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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N. Majdi (✉)
Abteilung Tierökologie, Universität Bielefeld, Konsequenz 45, 33615 Bielefeld, Germany
e-mail: nabil.majdi@uni-bielefeld.de

C. Hubas
Muséum National D'Histoire Naturelle, UMR BOREA, MNHN-CNRS-UCN-SU-IRD-UA, Place de La Croix, Station Marine de Concarneau, Concarneau, France

T. Moens
Biology Department, Marine Biology Lab, Ghent University, Krijgslaan 281/S8, 9000 Gent, Belgium

D. Zeppilli
IFREMER Centre Brest, REM/EEP/LEP, ZI de La Pointe du Diable, CS10070 Plouzané, France

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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,

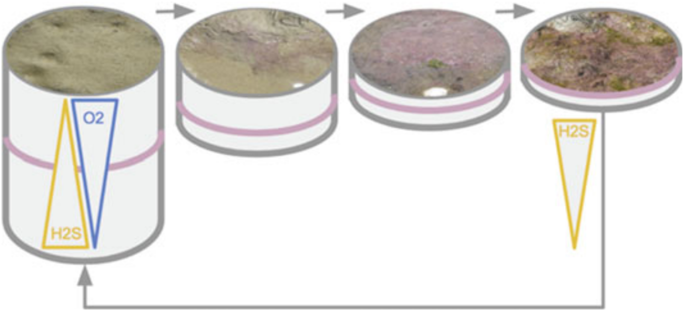

Fig. 3.2 Seasonal development of a photosynthetic microbial community in coastal sediments. The community develops from a typical microphytobenthic mat to a purple anoxygenic bacteria biofilm. From left to right, the images represent the evolution of the sediment surface from winter (left) to the end 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

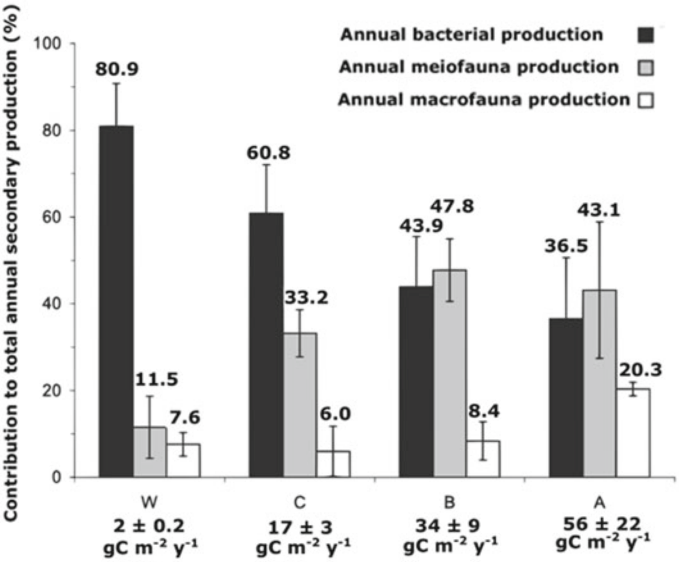

Fig. 3.3 Contribution of the different benthic heterotrophic compartments to total secondary production (in gC m^{-2} y^{-1}) along a productivity gradient. Stations A, B and C correspond to muddy to sandy sediment (median grain sizes are, respectively, 132 ± 54, 215 ± 43 and 251 ± 10 µm) of the Roscoff 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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