Macrobenthos structuring the sea floor: importance of its functional biodiversity for the benthic ecosystem

Braeckman Ulrike

Research Group Marine Biology, Biology Department, Ghent University, Krijgslaan 281, S8,
B-9000 Ghent, Belgium
E-mail: Ulrike.braeckman@ugent.be

The wealth of organisms and the accessibility of coastal zones have increasingly triggered exploitation of our seas in the last 150-300 years. Direct human impacts such as overfishing and associated habitat destruction, and indirect anthropogenic impacts such as sea temperature rise, eutrophication-driven or global warming-induced anoxia and the introduction of invasive species have pushed coastal ecosystems far from their historical baseline of rich, diverse, and productive ecosystems. As such, biodiversity loss can lead to a decline in ecosystem functioning, though this is often mediated through a loss in *functional* diversity (i.e. feeding and locomotion modes and biological traits such as longevity and body size).

Coastal systems are very important sites for organic matter (OM) cycling where, despite their small areal extent of about 10% of the global sea surface, about 80% of global marine benthic OM mineralisation occurs. Thus, a loss in ecosystem functioning in these areas can have important consequences at the global scale. In shallow seas like the North Sea, the main source of OM is the seasonal phytoplankton bloom. Owing to the shallowness of coastal seas, and their often mixed water columns, bentho-pelagic coupling is often tight in these systems and the benthic realm of depositional areas is therefore important in the mineralisation of the primary produced OM.
Bioturbation (solid transport) and bio-irrigation (solute transport) by macrobenthos (sediment inhabiting organisms > 1mm) play an important role in the cycling of this OM. This is because macrobenthic burial reallocates fresh detritus to the deeper, anoxic horizons of the sediment where mineralisation is retarded, delaying nutrient release to the water column, hence influencing primary production. At the same time, macrobenthic irrigation flushes the sediment with oxygen-rich water, removes toxic metabolites and stimulates denitrification, a nitrogen-eutrophication counteracting mineralisation process. These activities are crucial in OM cycling, but also provide favourable niches to other infauna, such as meiofauna (organisms between 38µm and 1mm) and bacteria.

In the Belgian part of the North Sea, the area of focus of this PhD thesis, multiple stressors act on the benthic ecosystem (*cf. supra*). As such, assessing the importance of macrofaunal density and functional identity for benthic ecosystem functioning is of paramount importance. Benthic ecosystem functioning covers amongst others, carbon and nitrogen cycling and maintenance of benthic biodiversity. These processes are outlined in **Chapter 1**, along with a description of the study site and the model organisms. Three model organisms were chosen for this study, each displaying a specific functional bioturbation/bio-irrigation behaviour: *Abra alba* (Bivalvia - Semelidae), *Lanice conchilega* (Polychaeta - Terebellidae) and *Nephtys hombergii* (Polychaeta - Nephtyidae).

In **Chapter 2**, a microcosm approach is applied to investigate the role of the three model organisms displaying functionally different traits in OM mineralisation and bioturbation. The three species were incubated in single species treatments in microcosms containing defaunated fine sandy sediment. Three density treatments of the model organisms were incorporated in the experimental design (natural, lower and a very low density). The functionally different traits in the experiments appeared to give rise to specific biogeochemical environments: whereas *Abra alba* displayed a substantial biodiffusive sediment reworking, the burrowing behaviour of *Nephtys* sp. was minimal. In contrast, the bio-irrigating activities of *Lanice conchilega* were important for oxygenation of the subsurface sediment layers. This oxygenation was linked to the stimulation of mineralisation processes such as nutrient release and denitrification by a factor 2 compared to defaunated controls. Densities of *Abra alba* appeared important in bioturbation potential, hence OM burial, whereas high *Lanice conchilega* densities sustained denitrification. These species can therefore be classified as allogenic ecosystem engineers. As such, both bioturbation and bio-irrigation, hence functional diversity, are of vital importance for ecosystem functioning in fine sandy sediments receiving high loadings of organic matter. A decrease in density of bioturbators entails a decrease in OM burial, whereas a concomitant decrease in bio-irrigators implies a decline in sediment oxygenation and denitrification, an important nitrogen-eutrophication-counteracting process in shallow coastal seas.

Establishment of enhanced biogeochemical processes such as oxygenation and removal of toxic metabolites as observed in Chapter 2, promotes co-habiting infauna, but studies on a detailed taxonomic level and high spatial resolution are very scarce. In **Chapter 3**, therefore the effect of macrofauna with functionally different bioturbation traits on the distribution and diversity of smaller infauna as nematodes, was investigated. The three model species were introduced in microcosms containing fine sandy sediment, however this time inhabited by the natural nematode population. Nematode survival was especially enhanced in bio-irrigated sediments as opposed to bioturbated and control sediments. Mainly non-selective deposit feeding and epistratum feeding nematodes responded to the presence of macrofauna, and the effect on these nematodes was most pronounced in sediments irrigated by *Lanice conchilega*. Along the length of the tube, increased densities and diversity were observed. In sediments reworked by *Abra alba*, mainly subsurface peaks in density were noted and nematodes clearly avoided the surface layer that is constantly cleared by the bivalve's siphons. These patterns demonstrate the ecosystem engineering capacities by *Abra alba* and *Lanice conchilega*. Apart from the sheltering effect of the tubes or shells (autogenic ecosystem engineering), bioturbation and bio-irrigation create specific biogeochemical niches through oxygenation, metabolite removal and probably stimulation of bacteria in the mucous tube linings and faecal pellets (allogenic ecosystem engineering).

Yet, the question whether the positive effects of bioturbation and bio-irrigation on nematodes were linked to oxygenation, to food supply or to both remained unresolved. In **Chapter 4**, we explored the nematode feeding dynamics after a simulated food pulse in both biologically mixed and physically mixed sediments. Indirect, facilitative actions go along with negative, direct actions such as disturbance, predation and competition in biologically mixed sediments, while physically mixed sediments are, apart from disturbance, free of direct interactions. A ^{13}C labelled diatom was added to microcosms containing single species treatments of the bioturbator *Abra alba* or the bio-irrigator *Lanice conchilega*, to control microcosms and to a treatment in which the upper 2cm was regularly mixed manually. On the one hand, positive effects of macrofauna were expected through their mixing of diatoms into the sediment and concomitant increased food accessibility for nematodes. On the other hand, negative structuring effects of macrofauna were surmised, through competition, predation and disturbance. Nematode survival and subsurface peaks in nematode density profiles appeared again most pronounced in the bio-irrigator treatment. Nematode specific uptake of the added diatoms was highest in absence of macrobenthos and where the diatoms were homogenised in the sediment. This could be related to enhanced accessibility in the physically mixed sediments (dilution over upper 2cm). However, fresh diatoms revealed to represent only a limited food source for nematodes and therefore the macrobenthic effect consisted essentially of *facilitating nematodes through niche creation*.

Chapter 5 explores the functional role of the selected macrobenthic species in terms of bentho-pelagic coupling. Benthic and pelagic food sources on the one hand and macrobenthic model organisms as consumers on the other hand were sampled from early spring till autumn. Fatty acid biomarkers were applied as tracers for the assimilation of food sources. The diet of *Lanice conchilega* was characterised by bacteria and diatoms, while that of *Nephtys hombergii* also showed diatoms, but more dinoflagellates and invertebrates as prominent food sources. The diet of both species demonstrated a seasonal transition from bacteria and *Phaeocystis* to assimilation of poly-unsaturated fatty acids (PUFA) originating from diatoms. In addition, accumulation and/or biosynthesis of PUFA in *L. conchilega* upon bloom deposition was demonstrated, which is probably related to energy storage for gametogenesis. PUFA are *essential fatty acids* in the metabolism of higher organisms and therefore, increased concentrations in benthic invertebrates such as *Lanice conchilega* and *Nephtys hombergii* constitute an important trophic link towards the flatfish species preying on the latter.

The knowledge on the functional role of the selected macrobenthic species is summarised and a "functional ID-card" for *Abra alba*, *Lanice conchilega* and *Nephtys hombergii* is created in **Chapter 6**. The results of the PhD thesis are put in a wider perspective through comparison with literature on bioturbators co-occurring with the selected species and by framing their importance in the actual threats marine ecosystems are confronted with upon loss of such allogenic ecosystem engineers.

In conclusion, it is clear that beneath the sediment surface, allogenic ecosystem engineers such as *Abra alba* and *Lanice conchilega* establish favourable niches for co- habiting infauna through oxygenation and OM processing and burial; functions that do not only have a large impact on infaunal biodiversity in se, but also on global carbon and nitrogen cycling. Given the large anthropogenic pressure in the North Sea, our study area, it is conceivable that for the maintenance of benthic ecosystem functioning, losing large bioturbators from muddy and fine sandy areas may be similar to losing epifaunal species such as bryozoans and sponges from areas of coarser, mixed sediment. Because these species obviously have multiple ecological roles, their loss could have effects that extend beyond their own demise to resonate throughout the ecosystem. Their management, therefore, requires particular attention to their function in ecosystems.