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Review

# Effects of widespread human disturbances in the marine environment suggest a new agenda for meiofauna research is needed

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## HIGHLIGHTS

- Marine meiofauna respond rapidly to fishing, invasive species and climate change
- Disturbance effects on habitats interact critically with effects on meiofauna present
- Proliferation of broadly adapted generalists homogenises meiofauna communities
- Research needed on meiofauna responses and adaptations to support conservation

## ABSTRACT

The response of an ecological community to a disturbance event, and its capacity to recover, are of major interest to ecologists, especially at a time of increasing frequencies and intensities of environmental change brought about by humans. Meiofauna, a group of small-sized metazoan organisms, are an abundant and ubiquitous component of seafloor communities that respond rapidly to environmental change. We summarise the available research on the response of meiofauna to the most widespread anthropogenic disturbances in the marine environment, including bottom fishing, the introduction of invasive species and anthropogenic climate change. We show that disturbance effects on habitats interact critically with effects on resident meiofauna species. Their responses are consistent with competitive replacement, where disparate disturbance effects on competing species drive shifts in dominance and intra- and interspecific interactions. The widespread replacement of habitat-specific ecological specialists by broadly adapted ecological generalists and opportunists results in biotic and functional homogenisation of once disparate biotas. Anthropogenic disturbances may facilitate novel interactions amongst meiofauna species, and between meiofauna and other benthic organisms, but the number and breadth of these interactions is likely to be limited. Knowledge on the dependence of meiofauna species on their environment and on other benthic species has been growing. Future studies will be most meaningful if this knowledge is expanded alongside understanding the potential of locally adapted species to respond to shifts in environmental conditions.

***Keywords:*** Meiofauna; Anthropogenic disturbance; Bottom fishing; Invasive species; Climate change; Ecosystem consequences

## 1. Introduction

The seafloor is the largest ecosystem on Earth by area, home to mostly unexplored biodiversity that provides numerous services to society (Snelgrove, 1997; Costanza et al., 2014), and is vulnerable to global change (Worm and Lenihan, 2014). Humans cause damage to the seafloor, and hence to benthic habitats and species, across spatial scales from local to global.

Benthic biota is frequently used to indicate the quality of seafloor ecosystems and how they are changing over time (Pinto et al., 2009, Pereira et al., 2013). Meiofauna, a group of small-sized organisms (< 1 mm) whose morphology, physiology and life history characteristics have evolved to utilise seafloor habitats, are the most abundant and phyletically diverse metazoans on Earth (Warwick, 1993; Giere, 2008). The small size of meiofauna organisms coupled with their often high abundance and diversity, and continuous reproduction, make them amenable to *in situ* studies and experimental manipulation (Fleeger and Carman, 2011). Meiofauna organisms have high site fidelity and are short-lived (generation times vary from weeks to a few months; Coull, 1999). Their populations and communities respond to both short-term fluctuations of, and longer-term trends in, local environmental conditions (Schratzberger et al., 2000). Most meiofauna organisms live in spaces and channels between sediment particles and are therefore susceptible to changes in seafloor physico-chemical composition (e.g. texture, bed forms, oxygenation, etc.) and biological properties (e.g. biofilms on sediment particles, content of organic matter).

Research over the past five decades has uncovered the influence meiofauna organisms, and their interactions with microorganisms and larger macrofauna, have on globally important ecosystem processes (Schratzberger and Ingels, 2018). Experiments (Nascimento et al., 2012) and field studies in benthic habitats where macrofauna is rare or absent (e.g. deep sea: Danovaro et al., 2008; Baltic Sea: Bradshaw et al., 2006) showed that meiofauna organisms can mediate ecosystem processes with little or no macrofauna. The continuous reproduction strategy of meiofauna organisms has two important consequences. Firstly, it renders them less vulnerable to the timing of disturbance than larger fauna, for which a disturbance event during the recruitment period can destroy the population until the next recruitment. Secondly, a constant supply of individuals facilitates rapid recolonisation of disturbed habitats, whereas recolonisation by larger fauna which recruit seasonally or sporadically may be less rapid (Bolam et al., 2006; Whomersley et al., 2009). The response of meiofauna organisms to, and recovery from, environmental change may, therefore, have important implications for seafloor habitats worldwide.

Some human activities have relatively local effects, whereas others have widespread effects which can alter whole ecosystems. Human activities that are considered to have the most widespread consequences for marine ecosystems include bottom fishing, the introduction of invasive species and anthropogenic climate change (Sutherland et al., 2013). Meiofauna has been widely used to determine the effects of humans on aquatic ecosystems, particularly pollution (Coull and Chandler, 1992; Balsamo et al., 2012; Zeppilli et al., 2015), but a critical evaluation of current research-derived knowledge about meiofauna responses to these most widespread anthropogenic perturbations is lacking. Here, we summarise recent scientific progress. In our summary we address the following questions:

1. What are the effects of bottom fishing, the introduction of invasive species and anthropogenic climate change on metazoan meiofauna species, populations and communities?

2. What are the potential consequences of these altered metazoan meiofauna communities for the overall structure and function of seafloor habitats?

We conclude by proposing future ecological research to better understand the role of meiofauna in determining how seafloor systems may respond to accelerating environmental changes and what the ecosystem consequences of these responses are likely to be. We focus on scientific fields that we think could yield promising scientific advances in the near future.

## 2. Methodological approach

### *2.1 Literature search*

A survey of the available published peer-reviewed literature was conducted to complement our own extensive knowledge of relevant literature. The Thomson Reuters Web of KnowledgeSM (formerly ISI Web of Knowledge) was used (https://apps.webofknowledge.com/WOS). This academic citation indexing and search service provides bibliographic content and the tools to access, analyse, and manage research information. In order to keep the search wide and to include the most relevant journal articles, a topic search was carried out with the search terms 'meiofauna' OR 'meiobenthos' in any topic, title or text words [TS = (meiofauna* OR meiobenth* OR nematod* OR harpacticoid*) AND TS = (disturb*); Databases = WOS; Timespan = All years; Search language = Auto]. The search, on 9 October 2019, returned a total of 2,253 articles. A total of 411 of all articles focused on marine meiofauna and abstracts of these articles were read. Approximately one third of these articles (142 articles) mostly presented results from field surveys with meiofauna where anthropogenic disturbance was inferred, but not explicitly tested, as a driver of community changes observed. These articles were therefore not considered further, nor were the 32 articles investigating the utility of meiofauna as indicators of environmental status (Fig. 1). A further 94 articles investigated pollution effects and 34 articles examined the effects of deep-sea mining and other physical disturbance effects. These articles were also excluded from further analysis. The remaining 110 articles were considered within the context of our review (Fig. 1), together with other relevant articles that were not picked up by the formal literature search.

### *2.2 Attributing changes in meiofauna to anthropogenic disturbance*

In many of the studies reviewed, a single type of human activity triggered a large number of ecological responses which often merged with patterns of natural variability. The responses of meiofauna to disturbance (*sensu* White and Pickett, 1985) seldom followed linear chains, but more often interacted with each other, sometimes damping the effects of the anthropogenic disturbance and at other times amplifying them (Steffen et al., 2006). Ideally the attribution of changes in meiofauna to the consequences of anthropogenic disturbance would involve long-term parallel time series of the disturbance, the meiofauna and their habitat across appropriate spatial scales, using *a priori* hypotheses on the spatio-temporal ecological changes expected (Duarte et al., 2015). Simple cause-effect responses are elusive, however, and the ecological consequences of a specific anthropogenic disturbance may be confounded with those of other anthropogenic disturbances, and its effects on meiofauna over- or under-estimated (Buma, 2015). The direct effects of bottom fishing, for example, could be confounded with the combined and cumulative effects of habitat modification (either by the fishing gear itself or from other unrelated sources), natural variability and/or anthropogenic climate change (Worm and Lenihan, 2014). Controlled experiments, carried out in the laboratory or in field mesocosms where such effects are disentangled using specific, identifiable treatments provided a means for testing *a priori* hypotheses and gaining a mechanistic understanding of ecological responses to specific disturbances (Schratzberger et al., 2009).

Most relevant meiofauna studies reviewed here focused on establishing the effects of identified anthropogenic disturbances in isolation. Notable exceptions were experiments designed to investigate interactive effects, such as between productivity and physical disturbance (Austen and Widdicombe, 2006), biotic physical disturbance and reduced pH (Dashfield et al., 2008) or elevated temperature and elevated $CO_2$ or reduced pH (see section 3.3). The following sections focus on the effects of widespread anthropogenic disturbances (including bottom fishing, the introduction of invasive species and anthropogenic climate change) on meiofauna.

## 3. What are the effects of bottom fishing, the introduction of invasive species and anthropogenic climate change on meiofauna species, populations and communities?

Each meiofauna species (and individual) has its own specific physiological optimum, and interactions with abiotic conditions in its habitat, so anthropogenic disturbances may cause changes in meiofauna communities by altering abiotic factors (Fig. 2). Anthropogenic disturbances may influence the physiology and behaviour of individuals directly, affecting their survival and fitness (Pirotta et al., 2018), as well as their distribution (Boldina et al., 2014). For example, changing temperature can alter the metabolic rates of meiofauna organisms, which affect activity patterns, survival, individual growth, or reproductive rates (Giere, 2008). Changes in activity can modify encounter rates among species if individuals avoid exposure to stress or increase foraging to meet metabolic needs. Changes in growth rates can alter body sizes and influence the outcome of species interactions (Gilman et al., 2010). Species-specific sensitivities to disturbance propagate through population dynamics to community-level responses which are mediated by shifts in species interactions. Too little is known, however, about the physiology and ecology of individual meiofauna species to enable predictions about community responses.

In the absence of such predictive ability, an alternative approach is to measure community responses directly, for example by using a community-level metric that reflects changes that might be expected to occur if species with similar physiological and ecological requirements respond to change differently to species with different requirements. An example is the family of measures which reflect the taxonomic spread of species in a community (Warwick and Clarke, 2001), where a symptom of anthropogenic disturbance is the removal of rarer (and less closely related) species and the relative success of (more closely related) species which tend to share physiological and ecological traits.

### *3.1. Bottom fishing*

Halpern et al. (2008) estimated that 75% of the world's continental shelf area (approximately 20 million km$^2$) has been trawled or dredged at least once, and it is the first pass of the gear that is most damaging for the seafloor (Cook et al., 2013). While global fishing effort has increased since the 1950s, and fisheries have expanded their geographic reach, catches have been declining since the mid-1980s, suggesting that biomass of target species has been reduced substantially over the past few decades (Watson et al., 2013). A wide variety of methods are employed to capture target species, including fixed (e.g. traps, bottom longlines, gill nets) and mobile (e.g. trawls, dredges) gears. Physical contact of mobile gear on the seafloor leads to scraping, scouring and resuspension of surface sediment (Jennings and Kaiser, 1998; Kaiser et al., 2006). This reduces the small-scale heterogeneity and topography created by epifauna and flora, large burrowing infauna and demersal fish, and alters hydrodynamic and biogeochemical processes (Pilskaln et al., 1998; Pusceddu et al., 2014). There is consensus in the scientific literature that bottom fishing can have far-reaching, mostly adverse, effects on the biodiversity, biomass, and production of benthic communities. The removal of certain species and size classes directly alters the composition and diversity of target and non-target communities (Crowder et al., 2008). These alterations are further amplified by species interactions, which mediate indirect effects through changes in, for example, trophic relationships (Table 1).

Whilst the effects of, and recovery from, bottom fishing on demersal fish and macrobenthic communities are well documented (Jennings and Kaiser, 1998; Kaiser et al., 2006; Tillin et al., 2006), studies on meiofauna are more limited. We were unable to find studies that document the effects of bottom fishing on meiofauna assemblages in sublittoral epifaunal turfs and biogenic reefs, the removal of which is one of the first impacts of bottom fishing. The effects of this impact can only be inferred from the fact that habitat heterogeneity is altered (see section 3.4). Most studies examined the effects of bottom fishing on infaunal meiofauna, often in areas that had already been subject to considerable fishing pressure. The small size of meiofauna organisms implies that they are resuspended rather than killed by bottom gear and that their response is thus mediated primarily *via* fishing-induced modifications to the seafloor habitat (e.g. removal of larger biota; changes to sediment sorting, grain size, and organic matter profiles; increase in silt content; loss of surficial sediment through resuspension and the winnowing of fines; see Kaiser et al., 2002; Puig et al., 2012). The short generation times of meiofauna organisms would allow their populations to increase following trawling (Schratzberger et al., 2002). If this is indeed the case, meiofauna may continue to process energy in the benthic ecosystem when the productivity of more sensitive and fragile macrofauna is reduced. Meiofauna organisms could even proliferate as a result of reduced competition and predation from target and non-target species (Schratzberger and Jennings, 2002).

The response of meiofauna to bottom fishing depends on the type of fishing gear, the intensity and frequency of fishing and its magnitude relative to other natural disturbances, and the habitat with its resident biota (Rosli et al., 2016). To date, *in situ* studies at fishing grounds in shallow-water and deep-sea habitats suggest that meiofauna abundance has increased (Liu et al., 2011; Pranovi et al., 2000), decreased (Hinz et al., 2008; Schratzberger and Jennings, 2002; Pusceddu et al., 2014), or exhibited only minor changes (Lampadariou et al., 2005; Schratzberger et al., 2002) in response to bottom fishing. Effects on meiofaunal biomass were relatively weak and chronic effects were more pronounced than acute effects (Alves et al., 2003; Pranovi et al., 2000, 2004). Although meiofauna communities are generally considered more resilient to anthropogenic disturbance than the larger macrofauna, any increases of meiofaunal biomass or production in trawled areas were small in relation to the losses in overall community biomass and production that resulted from the depletion of larger individuals (Schratzberger et al., 2002).

The most consistent response of meiofauna organisms to varying intensities and frequencies of *in situ* bottom fishing were changes in abundance of individual species and genera, mediated *via* fishing-induced modifications of the sediment. Hinz et al. (2008) and Liu et al. (2011) recorded both beneficial and adverse effects on nematode species. For example, mixing of sediments following the passage of fishing gear releases previously buried organic material and benefits those species that are able to use this surplus either directly or *via* increased primary production. Similarly, increased organic loading of the sediment can lead to a shift towards microbial-dominated, anaerobic food chains, resulting in the proliferation of the few species that can survive in oxygen-poor sediments and are able to exploit microbial food sources (Franco et al., 2008). Results from a mesocosm experiment suggested that removal or reduced densities of larger macrofauna species as a result of bottom fishing may lead to increased nematode abundance, most likely mediated by increased accessibility to food in the absence of macrofauna (Ingels et al., 2014), although evidence for close relationships between meiofauna-sized and larger organisms in the field is equivocal (Austen et al., 2003).

### *3.2. Introduction of invasive species*

Only a small fraction of the many marine species introduced by human action outside their native range are able to thrive and invade new habitat. However, the most invasive of these species create one habitat at the expense of another habitat. Levels of invasion are highest in temperate regions of Europe, North America and Australia, and the main means of introduction are international shipping and aquaculture. At least one invasive species has been recorded in 84 % of the world's 232 marine ecoregions (Molnar et al., 2008). More than half of all non-native species are benthic invertebrates while macroalgae rank second in numbers (Reise et al., 2006; Tricario et al., 2016). Invasive species can affect the seafloor in various ways (Crooks, 2002): they may use resources (e.g. space, food etc.) differently, thereby affecting resource availability for native species and potentially outcompete them; they may change the flow of energy or biomass, thereby changing biogeochemical cycles and food webs; and they may change the physical structure of the ecosystem itself, thereby either increasing or decreasing habitat heterogeneity (Table 2).

The close association between meiofauna organisms and their seafloor habitat, coupled with their direct benthic development (i.e. lack of planktonic larvae) and generally short generation times, suggests that they may respond rapidly to local habitat changes brought about by invasive species. The introduction of invasive habitat-forming species such as seagrasses and reef-building polychaetes, for example, may alter flow regimes, change the availability of food for meiofauna, provide refuges from predation and resuspension, and ameliorate exposure to physical conditions (Hendricks et al., 2010). In addition, meiofauna organisms are likely to respond to invasion-induced changes to chemical and textural characteristics of the seafloor, especially if physico-chemical properties in invaded habitat differ considerably from those to which resident meiofauna is adapted. The combined effects of invasive species on meiofauna will depend, at least in part, on the life habits both of the invader and the resident meiofauna organisms, as well as the magnitude of invasion and the time since invasion.

The most relevant meiofauna studies to date investigated how the proliferation of invasive canopy-forming (i.e. engineering) seaweeds and seagrasses affect rocky littoral (e.g. Smith et al., 2014; Veiga et al., 2016; Wagensteen et al., 2018) and soft sediment (e.g. Chen et al., 2007; Gallucci et al., 2012; Pusceddu et al., 2016) meiofauna communities in shallow waters. Adverse effects of invasive plant species (algae and angiosperms) outcompeting native plant species were mediated by loss of spatial variability in invaded habitats. Such effects were potentially counteracted by beneficial consequences arising from invasion of previously unvegetated seafloor, resulting in the generation of more microenvironments and increased protection from predation (see section 3.4). Macroalgal detritus can contribute to meiofauna diets (Queirós et al., 2019), but whether or not fresh organic matter derived from, and/or detritus trapped by, invasive seaweeds can easily be exploited as a primary resource by meiofauna organisms depends on the trophic ecology of the species in question (Chen et al., 2007). Overall, trends in meiofauna diversity and species distributions varied according to the extent to which invasive species created novel environments that differed from those to which the resident meiofauna was adapted. Field studies with invasive seaweed and seagrass species showed that changes in nematode diversity resulting from species-specific responses to habitat modifications were inconsistent at local scales (Chen et al., 2007; Gallucci et al., 2012; Pusceddu et al., 2016). At larger scales, however, invasive seaweeds promoted an overall increase in nematode diversity by favouring species that were absent from both vegetated and non-vegetated native environments (Gallucci et al., 2012). Conversely, the number of nematode species and diversity were reduced in mangroves invaded by *Spartina alterniflora* compared to uninvaded native mangroves. The invasive seagrass created physico-chemical habitat conditions (e.g. reductions in sedimentary carbon and nitrogen content) that were unfavourable for the majority of nematode species associated with uninvaded mangroves (Fu et al., 2017).

Experimental studies demonstrated that direct effects of invasive polychaetes on meiofauna organisms, such as sediment disturbance *via* burrowing, predation and creation of reefs, were generally weak and masked by indirect, cascading effects of their activities. The burrowing activity of the invasive polychaete *Marenzelleria* spp., for example, transported oxygen from the surface to deeper layers, thereby creating new niches in the microoxic environment near its burrows. This, in turn, facilitated the vertical penetration of some nematode species that were able to utilise additional food sources deeper in the sediment (Urban-Malinga et al., 2013). Like canopy-forming invasive seaweeds and seagrasses, the invasive reef-building polychaete *Ficopomatus* spp. added structure to the substratum. An *in situ* transplant experiment by Schwindt et al. (2001) revealed that the presence of *Ficopomatus* spp. regulated meiofauna density and diversity indirectly as increased numbers of the crab *Cyrtograpsus* spp. found shelter in the polychaete reefs and affected meiofauna *via* predation and sediment disturbance.

### *3.3. Anthropogenic climate change*

Atmospheric greenhouse gas emissions have doubled since 1980, raising atmospheric concentrations and increasing global average temperatures by approximately 0.2°C per decade over the past 30 years. Most of this added energy and atmospheric $CO_2$ are being absorbed by the oceans (Hoegh-Guldberg and Bruno, 2010; Brondizio et al., 2019). Owing to the enormous thermal mass of the oceans there is a considerable time-lag between warming of the atmosphere and increases in global ocean temperatures, but the average temperature of the upper layers of the ocean has increased by 0.6°C over the past 100 years and is expected to continue increasing. The dissolution of $CO_2$ acidifies ocean water, causing the pH of the Earth's oceans to shift towards pH-neutral conditions. Increased temperature decreases the ability of water to hold oxygen. These trends are ongoing (Brondizio et al., 2019). Although there is considerable uncertainty about the spatial and temporal details, anthropogenic climate change has so far been linked to decreased ocean productivity, altered food web dynamics, reduced abundances of habitat-forming species, shifting species distributions, and a greater incidence of disease (Table 3; Hoegh-Guldberg and Bruno, 2010). In addition, polar regions are experiencing rapid changes in sea ice duration, iceberg disturbance and melt water run-off (Sahade et al., 2015).

Meiofauna organisms, like other ectotherms, regulate their body temperature largely by exchanging heat with their surroundings. Their physiological performance, and hence distribution will, in part, depend on the range and extremes of temperatures that they experience throughout their life cycle (Giere, 2008). Changes in temperature can affect meiofauna directly by shifting the temperature experienced by individuals. Studies in exposed sandy beaches suggest that the distribution of meiofauna is largely determined by the maximum temperature experienced in their habitat rather than the range of temperatures at a given time (Wieser and Schiemer, 1977). Although species are able to acclimatise to a range of temperatures around the optimal values, beyond this range acclimatisation fails, fitness is reduced, mortality risk increases and populations decline. Whilst some species will not be able to withstand the frequency and/or magnitude of changes in thermal conditions, others may be able to disperse into areas that were previously too cold (Hiddink et al., 2015). Although meiofauna generally comprise non-calcifying taxa, physiological and metabolic functions common to both calcifying and non-calcifying organisms, such as reproduction and growth, are vulnerable to changes in pH (Vézina and Hoegh-Guldberg, 2008). Net effects of anthropogenic climate change on meiofauna organisms will be a combination of changes to the physiology and metabolism of individual species, and the interactive indirect effects of changing temperatures and pH on the quantity and quality of food, alterations to sediment properties such as oxygen penetration depth, changes in habitat-forming species, and the activity of, and interactions among, species and trophic groups (Coull, 1999; Ingels et al., 2012).

A range of laboratory experiments provided insights into the varied responses of meiofauna to single and combined treatments simulating climate change scenarios of elevated constant temperatures, fluctuating temperature regimes with extreme maxima, and changes in pH (Zeppilli et al., 2015). Most of these studies targeted shallow water temperate and tropical meiofauna communities and in particular nematode assemblages. Across habitats, nematode densities generally decreased under both elevated constant and fluctuating temperature treatments (Gingold et al., 2013; Mevenkamp et al., 2018; Vafeiadou et al., 2018a), as did those of other meiofauna taxa although their low abundances often precluded firm conclusions (Meadows et al., 2015). Densities of a few opportunistic nematode species in tropical subtidal communities increased, however, when the effects of elevated temperature were investigated in combination with reduced pH (Lee et al., 2017). Consistently observed shifts in dominance patterns of meiofaunal nematode species resulted from species-specific physiological tolerances to changes in temperature and pH (Mevenkamp et al., 2018), in combination with shifts in species interactions (Ingels et al., 2018). For example, De Meester et al. (2015) and Vafeiadou et al. (2018b) demonstrated that changes in fitness of individual nematode species in response to elevated temperature can alter their relative competitiveness, thereby affecting interactions between coexisting and competing species. Such shifts in interactions, rather than a differential temperature tolerance *per se*, might trigger changes in abundance of temperature-tolerant species.

Secondary effects of global temperature increases are generally longer-term and beyond straightforward manipulation, and thus poorly studied. In polar regions these include faster glacier retreat and related events which, in turn, lead to more frequent iceberg scouring, freshwater input and higher sediment loads. Although Somerfield et al. (2006) found little evidence for a specialised meiofauna in unconsolidated and nutrient-poor sediments close to a glacier front, field studies in polar regions investigating such secondary effects showed that meiofauna organisms may respond to high levels of ice disturbance and the newly available resource pool *via* rapid colonisation, followed by the establishment of more differentiated trophic niches during the early years after these events (Pasotti et al., 2015a). At locations where poor nutritional conditions were coupled with high sedimentation rates, macrofaunal biomass was reduced and meiofaunal biomass and production increased, most likely due to a release from macrofaunal predation and competition. Consequently, the partitioning of benthic biomass and production shifted towards meiofauna, which played a dominant role in the processing of sedimentary organic matter (Górska and Włodarska-Kowalczuk, 2017). The capacity of some nematode species to colonise sedimentary habitats following glacier retreat depended on their tolerance to high sediment deposition (Lee et al., 2001; Pasotti et al., 2015b). A recent study by Vause et al. (2019), using eDNA metabarcoding of meiofauna in Antarctic soft sediments, suggested that the increase in glacial sediment input as glaciers melt may be more important in structuring meiofauna communities than increased iceberg disturbance.

Over the last decade, various studies have used meiofauna to address the effects of increased $CO_2$ concentrations (> 5000 ppm) in relation to carbon capture and storage projects (Thistle et al., 2005; Fleeger et al., 2006; Thistle et al., 2006). More recently, sublethal effects of exposure to longer-term reduction in pH and increase in $pCO_2$ (< 1600 ppm), akin to anthropogenic climate change effects, have been demonstrated for intertidal harpacticoid copepod species in laboratory experiments (Fitzer et al., 2012; Sarmento et al., 2017). Exposure of laboratory-reared harpacticoid copepods to lower pH resulted in reduced developmental time, fecundity and body length. This suggests that harpacticoid copepods subjected to ocean acidification-induced stress preferentially re-allocated resources towards maintaining reproductive output at the expense of somatic growth. The physiological response of test species manifested in alterations to their redox system and an up-regulation of stress-related genes (Lee et al., 2019). Wild-caught organisms were generally more sensitive to experimental treatments of increased $CO_2$ than culture-derived ones (see section 4.2), and nauplii more sensitive than adults (Oh et al., 2017). Studies investigating the effects of low pH on meiofauna organisms in the field, however, showed that shifts in their community structure were driven by the indirect effects of acidification. These included changes to habitat type and structure, and shifts in species interactions resulting from, for example, release from predation pressure and altered quantity and type of food available, rather than physiological intolerance to low pH (Garrard et al., 2014; Ravaglioli et al., 2019).

### *3.4. Changes in seafloor habitat diversity*

Diverse physical and biogenic seafloor habitats are modified and/or lost as a result of bottom fishing, introductions of invasive species and anthropogenic climate change (Tables 1 to 3). Consequently, the seafloor is becoming more homogeneous (Thrush et al., 2006; Worm and Lenihan, 2014). Reise (2002) reviewed the role of sediment-dwelling organisms as bioengineers that alter the abiotic and biotic environment with effects on other species. Autogenic engineers, such as corals, macroalgae and seagrasses, provide and alter habitat with their body structure whereas allogenic engineers, such as burrowing macrofauna, transform their surroundings through their activity and thus alter resources for other organisms. While autogenic engineers offer shelter and food resources for other organisms, they may also be subject to considerable grazing pressure. Globally, ecosystem engineering is a facilitative process involving addition, removal, reconfiguration or redistribution of habitat, or a combination of these (Jones et al., 2010), with varying effects on biodiversity and ecosystem functioning (Guy-Haim et al., 2018). Generally, invertebrates are more effective as engineers than vertebrates and invertebrate species richness is particularly responsive to engineering effects (Romero et al., 2015). Biomass and volume of habitat-forming species have been widely used as indices of their heterogeneity whereas the structural heterogeneity of soft sediments is generally accounted for by measures of sediment form and texture (Danovaro and Fraschetti, 2002).

The morphology and life-history characteristics of meiofauna organisms tie them closely to the habitats in which they live. When patches of suitable habitat are spatially or temporally discontinuous, an organism’s dispersal capability will greatly affect its ability to colonise available space. Where the dispersal mechanism is closely related to the transport mechanisms of the associated sediment, as is the case for many sediment-dwelling meiofauna organisms, the distribution and location of the habitat is a key factor in controlling faunal distribution patterns (Schratzberger and Larcombe, 2014). A decline in the structural heterogeneity of sedimentary and biogenic seafloor habitats could affect their suitability for meiofauna. Autogenic engineers, for example, supply living space, food (directly, or indirectly by trapping detritus or providing attachment sites for microalgae and bacteria), or shelter from resuspension, physical stress, and invertebrate and fish predators (Reise, 2002). The activities of allogenic engineers modify physical, chemical and biological properties. They often do so simultaneously by, for example, displacing sediment grains during burrow construction and displacing/removing organic matter and/or associated meiofauna and microorganisms within the sediment matrix during feeding (Kristensen et al., 2012). Changes in the abundance and diversity of allogenic and autogenic engineers in response to anthropogenic disturbance may be brought about by differential survival and/or species-specific recovery rates. These, in turn, can affect recovery of associated meiofauna (Guerrini et al., 1998).

Many studies investigating meiofauna communities under similar environmental conditions but differing in major bioengineers, either naturally, accidentally or experimentally manipulated, were carried out at low taxonomic resolution (e.g. Bell, 1985; Dittmann, 1996; De Troch et al., 2001; Passarelli et al., 2012; Ataide et al., 2014; Ape et al., 2018), and were found to report weaker responses of meiofauna to changes in the type and density of bioengineers than studies reporting data at either meiofauna family or species level. The latter studies provide evidence of a generally positive relationship between the heterogeneity of physical and biogenic habitat and the diversity and abundance of meiofauna that they support (see Ólafsson, 2003; also macroalgae: Hicks, 1980; Warwick, 1977; Gee and Warwick, 1994; Arroyo et al., 2006; Frame et al., 2007; seagrass: Fonseca et al., 2011; coral reefs: Netto et al., 1999; Semprucci et al., 2010; polychaete tubes: Tita et al., 2000; burrowing crustaceans: Pillay and Branch, 2011; Citadin et al., 2016); echinoderms: Austen and Widdicombe, 1998).

Somerfield and Jeal (1995, 1996) demonstrated the importance of microenvironmental conditions in determining distributions of intertidal meiofauna among macroalgae, lichens and barnacles, while Norling and Kautsky (2007) showed that the diversity of mussel-associated meiofauna is almost entirely controlled by structural properties of the bioengineer, modifying meiofauna distributions by providing contrasting microhabitats. Conversely, the biological activities of mussels (i.e. biodeposition, nutrient recycling and water clearance) appeared to determine the carrying capacity (i.e. abundance and biomass) of meiofauna communities. Benthic mesocosm experiments showed that burrowing macrofauna species altered the structure of natural subtidal nematode assemblages in different ways, depending on the bioturbator’s feeding behaviour and mobility (Austen et al., 1998). Similarly, bioturbating and bioirrigating activities of macrobenthic infauna in subtidal soft sediments transport organic matter and oxygen from the surface to deeper layers, thereby extending and diversifying the habitat suitable for meiofauna (Pinto et al., 2006; Braeckman et al., 2011). The spatio-temporal extent of such facilitative effects, however, is currently unclear. A 3-year field manipulation experiment at a tidal flat in the German Bight, for example, recorded increased diversity of harpacticoid copepod assemblages in surficial sediments of sites where the burrowing polychaete *Arenicola marina* was excluded (Kuhnert et al., 2010).

Sediment transport processes operating at different magnitudes and frequencies create a wide range of habitats for meiofauna organisms in soft sediments free from biogenic structures. Sedimentary bedforms (e.g. ripples, sandwaves, sandbars) that differ in the intensity and frequency of sediment mobility, with associated changes in oxidation state and other biogeochemical parameters, support distinct nematode communities in intertidal (Gingold et al., 2010), subtidal (Schratzberger and Larcombe, 2014) and deep sea (Van Gaever et al., 2009) sediments. Somerfield et al. (2007) found that spatial patterns of meiofauna suggested an interaction between effects of physical processes affecting sediment properties and food supply at the sediment surface, and the homogenisation of sediment by the activities of burrowing urchins deeper within the sediment. Across habitats, structurally heterogeneous sediments generally feature higher levels of taxonomic and functional diversity, unique species, and communities that differ from those found in more homogeneous habitats (Norling and Kautsky, 2007; Gingold et al., 2010; Braeckman et al., 2011; Bianchelli et al., 2016; Zeppilli et al., 2016; Gallucci et al., 2020).

## 4. What are the potential consequences of altered meiofauna communities for the overall structure and function of seafloor habitats?

Warwick (1989) suggested that meiofauna organisms have had a profound influence on many structural and functional attributes of ecosystems, both in the benthic and pelagic realms. Size spectra, the life-history characteristics of the macrobenthos, and the energetic balance between ecological compartments of the marine ecosystem are considered to result from interactions involving meiofauna organisms. Meiofaunal species that persist in space and time will be those that are able to tolerate the natural variation in their environment. Their abundance will change as a function of alterations in the physical environment and in interactions among species in the local assemblage. The bounds over which seafloor habitats change in response to most natural events are limited, on the relevant time-scales, when compared with the changes imposed by anthropogenic disturbances (Karr, 1996; Schratzberger et al., 2009). Studies investigating meiofaunal responses to bottom fishing, the introduction of invasive species and anthropogenic climate change indicated that anthropogenic modifications primarily disrupt community assembly by altering habitats (Fig. 3), with implications for their ecological integrity (*sensu* Parrish et al., 2006).

### *4.1 Biotic homogenisation of meiofauna communities and simplification of species interactions*

Experimental and observational studies with meiofauna showed that often weak and inconsistent changes in community metrics (i.e. abundance, diversity and biomass) masked generally stronger responses of species with physiologies and life histories that either allowed them to, or prevented them from, thriving in disturbed conditions. Individual species often exhibited high spatial and temporal sensitivity to anthropogenic disturbance when the modified environment could not meet their requirements. Conversely, species with niches better suited to the new environmental conditions often proliferated, thereby compensating for species lost (Supp and Ernest, 2014). In many meiofauna studies, these compensatory mechanisms resulted in disturbances having low influence on community-level properties despite larger changes at the species level (Somerfield and Clarke, 1995). Population changes were the result of disturbance-resistant species persisting in the altered environmental conditions, the loss of disturbance-sensitive species, and the proliferation of other, often opportunistic, species. The combined effects of these population-level changes were sometimes detectable at the community level as a decline in taxonomic relatedness in disturbed assemblages (Warwick and Clarke, 1995; Clarke and Warwick, 1998).

Although responses of meiofauna communities to anthropogenic disturbances were complex, generally severe disturbance led to dominance by opportunistic species. The often high phenotypic plasticity of those species was illustrated by their ability to alter their growth rate, physiology or behavior to better suit the environmental conditions with which they were faced (Schratzberger et al., 2009). This widespread replacement of habitat-specific ecological specialists by broadly adapted ecological generalists and opportunists mixed the taxonomic and functional composition of once disparate biotas, resulting in biotic and functional homogenisation (*sensu* McKinney and Lockwood, 1999) of meiofauna communities under various regimes of anthropogenic disturbance, reflected in the decline in the taxonomic breadth of species mentioned above.

Meiofauna studies investigating the effects of invasive species introductions have, at times, provided equivocal or contrasting results, with species richness increasing in some cases and declining in others. Increased species richness, however, was often the consequence of habitat modification caused by invasive species that facilitated the colonisation of opportunistic meiofauna species or meiofauna species characteristic of other habitats (see section 3.2). Therefore, either increased or decreased species richness of meiofauna may result from biotic and functional homogenisation of meiofauna communities in invaded habitat.

Results from controlled defaunation experiments with meiofauna and macrofauna in the laboratory and in the field showed that colonisation of disturbed habitat by meiofauna organisms generally proceeded more rapidly than macrofaunal recolonisation (Bolam et al., 2006). The generally high colonisation capacity of meiofauna organisms, which is defined by their life history traits rather than their mobility (Fonsêca-Genevois et al., 2006), can lead to shifts in the partitioning of benthic biomass and production. Consequently, meiofauna would be expected to play a more dominant role in the processing of sedimentary organic matter in disturbed habitat compared to macrofauna, even after disturbance has ceased. Meiofauna studies in fishing grounds, however, clearly demonstrated that despite their small size and fast life cycles, nematodes were negatively affected by chronic bottom fishing and unable to compensate for the loss in production by larger macrofauna (see section 3.1). Further reduction in secondary production in chronically fished areas is thus likely. Given the intermediary role of meiofauna organisms, as consumers of a range of carbon sources and as a food source for secondary consumers (Schratzberger and Ingels, 2018), homogenisation of meiofauna communities may have cascading effects through the benthic compartments.

The evidence-base surrounding the direct response of meiofauna species to bottom fishing, the introduction of invasive species and anthropogenic climate change has been growing steadily over the past five decades, with individual studies implying that sensitive species drive most ecosystem responses. Our review of existing literature, however, emphasised the importance of shifts in species interactions. Such shifts can attenuate or amplify non-lethal physiological responses of opportunistic, disturbance-tolerant species and lead to further ecosystem change, or indeed buffer against such changes (Wolfe et al., 2017). Although anthropogenic disturbances may facilitate novel interactions amongst meiofauna species, and between meiofauna and other benthic organisms (see section 3), the number and breadth of these interactions is likely to be limited owing to the biotic and functional homogenisation of communities (Olden et al., 2004).

The taxonomic and functional diversity of meiofauna assemblages was generally highest in structurally heterogeneous seafloor habitats that provided resources for herbivores, bacterivores, omnivores and predators (Gingold et al., 2010). Bacterivorous and omnivorous nematodes, for example, feed on microorganisms and excrete nutrients in excess of their metabolic need. The abundance and activity of these nematodes may, in turn, be regulated by predatory nematodes, thus preventing over-grazing by those groups and further controlling nutrient availability (Schratzberger et al., 2019). At the same time, nutrients excreted by nematodes regulate microbial biomass and activity (Fig. 4). Reduced trophic diversity was a consistent response of meiofaunal nematode assemblages to habitat homogenisation (Gingold et al., 2010; Schratzberger and Larcombe, 2014). Larger-bodied predators, with generally lower fecundity and lower growth rates compared to other trophic groups, were particularly sensitive to the anthropogenic disturbances investigated here. The compensatory proliferation of less sensitive species may result in little detectable effect on community-level properties. However, homogenisation across multiple trophic levels will undoubtedly alter the pattern of energy flow through the benthic food web. Owing to the interdependence of bacteria and meiofauna and macrofauna production, the fate of unutilised benthic resources (such as particulate organic matter) in areas heavily defaunated by bottom fishing and other anthropogenic disturbances remains unclear (Fig. 4; Schratzberger et al., 2002; Hinz et al., 2008; Ingels et al., 2014)

### *4.2 Capacity of meiofauna organisms to adapt to environmental change*

The seafloor is subject to natural disturbance regimes that operate across a range of temporal and spatial scales. Natural disturbances tend to be pulse disturbances with a characteristic magnitude and frequency distribution to which local species assemblages are adapted, and from which they can recover. Human activities transform some pulse disturbances into press or chronic disturbances of greater magnitude, higher frequency and/or longer duration (Bengtsson et al., 2003). Meiofauna studies reviewed here demonstrated that biotic and functional homogenisation of meiofauna communities in response to anthropogenic disturbance inevitably narrowed the available range of species-specific responses to environmental change (Olden et al., 2004; Angeler and Allen, 2016), thereby affecting the availability of functional groups of species for renewal and reorganisation following disturbance (Elmqvist et al., 2003). The long-term consequences will, in part, depend on the capacity of meiofauna communities to adapt to environmental change.

For example, observed shifts in dominance patterns of meiofauna species in response to anthropogenic climate change resulted from species-specific physiological tolerances to changes in temperature and pH, in combination with shifts in species interactions (see sections 3.3 and 4.1). Existing studies are constrained by the necessity of compressing millennia of exposure into workable laboratory and field studies. Published work has therefore focused on the effects of future climate conditions (especially increased $pCO_2$/decreased pH) on contemporary meiofauna populations in the laboratory, or the exposure of field populations to natural acidification that occurs at $CO_2$ vents, largely ignoring the potential effects of adaptation. As Lee et al. (2017) pointed out, the increase in temperature and reduction in pH will be gradual processes occurring over a period of time that will encompass hundreds of thousands of meiofauna generations. To some extent, multi-generational laboratory experiments enable the investigation of the capacity for adaptation. Inevitably, such experiments rely on meiofauna test species that are easily cultured and maintained, have a rapid and predictable life cycle, and high fecundity. Laboratory experiments reviewed here generally succeeded in capturing an immediate stress response of test organisms, reflected in increased reproductive output followed by decreases in offspring production in future generations. The longer-term consequences of these short-term physiological and metabolic responses, or indeed how these responses are manifested under (future) conditions in the field, are currently unknown.

Meiofauna organisms, and nematodes in particular, are characterised by high phenotypic plasticity (see section 4.1), a process by which one genome can produce different phenotypes in response to variation in the environment (Viney and Diaz, 2012). This allows genotypes to better match their phenotype to the prevailing conditions. This, at least in part, explains the persistence of nematodes in disturbed sediments where other (meio)fauna is absent. Meiofauna, and in particular generalist species, have been, are, and will be adapting to tolerate variations in environmental conditions. We do not yet know under what circumstances, and how rapidly, adaptation will take place in specialist species, and whether adaptation occurs rapidly enough to outpace potential population declines.

## 5. Conclusions and future meiofauna research

Despite the recognised importance of meiofauna in marine ecosystems (Schratzberger and Ingels, 2018), and the ecological and evolutionary success of free-living meiofauna such as nematodes *across* ecosystems (Schratzberger et al., 2019), there are many areas of the world where our knowledge of meiofauna, even in terms of the species living there, is poor. This is particularly true for the polar regions (Vause et al., 2019) and extreme habitats (Sweetman et al., 2017) which have been experiencing rapid rates of regional change. It is imperative that we sharpen our scientific focus so as to examine and better understand how meiofauna species across geographic regions and habitats *respond and adapt* to environmental changes over scales of time and space, and what the ecosystem consequences of these responses and adaptations are likely to be. Existing meiofauna studies are mostly based on statistical relationships between environmental and species distribution data. Physiological limits of species and altered biological interactions are often identified, but not directly tested, as the main factors driving changes of meiofauna distribution patterns under varying regimes of anthropogenic disturbance.

Most meiofauna species lack dispersal stages and are thus assumed to have low dispersal ability and low levels of gene flow between populations. Yet, most species are widely distributed, and this creates a paradox (Giere, 2008; Cerca et al., 2018). Oncholaimid nematodes, for example, often show a surprising capacity to colonise suitable habitat (i.e. disturbed or defaunated areas) rapidly, even to such an extent that passive dispersal alone, or passive dispersal in combination with the presumed limited active dispersal capacities of meiofauna, may no longer explain these colonisation events (Fonsêca-Genevois et al., 2006; Worsaae et al., 2019). Molecular studies with meiofauna suggest that the morphological similarity of many meiofauna species hides high genetic diversity (Todaro et al., 1996; Warwick and Robinson, 2000; Jörger et al., 2012; Kieneke et al., 2012; Derycke et al., 2016). The perceived “meiofauna paradox” is therefore partly an artefact of our incomplete understanding of diversity in meiofauna. Cryptic species may have different environmental preferences and changing environmental conditions can affect the fitness of individual species and the interactions between them (Derycke et al., 2016).

A common assumption behind most of the meiofauna studies considered here is that relationships between the observed patterns of environmental conditions and species distributions will remain unaltered. This assumption is, however, unrealistic especially given future climate conditions (Scheffer et al., 2001). Generally, variation in meiofauna life histories is generated either through the plastic response of a single genotype to environmental conditions (see section 4.1) or through local adaptation of genotypes to specific sets of environmental conditions. In either case, the mechanistic links between the environment and the phenotype that is expressed are complex and often difficult to discern.

Based on the results of our review, future meiofauna research that holds particular promise includes studies aimed at:

- investigating the effects of multiple stressors concurrently over longer time periods and at lower rates of exposure to simulate more realistic scenarios of environmental change;
- understanding the physiological tolerances of meiofauna species to varying types, intensities and frequencies of environmental change;

- obtaining comprehensive estimates of the absolute and relative importance of biotic and abiotic factors affecting the fitness of meiofauna;
- examining the response of different meiofauna taxa, and cryptic species within taxa, to environmental change;
- understanding the genetic basis of biotic interactions and local adaptation/phenotypic plasticity of meiofauna species;
- quantifying the relative energetic and physiological costs of adaptation to abiotic factors (e.g. tolerance to warmer waters) and biotic factors (i.e. tolerance to shifting inter- and intra-specific interactions), and trade-offs between them.

Knowledge on the dependence of meiofauna species on their environment and on other benthic species has been growing. Future studies will be most meaningful if this knowledge is expanded alongside an understanding of the potential of locally adapted species to respond to shifts in environmental conditions. Integrating outcomes from such empirical research into spatial predictive models could undoubtedly improve the reliability of species distribution projections under future disturbance scenarios (Kotta et al., 2019).

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## Authors' contributions

M.S. conceived the research idea and carried out the data collation. M.S and P.J.S. participated in the analysis, interpretation of results, and the writing of the manuscript. Both authors gave final approval for submission.

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**Figure captions**

**Fig. 1.** Number of studies (percentages in parentheses) considered for this review following a Thomson Reuters Web of KnowledgeSM (https://apps.webofknowledge.com/WOS) topic search [TS = ((meiofauna* OR meiobenth* OR nematod* OR harpacticoid*) AND TS = ( (disturb*); Databases = WOS; Timespan = All years; Search language = Auto] on 9 October 2019. The search returned a total of 2,253 articles, 411 of which dealt with meiofauna responses to disturbance. The 411 articles are categorised here by disturbance type. See text for details.

**Fig. 2.** Conceptual diagram depicting the response of different levels of biological organisation (individual, population and community) to anthropogenic disturbance.

**Fig. 3.** Conceptual diagram depicting how physico-chemical- and meiofauna-mediated responses to anthropogenic disturbances affect the integrity of seafloor habitats (see text for details).

**Fig. 4.** Conceptual diagram (adapted from Schratzberger and Ingels, 2018) indicating potential cascading effects of changes in meiofauna activity. POM = particulate organic matter, OM = organic matter, EPS = extracellular polymeric substances, MPB = microphytobenthos. Effects of microbiota and macrofauna on meiofauna are not shown; size of boxes and arrows is not indicative of effect size.

**Table 1**. Effects of bottom fishing on the abiotic and biotic seafloor environment. See text for details.

| Bottom fishing | |
|---|---|
| **Abiotic seafloor environment** | **Biotic seafloor environment** |
| Scraping/scouring of the seafloor | Removal of larger target species |
| 'Flattening' of the seafloor, decreased habitat heterogeneity | Removal and/or increased mortality of (habitat-forming and fragile) non-target species |
| Resuspension of surface sediment | Shifting species distributions |
| Release of previously buried organic matter | Modification of trophic relationships |
| Increased organic loading of sediments (bycatch) | |
| Modification of biogeochemical cycles | |

**Table 2**. Effects of the introduction of invasive species on the abiotic and biotic seafloor environment. See text for details.

| **Introduction of invasive species** | |
|---|---|
| **Abiotic seafloor environment** | **Biotic seafloor environment** |
| Changes in availability of resources (space, food) | Increased/decreased faunal settlement |
| Changes in physical and chemical characteristics of the seafloor | Protection from/exposure to predators, resuspension, environmental conditions |
| Increased/decreased habitat heterogeneity | Shifting species distributions |
| Changes in availability of organic pools derived from and/or trapped by invasive species | Modification of trophic relationships |
| Changes in flow of energy and biomass | |
| Modification of biogeochemical cycles | |

**Table 3**. Effects of anthropogenic climate change on the abiotic and biotic seafloor environment. See text for details.

| Anthropogenic climate change | |
|---|---|
| **Abiotic seafloor environment** | **Biotic seafloor environment** |
| Increased temperature of upper ocean layers | Changes in survival and physiological performance |
| Altered carbon chemistry of seawater, shift towards pH-neutral conditions | Removal/increased mortality of habitat-forming and fragile calcifying species |
| Changes in sediment properties | Shifting species distributions |
| Modification of biogeochemical cycles | Change in life history traits |
| Changes in the availability and quality of organic pools | Modification of trophic relationships |
| Reduction in habitat heterogeneity | |

**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.

Graphical abstract

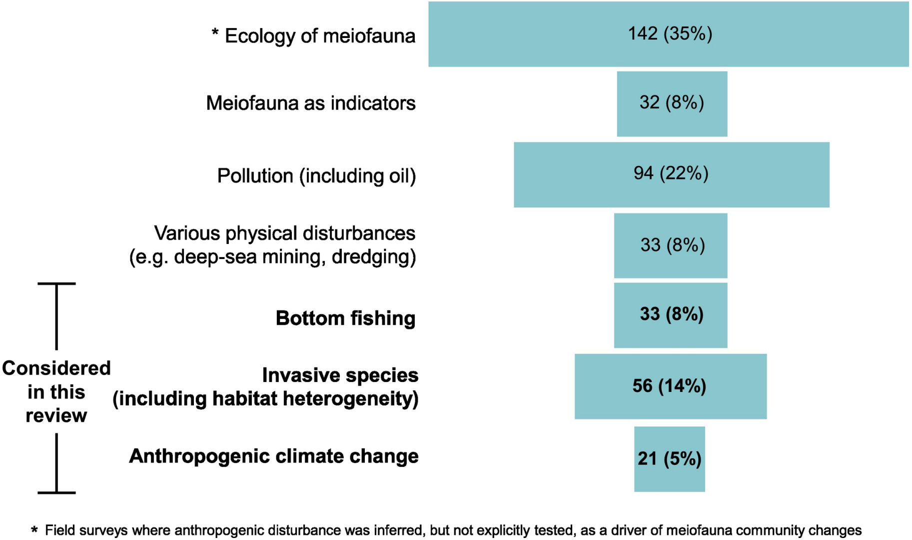
* Ecology of meiofauna
142 (35%)
Meiofauna as indicators
32 (8%)
Pollution (including oil)
94 (22%)
Various physical disturbances (e.g. deep-sea mining, dredging)
33 (8%)
Bottom fishing
33 (8%)
Invasive species (including habitat heterogeneity)
56 (14%)
Anthropogenic climate change
21 (5%)
Considered in this review
* Field surveys where anthropogenic disturbance was inferred, but not explicitly tested, as a driver of meiofauna community changes

Figure 1

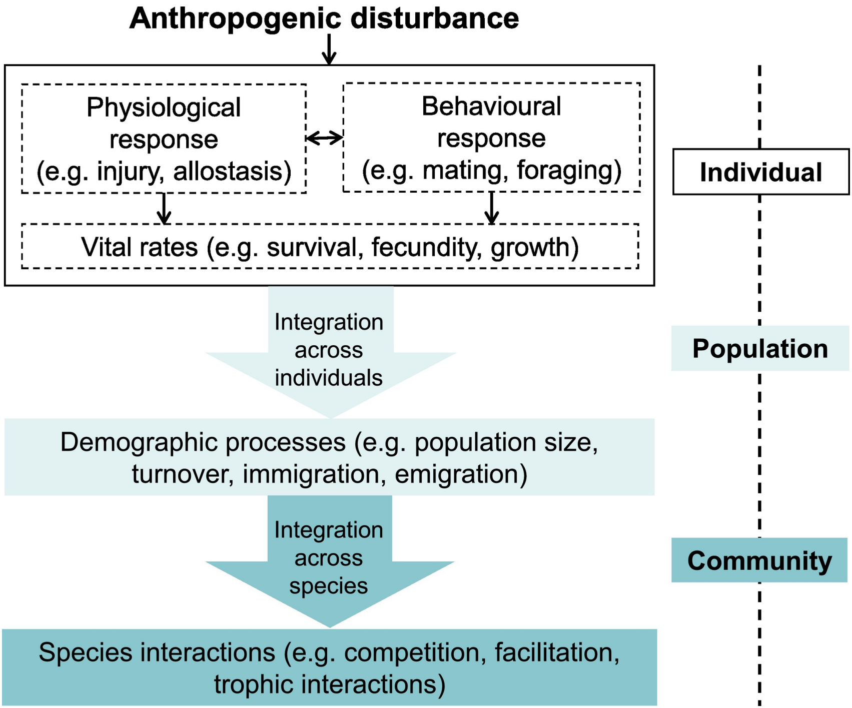
Anthropogenic disturbance
Physiological response (e.g. injury, allostasis)
Behavioural response (e.g. mating, foraging)
Vital rates (e.g. survival, fecundity, growth)
Individual
Integration across individuals
Population
Demographic processes (e.g. population size, turnover, immigration, emigration)
Integration across species
Community
Species interactions (e.g. competition, facilitation, trophic interactions)

Figure 2

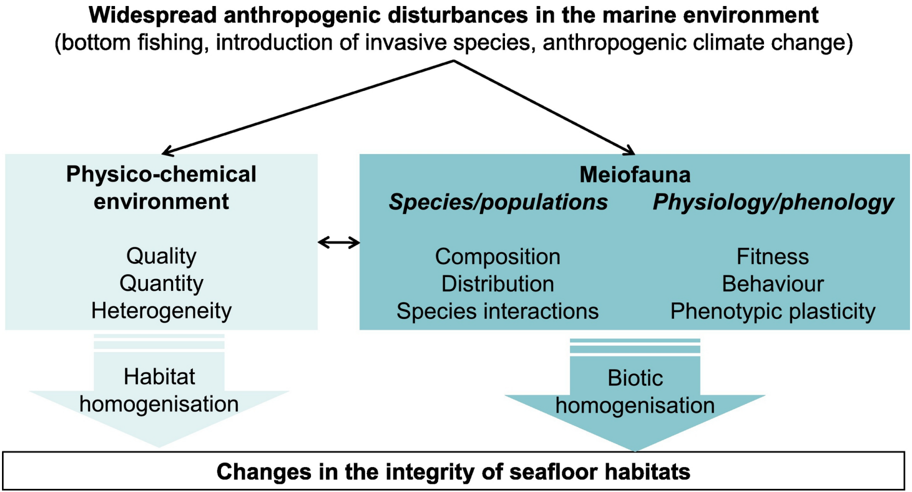
Widespread anthropogenic disturbances in the marine environment
(bottom fishing, introduction of invasive species, anthropogenic climate change)
Physico-chemical environment
Quality
Quantity
Heterogeneity
Meiofauna
Species/populations
Physiology/phenology
Composition
Distribution
Species interactions
Fitness
Behaviour
Phenotypic plasticity
Habitat homogenisation
Biotic homogenisation
Changes in the integrity of seafloor habitats

Figure 3

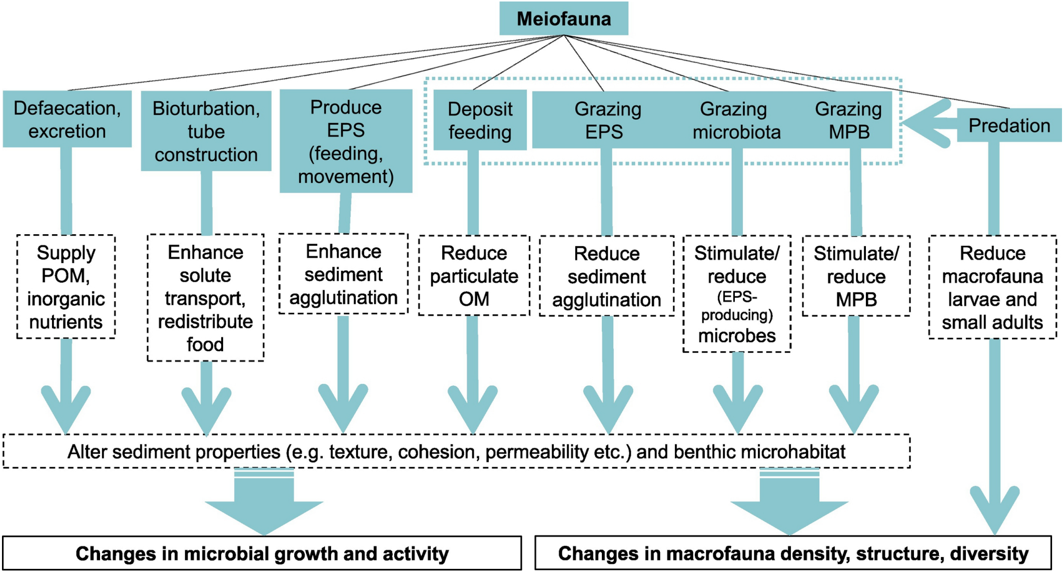
Meiofauna
Defaecation, excretion
Bioturbation, tube construction
Produce EPS (feeding, movement)
Deposit feeding
Grazing EPS
Grazing microbiota
Grazing MPB
Predation
Supply POM, inorganic nutrients
Enhance solute transport, redistribute food
Enhance sediment agglutination
Reduce particulate OM
Reduce sediment agglutination
Stimulate/ reduce (EPS-producing) microbes
Stimulate/ reduce MPB
Reduce macrofauna larvae and small adults
Alter sediment properties (e.g. texture, cohesion, permeability etc.) and benthic microhabitat
Changes in microbial growth and activity
Changes in macrofauna density, structure, diversity

Figure 4