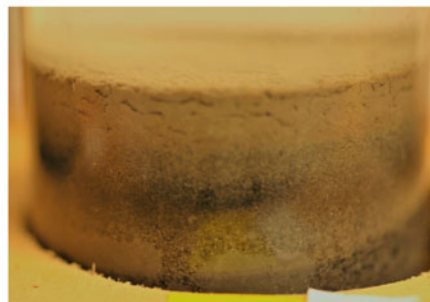
Regarding meiofauna, the organisms are often smaller than the surrounding sediment particles. Nevertheless, their population density affects sediment reworking. Bioturbation by meiofauna (Fig. 2.3), or meiobioturbation, as an active process was first identified and clearly distinguished from macrofauna 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

Low meiobioturbation



High meiobioturbation

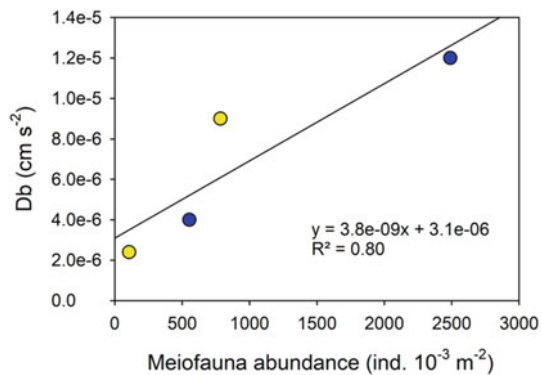


**Fig. 2.3** Visual impact of meiofauna bioturbation: left–low intensity: about  $130 \text{ ind.} \cdot 10^{-3} \text{ m}^{-2}$ ; right–high intensity: about  $850 \text{ ind.} \cdot 10^{-3} \text{ m}^{-2}$  (Bonaglia et al. 2014). Original

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 properties 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 ( $D_s$ ) and biodiffusivity ( $D_b$ ) 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 ( $D_b$ ). 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  $\text{cm}^2\cdot\text{m}^{-2}\cdot\text{day}^{-1}$  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  $\text{Pg C y}^{-1}$ ) and less than 4% of this carbon reaches the ocean floor (2  $\text{Pg C y}^{-1}$ ), 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).

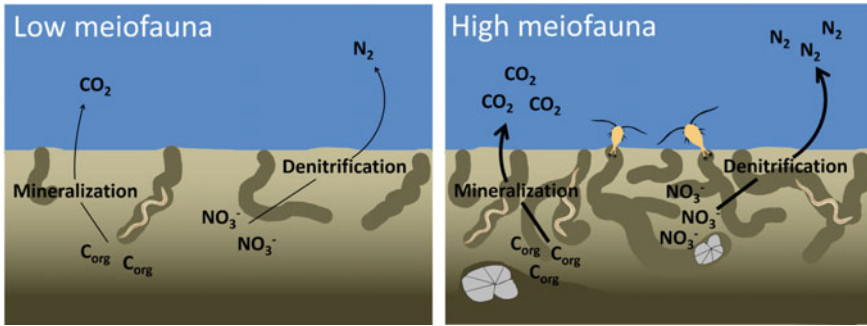
Summarizing, these works confirm that the importance of meiofauna for organic matter mineralization through direct grazing and carbon assimilation is limited. This pattern is consistent and independent of the geographical area or carbon source. Collected experimental and field data indicate that usually 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 thibios (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

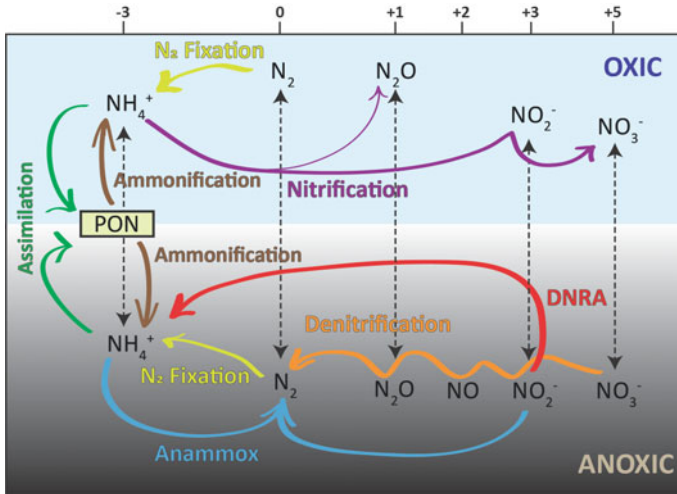
book, and overview in (Giere 2009). Often thiobiotic species have been found to live in symbiosis with chemosynthetic bacteria where the partners interact in complex metabolic pathways.

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 ( $\text{N}_2\text{O}$ , 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 ( $\text{CH}_4$ ) and nitrous oxide ( $\text{N}_2\text{O}$ ). While even the impact of macrofauna on these fluxes 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  $\text{CH}_4$  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 ( $15 \text{ Tg N y}^{-1}$ ) 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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