



## Meiofauna in a changing world

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### 1. Introduction

This special issue emerged under the umbrella of the 17th International Meiofauna Conference (SeventIMCO), which celebrated the 50th anniversary (1969–2019) of the International Association of Meibenthologists under the general theme “Meiofauna in a changing world”. Traditionally, the triannual IMCO is the major assembly for scientists who are active in very divergent disciplines such as taxonomy, phylogeny, ecology, ecotoxicology, impact assessment, ... using a wide array of methods, but who converge on the use of meiofauna as model organisms to address their scientific questions. Meiofauna are operationally defined as those organisms which, upon their extraction from aquatic sediments or other substrata, are retained on a sieve with a mesh size of 44 µm but pass through a sieve with a mesh size of 0.5 or 1 mm (but slightly different mesh sizes have been used) (Mare, 1942; Giere, 2009). While the Association of Meibenthologists has traditionally focused primarily on metazoans, some of the larger protists (mainly Foraminifera) also match this operational definition. The importance of meiofauna in aquatic ecosystems, from the sediments of inland waters to those of deep-sea environments, results from an intricate web of relationships that collectively affect a range of ecosystem processes, including several that contribute to important ecosystem services (Schratzberger and Ingels, 2018). Their activities in interstitial environments modify a series of physical, chemical and biological sediment properties, and these modifications directly and indirectly affect ecosystem dynamics and services at various spatial and temporal scales, including food-web dynamics, sediment stabilization and bioturbation, biogeochemical cycling and waste removal (e.g., Hubas et al., 2010; Nascimento et al., 2012; Bonaglia et al., 2014; D’Hondt et al., 2018; Deldicq et al., 2021). Due to their omnipresence and abundance, meiofauna can mediate ecosystem processes in sediments with little or no macrofauna, thereby increasing the resilience of those benthic ecosystem processes that are essential for the continued delivery of ecosystem services (Schratzberger and Ingels, 2018; Ridall and Ingels, 2021).

Meiofauna can also be an effective “ecological tool” to assess impacts

of natural and anthropogenic disturbances on benthic ecosystems, their biodiversity and functioning. Not only are they ubiquitous and very abundant, sometimes rendering them the best alternative to macrofaunal indicators wherever these are scanty or lacking, they are also highly species-rich at local scales, they are involved in multiple trophic and non-trophic interactions, they cover a broad range of sensitivities to various kinds of environmental disturbance, and because they have limited active mobility, they cannot escape from local disturbances (Bongers and Ferris, 1999; Yeates et al., 2009; Ridall and Ingels, 2021).

This “Special Issue” is dedicated to recent developments and advances in the use of meiofauna as indicators of the impacts of environmental change on aquatic communities, allowing a forum for field as well as laboratory studies, and for both case studies and more methodologically oriented papers. Among the major challenges for an optimal use of the potential of meiofauna as environmental indicators are the needs 1) to better understand the functional implications of shifts in the complex community composition and interactions, 2) to embrace innovative technologies and approaches which can facilitate a broader implementation of meiofauna in impact studies, and 3) to translate the contribution of meiofauna studies in support of management decisions regarding the sustainable use of the oceans, seas and freshwater ecosystems.

### 2. Selected topics and papers

Out of thirty - six submitted manuscripts, we selected twelve that we considered both to have the potential to appeal to a broad audience of aquatic environmental biologists and ecologists, and to meet the high scientific standards of this journal. A majority of these papers were dedicated to the responses of meiofauna to current environmental issues of global concern such as climate warming (Majdi et al., 2020; Leasi et al., 2021; Vafeiadou and Moens, 2021; Pontes et al., 2021), (micro) plastic pollution (Mueller et al., 2020), industrial and domestic pollution (Sahraeian et al. 2020; Brüchner-Hüttemann et al., 2021; Francolino et al., 2021; Hua et al., 2021) and fish farming (Bouchet et al., 2020). This selection of papers comprises both field and laboratory studies and

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<https://doi.org/10.1016/j.ecolind.2022.108769>

Received 6 March 2022; Accepted 8 March 2022

Available online 24 March 2022

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includes community as well as species-level approaches.

### 3. Field studies

#### 3.1. Novel approaches and methodologies

Among the approaches used to tackle pressing environmental issues, some interesting trends could be discerned.

First and foremost, several field-sampling based papers surpassed the traditional focus on single, or at most two (most commonly Nematoda and/or Harpacticoida), meiofaunal taxa (Grego et al., 2014; Semprucci et al., 2014; Fonseca and Gallucci, 2016; Branco et al., 2018). Leasi et al. (2021) assessed the diversity and community composition of Arctic sea-ice and sediment-associated small metazoans using metabarcoding of the 18S rRNA gene. By using ‘universal’ eukaryotic primers and selectively removing amplicon sequence variants belonging to ‘undesired’ taxa, they could demonstrate significant effects of season and habitat on the diversity and taxonomic composition across more than a dozen metazoan phyla. Attaining such a broad taxonomic coverage is virtually impossible using traditional sample processing and identification protocols, which are highly time-consuming and require specialized taxonomic skills that, unfortunately, are not always easy to find. The authors do make a plea for dedicated barcoding efforts of morphologically vouchered and identified specimens of as many meiofaunal taxa as possible, since meiofauna tend to be strongly underrepresented in reference sequence databases, thereby limiting our ability to properly assess species richness and community composition (Bik, 2016; Macheriotou et al., 2019).

Although several earlier studies have investigated the pro’s and con’s of using macrobenthos vs meiobenthos in impact monitoring (e.g. Warwick et al., 1990; Kröncke et al., 2000; Flach et al., 2002; Schratzberger et al., 2003; Patricio et al., 2012), only very few authors have addressed a larger part of the size spectrum of benthic organisms, spanning the entire range from micro- over meio- to macrobenthos (but see Franzo et al., 2015; Baldrighi et al., 2018). In this issue, Udalov et al. (2021) present a rare effort in which the environmental drivers of estuarine benthic community structure are investigated across diatoms, Foraminifera, Nematoda, Copepoda, macrobenthos and mobile megafauna, all at the (morpho)species level. They conclude that the principal drivers of the large-scale distribution of benthos along an estuarine gradient are generally similar across taxa and size groups, whereas partly different drivers are responsible for their finer-scale distribution. Given that there is no such thing as a single set of common drivers of the distribution of benthic biota at smaller spatial scales, the best choice of environmental indicator group for ecological quality assessment will depend on the specific impacts that are acting on a system (change in salinity, climate, sediment characteristics, eutrophication, etc.).

Other field-based impact studies included in this special issue did focus on single phyla. Sahraeian et al. (2020) and Hua et al. (2021) used free-living nematode assemblages to investigate the impacts of domestic and industrial waste inputs on beaches from the Persian Gulf area, and to assess effects of pollution status – with a focus on heavy metals – on subtidal sediments of Bohai Bay in China, respectively. Bouchet et al. (2020) used effective species diversity of benthic Foraminifera in the assessment of ecological quality status (EcoQS) in relation to salmon-culture impacts on marine sediments. A pronounced and consistent relationship between effective species diversity and community composition on the one hand, and dissolved oxygen concentration on the other, indicates that assemblages of benthic Foraminifera may indeed be a good tool for monitoring, in particular, effects of eutrophication and other factors that increase the organic-matter load in marine sediments (Bouchet et al. 2012, 2020). In addition, analysis of the fossil foram assemblages holds potential for defining proper reference conditions and past changes against which to compare present-day assemblages and their (rate of) change (Bouchet et al. 2012).

#### 3.2. The quest for the right ind(ex)(ices) to detect impact

Despite a growing body of evidence demonstrating their potential as good indicators of environmental impacts and ecological change (Adão, 2021), meiofauna is currently being overlooked by relevant legislative frameworks and is therefore not included in the biological compartment of the tool box to assess good environmental status of aquatic ecosystems, such as the Marine Strategy Framework Directive (MSFD). Several explanations contribute to this situation.

First and foremost, when compared to sample processing and assessment of macro- and microbenthos abundance, community composition and diversity, the analysis of meiobenthic communities with high (i.e. at least genus-level) taxonomic resolution is highly time-consuming and therefore not always suited for larger-scale monitoring programmes. Metabarcoding is currently the most promising way forward towards a rapid and accurate community analysis of meiofauna, and is therefore rapidly gaining interest (Fonseca et al., 2010; Creer et al., 2010; Rzeznik-Orignac et al., 2017; Tytgat et al., 2019; Macheriotou et al., 2019; Panto et al., 2021); however, the technique still suffers from many limitations. Among others, shortcomings relate to the underrepresentation of most meiofaunal clades in sequence databases (Macheriotou et al., 2019) and to the potentially very different copy numbers of barcoding genes in multicellular organisms, rendering quantitative estimates of the abundances of particular species in a metabarcoding approach highly problematic. As a consequence, the only diversity number that can at present be reliably deduced from metabarcoding of metazoans is richness, and even this may be problematic because of a) the occurrence of multiple divergent alleles of barcoding genes in single individuals (e.g. 18S rRNA in Nematoda (Qing et al., 2020)), b) the inability of universal and even taxon-specific primers to detect all species (Derycke et al., 2010), and c) the inability of primers to amplify every copy of a target gene amongst thousands of other copies. Problem a) may cause overestimations of richness (Qing et al., 2020), whereas c) may cause rare species to be overlooked and may therefore result in severe underestimates of true richness, particularly given the often skewed abundance distribution of species in meiobenthic communities (Moens et al., 2013). In this issue, Sevigny et al. (2021) present a methodological breakthrough that should help to alleviate this limitation. They use hybridization capture probes to enrich mitochondrial DNA of either complete animal communities or of selected taxa by almost 500-fold when compared to standard preparation methods for NGS sequencing libraries, thereby ensuring that even DNA of rare species is sufficiently present to be sequenced.

A second reason for the absence of meiofaunal indicators in environmental legislation frameworks relates to the indecisiveness among researchers as to what are the most suitable descriptors of change in meiofaunal communities that are exposed to environmental stressors. Traditionally, abundance, species richness, other diversity measures such as evenness, and community composition are the most commonly reported descriptors. While shifts in abundance may provide a sensitive indicator of a more general impact on a community (e.g., Hägerbäumer et al., 2018; Monteiro et al. 2019), their interpretation may be all but straightforward. Diversity indices, preferentially reporting on different aspects of diversity such as richness and evenness, are common practice, but do not always properly reflect the mechanistic basis of the observed responses. They often exhibit much less significant change when compared to community composition (see below), possibly because of contrasting responses of species. In this special issue, the interaction between season and habitat did not significantly affect richness but did impact community composition of polar meiofauna (Leasi et al., 2021). In their study of nematode communities from beaches in the Persian Gulf, Sahraeian et al. (2020) found highly significant effects of the interaction month by location and of both separate main factors on total nematode abundance, community composition and richness, but not on evenness, despite the logical expectation that the strongest anthropogenic impacts should have decreased evenness. In their comparison of

station groups with different pollution loads in Bohai Bay, Hua et al. (2021) found by far the most significant differences among pairs of station groups when using community composition as a descriptor, followed by Shannon-Wiener diversity, richness and total nematode abundance. Although there was a marginally significant overall effect of station group on evenness, no significant pairwise differences were observed. In all, with the exception of Bouchet et al. (2020), the different field studies presented here align with other recent work which reported that community composition is almost consistently the most sensitive indicator of an environmental impact on meiobenthos, while diversity indices provide much more variable and often weaker resolution (Meadows et al. 2015; Sahraean et al. 2017; Vafeiadou et al. 2018). The main drawback of this conclusion is that unlike indices, which are mere numbers, the increase or decrease of which can usually be translated in a relatively straightforward message to decision makers, the relevance of shifts in community composition is often difficult to explain, in particular when dealing with inconspicuous and poorly known organisms like meiofauna.

In this respect, the use of UniFrac distances as a metric of (dis)similarity among communities, as in the paper by Leasi et al. (2021), may offer an attractive way of quantifying change in community composition. UniFrac distance differs from more commonly used dissimilarity measures such as Bray-Curtis in that it incorporates information on the phylogenetic relatedness of recorded taxa in the observed community (Lozupone et al., 2006). In this way, it is conceptually similar to the indices of taxonomic diversity and taxonomic distinctness, which have been used to demonstrate how the phylogenetic diversity of communities is affected by environmental impacts (Warwick and Clarke, 1995; Leonard et al., 2006). These indices essentially give the mean phylogenetic distance between, respectively, any two individuals or any two taxa in a community; in other words, the former takes into account abundances, the latter does not (Warwick and Clarke, 1998, 2001). UniFrac distances also come in abundance-weighted and unweighted variants; since they are used on metagenomic datasets, and given the quantification problems inherent to such datasets (see above), we currently recommend unweighted analyses.

So far, we have only discussed descriptors of community structure. Several of the papers in this special issue have also included descriptors that link to functional aspects and/or to the sensitivity of organisms. The index of trophic diversity (ITD (Heip et al., 1985)), for instance, is commonly used as an indicator of the 'health' of a nematode community, under the assumptions that an unimpacted environment a) is likely to harbour a diversity of feeding strategies, from bacterivores to predators, and b) could be expected to have a more or less even distribution of different feeding types. Indeed, the ITD is nothing else than the Simpson index calculated using feeding types instead of species. The commonly used reciprocal of this ITD avoids the counterintuitive behaviour of the Simpson index, which decreases when evenness increases; it is also readily interpretable as the number of equally abundant feeding types present in a community (Jost, 2007). The ITD did discriminate station groups in Bohai Bay, but the number of significant pairwise differences was considerably smaller than for species composition (Hua et al., 2021), suggesting this index to be of moderate applicability, in line with taxonomic evenness.

The maturity index determines the weighted mean score of a nematode in a community along an axis spanning life-history strategies from extreme 'r'-selected species to species with a pronounced 'k' strategy (Bongers, 1990; Bongers and Ferris, 1999). The basic idea is that r-selected species have a life strategy that allows them to rapidly (re)colonize disturbed habitat as well as to tolerate various kinds of pollutants, whereas 'persisters' have characteristics of k strategists, such as a long life cycle and high fecundity, thereby making them successful only when a habitat remains fairly stable over a sufficiently long period of time. In addition, many k-selected species have a more limited tolerance to various kinds of pollution (Bongers, 1999), although this should not be generalized (Moreno et al., 2011). While the MI has

become an intricate part of many impact and monitoring studies in terrestrial soils (Bongers and Ferris 1999; Neher, 2001), it is mainly successful in describing impacts acting on a particular community and/or in comparing communities from the same habitat type. It is much less informative for comparisons between different habitats (Semprucci et al. 2016). In aquatic environments, and particularly in the marine realm, the success of the MI as a descriptor of environmental impact has been limited. Among other reasons, the lack of knowledge about the life histories of a majority of aquatic nematode species and the (near-)absence of extreme colonizers, which are a crucial element in the use of the MI, has resulted in a more limited use and variable success of the index (Moreno et al., 2011). This ambiguity is reflected in the present issue, where the MI was the least informative descriptor of differences in nematode communities in Bohai Bay (Hua et al., 2021), in line with (Schratzberger et al., 2007), whereas it did exhibit highly significant differences among pollution-impacted locations on Persian Gulf beaches (Sahraean et al., 2020).

Brüchner-Hüttemann et al. (2021) evaluated the performance of the NemaSPEAR-index in assessing the ecological status of stream sediments and compared the results with macrofauna-based indices. SPEAR is an abbreviation of 'species at risk', referring to species that are sensitive to pollution or disturbance. A high SPEAR index implies that sensitive species comprise a substantial portion of the total community. The SPEAR-index was originally developed for macrobenthos (Liess and Von der Ohe, 2005), but the paucity of macrobenthos in many fine sediments of freshwaters precludes the use of macrofauna-based SPEAR indices in many locations. Höss et al. (2011) therefore introduced a nematode-based SPEAR-index, which in the study by Brüchner-Hüttemann et al. (2021) clearly correlated with known sediment contamination levels; moreover, it did so in a robust way, across – and despite – seasonal variations in communities, which renders the NemaSPEAR-index superior to macrofauna-based analogs. Still, a reliable SPEAR-index requires that substantial knowledge on the sensitivity of a majority of species in a community is available; moreover, particular species may be sensitive to some kinds of disturbance while much less to others (Höss et al., 2011), implying that a broader-scale application of the index requires considerable extra knowledge on the sensitivity of a broad range of nematode species to a variety of stressors. Nevertheless, in well-studied areas such as the North Sea and several European estuaries, substantial data is available on a wide range of pollutant concentrations as well as on nematode communities, suggesting that a sound basis for the development of a marine NemaSPEAR-index is probably available.

Like Brüchner-Hüttemann et al. (2021), Bouchet et al. (2020) also compared the performance of a benthic meiofauna (here: Foraminifera)-based index for assessing ecological quality status with that of macrofauna-based indices, and found both to have a similar reliability.

## 4. Experimental approaches

### 4.1. Population assays and model species

Just under half of the papers of this special issue used experimental approaches in laboratory (four papers) or field (one paper) settings.

All four laboratory studies included in this special issue have performed population assays which allow detailed investigation of stressor effects on multiple traits that can contribute to fitness (see under 4.2). The need for such population assays inevitably limits the choice of model organisms, since the range of meiofaunal species that can easily be raised in lab cultures is altogether limited. Nematodes are best represented, but even in nematodes, most species that are amenable to laboratory culture share certain key traits: they are bacterial feeders with r-selected life-history traits, such as a fast development and high fecundity (Moens and Vincx, 1998). At the same time, these characteristics render multigenerational effect studies feasible, which is of prime importance for a proper understanding of impacts, both because first-generation effects may be biased by the stock culture conditions in

which the parental generation was raised (dos Santos et al., 2008; Lira et al., 2011), and because they do not allow to assess adaptive responses (Sanford and Kelly, 2011). The importance of multigeneration experiments is illustrated in the current special issue by the results of Mueller et al. (2020) that the reduction by almost 50% of the carrying capacity of a *Caenorhabditis elegans* population exposed to microplastics (MP) only became visible from the third exposed generation onwards; and by the observation that fitness impacts of the exposure of *L. marina* to the pesticide atrazine were more pronounced in the second than in the first generation (Francolino et al., 2021).

*Litoditis marina* cryptic species PmIII (Francolino et al., 2021) and *Diplolaimelloides delyi* (Pontes et al., 2021) are proposed in this issue as novel model organisms for impact studies, in line with previous ecotoxicological and other impact studies using marine nematode model species, which have invariably used representatives of the Monhysteridae and of the few Rhabditidae that live in marine environments (Vranken et al., 1985, 1988; Derycke et al., 2007; Lira et al., 2011). These are opportunistic species which thrive best in organically enriched microhabitats and typical examples of r-selected species, yet this does not necessarily imply that they are highly tolerant to all kinds of stressors, since stress sensitivity of Nematoda does not appear to follow a clear link with life history traits (Kammenga et al., 1994). While many laboratory impact studies on freshwater meiofauna draw on the best studied terrestrial model organism, *Caenorhabditis elegans*, a species for which several certified toxicity assays are available (e.g. ISO/DIS 10872, 2010), there is no 'parallel' model species for marine meiofauna. However, several cryptic species of the *L. marina* complex, as well as several marine Monhysteridae, are available in monospecific culture; using them for ecotoxicological testing does not require very extensive expertise nor high-tech lab facilities, bringing toxicity assays with such model organisms within reach of laboratories worldwide. *Litoditis marina* is of particular interest here because of its close phylogenetic relation with *C. elegans* and because of its extremely fast development, allowing as much as 6–7 generations to be assessed within one month. Moreover, the complete genomes of these species will soon become sequenced and annotated (Blaxter et al., pers. comm.), which may greatly facilitate in-depth studies of how stressors affect the physiology and metabolism of these nematodes, which in turn is likely to reveal novel and highly sensitive stress response variables, such as expression levels of stress-related proteins like heat shock proteins. This may in time open up a whole new avenue of experimental approaches complementary to the ones that are commonly practised now, although the application of many metatranscriptomic and/or metabolomic approaches to small-sized organisms like meiofauna still remains a challenge.

#### 4.2. Choosing the best (combination of) traits with indicator value

In their multigenerational assessment of MP effects on the growth of populations of three freshwater bacterivorous nematode species, Mueller et al. (2020) observed trends – albeit in most cases statistically not significant – which combine a lower carrying capacity of the nematode populations exposed to MP (significant only for *C. elegans*) with a higher population growth rate and faster population doubling times. At first glance, it is difficult to reconcile a faster population growth rate with a lower carrying capacity in microcosms which receive the same amount of resources, unless MP ingestion decreased energy intake over time to an extent where fecundity became negatively impacted; alternatively, MP may have caused increased mortality, but neither fecundity nor mortality were specifically reported on in this population-level study.

Francolino et al. (2021) traded much of the multigenerational approach of Mueller et al. (2020) for a more detailed dissection of stressor (here: organochlorine herbicides) effects on *L. marina* using a range of life-history traits which all contribute to an organism's fitness. In addition to survival, these included fecundity, time until first progeny production, development times of eggs, juveniles and adults, all of

which are essentially individual-based traits. At the same time, they counted population abundance. While there were sublethal stressor effects on most of the traits considered, sensitive traits that were already impacted at low doses of the herbicide included fecundity and maximal population abundance. Given the fact that their experiments were not conducted long enough to reach carrying capacity, the effect on population abundance can be explained by the impact on fecundity, on survival and/or on energetic tradeoffs leading to a lower energy investment in reproduction and/or a slower maturation. In a similar approach, Pontes et al. (2021) assessed the impact of the PAH phenanthrene on *D. delyi*. They found population growth rate to be a more sensitive response variable than any of the individual-based traits. It is tempting to conclude from these three studies that counting abundances over time and calculating population growth rates provides a rapid, sensitive and sufficient indicator of stressor impacts on nematode populations. While we do not argue against the value of such approach, particularly in more routine assessments of large-scale impact studies, we feel that there is substantial added value in determining individual-based traits like fecundity, generation time, and (ideally age-specific) survival to allow a better interpretation of the population trends. Furthermore, additional traits like behaviour may shed further light on the impact of a changing environment on model organisms. Behavioral changes are often among the first responses that can be observed when animals are subjected to a changing environment (Tuomainen and Candolin, 2011; Van Colen et al., 2020), but they have not hitherto been routinely incorporated into impact studies on meiobenthic model species (but see, e.g., Monteiro et al., 2014, 2018). An important added advantage of an approach which takes into account individual-based traits, is that it allows a better estimate of inter-individual variation, the importance of which for population dynamics and resilience may at least equal that of mean rates (Violle et al., 2012).

#### 4.3. Incorporating complexity into experimental approaches

Laboratory experiments typically take a reductionist approach in which one or more factors of potential impact are varied in an otherwise maximally controlled environment. Such approaches, especially when applied to single populations or to very simple artificial communities, have the advantage of allowing a firm mechanistic understanding of stressor effects. At the same time, their results cannot be readily extrapolated to the performance of species, let alone entire communities, in natural settings (see, e.g., Lawton et al., 1996 and the different contributions to that special issue). In order to bridge the gap from lab to nature, field experiments may be needed, even though these generally do not allow similarly firm mechanistic conclusions. A complementary contribution to bridging this gap should come from laboratory experiments a) studying stressor impacts on species interactions instead of on single species (Vafeiadou and Moens, 2021), or b) focusing on realistic combinations of stressors such as a toxicant and temperature (Pontes et al., 2021), or temperature and competition (Vafeiadou and Moens, 2021).

Using dedicated monospecific experiments, Pontes et al. (2021) demonstrated that a temperature increase according to a realistic future climate scenario substantially increased the toxicity of phenanthrene to the nematode *D. delyi*, resulting in a reduced population growth and fecundity. We cannot overstate the importance of such results, since these novel insights should echo loudly into the offices of environmental managers and decision makers who have to adequately forecast future risks of current environmental concerns. Of similar importance, particularly from a conservationist point of view, is the observation that species interactions such as competition may weaken a species' intrinsic tolerance to environmental change (Collins, 2011; Vafeiadou and Moens, 2021). This implies that tolerance levels observed in traditional monospecific assays may largely overestimate the real tolerance and/or adaptive potential of a species in its natural environment.

Whilst both above-mentioned studies already underpin the

complexity of climate-change related effects on populations and simple artificial communities of free-living nematodes, they also open an exciting avenue for research on how such findings might affect entire food webs and ecosystem functioning. To bridge the large gap between the very basic complexity in the studies by Pontes et al. (2021) and Vafeiadou and Moens (2021), and that in real in situ communities, experiments at community-level are direly needed. Majdi et al. (2020) studied the effect of climate warming on entire biofilm communities in an in situ experimental set up in the Garonne river in France. The authors tested how climate warming affects the structure of biofilms and biofilm-inhabiting invertebrate communities. Interestingly, while the biomass of algae and invertebrates did not differ significantly between the treatments, authors observed significant shifts in the structure of the communities, encompassing body-size spectrum, species composition, distribution of feeding types and age structure, but also functional diversity, at least in Nematoda. The next step will be the translation of these results to ecosystem functions in which meiofauna are involved, ranging from stability and productivity of the biofilm to biomass production of meiofauna which can serve as prey for higher-order consumers (Schratzberger and Ingels, 2018).

## 5. Conclusion

The papers in this special issue demonstrate that meiofauna hold substantial potential as indicators of a broad range of environmental impacts on benthic communities. Because of their omnipresence, high abundances and substantial local diversity, changes in meiobenthic communities in response to environmental disturbance can hold powerful clues in impact assessment in almost any freshwater or marine sediment, including habitats devoid of – or at least very depauperate in – macrobenthos. Several studies presented here demonstrate that community composition at genus or even species level is often the most sensitive community-based variable demonstrating a response to environmental disturbance, outperforming the information contained in simple community-based metrics such as diversity indices or the maturity index. In the quest for sensitive community-based metrics, a nematode-based species-at-risk (SPEAR) index holds considerable potential in areas where substantial information is available on the sensitivity of a majority of species to various kinds of disturbance. Hitherto, this approach has only been applied to freshwater sediments; however, the development of a marine nematode SPEAR index for at least estuarine and shallow coastal waters should be within reach.

An important asset of meiofauna, and in particular nematodes, is the availability of a set of suitable model species for laboratory assays under controlled conditions. The species that are amenable to cultivation are all characterized by a fast development and high fecundity, allowing for both single- and multigenerational exposure experiments to be performed within a limited time span. Both population-level parameters, like rate of population increase, and individual-based traits like fecundity prove to be sensitive and complementary indicators of fitness effects of various stressors. The relative ease of working with these laboratory models allows impact screening of both single stressors and combinations of stressors, and the existence of well-documented interspecific interactions between several nematode model species also allows assessment of stressor impacts on species interactions. Such experiments can provide a first step to bridge the large gap between lab experiments and field studies, however, laboratory and in situ experimental manipulations of entire communities are needed to reach that goal.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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