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Meiofauna matters: The roles of meiofauna in benthic ecosystems

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ABSTRACT

Sedimentary habitats cover most of the ocean bottom and therefore constitute the largest single ecosystem on Earth in spatial coverage. The benthic ecosystem contributes to human well-being by providing essential services such as food production and nutrient cycling. Although meiofauna are well-recognised as an abundant and ubiquitous component of benthic communities, empirical evidence of their wider role in marine ecosystems is scattered across the literature. Some ecologists and decision-makers thus remain sceptical about what meiofauna can tell them about the provision of ecosystem services. This article investigates empirical evidence on the roles of meiofauna in benthic ecosystems using a conceptual model that links the supply of an ecosystem service, the ecosystem processes that contribute to that service (e.g. production, consumption and decomposition of organic matter, nutrient regeneration, and energy transfer to higher trophic levels) and the meiofaunal activities (e.g. bioturbation and feeding) that regulate these processes. Meiofauna activities modify a series of physical, chemical and biological sediment properties. They often do so simultaneously by, for example, displacing sediment grains during burrow construction and displacing organic matter and microorganisms within the sediment matrix during feeding. These modifications directly and indirectly, positively and negatively affect various ecosystem services including sediment stabilisation, biochemical cycling, waste removal and food web dynamics, at various spatial and temporal scales. 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 desired by society. This is of growing importance since benthic ecosystems are under increasing anthropogenic pressure. Whilst studies over the past five decades have emphasised the important roles meiofauna play in benthic ecosystems, future studies will need to determine how consistent and widespread these roles are.

1. Looking closer at a miniature world

Marine sediments are, by surface, the largest habitat on Earth. A wide diversity of organisms inhabits these sediments that by their actions mediate many ecosystem processes (Snelgrove, 1997, 1999). Several of these processes, such as the reworking of sediments, the recycling of nutrients, food web dynamics, the degradation and distribution of pollutants, and the decomposition, mineralisation, burial and storage of organic matter are important on a global scale and are essential to sustain life on Earth. These processes are maintained and shaped by intra- and interspecific interactions as well as the interplay between organisms and their physical and chemical environment (Giere, 2009).

Society obtains great benefits from benthic ecosystems in the form of provisioning (e.g. food, biotic materials and biofuels), regulating and maintenance (e.g. nutrient cycling and waste processing), and enriching (e.g. recreation and tourism) services, all of which are provided on multiple scales and at no charge to society. The protection of ecosystem services (i.e. the direct and indirect contributions of ecosystems to human well-being) forms an important part of current environmental management practice, designed to ensure ecosystem services are conserved for human benefit (TEEB, 2010). Ecosystem services are ecological in nature and are delivered by the living components of the ecosystem (Boyd and Banzhaf, 2007). The number and composition of species influence ecosystem processes in concert with the effects of climate and disturbance regimes. Human activities can modify these factors. It is now widely acknowledged that degradation of marine sediments which harbour the organisms essential to benthic ecosystem processes will in turn degrade a range of ecosystem services (Hooper et al., 2005).

Although ecosystem services are properties of whole ecosystems or communities, the processes that support them often depend on particular populations, species, species guilds or habitat types (Prather et al., 2013). Of the studies that have explicitly tested the effects of species on benthic ecosystem processes, relatively few have attempted to reconcile the role of those species which, for the most part, are invisible

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to the naked eye, yet which are crucial elements of the biosphere (Sheppard, 2006; Schratzberger, 2012). Meiofauna, a discrete group of small-sized organisms (<1 mm) whose morphology, physiology and life history characteristics have evolved to exploit a range of terrestrial and aquatic environments, occur in often high abundance and diversity in soils and sediments worldwide. They are the most phyletically diverse fauna on Earth. Some meiofauna species are ancestrally miniature and were most likely involved in the earliest stages of the diversification of metazoan life. Others have secondarily evolved miniature morphologies from macroscopic ancestors (Rundell and Leander, 2010; Laumer et al., 2015). The microscopic size reflects the evolutionary benefit these organisms have that enables them to survive and thrive in interstitial space. Conversely, the larger macrofauna more often exhibit a lifestyle whereby they rely on sediment displacement or burrowing. The highly conservative bimodal body size pattern within the benthos is postulated to result from the evolutionary optimisation of functional traits such as body size, with intermediate traits being either impossible or non-viable. Body size bimodalism may, however, be modified by local ecological constraints and disturbances (Warwick, 2014).

There is considerable debate as to whether high meiofauna abundance and diversity translate into a significant effect on ecosystem processes. Meiofauna biomass is low compared to other benthic components and meiofaunal contributions to ecosystem processes will therefore be, at least partially, dependent on their biomass turn-over and activity (Moens et al., 2013). This article investigates empirical evidence on the roles of meiofauna in benthic ecosystem processes and in particular those processes that underpin ecosystem services. The primary motivation is to define the current state of scientific knowledge, to provide useful information for scientists and environmental managers, and to identify critical gaps to be filled by future research. To that aim, the following questions are addressed:

1) What is the contribution of meiofauna to fundamental ecosystem processes that operate within benthic ecosystems? This question focuses on how ecosystem processes are affected by the presence of meiofauna in order to clarify their trophic position and roles in benthic ecosystems.

2) How do meiofauna-mediated effects on sedimentary, trophic and ecological processes modulate the delivery of ecosystem services? The focus here lies on how meiofaunal activities (e.g. bioturbation and feeding) regulate those ecosystem processes that underpin outcomes that humans find useful.

3) How can scientists best incorporate what is known about the roles of meiofauna in benthic ecosystems into evidence supporting environmental management and policy? This includes some suggestions of how meiobenthologists can feed relevant information into decision-making.

Findings are synthesised in a systematic way, using a simple conceptual framework that links natural systems with socio-economic systems via the flow of ecosystem services (adapted from Haines-Young and Potschin, 2010; Liquete et al., 2013; Maes et al., 2016). This is the first attempt that places meiofauna contributions to ecosystem processes into a socio-economic ecosystem services framework. The flow of ecosystem services may be translated into specific societal benefits and values (Fig. 1). Whether a particular process is regarded as a service or not depends upon whether it is considered as a benefit (De Groot et al., 2010). Society will value a particular process differently in different places at different times. Therefore, all fundamental ecosystem processes that operate within benthic ecosystems (including processes that humans find useful) are included here to determine the role of meiofaunal organisms within those systems (Jax, 2005). The adapted model in Fig. 1 distinguishes between the supply of an ecosystem service (e.g. sediment stability and nutrient cycling), the ecosystem processes that contribute to that service (e.g. a range of sedimentary, trophic and ecological processes) and the meiofaunal activities (e.g. bioturbation and feeding) that regulate these processes (De Groot, 2006).

By virtue of their dominance in marine sediments, universality and robust bodies, nematodes and harpacticoid copepods are the most frequently studied components of the meiofauna. Various taxonomic keys for the identification of nematode and harpacticoid copepods have been published, further stimulating interest in these two groups (Schratzberger et al., 2000). Consequently, the great majority of meiofauna articles published in the peer-reviewed scientific literature to date deals with either nematodes or harpacticoid copepods which adds inevitable bias to this review.

2. Biological activities of meiofauna and their effects on benthic ecosystems - a pre-21st century perspective

Meiofauna carry out a range of biological activities. These include moving through or along the sediment (Cullen, 1973), active sediment particle reworking as a result of burrowing, construction and maintenance of burrows and ingestion and defecation of particles (bioturbation sensu Kristensen et al., 2012), and excretion of metabolic wastes. Meiofauna, and nematodes in particular, produce sticky mucus which serves for attachment to the sediment for eggs and to stabilise burrows (Riemann and Schrage, 1978). Reviews published between 1970 and 2000 suggest that these activities are pivotal in shaping benthic ecosystems in shallow-water and deep sea environments.

Many meiobenthic species construct microscale burrows in sandy and muddy sediments where the sediment particles are bound together by extracellular polymeric substances (EPS) secreted by the organisms

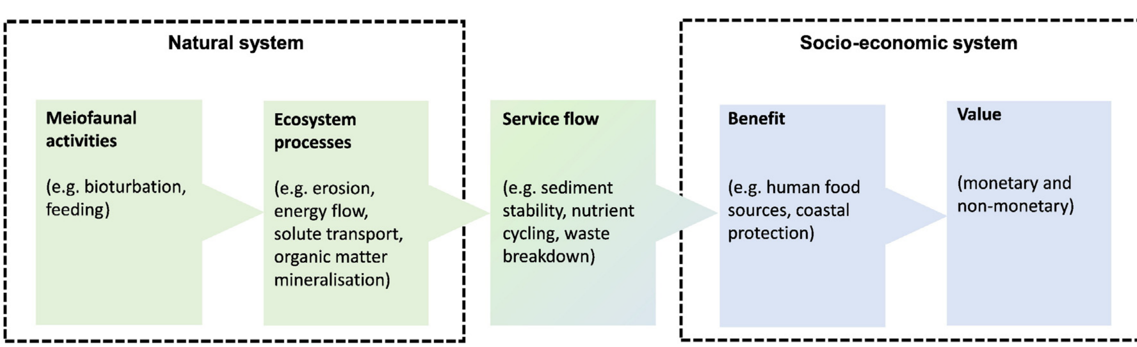

Fig. 1. Conceptual model linking the supply of an ecosystem service (e.g. sediment stability, nutrient cycling), the ecosystem processes that contribute to that service (e.g. sedimentary, trophic and ecological processes) and the meiofaunal activities (e.g. bioturbation and feeding) that regulate those processes (adapted from Haines-Young and Potschin, 2010; Liquete et al., 2013; Maes et al., 2016).

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