

THE ECOLOGY OF ESTUARINE INTERTIDAL FLATS – THE EXAMPLE OF THE WESTERSCHELDE

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ABSTRACT

The ecology of estuarine intertidal flats is characterised by low species diversity and high productivity. The consequences of these two main characteristics have been investigated in detail on an intertidal flat in the Schelde estuary in the Netherlands. The existence of a species minimum in the oligohaline section of the estuary, as postulated by Remane, could not be confirmed for nematodes and macrofauna for the Schelde, nor for several other European estuaries. Rather, a linear decrease in species richness from the sea to the freshwater was observed.

The productivity of estuarine tidal flats depends on an *in situ* source of primary produced material, the microphytobenthos, as well as on the capacity of the macrofauna to transfer material from the water column to the sediments. A very rapid transfer of ^{13}C labelled carbon from primary production to the higher trophic levels was observed.

INTRODUCTION

Tidal flats, like other intertidal habitats, are on the border between the marine and terrestrial biosphere. During the tidal cycle they are exposed either to the atmosphere or to the overlying water, and the substrate gradually transforms from sediment to soil as one approaches the upper tidal levels. In contrast to rocky shores and sandy beaches, estuarine tidal flats can completely drown and lose their connection to the land at high water. The resident biota therefore must be able to cope with this change from an aquatic to a semi-terrestrial environment twice a day, and to resist the pressure from both aquatic and terrestrial predators and competitors. Because of that, tidal flats are unique in the biosphere, and, although quite limited in surface, they are of great importance to fish and

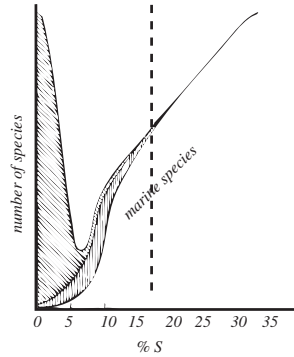


Figure 1. The Remane diagram showing the hypothetical distribution of benthic invertebrate diversity along a marine–freshwater salinity gradient, with a species minimum in brackish waters. Vertical hashed area corresponds to brackish water species, slanted hashed area freshwater species. (from Remane and Schlieper 1971).

birds as feeding areas. Moreover, they have high commercial value as areas of shellfish exploitation and eco-tourism.

Ecological wisdom has it that, at least in temperate areas of the world, estuarine tidal flats are characterised by few species and high productivity. Brackish waters in general are assumed to show a species minimum in the oligohaline zone (Remane and Schlieper 1971) (Figure 1). This implies that system functioning can be understood from the knowledge of resident species, that ecosystem models can be built based largely on population characteristics, and that management of these systems can be based at least partially on knowledge of population biology. Moreover, if we are able to predict the number of species and their distribution, then we may explore the direct link between biodiversity and ecosystem functioning and use this information in operational ecological models. Such comparative and experimental studies are now increasingly being reported (e.g. Emmerson *et al.* 2001), but the full potential of the estuarine soft-bottom system to serve as a model case for the link between biodiversity and ecosystem functioning is not yet exploited. Many studies in the rocky intertidal have significantly contributed to ecological theory (see e.g. recent review by Robles and Desharnais 2002), but although comparisons with soft-sediment systems have been analysed (Seitz 1998), it is clear that more progress could be made, especially in a better understanding of trophic and biogeochemical interactions in soft sediments.

Predictability is also an important aspect of ecosystem monitoring. The use of biological indicators for water quality and ecosystem health has gained support in the last two decades. Within this ecological indicator system approach, many studies have investigated macrobenthic communities in relation to the abiotic environment and how human activities affect them. Examples include the ABC method (Warwick 1986) where dominance patterns are investigated, and studies on functional life-history characteristics (trophic structure) (Pearson and Rosenberg 1978; Boesch and Rosenberg 1981; Gaston *et al.* 1998). As these indicators are weak in demonstrating cause-effect relationships and in general suffer from poor predictability and low explanatory power, the demands for

more reliable and quantitative predictive tools have become more and more pronounced (Constable 1999; Thrush *et al.* 1999). On the one hand, such tools are required for *post-hoc* interpretation of changes that have been observed in the estuarine environment. On the other hand, they are needed to predict the future response of the system to planned or anticipated changes in environmental conditions (Ysebaert *et al.* 2002).

The other part of the estuarine ecology paradigm is that estuarine intertidal flats are areas of high biological production. Here one usually refers to the yield in biomass that benefits humans and other vertebrate and invertebrate predators. This term can be estimated in a straightforward way, but to estimate total production (primary, secondary, tertiary. . .) and system mineralisation, or to evaluate whether estuarine intertidal systems are net exporters or importers of organic matter, is more complex. Indeed, although estuarine tidal flats are simple biological systems, they are quite complex biogeochemically and hydrographically, and the evaluation of autotrophic and heterotrophic processes in such a complex framework is very difficult (Heip *et al.* 1995). For instance, primary production occurs by microphytobenthos and macrophytobenthos on top of the sediments, but organic matter on the flats may or may not be derived from higher plants in salt marshes (Nixon 1980), or derived from import of primary produced organic matter from the river and often from the seas as well (Soetaert and Herman 1994). All these processes vary in space and time depending on the conditions in the estuaries.

These primary sources of organic matter serve as food for microbial, microbenthic, meiobenthic and macrobenthic life forms, which often attain considerable biomass on intertidal flats (Heip *et al.* 1995) and are directly responsible for a substantial fraction of the whole system energy flow in these estuarine systems (Herman *et al.* 1999). Part of the biomass of these secondary producers on intertidal flats is consumed by highly mobile organisms (crabs, fish, birds and mammals) that may export the production very rapidly. The main part of organic matter is, however, not exported but ultimately mineralised (respired) locally in the intertidal sediments (Middelburg *et al.* 1996). This process is mainly attributed to microbes, although the benthic fauna is an important player as well, both directly and indirectly (D'Andrea *et al.* 2002).

MATERIAL AND METHODS

In what follows, we will elucidate some of these important paradigms, using research performed in a well-known estuary, the Westerschelde and especially from a small intertidal flat in that estuary, the Molenplaat (Figure 2). The Westerschelde is a temperate, macrotidal, turbid, nutrient-rich and heterotrophic estuary in the Netherlands. The Molenplaat (51° 26' N, 3° 57' E) (Figure 2) is located in a region where salinity varies around 20–25. Most of the intertidal flat is located between -1 m and +1 m relative to mean tidal level. Mean tidal range is approximately 5 m. The average period of emersion varies between 4.5 h (site 1), 7 h (sites 2, 3, 4) and 8 h (site 5) per tidal cycle. Other areas in the Dutch delta in which our studies have taken place are the Oosterschelde, Veerse Meer and Grevelingen. Description of those areas can be found in Heip (1989) and Nienhuis and Smaal (1994).

The diversity of several groups of benthic and pelagic biota was examined during the EC-supported JEEP project (Major Biological Processes in European Tidal Estuaries), the results of which have been summarised by Heip (1995) and partly in Herman and Heip (1999). During this project the species composition of phytoplankton (Muylaert and Sabbe, 1999), zooplankton (Soetaert and Van Rijswijk 1993), hyperbenthos (Mees *et al.* 1995), microphytobenthos and metazoan meiofauna (nematodes) (Soetaert *et al.* 1995) was compared along the estuarine gradient between several European estuaries. We will discuss only those studies dealing with tidal flats.

Much of our discussion will deal with the macrofauna, of which an extensive data set exists for the Schelde estuary. To evaluate the impacts of the dredging activities, the macrobenthos has been monitored extensively since 1990, resulting in a database containing over 5000 macrobenthos samples at present. Parts of this large dataset on macrobenthic species and community composition in the Schelde estuary have been analysed very recently (Ysebaert *et al.* 2002; Ysebaert and Herman 2002).

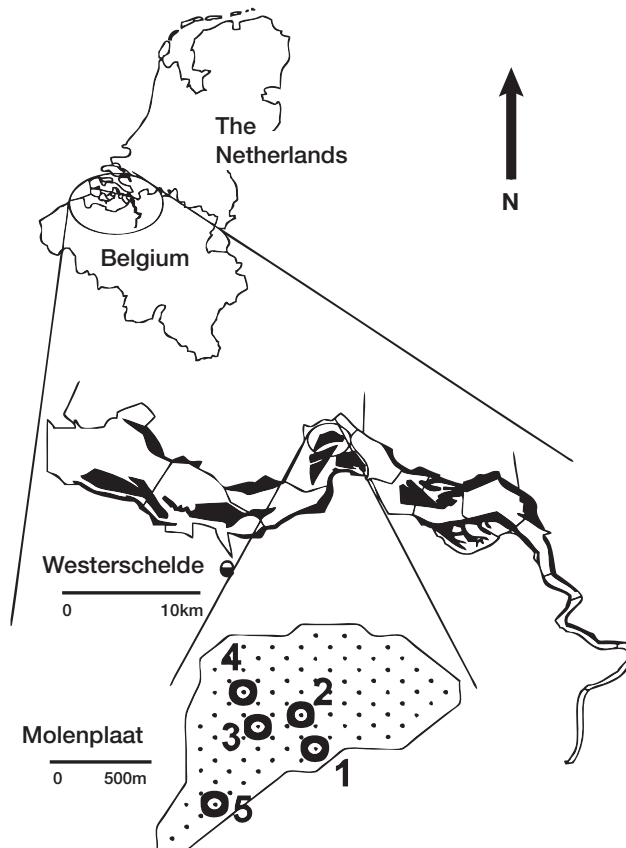


Figure 2. Map of the Westerschelde estuary (The Netherlands) showing the intertidal flat Molenplaat with the five sampling sites

RESULTS AND DISCUSSION

Species richness

Soetaert *et al.* (1995) made a detailed study of meiofauna and especially nematode communities in six European estuaries. Total meiofauna densities showed an idiosyncratic picture, with nematodes dominating the meiofauna everywhere. However, the groups ranking second in importance were quite different between the estuaries, but the cause of this was unclear. For instance, the Ems had the lowest dominance of nematodes in the mesohaline reach, and soft-shelled foraminiferans and copepods were more abundant relative to other estuaries. For nematodes Soetaert *et al.* (1995) observed a general increase of nematode genus diversity from freshwater to the sea and remarkably similar values in six estuaries (including literature data from the Tamar) of α -diversity (number of genera per sample) but no sign of an estuarine species minimum (Figure 3). This similarity is even more striking when one realises that the identity of these species is very different, that most species only occur in one estuary and that only three species out of 220 were found in all six estuaries. Meso-scale variation (in the order of kilometres) due to salinity changes or grain size differences along the estuarine axis is more important than regional variation (hundreds of kilometres) among estuaries and micro-scale variation (centimetres).

Based on a very large dataset for macrobenthos, Ysebaert *et al.* (2003) demonstrated the role of both salinity and depth in explaining large-scale patterns in diversity, abundance

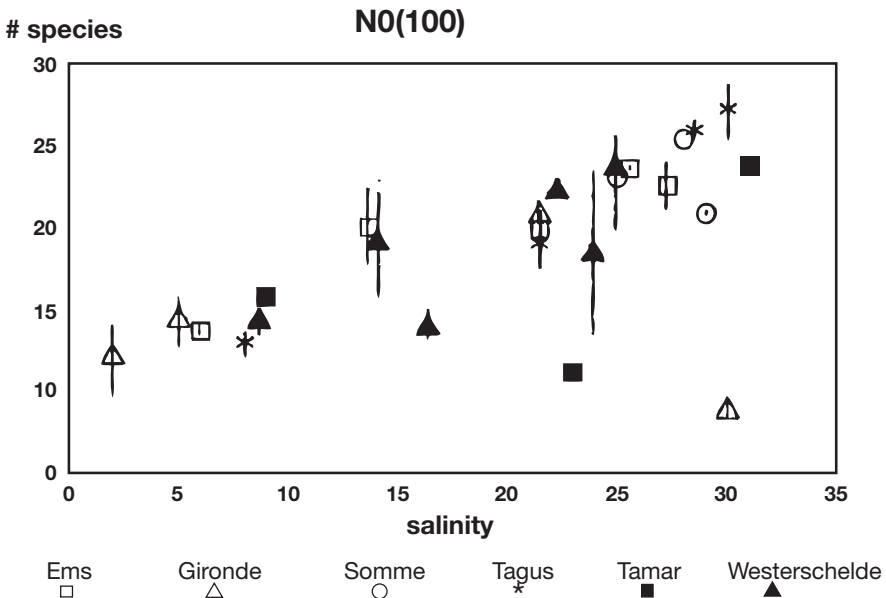


Figure 3. Expected number of nematode genera per 100 individuals in six European estuaries (from Soetaert *et al.* 1995)

and biomass of the macrobenthos in the Schelde estuary. Overall, the subtidal zone had a relatively higher number of species (γ -diversity) as compared to the intertidal zone, but α -diversity (mean number of species per sample) was higher in the intertidal zone (Ysebaert *et al.* 2000; Ysebaert *et al.* 2003). Not only α -diversity but also total number of species found decreased with decreasing salinity. Based on an analysis of the intertidal zone for the period 1990–2001 with a yearly effort of 30 samples, a total of 93 taxa were observed in the polyhaline zone of the Westerschelde, 86 in the poly-mesohaline transition zone and 59 taxa in the mesohaline zone.

Multivariate analyses indicated that the structural complexity of the macrobenthic assemblages decreased from the polyhaline zone towards the meso-oligohaline zone. In the meso-oligohaline transition zone, where salinity shows large seasonal fluctuations, benthic communities change frequently (with sudden dramatic events linked to peak river discharges), resulting in communities that seldom progress beyond early succession stages. Similar patterns were observed in the Loire estuary (Marchand and Gascuel 1988).

In the freshwater tidal zone of the Schelde estuary, no increase in the number of species was observed, probably due to a high degree of pollution in this part of the estuary. Only an impoverished benthic fauna, consisting solely of a few Oligochaeta species, was observed here (Ysebaert *et al.* 1993; Seys *et al.* 1999).

Heip *et al.* (1995) summarise data from many estuaries on biomass and productivity of macrofauna. In many cases, in particular estuaries with a well-developed maximum turbidity zone in the oligohaline zone, biomass increases dramatically from the freshwater upper part to the downstream part of the estuary. Exceptions to the rule are lake-like estuaries where the downstream shallow part is an area of fine sediment deposition unsuitable for suspension feeders, or intermittent estuaries where occasional freshwater runoff is the main source of nutrients.

Productivity

Estuarine intertidal systems are reputedly highly productive systems. The net yield of organic matter from the system is probably the best measure for productivity but is difficult to calculate. We will restrict our discussion to the benthos, as it is the main intermediate between primary production and biomass export from the system and, is responsible for an important part of the total consumption of the primary produced material. Heip *et al.* (1995), extending previous data compilations by Nixon (1980), Dollar *et al.* (1991) and Kemp *et al.* (1992), presented a general relation between system-averaged water depth and the fraction of total estuarine primary production mineralised in the sediment.

The relation is given by the equation

$$\log_{10}(F) = 1.6 - 0.0146 H$$

where F is the percentage of the system mineralisation in the sediment, and H denotes water depth (m). The factor -0.0146 has the dimension m^{-1} and was interpreted by Heip *et al.* (1995) as representing the multiplicative effect of two factors: a degradability constant ($time^{-1}$) and an effective sinking speed ($m \cdot time^{-1}$).

Drawing upon this equation, an order-of-magnitude estimate for sediment mineralisation in shallow estuaries can be made. The fraction mineralised in shallow

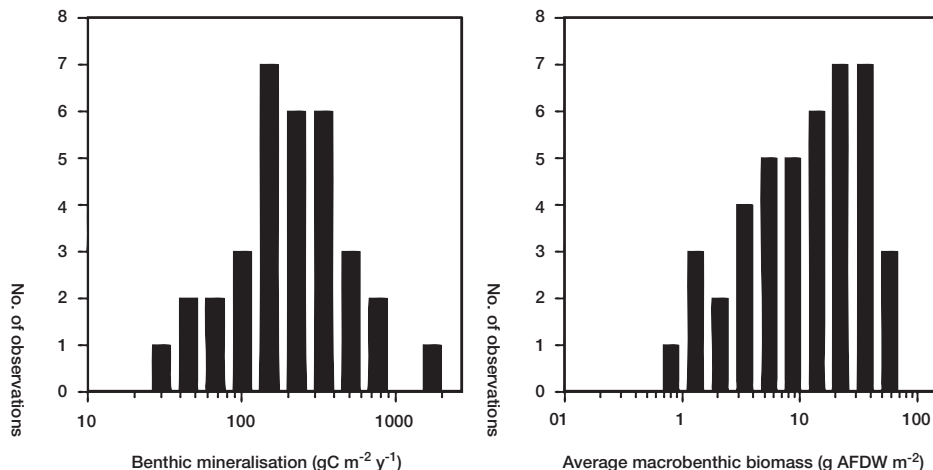


Figure 4. Frequency distribution of observations of (A) total sediment mineralisation (measured as either total inorganic carbon production or oxygen consumption) and (B) system-averaged benthic biomass. Most observations are listed in tables 23 and 29 of Heip *et al.* (1995); for Figure 4A additional data (Herman *et al.* 1999) have been taken into account.

systems (~10m) is around 60% of the total primary production. Taking an estimate for yearly primary production of ~200g C m⁻² yr⁻¹, one would arrive at ~120g C m⁻² yr⁻¹ for sediment mineralisation, coinciding with the mean value obtained by Heip *et al.* (1995) from (highly variable) measurements in 13 estuarine systems. These values were later complemented by Herman *et al.* (1999) to a total of 33 sites, with several Westerschelde sites included. The frequency distribution shown in Figure 4A was obtained. The median value for this data set, which however is probably biased by intertidal Westerschelde sediments, is 181g C m⁻² yr⁻¹.

Benthic microalgae can contribute significantly to total system primary production of estuarine systems (Colijn and de Jonge 1984) and can present a primary food source for intertidal food webs. Cahoon (1999) made an extensive compilation of benthic primary production by microalgae and reported a mean (\pm SD) of 111 \pm 99g C m⁻² yr⁻¹ for temperate intertidal sediments. This estimate is about 50% of typical coastal and estuarine pelagic primary production (Heip and Herman 1995; Cahoon 1999) and remarkably similar to estimates of mineralisation in estuarine sediments (about 120g C m⁻² yr⁻¹ (Heip and Herman 1995). This indicates that all benthic primary production could be mineralised in the sediments, consistent with reports for sandy sediments by Middelburg *et al.* (2000) and D'Andrea *et al.* (2002). It is also consistent with rapid and efficient transfer of microalgal-derived carbon within intertidal food webs (see below) and the lack of stable isotope evidence for significant burial of microalgal-derived carbon in intertidal sediments (Herman *et al.* 2000).

It is difficult to establish which fraction of the carbon mineralised in estuarine sediments is directly attributable to the metabolism of the macrobenthic animals. At a system scale, one would need concurrent estimates of sediment respiration and of benthic

production or respiration from a representative sampling of the different strata in the system. From the median figures on macrobenthic biomass and benthic mineralisation from the database discussed by Herman *et al.* (1999) it can, however, be qualitatively deduced that this fraction is significant. Taking a median ash-free dry weight (AFDW) biomass of 15g AFDW m⁻² (Figure 4B), a carbon: AFDW ratio of 0.5, a P/B of 2 yr⁻¹ (Heip *et al.* 1995) and a respiration/production ratio of 1.8 (Banse and Mosher, 1980), one would estimate a typical macrobenthic respiration rate in estuaries of the order of 25g C m⁻² yr⁻¹, which constitutes around 15–20% of the median total respiration of the sediment. The general conclusion, as repeated from the recent review by Herman *et al.* (1999), is that a substantial fraction of the carbon flow in estuarine systems passes through macrobenthic populations.

Conversely, macrobenthic populations at a system level may be limited by food fluxes to the sediments. This is confirmed by several studies. Beukema and Cadée (1997) provided direct observational evidence for limitation of system-averaged benthic biomass by estuarine productivity. They showed that in the Balgzand area (Dutch section of the Wadden Sea) a substantial increase of pelagic primary production between the 1970s and the 1980s (nearly a doubling), was followed by a nearly proportional increase of system-averaged benthic biomass. The proportional increase was equally large for suspension feeders and deposit feeders.

Field evidence for a direct coupling between benthic biomass and pelagic primary production was also produced by Josefson *et al.* (1993) who showed an increase in biomass and a change in community structure in the Skagerrak-Kattegat area between the 1970s and 1980s. The increase in biomass correlated (with a time lag of 1–2 years) with runoff variables known to be directly related to phytoplankton primary production. Austen *et al.* (1991) described similar long-term changes correlated to (indirectly determined) increases in primary production for two widely spaced sites, one in the Western North Sea and one in the Skagerrak.

In Figure 5 the relationship between benthic biomass and system productivity is given for a series of estuarine systems (see Herman *et al.* (1999) for more details). The resulting relation suggests that for these shallow estuarine systems between 5% and 25% of the annual primary production is consumed by macrobenthos and shows up as macrobenthic respiration. On a system-averaged basis, suspension feeders are often the dominant component (with respect to biomass) of estuarine benthic assemblages. They typically occur in much higher local biomass than deposit feeders, which are much more equally spread over (generally lower) biomass classes. In the Oosterschelde, over 75% of the total biomass of suspension feeders was found at local biomass values of more than 100g AFDW m⁻² (Figure 6), whereas 53% of the samples contained less than 1g AFDW m⁻² of suspension feeders and 28% of the samples contained no suspension feeders at all (Herman *et al.* 1999). For deposit feeders, only 15% of the system biomass was found at local biomass values of more than 100g AFDW m⁻² (Figure 6) but only 20% of the samples contained less than 1g AFDW m⁻² of deposit feeders and there were virtually no samples without deposit feeders (Figure 6). Similar patterns were observed for the Westerschelde (Ysebaert *et al.* 2003).

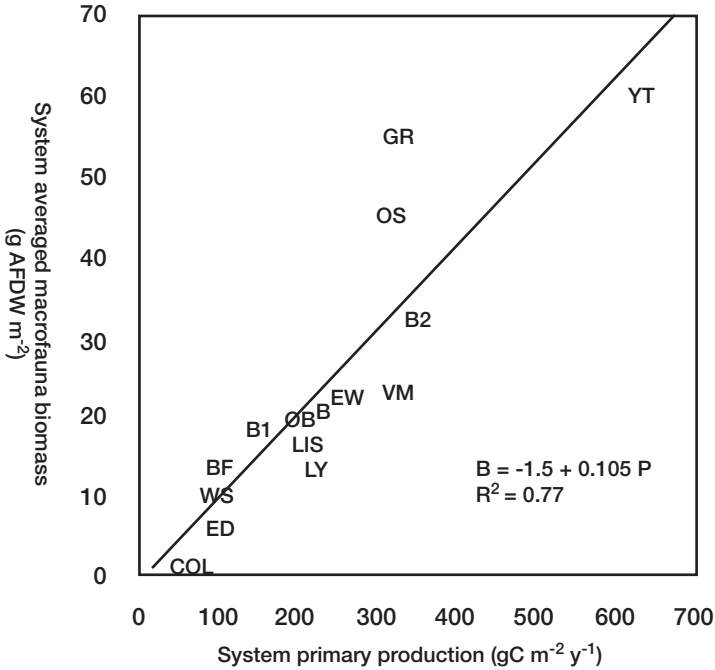


Figure 5. Relation between system-averaged macrobenthic biomass and primary productivity of shallow well-mixed estuarine systems. Data points are indicated by the abbreviation of the name of the system. The regression line is a predictive linear least squares line. System abbreviations (for sources see Herman *et al.* 1999) are: YT: Ythan estuary; GR: Grevelingen; OS: Oosterschelde; B1: Balgzand (Dutch Wadden Sea) in the 1970s; B2: Balgzand (Dutch Wadden Sea) in the 1980s; VM: Veerse Meer; EW: Ems Estuary near the Wadden Sea; ED: Ems Estuary, inner part ('Dollard'); SFB: San Francisco Bay; LY: Lynher estuary; WS: Westerschelde; BF: Bay of Fundy; COL: Columbia River estuary; LIS: Long Island Sound; CB: Chesapeake Bay. (from Herman *et al.* 1999).

Heip *et al.* (1995) showed a dependence of total system biomass of commercial benthic suspension feeders on residence time of the water in the system. This pattern was modelled assuming that residence time was an inverse measure of food exchange with the coastal sea, and that system productivity was the basic limiting factor for the suspension feeder biomass (as in the relation between system productivity and benthic biomass presented above). Dame and Prins (1998) and Dame (1996) tested the model proposed by Heip and Herman (1995) for a number of systems. They concluded that commercial bivalve filter-feeder populations are mostly found in systems with short residence times and high relative rates of primary production.

The benthic food web

As argued above, an important part of the primary production in the estuary is captured on the intertidal flats by the benthic fauna and transferred into the benthic food web. This transfer has been studied in detail at the Molenplaat stations 2 (muddy) and 4

(sandy) using natural stable isotope ratios in different components of the food web, and using stable isotope labelling experiments (Middelburg *et al.* 2000; Herman *et al.* 2000; Moens *et al.* 2002).

Herman *et al.* (2000) compared three different approaches to estimate the relative importance of planktonic microalgae, benthic microalgae and bulk detritus in the sediment as a food source for macrofauna: natural stable isotope ratios in the animals, an *in situ* labelling experiment reported by Middelburg *et al.* (2000) and a dual labelling flume experiment where planktonic and benthic microalgae were labelled with ¹⁵N and ¹³C, respectively. They showed that macrobenthic species differed in their relative dependence on benthic and pelagic microalgae. Suspension feeders (*Cerastoderma edule*, *Mya arenaria*) were directly dependent on pelagic microalgae and had little traces of uptake of benthic microalgae. Surface grazers (e.g. *Hydrobia ulvae*) had a pure signature of benthic microalgae. Deposit feeders (e.g. *Macoma balthica*, *Arenicola marina*) were intermediate in their signature, but benthic microalgae were an important fraction of their food. The biomass of (surface) deposit feeders correlated significantly with the primary production by benthic microalgae.

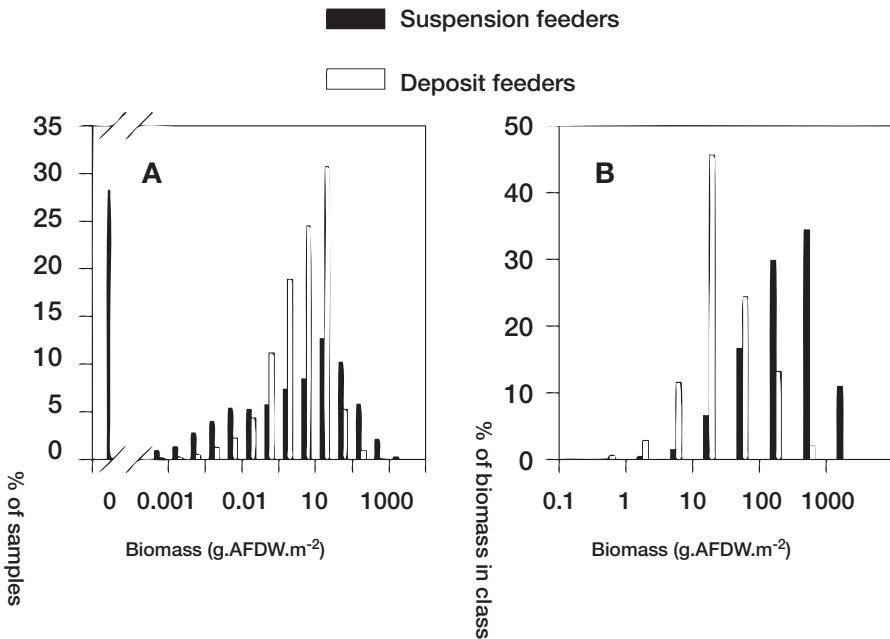


Figure 6. (A) Frequency distribution of suspension and deposit feeder biomass in the Oosterschelde (n = 2368, data collected between 1990 and 1998) over logarithmic biomass classes. Suspension feeders are absent from a large number of samples, and occur more frequently in very high local biomass classes. (B) Percentage of the total recorded biomass found at local biomass values in logarithmic classes. Over 75% of the recorded suspension feeder biomass is found at a local suspension feeder biomass of over 100 g.AFDW.m⁻², whereas the largest fraction of deposit feeder biomass is within the 10–100 g.AFDW.m⁻² class. (from Herman *et al.* 1999).

Stable carbon isotope signatures of nematodes from a salt marsh and 4 tidal flat stations in the Westerschelde were determined in spring and winter situations, and compared to isotope ratios of organic matter sources within the estuary by Moens *et al.* (2002). Nematodes collected from a fine sandy tidal flat sediment in late spring and during mild and sunny late winter weather had ^{13}C values consistent with microphytobenthos being their prime carbon source. Nematodes from a silty station and individuals sampled under cold and dark winter conditions had ^{13}C values intermediate between those of microalgae and particulate organic matter. In combination with experimental results, this suggests that tidal flat nematodes preferentially utilise labile organic carbon derived from microphytobenthos or settling phytoplankton; organic matter from terrestrial or riverine origin does not contribute significantly to the diet of nematodes at the sites studied (Moens *et al.* 2002).

Whereas the above-mentioned studies elucidated the *nature* of the food of benthic animals, other studies have explored the *rate* at which food cascades into the trophic web.

Moodley *et al.* (2000) used ^{13}C -labelled *Chlorella* to study the utilisation of phytodetritus by bacteria, foraminifera and other meiofauna in intertidal estuarine sediments. The response of the community was rapid: about 5% of the added carbon was respired to CO_2 within 6h and bacteria assimilated 2% to 4% of the added carbon within 12h. Among the foraminifera, the dominant genus *Ammonia* exhibited rapid uptake and

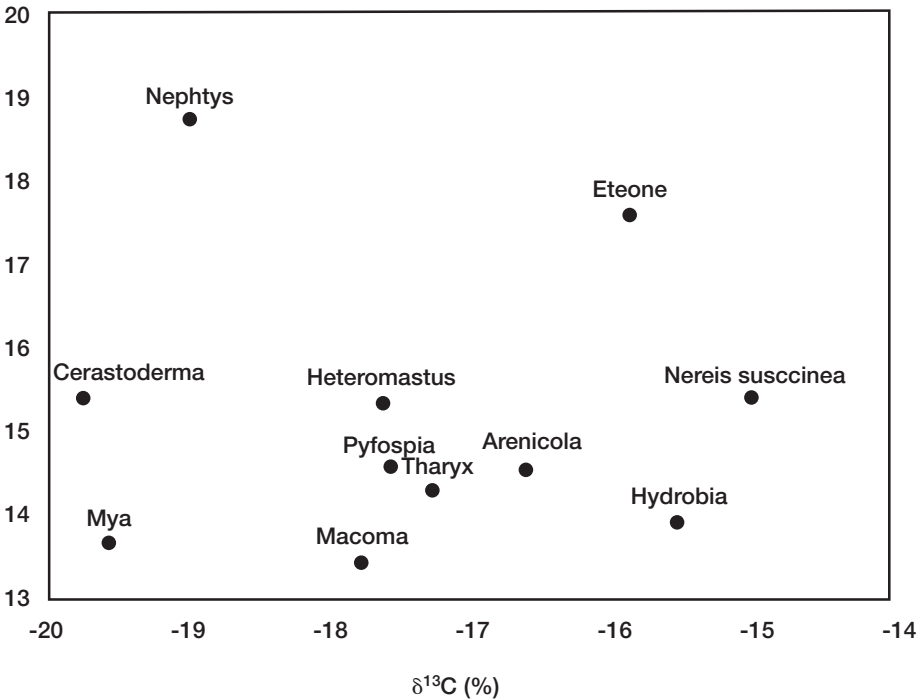


Figure 7. Natural stable-isotope signatures of macrobenthic species sampled at sample site 2 in June 1997 on the Molenplaat tidal flat (see Figure 2). (from Herman *et al.* 2000).

it is estimated that 1–7% of the added carbon was ingested within 3h to 53h. Limited ^{13}C enrichment was recorded for two other genera. This suggests a preference for other carbon sources and implies resource partitioning among the foraminifera. The rapid uptake and significant contribution of *Ammonia* to meiobenthic abundance and biomass indicates that this genus plays an important role in moderating the carbon flow within intertidal food webs.

Middelburg *et al.* (2000) sprayed inorganic $\text{NaH}^{13}\text{CO}_3$ onto the sediment surface at the beginning of low tide, and followed the fate of the ^{13}C label through the benthic food web during the consecutive days. They showed a linear uptake of the label by the benthic microalgae with time during the first ebb period. The label was transferred quickly to bacteria, presumably to a large extent *via* extracellular excretions. Bacterial labelling peaked after one day, and decreased afterwards. Nematodes were significantly labelled within a period of a few hours; their specific labelling increased during the following days. This corroborated the importance of microphytobenthos as a carbon source for nematodes, yet at the same time contradicted the hypothesis that direct grazing would be the main pathway of microalgal carbon to nematode consumers (Moens *et al.* 2002). Mixing of the label into deeper sediment layers was fast at the sandy station. After 3–4 days, the major groups in the benthic food web that were measured (bacteria, meiofauna, macrofauna) had attained similar specific labelling levels and the amounts of label incorporated were proportional to their biomass.

These studies demonstrate that organic matter produced *in situ* by benthic microalgae is transferred very rapidly and efficiently into the benthic food chain. At the sandy station, there was loss due to resuspension, but this loss was not extremely high (about 34% after 3 days). No major loss due to resuspension could be demonstrated for the muddy station. This study also demonstrated that the turnover of the benthic microalgae was much faster at the sandy than at the muddy station: primary production levels were similar, although the microalgal biomass at the sandy station was almost an order of magnitude lower than at the muddy station.

Benthic organisms as system engineers

Disciplinary studies during the last few decades have resulted in detailed knowledge on tidal flat microbial ecology (e.g. degradation pathways), trophic interactions within the macrobenthos domain (e.g. predator-prey, competition) and sedimentology, but our understanding of interactions between different size classes of benthic organisms and between the sediments and benthic organisms is rather limited. Heip (1976), Jones *et al.* (1994) and Jones *et al.* (1997) advanced the concept of organisms as ecosystem engineers in which they provide structure or modify their physical or chemical environment and thus affect the availability of resources to other organisms. This may generate organism-organism interactions via the environment. Tidal flats provide numerous examples (e.g. Van De Koppel *et al.* 2001; Reise 2002) including stabilisation of sediments by microalgae, destabilisation of sediments by moving fauna, deposition of (pseudo)faecal pellets by suspension feeders, mixing of sediments by animals (bioturbation) and the construction of tubes and burrows by macrofauna. The construction of burrows has dramatic effect

on the biogeochemical processes (e.g. Aller 1983; Herman *et al.* 1999), the bacterial community structure (Marinelli *et al.* 2002) and meiofauna communities (Levin *et al.* 2001). Macrofauna-induced structures and processes may generate (via coupled positive and negative feedbacks) a diversity of microhabitats that can host a diverse community of bacteria and micro and meiofauna.

GENERAL CONCLUSIONS

Conventional ecological wisdom has it that species diversity is lowest in the brackish water regions of estuaries. The 'brackwasserminimum' as described by Remane and Schlieper (1971) from the Baltic Sea is usually ascribed to the low tolerance of most species to the salinity fluctuations existing in those areas. In the data series we investigated there is indeed a reduction in α -diversity going from marine to freshwater reaches of the estuary, but this reduction is gradual and often linear and there is no indication of a real species minimum in the oligohaline brackish water region of Western European estuaries in several groups of animals that were studied in more detail. Unfortunately, most detailed studies from tidal areas in Western Europe fail to include the freshwater tidal areas or freshwater biotopes adjacent to the main channel of the estuary, which may serve as refuges for many species. It is therefore still unclear how the total species richness of an estuary and its intertidal flats is distributed. This is mainly a problem of sampling methodology and spatial scale. Spatial scale has been discussed by Ysebaert and Herman (2002) who showed that at meso-scale (>100m–10 km) a considerable fraction of the variation in occurrence, density and biomass of eleven dominant macrobenthic species correlated very well with physical factors (depth, tidal current velocity, sediment composition). At larger scales within the estuary salinity changes these relations significantly (Ysebaert *et al.* 2003). One important conclusion from the analysis of spatio-temporal variance components (Ysebaert and Herman 2002) was that a significant amount of variation occurs in the 'station*year' interaction factor. Stations (characterised by replicate samples within 1 m²) varied significantly from year to year in their macrobenthic species composition, and this variation was not part of a general trend at larger scales, nor could it be correlated to fluctuating physical factors. It shows that patchiness at relatively small scales (10–100 m) is an important feature of these communities.

The other general perception, that estuarine intertidal flats are highly productive ecosystems, is supported when one considers the biomass of higher trophic levels, including the benthos. An important part of total system production is mineralised in the sediments and much of this can be attributed by benthic animal activity. Moreover, our food web studies have demonstrated that the transfer of organic matter in the benthos is very rapid.

Often one assumes that high productivity is associated with silty sediments. Sandy sediments have traditionally been neglected by biogeochemists and microbial ecologists because stocks of carbon (food for benthos) were low. However, recent studies presented convincing evidence that mineralisation rates of sandy sediments are not necessarily lower than those of organic-carbon-rich silty or muddy sediments (Boudreau *et al.*

2001; D'Andrea *et al.* 2002). Organic matter mineralisation in sandy sediments can be significant because of the high quality (i.e. degradability) of the organic carbon (Dauwe *et al.* 1999). The consequent high rates of turnover are maintained by steady resupply of fresh carbon derived from microphytobenthos production (Middelburg *et al.* 2000) and benthic filtration of water column phytoplankton (Huettel and Rusch, 2000). This high-quality microalgal-derived organic matter provides the base resource for the complex and diverse micro and meiobenthos food webs characteristic of sandy tidal flat sediments.

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