

5. The structure and functional roles of tidal flat meiobenthos

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Abstract

Meiofauna comprise the smallest multicellular and largest unicellular metazoans in benthic food webs. They are highly abundant and species-rich, yet essential aspects of the factors driving their community structure and abundance remain poorly understood. Similarly, their functional roles in benthic carbon cycling remain poorly characterized and even more poorly quantified. In the frame of two projects, we addressed questions regarding both the biotic and abiotic factors that drive meiobenthic assemblage structure, and their roles in benthic carbon cycling. Our research involved an intricate combination of manipulative laboratory experiments and field work, the latter mostly focusing on the intertidal flats bordering the Paulina salt marsh in the Scheldt estuary.

The results add considerably to our understanding of the factors that drive meiobenthic assemblage structure. They clearly demonstrate that biotic interactions among different meiofauna, and between meio- and macrofauna, are extremely important and moderate the impacts of prominent abiotic drivers of assemblage structure such as granulometry and oxygen availability.

From a functional point of view, we demonstrated that tidal flat meiofauna rely predominantly on carbon derived from *in situ* primary production by microphytobenthos. Quantification of grazing rates of meiofauna on microphytobenthos and benthic bacteria does not, however, point at an important direct contribution of meiofauna to benthic carbon cycling. The role of meiobenthic species diversity remains to be established, but laboratory experiments into the role of nematodes in OM decomposition reveal that in addition to species identity, species diversity does have a significant, yet largely unpredictable effect on OM decomposition rates.

i. Problem

The past two decades have witnessed an explosive increase in research efforts devoted to the relationship between biological diversity and ecosystem functioning (Loreau et al., 2001, Hooper et al. 2005). A majority of studies have focused on terrestrial systems and on the relationship between plant species diversity and primary productivity. Estuaries, however, are ecosystems

which provide an array of ‘functions’ or ‘services’ of great importance and economic value to men. Further, in addition to offering food, shelter etc... to impressive numbers of animals and they often present natural gradients of animal diversity (Kaiser et al., 2005). Whether and how both these high abundances and varying diversity levels affect key ecosystem functions in estuaries remains largely unknown.

In terms of density and species diversity, the meiofauna (multicellular and unicellular organisms in the size range between 100 μm and a few mm) are prominent members of sediment communities in all marine and estuarine soft sediments (Heip et al., 1985) (Fig. E-5.1).



Fig. E-5.1: Picture of meiobenthos elutriated from a small tidal flat sediment subsample, showing nematodes, harpacticoid copepods, polychaetes (large) and a turbellarian.

The combination of small body size, comparatively short life cycle and limited active mobility, disabling them from escaping local impacts on sediments, renders them highly interesting instruments for biomonitoring of marine sedimentary environments (Bongers and Ferris, 1999, Schratzberger et al., 2000). Their very high abundances (usually $> 10^6$ individuals m^{-2}) and suspected high metabolic activity per unit body weight, raise questions on their importance in carbon and nutrient fluxes in estuarine sediments (Heip et al., 1985). Moreover, their high species diversity at local scales (usually several tens of species in every m^2 of sediment) provides a challenging research model for the study of how species diversity is structured and how it contributes to ecosystem functioning (De Mesel et al., 2006).

Although field studies have shown consistent patterns in meiofaunal assemblage composition, we still lack an understanding of how these patterns are established. More importantly, their actual roles in benthic carbon cycling remain poorly understood and even more poorly quantified.

Meiofauna as a group are generally considered microbial feeders and/or grazers of microalgae; hence, they are likely involved in detritus decomposition and may affect primary production. Since meiofauna are also food to higher animals such as hyperbenthic crustaceans and fish, their importance in channeling carbon and energy from basal to higher trophic levels remains to be established (Gee, 1989). Hence, it is currently hard to describe exactly whether and how a square meter of sediment comprising a million meiofaunal individuals and tens of species function differently from a hypothetical identical sediment completely devoid of meiofauna.

ii. Aims

The aims of the projects were twofold:

- 1) To elucidate the importance of selected environmental drivers for the structure and activity of meiofaunal communities. We have chosen to focus on a combination of sediment granulometry, organic matter/food availability and sediment oxygenation. These parameters have shown to exert major impacts on benthic fauna in different systems (Heip et al., 1985). They are often subject to fluctuations of anthropogenic origin and they are strongly interrelated. We have further tried to emphasize the role of macrofauna, which, through their burrowing activities, affect sediment oxygenation, while at the same time they may cause meiofaunal mortality through both physical disturbance and direct predation (Olafsson, 2003).
- 2) To further increase our understanding on the functional roles of meiofauna in benthic metabolism and how these roles relate to taxonomic identity and/or species diversity.

The first goal has been addressed mainly during the first project: Food, oxygen and bioturbation: an experimental study of the structure of meiofaunal communities. Whereas the second goal formed the core of the second project: Functional role of nematodes and foraminifera in benthic metabolism' and derived projects.

The results are based on an intricate interplay between manipulative laboratory experiments and field studies, including an in situ disturbance and recolonization experiment, in the Scheldt estuary during the years 2002 till 2007 (Fig. E-5.2).

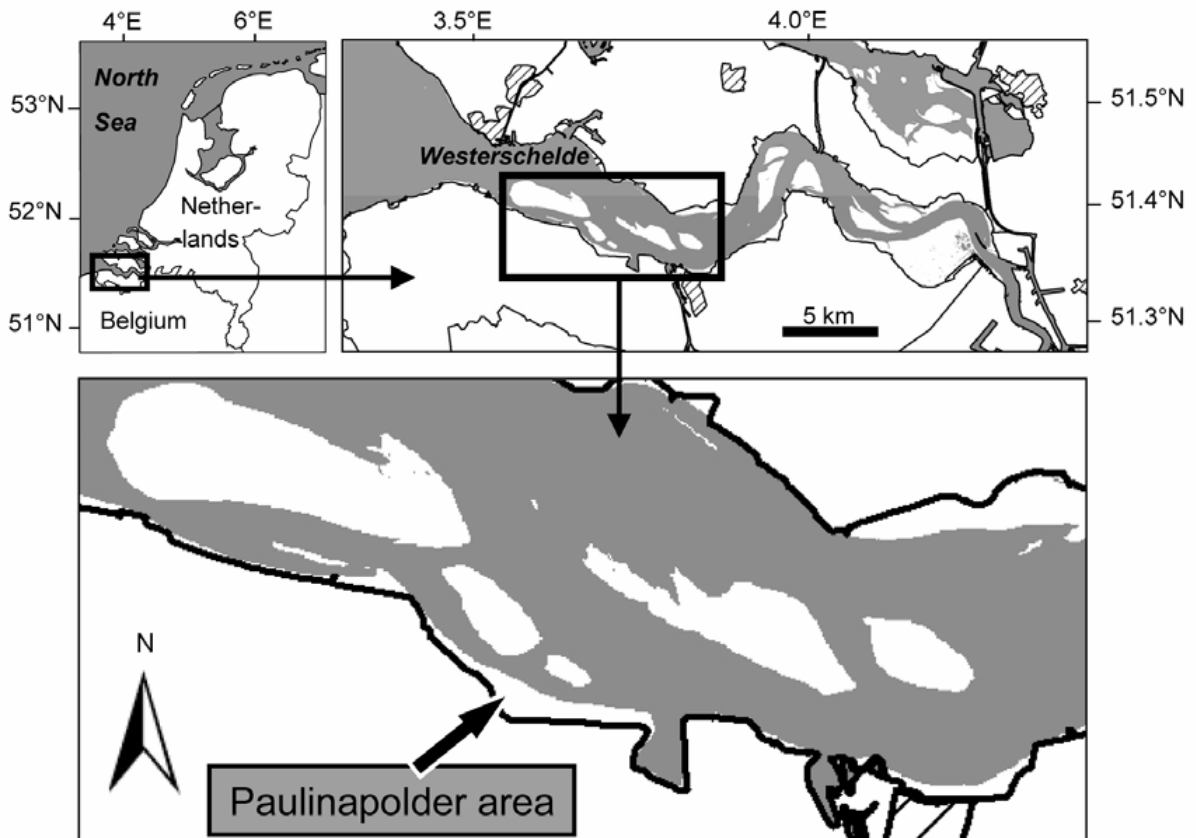


Fig. E-5.2: Map of the Scheldt Estuary with indication of the Paulinapolder salt marsh and intertidal flat area where most of the field work described in this paper was performed and where most live organisms for lab experiments were collected.

iii. Results

Project I – Although a considerable body of literature points at the importance of sediment granulometry as the main structuring factor for meiofaunal communities, with oxygenation and organic matter loading as derived factors. However, the results of the project paint a more complex picture in which biological interactions strongly modify these abiotic sedimentary impacts. This is illustrated by the comparison of the vertical profiles of nematode assemblages in sediments with contrasting granulometry. The main differences in nematode assemblages between these sediments are found in the upper 2 cm, while assemblages in deeper layers exhibit substantial similarity (Steyaert et al., 2003). In fine-grained but silt-poor sediments, the upper 2 cm are often characterized by a high prominence of nematodes predacious on other nematodes. Both in terms of biomass and abundance, other nematodes in this sediment horizon are often low, much lower than in nearby silty sediments (Steyaert et al., 2001, 2003). Manipulative laboratory experiments and correlative studies based on field samples clearly indicate that the prey nematode assemblages in this surficial sediment stratum are primarily governed by top-down control in which predation controls prey abundance, species composition and perhaps diversity (Moens et al., 2000, Gallucci et al., 2005). Interestingly, prominent species in deeper sediment strata are often the same as in surface layers of nearby silty sediments. A logical explanation for the segregation between a surface- and a deeper-living assemblage in silt-poor sediments would

be that the predatory nematodes are more susceptible to oxygen stress than most of their prey, but this was not confirmed by our lab experiments (Steyaert et al., 2005). We did observe that even minor differences in sediment texture – in particular silt content – and sediment water content (during low-tide exposure on intertidal flats) profoundly impact the predation success of the predatory nematodes: even small amounts of silt create extra refuges for prey and greatly reduce predation rate, which corresponds very well with the in situ distribution pattern of the dominant predatory species (Gallucci et al., 2005) (Fig. E-5.3).

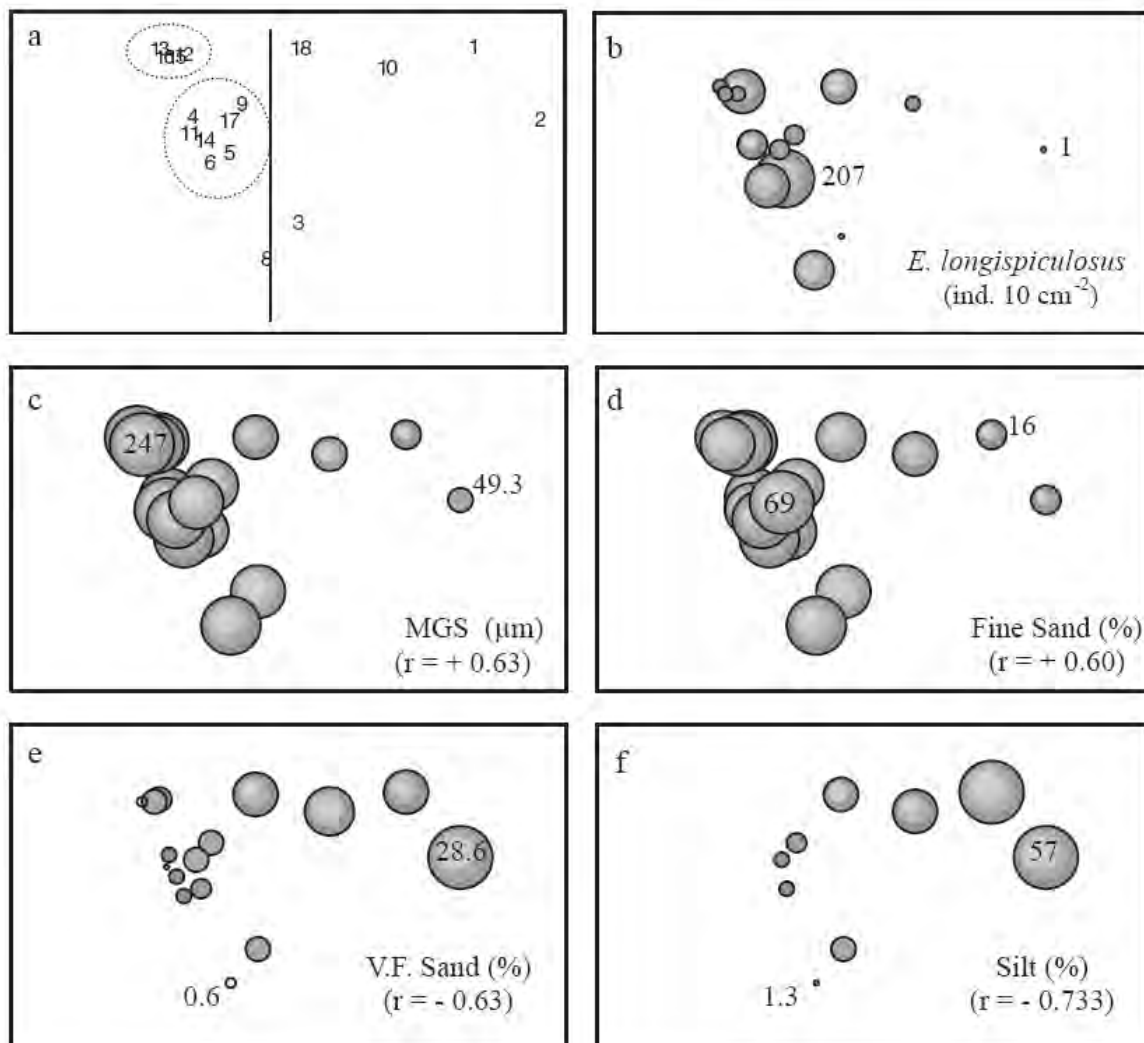


Fig. E-5.3: Bubble plot of the abundances of *Enoploides longispiculosus*, a dominant predatory nematode, in 18 stations on the Paulina tidal flat in the Schelde Estuary (b). The data are superimposed on an ordination (PCA) of these same stations based on sediment characteristics (a). Figures (c) - (f) plot mean grain size (MGS), % fine sand (125-250 µm), % very fine sand (63-125 µm) and % silt (< 63 µm) of the 18 stations. The figures clearly show a strong positive correlation between *Enoploides* abundance, MGS and proportion of fine sand, and a negative correlation between *Enoploides* abundance and the proportions of very fine sand and silt. Figure taken from *Marine Ecology Progress Series* 134, p. 172.

Similarly, drying of surficial sediment during low-tide exposure immobilizes predators, reducing the prey's risk of being caught (Gallucci et al., 2005). This corresponds remarkably well with observations of tide-induced vertical migrations of different nematode species: as the tide moves

out, predatory nematodes tend to burrow deeper to avoid the dryer surface sediment, while several prey species do exactly the opposite, allowing them to feed on the diatom biofilms at the sediment surface (Steyaert et al., 2001). The general net effect, nevertheless, is still such that prey abundances in surface layers remain low (Gallucci et al., 2005). Interestingly, none of the above factors explain the absence of predatory nematodes beneath a depth of 2 cm. Pressure plate experiments suggest that the higher sediment compaction in deeper layers is the main reason for this, as it reduces the available pore space in which predators can forage (Steyaert et al., unpubl.). While mainly of fundamental interest, these results are highly relevant to understand seasonal changes in meiofaunal communities, since intertidal sediments in estuaries are often subject to seasonal siltation-desiltation cycles (Herman et al., 2001). They also have implications for the consequences of any anthropogenic actions that may alter – even to a small extent – the granulometry of intertidal sediments. Since other studies have suggested that the larger predatory nematodes in turn are more susceptible to predation by hyperbenthic predators such as shrimps and fish (Hamerlynck and Vanreusel, 1993), and since predatory nematodes also impact on the microbial loop in sediments through predation on ciliates (which in turn feed on diatoms and bacteria) (Hamels et al., 2001), the current findings may have important implications.

While interactions among meiofaunal species thus appear important in determining meiofaunal assemblage structure, this certainly also holds for interactions between meio- and macrobenthos. This was illustrated by an *in situ* defaunation experiment at the Paulinapolder tidal flat (Fig. E-5.2) in which silty sediment plots were defaunated by induced hypoxia, and their recolonization followed over a period of 3 years in comparison to neighbouring control spots. The induced hypoxia completely eliminated macrobenthos but not nematodes, several species of which survived, albeit at low abundance (Van Colen et al., 2009). Recovery after hypoxia – even after 3 years – did not result in assemblages identical to those in the surrounding sediments for either meio- or macrobenthos (Van Colen et al., 2008, 2009, 2010). The nematode assemblage changed mainly as a function of microphytobenthos and of abiotic factors such as sediment ammonium content. Both microphytobenthos biomass and several sediment abiotic factors in turn were profoundly affected by the activity of, and changes in, the macrofauna communities which recolonized the disturbed plots. Bioturbation and grazing by macrofauna affect microphytobenthos abundance and sediment accretion (Montserrat et al., 2008, Van Colen et al., 2008), while bio-irrigation impacts nitrification/denitrification processes (D’Andrea and DeWitt, 2009). Hence, the recovering macrobenthos drives the ecosystem changes which in turn control the evolution of the nematode community (Van Colen et al., 2009).

We had rather expected a direct impact of macrobenthos on meiofauna as a result of the deeper oxygen penetration caused by bio-irrigation. We performed several lab experiments in which bio-irrigation of macrofauna was mimicked by flushing artificial tubes with oxygen. These experiments revealed clear species-specific effects on the location and activity of meiofauna (Steyaert et al., 2005). Additional lab experiments documented species-specific survival and recovery rates of nematodes during and after induced hypoxia or anoxia (Steyaert et al., 2007). Even so, the above field experiment illustrates that oxygen in itself is not the sole or even the principal driver of community changes during recovery from hypoxia. Rather, an intricate combination of biological interactions and abiotic drivers, including oxygen, is responsible for the observed structural changes in nematode communities.

Project II – In order to further increase our understanding on the roles and importance of meiofauna in benthic carbon fluxes, an improved insight into their trophodynamics, feeding selectivity and metabolic activity is required. We investigated the relative contributions of different carbon inputs to the diet of nematodes on intertidal flats using stable isotopes. Tidal flats receive a variety of inputs with different quality and palatability (e.g., detritus and algae). The carbon and nitrogen isotopic signatures of these sources often differ. Since isotopic signatures of consumers closely resemble those of their food, natural isotope abundances are good trophic tracers. Using this approach, we demonstrated that nematode assemblages of bare intertidal flats rely predominantly on microphytobenthos-derived carbon. In sediments of salt marshes, which act as traps of suspended particulate (organic) matter and to a lesser extent in bare silty tidal flat sediments, settled phytoplankton also contributes to the diet of nematodes (Moens et al., 2002, 2005). For many nematode species, microphytobenthos carbon uptake is indirect and involves predation on a herbivore which grazes microphytobenthos (Moens et al., 2005) (Fig. E-5.4).

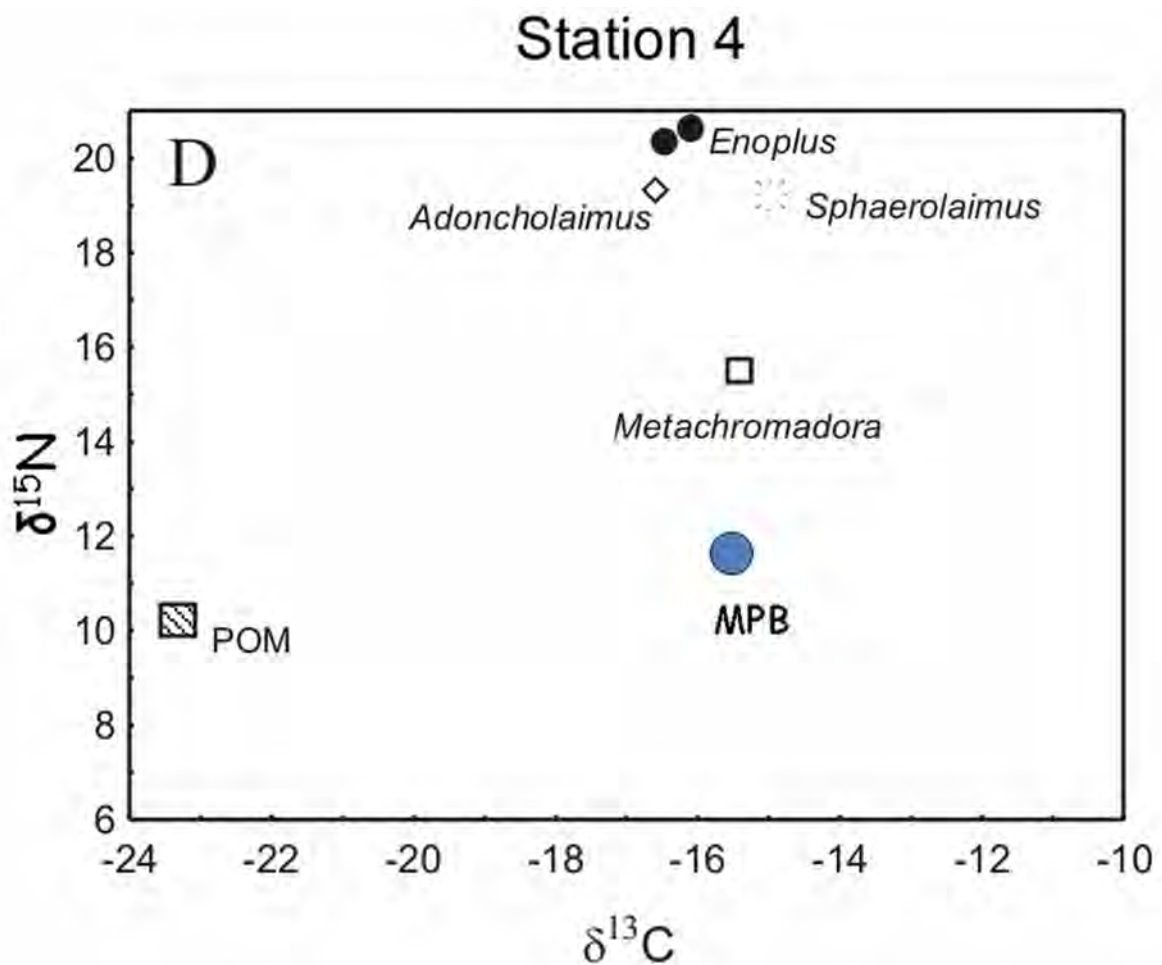


Fig. E-5.4: Plot of the stable carbon and nitrogen isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of 4 nematode genera and of microphytobenthos (MPB) and suspended particulate organic matter (POM) at a station on the Paulina tidal flat (Schelde Estuary). The high similarity in $\delta^{13}\text{C}$ between MPB and all nematode genera demonstrates that MPB is the predominant carbon source for nematodes on this tidal flat. The offsets between $\delta^{15}\text{N}$ of MPB, *Metachromadora* and other nematode genera illustrates that MPB feeds directly on MPB, while the other nematode genera are predators of herbivores such as *Metachromadora*. Figure redrawn after *Journal of the Marine Biological Association of the United Kingdom* 85, p. 143.

This again illustrates the importance of predation on other meio- and microfauna as a feeding strategy in a variety of nematodes. We further substantiated the link between microphytobenthos (mainly diatoms) and meiobenthos in several tracer experiments in which ^{13}C -labeled diatoms were offered as food, or in which diatoms were labeled *in situ* with ^{13}C and the fate of the freshly produced diatom carbon into different consumers was followed.

In spite of the importance of diatom carbon to the diet of nematodes, harpacticoid copepods and foraminiferans, none of these meiofaunal groups grazed a significant part of the MPB primary production (Moens et al., 2002, Van Oevelen et al., 2006b). Similarly, while up to 40 % of the carbon requirements of nematodes could be met by their grazing on bacteria, this grazing removed only a marginal portion of the bacterial secondary production (Van Oevelen et al., 2006a). Hence, the direct contribution of meiobenthos to carbon cycling on intertidal flats is probably very small. In addition, our work also revealed that inputs of detrital carbon fuel a major share of bacterial production on intertidal flats. Less than 10 % of this microbial secondary production is consumed and transferred up the food chain, leaving the majority of the bacterial carbon production as a trophic dead end (Van Oevelen et al., 2006b).

In relation to the goals of first project, we also investigated the effects of hypoxia on carbon consumption by meio- and macrobenthos. Since meiobenthos exhibit much better survival under hypoxia than macrobenthos, we hypothesized that meiobenthos could perhaps partly take over the role of macrobenthos in benthic carbon cycling under low-oxygen conditions. However, our results demonstrated that while many nematodes survived episodes of hypoxia, their metabolic activity during hypoxia was severely depressed (Moodley et al., unpubl.).

The two projects also provided the facilities and the impetus for expanding tools and methods to study trophic relations and dynamics in meiofauna. The above-mentioned studies were among the first in which the relative importance of different carbon sources to the diet of meiofauna was studied at genus or even species level, thanks to proper adaptation of existing protocols for larger organisms to the small-sized metazoans. Further, we developed a novel respiration chamber for highly sensitive measurements of oxygen consumption in meiofauna (Moodley et al., 2008). We applied this method to selected species of nematodes, foraminiferans, ostracods and a gastropod. The results demonstrated similar biomass-specific oxygen consumption rates across taxa, averaging 1.5 to $2.5 \mu\text{mol O}_2\text{h}^{-1}\text{mg}^{-1}\text{C}$ (Moodley et al., 2008). We also pioneered the use of fatty acid profiles as trophic tracers in meiobenthos, where they provide a complementary method to stable isotope signatures to elucidate the importance of different food sources. We applied both approaches (stable isotopes and fatty acids analyses) to two nematode species, two harpacticoid copepods, a foraminiferan and an ostracod from a muddy tidal flat in the Oosterschelde. The results again highlighted the importance of microphytobenthos as a carbon source for most tidal flat meiofauna. One nematode species and one harpacticoid species clearly relied on chemosynthetic bacteria as food (Moodley et al., unpubl.). That chemoautotrophic prokaryotes are food to some meiobenthos had previously only been documented from deep-sea hydrocarbon seeps (Van Gaever et al., 2006) and from mangrove sediments (Moens et al., unpubl.).

Finally, we also performed closed microcosm experiments into the role of bacterial-feeding nematodes in organic matter decomposition. We found that nematodes can both stimulate and slow down decomposition rates through their interactions with bacteria, but the underlying mechanisms have only partly been elucidated (De Mesel et al., 2003, 2004). Even very closely related nematode species may differentially affect decomposition, and strongly interact – often in

an inhibitory way – with each other. As a result, while we were able to demonstrate highly significant effects of species diversity and identity on decomposition rates, the diversity effect was largely unpredictable (De Mesel et al., 2006).

iv. Conclusions

The results of the Vlanezo projects add considerably to our understanding of the factors that drive meiobenthic assemblage structure. They clearly demonstrate that biotic interactions among different meiofauna, and between meio- and macrofauna, are extremely important and moderate the impacts of prominent abiotic drivers of assemblage structure such as granulometry and oxygen availability.

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