



PERGAMON

Continental Shelf Research 21 (2001) 2055–2071

CONTINENTAL SHELF
RESEARCH

www.elsevier.com/locate/csr

Review article

Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project

Peter M.J. Herman*, Jack J. Middelburg, Carlo H.R. Heip

Netherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology, P.B. 140, 4400 AC Yerseke, Netherlands

Received 10 April 2000; accepted 12 February 2001

Abstract

Interactions between physical and biological processes in intertidal sediments have been the focus of studies in the framework of the ECOFLAT project. Process studies were focused on the Molenplaat, a 1.5 km² intertidal flat in the Westerschelde estuary, The Netherlands. Distinct spatial patterns in the biological community on the flat were found and related to patterns in bottom shear stress as derived from a hydrodynamic model. Based on these survey results five stations were selected with contrasting sediment composition and benthic communities.

Long-term net sedimentation of mainly sand was deduced from radionuclide profiles. Sedimentation of mud on the surface of part of the intertidal flat was shown to be a seasonally cyclic process, with a magnitude sufficient to significantly affect the mud balance of the estuary. Measurements of erodability as a function of tidal current showed a biological control on this variable. Benthic microalgae stabilise the sediment surface, whereas the benthic macrofauna has a destabilising effect.

Food web studies show that the contrasting biological communities (microbenthos, meiobenthos, macrobenthos) at muddy and sandy sites have substantial differences in the quantitative aspects of their food web. Turnover of microalgae is much lower at muddy than at sandy sites, and this is mostly related to a lower grazing pressure. It is hypothesised that high mud content decreases the availability of benthic microalgae to grazers.

We demonstrate a positive feedback between benthic microalgae and mud sedimentation which may lead to the existence of different stable states. This may explain the existence of relatively sharp boundaries and strong community contrasts in the presence of weak and smooth environmental gradients. © 2001 Elsevier Science Ltd. All rights reserved.

*Corresponding author. Tel.: +31-113-577475; fax: +31-113-573616.

E-mail address: herman@cemo.nioo.knaw.nl (P.M.J. Herman).

1. Introduction

Estuarine intertidal flats are sites of intense biological activity. The sediment surface is characterised by important in situ primary productivity by benthic microalgae, with production rates typically in the order of $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Underwood and Kromkamp, 1999). This constitutes an important source of organic matter to the sediment, which, together with deposition of suspended particulate organic matter, explains the high mineralisation rate in intertidal sediments (Middelburg et al., 1996). These primary sources of organic matter are the food base 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 energy flow in these estuarine systems (Herman et al., 1999).

The intertidal benthic biota have to survive in a harsh and variable environment. Physical stress is exerted by tidal currents and waves, the impact of which varies in space and time. Temperature, light and water saturation vary not only according to tidal and diurnal rhythms, but also with seasonal and short-term weather variations. Average salinity obviously varies spatially with the position in the estuarine gradient from freshwater to the sea, and temporally with freshwater runoff.

Organisms adapt to these variable and often adverse conditions in different ways. One of the most interesting ways from an ecological viewpoint is the strategy whereby biota actively modify their physical environment, so as to provide better conditions for their survival. This is generally known as 'ecosystem engineering' (Jones et al., 1994), where organisms physically change their environment to enhance the availability of resources, not only to themselves but also to other species. Ecosystem engineering may entail feedbacks between organisms and their environment, which is called 'extended phenotype engineering' because the engineered habitat has consequences for the fitness of the engineer (Jones et al., 1997). These feedbacks can be positive or negative. In the latter case, this may lead to local extinction of the engineer populations and unstable system dynamics (Gurney and Lawton, 1996). Where ecosystem engineering leads to stable interactions, it can typically lead to sharp boundaries between contrasting physical–biological community structures, even in the presence of weak and gradual physical gradients (Wilson and Nisbet, 1997).

Recently, several studies have shown that sediment stability in intertidal habitats can be substantially modified by biofilms and microbial mats (see review in Paterson and Black, 1999) and the effect of grazers on these surface types (Daborn et al., 1993; Willows et al., 1998; de Deckere et al., 2000). The consequences of these interactions and other aspects related to the benthic food web for the functioning of the system are still poorly understood. The central players in the biostabilisation of sediments, the benthic microalgae, are a potential food source not only for benthic deposit feeders, but also for other components of the benthic system. Grazing by meiobenthos and protists are still poorly quantified. Stabilisation of sediments involves the production of extracellular polysaccharides (EPS) which may be quickly consumed by bacteria (Middelburg et al., 2000); production rates of EPS may determine the composition and activity of the bacterial community (Yallop et al., 2000). When physically resuspended, benthic microalgae may constitute an important food source for macrobenthic filter feeders (de Jonge and van Beusekom, 1992). Food web studies, including the microbial benthic food web, may clarify the regulating mechanisms of the benthic microalgae, and therefore improve our insight in how they regulate the physical properties of the sediment.

The project Eco-metabolism of an estuarine tidal flat (ECOFLAT) aimed at describing the interactions between benthic biota, physical and biogeochemical processes. Composition, abundance and diversity of estuarine benthic macrofauna has been described as a function of physico-chemical forcing. We consider that biota (microalgae, heterotrophic microbiota, meiobenthos, macrobenthos) are not only a direct and straightforward reflection of abiotic physical factors, but rather highlight in this paper the two-way interactions between biota and physical processes. Hence, we consider both how biological communities undergo physical forcing and vice versa and how the biota are physically shaping the environment. If ecological processes are important for shaping the sedimentology, at what scale can the effects be assumed to be important? How do animals influence biogeochemistry of the sediment? Where do they find their food sources and how is the food web related to the production, sedimentation and mineralisation of organic matter in the sediment?

ECOFLAT studied processes of benthic–pelagic exchange and of benthic interactions at a relatively small scale, i.e. within a single intertidal flat (Fig. 1). We selected a small (1.5 km²) intertidal flat in the Westerschelde, SW Netherlands, and studied many processes at five locations situated a few hundred metres apart, showing a diversity in physical forcing and biological and chemical characteristics that spans almost the range observed in the whole estuary. Apart from these process studies, we also addressed the problem of upscaling this information to better describe distribution patterns of benthic macrofauna in the estuary. This subject is dealt with in Ysebaert et al. (2001).

In this contribution, we review the results of the process studies at the Molenplaat, and summarise their conclusions with respect to the interaction between biota and sediment.

1.1. Study site and general sampling set-up

All measurements were performed at the Molenplaat (51°26' N, 3°57' E), a small intertidal flat in the turbid, nutrient-rich and heterotrophic Westerschelde estuary (Fig. 1). Salinity in this region of the estuary varies around 20–25. Most of the intertidal flat is located between –1 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 2–4) and 8 h (site 5) per tidal cycle.

Five sites were selected for intensive measurements, based on sedimentology and composition of the fauna from a preliminary survey in 1995. This survey encompassed 92 sampling stations on a rectangular grid (small open dots in Fig. 1) where macrofauna density and biomass per species were determined, as well as grain size distribution in the top 1 cm (using Malvern laser diffraction). The grid had a node spacing of ca. 120 m. It was surveyed four times (March, June, September and December 1995). During ECOFLAT, four intensive campaigns were organised at the Molenplaat, in May–June 1996, September 1996, June 1997 and September 1997. Each campaign lasted 14 days and included a spring and neap tide. During each campaign a barge was anchored at one of the stations (stations 1–4 were occupied during the four campaigns), from which permanent measurements of current velocity at four heights above the bed were performed, as well as determinations of suspended sediment, chlorophyll, water temperature and salinity.

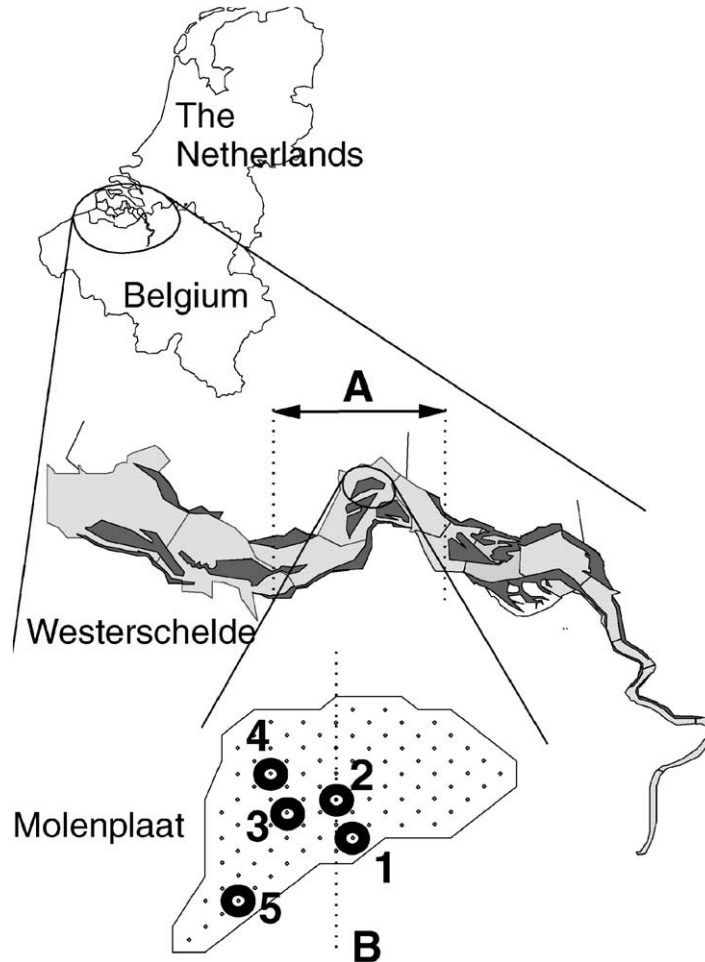


Fig. 1. Location of the study sites. The zone denoted 'A' was covered by the long-term measurements of suspended material in the water column (Fig. 5). The transect 'B' was used to show seasonal evolution of %mud in the surface sediment (Fig. 4).

2. Results

2.1. Spatial patterns of benthic macrofauna on the Molenplaat

At the scale of the entire flat, the seasonal surveys showed that the spatial distribution of the different species had distinct patterns. Fig. 2 shows the spatial distribution of the lugworm *Arenicola marina* and the cockle *Cerastoderma edule*. *A. marina* attained its highest average biomass in a ring-like pattern around the centre of the intertidal flat. The cockle *C. edule* had its highest biomass in this central part of the flat. In a multivariate analysis (correspondance analysis) of the species abundance data of the whole of the intertidal flat, the major distinction was between a limited set of samples taken on very dynamic sand megaripples (at the southwest corner of the

intertidal flat) with a very poor faunal abundance, and all other samples. Within the latter group, which no longer contained sites with very high physical stress, two major axes dominated the correspondence analysis. The first and most important axis again related to bottom shear stress, as calculated from the hydrodynamic model (see below). The second axis related to bathymetry (and therefore also inundation and exposure time). Feeding types of macrofauna separated out on the axes. In particular, the biomass of suspension feeders was highest in the central part of the flat, where bottom shear stress was minimal. Surface deposit feeders, and in particular *A. marina*, peaked at intermediate bottom shear stress, where the sediment was sandy with a low mud percentage (throughout the paper, we will use the term ‘mud’ as a generic name for the fraction smaller than 63 μm).

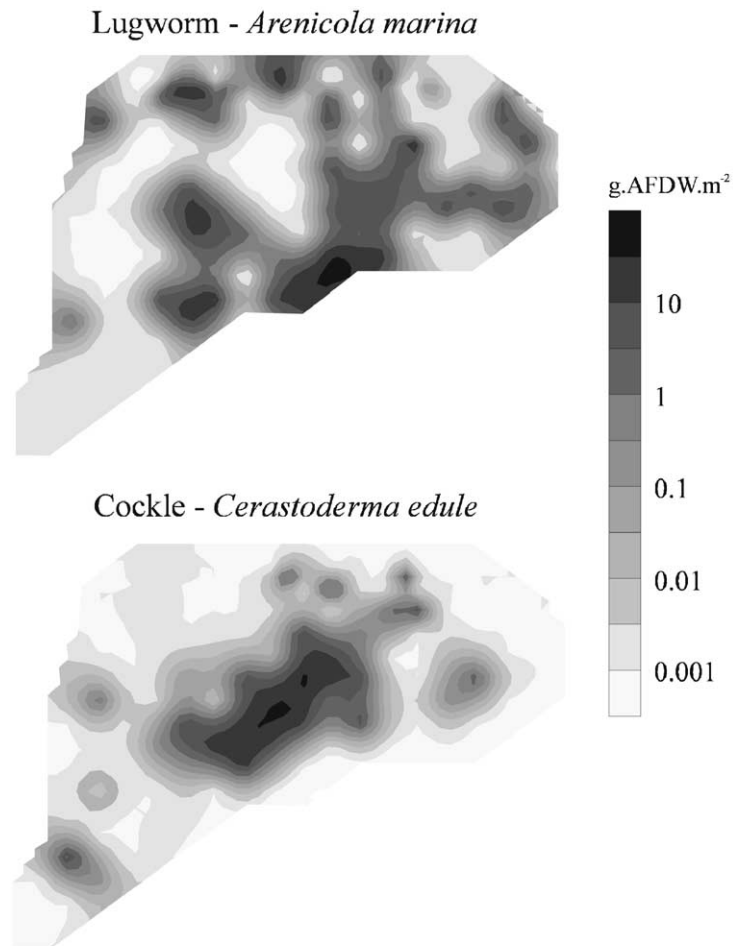


Fig. 2. Spatial distribution patterns of the biomass of the species *Arenicola marina* and *Cerastoderma edule* on the Molenplaat. Average biomass of the four seasonal campaigns of 1995 are shown. Interpolation was by kriging on the log-transformed biomass values.

These patterns were used to select the five ECOFLAT sites that represent the major faunal assemblages on the flat, and at which detailed process studies were made during the ECOFLAT project. Of the five selected sites, site 2 has the finest sediment, sites 4 and especially 5 are more dynamic and sandier and sites 1 and 3 are intermediate (Table 1).

2.2. Hydrodynamic model

A detailed 2-D hydrodynamic model was constructed for the Molenplaat and its surroundings. The model domain extended somewhat more than a tidal excursion upstream and downstream of the flat, to reduce undue dependence on the boundary conditions. A rectilinear grid with variable grid size was used, with its highest resolution (~ 30 m grid size) around the Molenplaat. The model was developed within the Delft Hydraulics TRISULA package. Boundary conditions were derived from the SCALDIS model (Dekker, 1993) which simulates the hydrodynamics of the whole Westerschelde estuary with a 100 m resolution. Model runs were calibrated on current velocity and water height measurements along a transect on the Molenplaat during a fortnight in June 1995. These measurements included data from vertical arrays of current meters used to estimate the logarithmic profiles of current velocity above the bottom. The model used a uniform wind speed of 5 cm s^{-1} and ran for an average tide in summer conditions. Preliminary calibration of the model showed that a good reproduction of current velocity at the different measurement sites on the intertidal flat necessitated the implementation of spatially variable bottom roughness. The muddy sediment at the centre of the flat was modelled as a smooth bed, with roughness proportional to the grain size of the sand fraction. At the outer edges of the flat the surface roughness was proportional to the height of the megaripples. At intermediate positions the height of the sand ripples was the determining factor for roughness length. With these spatially variable bottom roughness formulations, the hydrodynamic model reproduced the observations faithfully. Estimates of bottom shear stress were produced by the model.

Table 1

Characteristics of the sampling stations on the Molenplaat. Bottom shear stress is the maximal value during a tidal cycle, as derived from hydrodynamic modelling (Van de Koppel et al., 2001). Benthic primary production is based on oxygen microelectrode measurements (Hamels et al., 1998). Sediment grain size and organic carbon data are from 9/6/96

Site	Depth range (cm)	% mud < 63 μm	Median grainsize (μm)	Bottom shear stress (Pa)	Organic carbon (wt%)	Benthic primary production ($\text{mg C m}^{-2} \text{h}^{-1}$)
1	0–1	24	137	0.43	0.29	225
	0–25	11	171		0.18	
2	0–1	43	77	0.36	0.64	105
	0–25	30	94		0.41	
3	0–1	14	160	0.58	0.20	152
	0–25	10	168		0.22	
4	0–1	4	170	1.15	0.06	131
	0–25	5	167		0.07	
5	0–1	5	166	3.37	0.04	15
	0–25	4	174		0.05	

Bottom shear stress at the macrofauna sampling points was estimated as the average of the model grid points within an 80 m distance from the sampling point. Fig. 3 shows the spatial distribution of bottom shear stress as calculated from the model and compares this to the sample scores (projection of the biotic communities) on the first axis of the macrofauna correspondence analysis.

2.3. Sedimentation and erosion

Sedimentation and erosion are important processes for benthic life. Sedimentation of particles is one of the factors determining the flux of organic matter to the sediment, especially if the sedimenting material is fine-grained. Sedimentation and erosion also determine the physical stability of the bed, which is important for the maintenance and recruitment potential of the animals (Bouma et al., 2001a, b). We used profiles of radionuclides to estimate both long- and short-term sedimentation rates.

Based on profiles of ^{210}Pb and ^{137}Cs , Schmidt et al. (1999) estimated a long-term sediment accretion rate of $1\text{--}2\text{ cm yr}^{-1}$ at sites 1–5. The rate showed little spatial variation between the different stations. Grain size analysis in the vertical profiles showed that long-term sedimentation was mostly due to sand accumulation. A constant low proportion of mud accumulated in the deeper parts of the profiles. The organic carbon fraction of the accumulating material was relatively low (0.06–0.3 wt%). Nevertheless, due to the high accumulation rates, organic carbon burial rates varied from 10 to $105\text{ g C m}^{-2}\text{ yr}^{-1}$, which correspond with burial efficiencies of 28–39%.

On a monthly to seasonal time scale, the net effect of sedimentation and erosion was followed using ^7Be as a tracer (Schmidt et al., 1999; Widdows et al., 2000). ^7Be is a short-lived (half-life 53 days) radionuclide that is mainly attached to fine particles. Total inventories of ^7Be are consequently a good measure of recent mud accumulation. The depth distribution of ^7Be activities can be used to quantify particle mixing due to bioturbation, since its short half-life prevents accumulation below the surface in the absence of mixing. At station 2 (central muddy station) a bioturbation coefficient of ca. $5\text{ cm}^2\text{ yr}^{-1}$ was estimated. The ^7Be inventories clearly showed a seasonal build-up of fine material in the top 10 cm of the sediment. Between March and September 1997, the ^7Be inventory increased by one order of magnitude. This result was consistent with the field observation that the sediment is sandy over the entire intertidal flat in winter, but becomes increasingly muddy in the central part between March and June (Fig. 4). Since the whole intertidal flat shows net accumulation, and the mud percentages in the deeper layers are consistently low, it is clear that the mud deposition is temporary. The material disappears largely during winter, probably due to storms.

The seasonal cycle of mud deposition and erosion as observed on the Molenplaat shows a remarkable temporal correlation with the seasonal cycle of suspended matter concentration in this part of the Westerschelde. Fig. 5 shows the annual SPM cycle, averaged over the years 1989–1998 and over a zone approximately 10 km upstream and downstream of the Molenplaat (Monitoring data courtesy of Rijkswaterstaat). From the difference between winter and summer concentrations and the water volume in this part of the estuary, we calculated the total (dry) mass of fine sediments that is suspended in winter time, and not in summer time. If this total mass were deposited in summer as a sediment layer of 5 cm thickness with 30% (additional) mud content on a dry weight basis and a porosity of 0.6 (values taken from the Molenplaat observations) the seasonal deposition area should occupy 40% of the intertidal area. On the Molenplaat, the

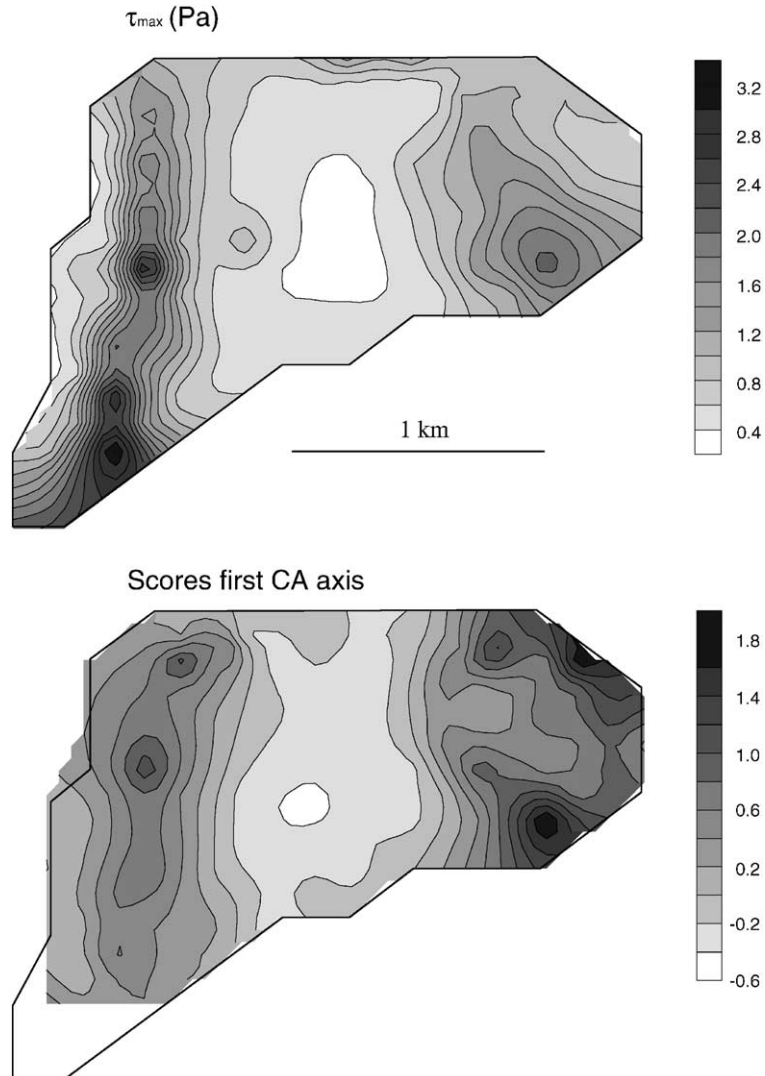


Fig. 3. Spatial pattern of (A) maximal bottom shear stress (Pa) in a tidal cycle as calculated from the hydrodynamic model and (B) first axis of correspondence analysis of fauna (species density, excluding sample points on the extremely dynamic southwest corner of the flat).

muddy area in summer occupies more or less this percentage of the surface, but this may be different on other intertidal flats. Other factors (e.g. runoff cycles, differential sedimentation in salt marshes) will undoubtedly also influence the seasonal cycle. However, this back-of-the-envelope calculation shows that seasonal deposition cycles on intertidal flats may be a significant factor in the mud balance of the estuary. The timing of the average seasonal cycle in suspended matter in the water corresponds well with the field observations on the Molenplaat. We observed little mud accumulation on the sediment in March of several years, but continued to observe

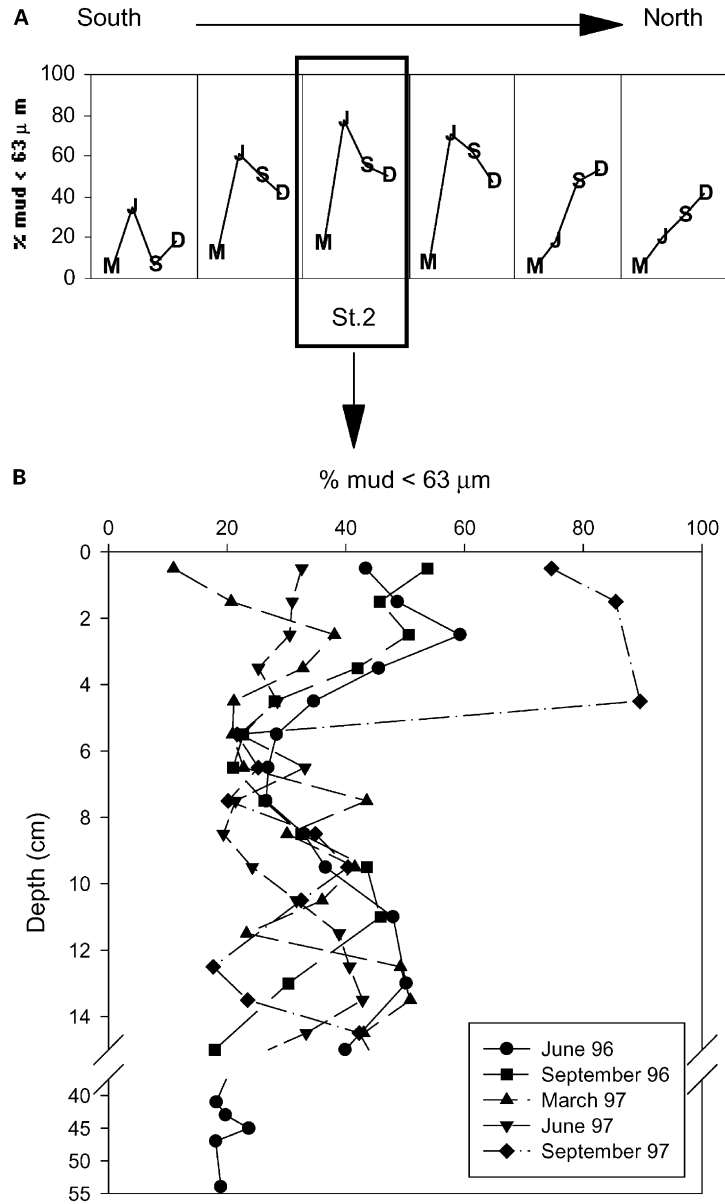


Fig. 4. (A) Temporal evolution of %mud < 63 μm at six stations along transect 'B' in Fig. 1, sampled in March, June, September and December 1995. (B) Depth profile of %mud at station 2, sampled at five occasions in 1996–1997.

muddy sediments throughout December (Fig. 4A). SPM data are highest in January–February, with appreciable decreases only in April–May, and continued low values until December (Fig. 5).

Spot measurements of erodability of the sediment have been made using an annular laboratory flume (Widdows et al., 1998a, b, 2000; Lucas et al., 2000). Sediment sampled on the flat was

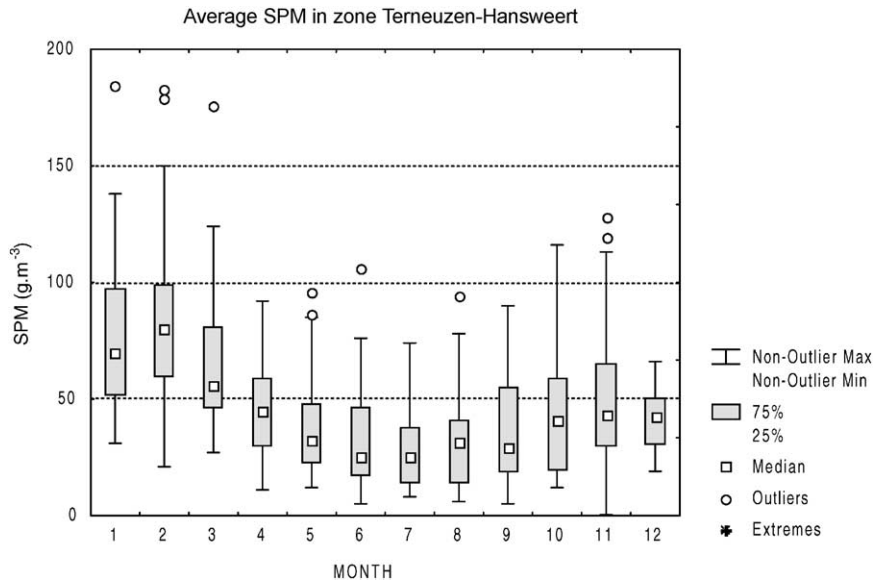


Fig. 5. Long-term average suspended matter concentration in the water column of the Westerschelde in the zone denoted by 'A' in Fig. 1. Data of the regular monitoring of the water quality courtesy of RIKZ, Ministry of Public Transport and Water Management. Data sampled between 1989 and 1998 have been binned per month.

introduced carefully into the flume to minimise disturbance of the surface, and then subjected to varying current velocities. Critical erosion thresholds and mass eroded at different current speeds were determined. Moreover, the quality of the eroded material (POC and PON content, pigment content, grain size) was determined in the experiments. Lucas et al. (2000) compared this to the quality of the material in suspension above the flat. Experimental results showed that the critical erosion threshold was very variable in space and time. It correlated significantly with the presence of biofilms on the surface of the sediment (Widdows et al., 2000). Generally, it was higher in May–June than in September for the same site, corresponding to the development of the biofilms in spring, and the increasing grazing pressure on the microalgae during summer (Barranguet et al., 1998; Lucas and Holligan, 1999; Lucas et al., 2000). Benthic macrofauna, and in particular bivalves, were shown to have two distinct effects on benthic–pelagic exchange (Widdows et al., 2000). Their filtration of suspended matter resulted in biodeposition of fines, thus increasing the flux of material from the water column to the sediment. The bioturbation caused by their movement through the upper sediment layers, and probably also (for *Macoma balthica*) their direct grazing pressure on the microalgae on the sediment surface, resulted in a significant increase of the mass eroded once the critical erosion current velocity had been reached. It is unclear, in the long term, which of the two opposing effects is the most important for sediment dynamics.

The dynamics of the microalgae–mud interaction was studied by van de Koppel et al. (2001). They based a dynamic model on two assumptions, corroborated by field and laboratory measurements during ECOFLAT and by literature reports: microalgal biomass accumulates faster on muddy than on sandy sediments (see also below), and microalgal biomass reduces the

erodability of the sediment. Given these properties, which were translated mathematically into generalised conditions of the type ‘*erosion rate of mud decreases with increasing microalgal biomass*’ without the need to specify the dynamic equations, they showed that the microalgae–mud system has two stable equilibrium states: one with low mud and low microalgal biomass and one with high mud and high microalgal biomass. At high bottom shear stress, only the latter equilibrium is expected to occur; at low shear stress only the former. However, there is an intermediate range of bottom shear stress where both states are possible, and the system may flip from one state to another. Fig. 6 illustrates the existence of these stable states as a function of bottom shear stress. Field data from the Molenplaat, using the modelled bottom shear stress from the hydrodynamic model, confirmed the existence of this intermediate range where the distribution of sediment mud content is clearly and significantly bimodal. The model illustrates the consequences of ecosystem engineering by the microalgae on the dynamics of the system. For at least part of the range of physical forcing, strong positive feedback mechanisms were shown to occur.

2.4. Benthic food web

We observed a strong feedback between sediment granulometry and the structure and functioning of the benthic food web. Hamels et al. (1998) summarised the structure of the biological community at several of the contrasting ECOFLAT stations, with an emphasis on the protist assemblages. It was shown that the microbenthic assemblage had much higher diversity, density and biomass at sandy than at muddy stations. Moens et al. (1999) and Steyaert (pers. comm.) similarly showed that the meiofauna (mainly composed of nematodes) was more diverse and abundant at sandy stations. Moreover, especially at the sandy station 4, the assemblage was dominated by predator/omnivore species. At station 2, which seasonally shifts from sandy to muddy and back to sandy, Hamels (pers. comm.) showed that the microbenthos shifted from a diverse and dense assemblage in winter to a species-poor and low-density assemblage in spring, well correlated with the onset of siltation. Seasonal variations of benthic macrofauna, which are

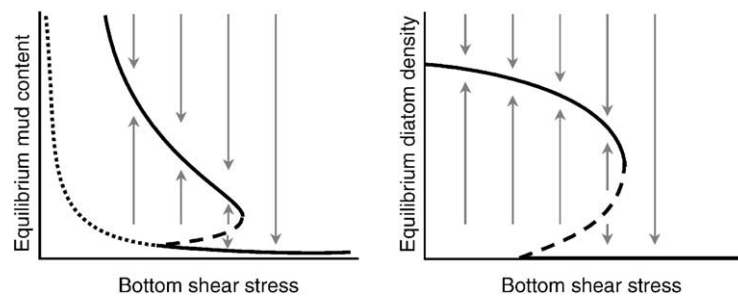


Fig. 6. Dynamics of the mud–microalgae interactions in the model by Van de Koppel et al. (2001). Equilibrium states for mud content and diatom density are shown in bold. Dashed lines indicate unstable equilibrium states, whereas the dotted line for mud content shows the mud content in the absence of microalgae. At intermediate values of bottom shear stress, two alternative stable states occur. Above and below this range of bottom shear stress, only one stable state is possible. Results are semi-quantitative, since the model was formulated only in terms of the qualitative properties of the dynamic interactions. (Reprinted from Van de Koppel et al. (2001) with permission.)

relatively long-lived, showed less dramatic variation. Biomass was higher in autumn than in spring, which is a normal pattern as a consequence of recruitment and growth processes in spring and summer (Ysebaert et al., 2001).

The benthic food web at the Molenplaat stations 2 (muddy) and 4 (sandy) was studied 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). 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. This 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. Mixing of the label into deeper sediment layers was fast at the sandy station. At the muddy station, the label was mixed according to a bioturbation coefficient very similar to the coefficient estimated on the basis of ^7Be distributions. After 3–4 days, the major groups in the benthic food web that were measured (bacteria, meiofauna, macrofauna) attained similar specific labelling levels; the amounts of label incorporated were proportional to their biomass. The study demonstrated 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.

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, the in situ labelling experiment of Middelburg et al. (2000) and a dual labelling flume experiment where planktonic and benthic microalgae were labelled with ^{15}N and ^{13}C , 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.

Our food web studies showed that, even in a mobile, ripple-forming sandy sediment, resuspension of benthic microalgae is relatively limited and that most algal carbon is consumed within the sediment where it is produced. Therefore, resuspended benthic algae are not a major component in the diet of suspension feeders. Although these animals may affect the physical structure of the sediment through bioturbation and biodeposition, they are relatively independent of the rest of the benthic system as far as food sources are concerned. In contrast, deposit feeders depend to a large extent on local benthic microalgal production. The accessibility of the benthic

microalgae for grazers and deposit feeders is a function of the granulometry of the sediment. It is far greater in sandy than in muddy sediments, leading to a higher buildup of microalgal biomass in the finer sediments, which in turn may facilitate the deposition of mud and close the positive feedback loop. Interface feeders (i.e. species switching between suspension and deposit feeding, e.g. *Macoma balthica*) also depend partly on pelagic algae. Biodeposition by suspension feeders, or direct sedimentation of pelagic algae, may be a further source of pelagic algae to deposit feeders. Meiofauna depends heavily on microphytobenthos, at least during spring and summer. Top-down control of benthic microalgae by grazers is stronger in sandy than in muddy sediments. It is a function of meiofaunal, (possibly) protist and deposit feeding macrofauna activities.

3. Discussion and conclusions

The dynamics of the mud–microalgae system at different bottom shear stress conditions, as determined by Van de Koppel et al. (2001), was based on two assumptions. The first, that microalgae stabilise sediments and decrease the erosion rate of mud, has been confirmed by a number of authors (Paterson, 1997; Grant and Gust, 1987; Sutherland et al., 1998) and has also been shown in the ECOFLAT studies using an annular flume (Widdows et al.; 2000, Lucas et al., 2000). Indirectly, the increase of mass eroded as the density of surface deposit feeders increases (Widdows et al., 2000) also lends support to this assumption. The second assumption was equally important: that microalgal biomass accumulates more easily with increasing mud content of the sediment. Van de Koppel et al. (2001) give experimental support for this hypothesis, based on laboratory experiments in flumes with different sediment types. This assumption has been further supported by the field investigations of food web structure at the Molenplaat stations 2 and 4. It was clearly shown by Middelburg et al. (2000) that the major difference between these stations was not in the primary production per unit of biomass and time, but in the biomass of the benthic microalgae. As a consequence, the turnover time (biomass to production ratio) was much lower at the sandy station (1.3–1.6 days) than at the muddy station (9.4–10.9 days). From this study we conclude (1) that biomass was not the prime limiting factor for primary production and (2) that specific loss rates of the benthic microalgae were much greater in sandy than in muddy sediments. Herman et al. (2000) showed that macrobenthic grazers and deposit feeders have a biomass proportional to microphytobenthic production, not standing stock. Their consumption can be estimated at ca. 10% of the microphytobenthic primary production. Protists and meiofauna have a greater density and biomass at the sandy station. Their grazing pressure on the microphytobenthos is very difficult to establish, but it is potentially high. Other losses include resuspension and burial to depths below the photic zone due to sediment mixing. Both are significantly higher at the sandy than at the muddy station. Note that the photic zone is deeper in sandy than in muddy sediments, but that mixing coefficients are orders of magnitude higher in the sandy sediment (e.g. Middelburg et al. (2000) estimate a mixing coefficient for labelled algal carbon of $4\text{ cm}^2\text{ yr}^{-1}$ at the muddy station 2, and $>1000\text{ cm}^2\text{ yr}^{-1}$ at the sandy station 4). All the factors responsible for biomass loss of benthic microalgae are therefore lower at the muddy than at the sandy station. In addition, nutrient resources for growth can be expected to be higher at the muddy than at the sandy station, as mineralisation rates are higher.

These dynamics may easily lead to a situation where accumulation of sufficient mud at the sediment surface leads to enhanced ‘protection’ of the benthic microalgae, further increase of the standing stock, further protection of the sediment surface against erosion, mud accumulation etc. If, however, sufficient mud never builds up, the microalgae are vulnerable to all the loss processes mentioned, are not able to stabilise the sediment and the situation stabilises in a state of low mud content and low microalgal biomass. These differences will also reflect in the species composition of the microalgal assemblage, e.g. the relative dominance of epipelagic and epipsammic forms. It would be interesting to investigate whether, and how, shifts in assemblage composition are a factor in itself causing differences in growth and loss process dynamics.

The effect of the biota on their environment fits the concept of ‘ecosystem engineering’ (Jones et al., 1994). Cohesiveness of the sediment and grazability of the benthic microalgae (which constitute a major primary source of energy to the system) are physical characteristics of the environment that are of major relevance to the fitness of the benthic organisms. It has been argued that a logical consequence of ecosystem engineering is the existence of positive feedback loops, as exemplified by salt marsh systems where the plants influence sedimentation processes and hence survival of the plants (Bertness and Leonard, 1997). Similar mechanisms could be important in intertidal flat systems, albeit in a less conspicuous way. Wilson and Nisbet (1997) made spatially explicit models of this type of interactions. They showed that sharp boundaries between types of ecosystem may develop in the presence of weak environmental gradients. These dynamics may explain, on our intertidal flat, why consistent spatial patterns in the occurrence of high mud percentages with concomitant high microalgal biomass develop. From the model calculations we can show that the muddy area develops where bottom shear stress is minimal (Fig. 3). However, as mentioned before, the model had to incorporate spatially variable bottom roughness in order to predict correctly the current velocity at the different measurement points. Measurements of the logarithmic profile near the sediment at the different sampling points have confirmed these differences in bottom roughness (Twisk, pers. comm.), which are much more pronounced than differences in maximum current velocity at our stations. Using a field minirig, Widdows et al. (2000) measured an approximately similar maximal current velocity at 10 cm above the bed at the different stations.

The ‘explanation’ of the spatial patterns by the difference in bottom shear stress is, therefore, circular: muddy situations develop where bottom shear stress is low, but bottom shear stress is low there mainly because the sediment is muddy and, therefore, hydrodynamically smooth. The question is further complicated by the fact that in winter little or no differences in mud content (and probably also roughness) of the sediments can be observed, since the siltation at the sediment surface is a seasonal phenomenon. Therefore, although siltation and the close microalgae–mud interaction are primarily restricted to the growing season of the microalgae, the question is which mechanism is responsible for carrying over this effect from one year to the next. Basically two options are open. The first is that there are subtle but important differences in the physical forcing, e.g. current velocities falling just short of critical levels in the centre of the intertidal flat and exceeding them at more lateral sites. These differences could be more pronounced in late spring situations when the centre of the flat is still sandy. Due to frictional drag, the greater bottom roughness could slow down currents to a level where deposition overtakes erosion. As the sediment becomes more muddy and the bed smoother, the current velocity could increase, without however exerting a higher bottom shear stress. In this hypothesis the amount of energy dissipated

on the bed in the central part of the flat would remain low in either case. The alternative hypothesis would be that some factors in the biological community prevent the central part of the intertidal flat developing into the sand-type community that persists in the lateral parts. This could be due to either the presence of suspension feeders causing high biodeposition of mud, or to the absence of major bioturbators, such as *Arenicola marina*, that may be able to keep the sediment free of siltation by their frequent reworking of the top layer. Experiments and observations showed that *A. marina* did indeed decrease cohesiveness of the sediment (Jones and Jago, 1993) and that its activity prevented settlement or maintenance of other macrofaunal species (*Corophium*—Flach and Beukema, 1994; Flach, 1992) or seagrass (Philippart, 1994). Goniurriza et al. (1999) report an interesting observation around a wreck that was buried in the sediment at shallow depth (10 cm), preventing the establishment of a local population of *Arenicola* (which was present in the sediment surrounding the wreck) without altering the sediment surface. The sediment without *Arenicola* had a higher percentage of fine particles and a different bacterial population, compared to the surrounding sediment, suggesting that bioturbation activities increased the removal rate of fine particles from the sediment.

We currently have insufficient winter observations to judge the likelihood of either of these hypotheses. However, we suggest that the hypothesis involving suspension feeders is most unlikely. Station 3, situated between stations 2 and 4, usually remains sandy throughout the year, despite its high biomass of suspension feeders (*Mya arenaria* and *Cerastoderma edule*). More field experiments and model runs for winter situations would be needed, however, to evaluate the respective roles of physical forcing and major bioturbators.

Our studies have demonstrated the existence of intense two-way interactions between biological and geomorphological processes on an intertidal flat. The resulting dynamics of the sediment are characterised by the existence of two quite different stable conditions characterised by different biological communities. These communities develop into contrasting situations under weak and gradual physical forcing. Their consequence, however, is probably significant for the mud balance of the estuary. More study at the scale of the estuary is needed to corroborate the causal link in the correlation between seasonal variation in suspended matter concentration and seasonal siltation of (part of) the intertidal flats. If temporal storage of mud on intertidal flats is indeed an important process, one could wonder whether the total availability of mud in the estuary influences the siltation: would a greater availability of mud lead to a higher percentage of the surface of the intertidal flats turning into the ‘muddy’ state? In any case, the positive feedback loops are the cause of major gradients in the benthic community structure and carbon and energy flow through the benthos under subtle physical differences.

Acknowledgements

We thank our colleagues in the ECOFLAT project for their stimulating cooperation that was indispensable for the development of the ideas expressed in this paper. We thank in particular J. Widdows, C. Lucas, P. Holligan, S. Schmidt, T. Moens, M. Steyaert, I. Hamels, W. Vyverman, M. Vincx, F. Twisk, H. Verbeek, P. Meire, T. Ysebaert, P. Thoolen, M. Baptist, C. Barranguet, J. van de Koppel for numerous discussions. Technical assistance was provided by B. Krebs, P. van Rijswijk, A. Sandee, J. Nieuwenhuize, P. Salkeld, M. Brinsley and the crews of the Luctor and the

Zeekat. The paper was substantially improved by constructive comments of R. de Wit, D. Paterson and P. Friend. The ECOFLAT project was supported by the EU Environment and Climate programme (ENV4-CT96-0216) and was part of the ELOISE programme (Publication no. 242). This Review forms part of the Delft Cluster 'Ecomorphology' project. It is Publication No. 2826 of the NIOO-CEMO.

References

- Barranguet, C., Kromkamp, J., Peene, J., 1998. Factors controlling primary production and photosynthetic characteristics of intertidal microphytobenthos. *Marine Ecology Progress Series* 173, 117–126.
- Bertness, M.D., Leonard, G.H., 1997. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78, 1976–1989.
- Bouma, H., Duiker, J.M.C., de Vries, P.P., Herman, P.M.J., Wolff, W.J., 2001a. Spatial pattern of early recruitment of *Macoma balthica* (L.) and *Cerastoderma edule* (L.) in relation to sediment dynamics on a highly dynamic intertidal sandflat. *Journal of Sea Research* 45, 75–93.
- Bouma, H., Duiker, J.M.C., de Vries, P.P., Herman, P.M.J., Wolff, W.J., 2001b. Migration of the bivalve *Macoma balthica* (L.) on a dynamic tidal flat in the Westerschelde estuary, The Netherlands. *Marine Ecology Progress Series*, in press.
- Daborn, G.R., Amos, C.L., Berlinsky, M., Christian, H., Drapeau, G., Faas, R.W., Gran, J., Long, B., Paterson, D.M., Perillo, G.M.E., Piccolo, M.C., 1993. An ecological cascade effect. Migratory birds affect stability of intertidal sediments. *Limnology and Oceanography* 38, 225–231.
- De Deckere, E.M.G.T., van de Koppel, J., Heip, C.H.R., 2000. The influence of corophium volutator abundance on resuspension. *Hydrobiologia* 426, 37–42.
- De Jonge, V.N., van Beusekom, J.E.E., 1992. Contribution of resuspended microphytobenthos to total phytoplankton in the Ems estuary and its possible role for grazers. *Netherlands Journal of Sea Research* 30, 91–105.
- Dekker, L., 1993. Scaldis: modeloriëntatie, randvoorwaarden, beginvoorwaarden en metingen. Rijkswaterstaat internal report. RIKZ, Middelburg, The Netherlands.
- Flach, E.C., 1992. Disturbance of benthic infauna by sediment-reworking activities of the lugworm *Arenicola marina*. *Netherlands Journal of Sea Research* 30, 8–89.
- Flach, E.C., Beukema, J.J., 1994. Density-governing mechanisms in populations of the lugworm *Arenicola marina*. *Marine Ecology Progress Series* 115, 139–149.
- Goniurriza, M., Demontaudouin, X., Guyoneaud, R., Bachelet, G., Dewit, R., 1999. Effect of macrofaunal bioturbation on bacterial distribution in marine sandy sediments, with special reference to sulphur-oxidising bacteria. *Journal of Sea Research* 41, 269–279.
- Grant, J., Gust, G., 1987. Prediction of coastal stability from photopigment content of mats of purple sulphur bacteria. *Nature* 330, 244–246.
- Gurney, W.S.C., Lawton, J.H., 1996. The population dynamics of ecosystem engineers. *Oikos* 76, 273–283.
- Hamels, I., Sabbe, K., Muylaert, K., Barranguet, C., Lucas, C., Herman, P.M.J., Vyverman, W., 1998. Organisation of microbial communities in intertidal estuarine flats, a case study from the Molenplaat (Westerschelde Estuary, The Netherlands). *European Journal of Protistology* 34, 308–320.
- Heip, C.H.R., Goosen, N.K., Herman, P.M.J., Kromkamp, J., Middelburg, J.J., Soetaert, K., 1995. Production and consumption of biological particles in temperate tidal estuaries. *Oceanography and Marine Biology Annual Reviews* 33, 1–150.
- Herman, P.M.J., Middelburg, J.J., van de Koppel, J., Heip, C.H.R., 1999. Ecology of estuarine macrobenthos. *Advances in Ecology Research* 29, 195–240.
- Herman, P.M.J., Middelburg, J.J., Widdows, J., Lucas, C.H., Heip, C.H.R., 2000. Stable isotope labelling experiments confirm the importance of microphytobenthos as food for macrofauna. *Marine Ecology Progress Series* 204, 79–92.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957.

- Jones, S.E., Jago, C.F., 1993. In situ assessment of modification of sediment properties by burrowing invertebrates. *Marine Biology* 115, 133–142.
- Lucas, C.H., Holligan, P.M., 1999. Nature and ecological implications of algal pigment diversity on the Molenplaat tidal flat (Westerschelde estuary). *Marine Ecology Progress Series* 180, 51–64.
- Lucas, C.H., Widdows, J., Brinsley, M.D., Salkeld, P.N., Herman, P.M.J., 2000. Benthic–pelagic exchange of microalgae at a tidal flat. 1. Pigment analysis. *Marine Ecology Progress Series* 196, 59–73.
- Middelburg, J.J., Klaver, G., Nieuwenhuize, J., Wielemaker, A., de Haas, W., van der Nat, J.F.W.A., 1996. Organic matter mineralization in intertidal sediments along an estuarine gradient. *Marine Ecology Progress Series* 132, 157–168.
- Middelburg, J.J., Barranguet, C., Boschker, H.T.S., Herman, P.M.J., Moens, T., Heip, C.H.R., 2000. The fate of intertidal microphytobenthos carbon: an in situ ¹³C labelling study. *Limnology and Oceanography* 45, 1224–1234.
- Moens, T., Van Gansbeke, D., Vincx, M., 1999. Linking estuarine intertidal nematodes to their suspected food. A case study from the Westerschelde Estuary (south-west Netherlands). *Journal of Marine Biology Association of the UK* 79, 1017–1027.
- Paterson, D.M., 1997. Biological mediation of sediment erodibility: ecology and physical dynamics. In: Burt, N., Parker, R., Watts, J. (Eds.), *Cohesive Sediments*. Wiley, Chichester, pp. 215–229.
- Paterson, D.M., Black, K.S., 1999. Water flow, sediment dynamics and benthic biology. *Advances in Ecology Research* 29, 155–194.
- Philippart, C.J.M., 1994. Interactions between *Arenicola marina* and *Zostera noltii* on a tidal flat in the Wadden Sea. *Marine Ecology Progress Series* 111, 251–257.
- Schmidt, S., Reyss, J.-L., Herman, P.M.J., 1999. Sedimentation patterns of a tidal flat in the Westerschelde estuary. In: Kraus, N.C., McDougal, W.G. (Eds.), *Proceedings of the Fourth International Symposium on Coastal Engineering and Science of Coastal Sediment Processes*, Vol. 3, pp. 1927–1935.
- Sutherland, T.F., Grant, J., Amos, C.L., 1998. The effect of buoyant biofilms on the erodibility of sublittoral sediments of a temperate microtidal estuary. *Limnology and Oceanography* 43, 225–235.
- Underwood, G.J.C., Kromkamp, J., 1999. Primary production by phytoplankton and microphytobenthos in estuaries. *Advances in Ecology Research* 29, 93–154.
- Van de Koppel, J., Herman, P.M.J., Thoolen, P., Heip, C.H.R., 2001. Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. *Ecology* 82 (12), 3449–3461.
- Widdows, J., Brinsley, M.D., Elliott, M., 1998a. Use of in situ flume to quantify particle flux (deposition rates and sediment erosion) for an intertidal mudflat in relation to changes in current velocity and benthic macrofauna. In: Black, K.S., Paterson, D.M., Cramp, A. (Eds.), *Sedimentary Processes in the Intertidal Zone*. Geological Society London, Special Publications, 139, pp. 85–97.
- Widdows, J., Brinsley, M.D., Bowley, N., Barrett, C., 1998b. A benthic annular flume for in situ measurement of suspension feeding/biodeposition rates and erosion potential of intertidal cohesive sediments. *Estuarine and Coastal Shelf Science* 46, 2–38.
- Widdows, J., Brinsley, M.D., Salkeld, P.N., Lucas, C.H., 2000. Influence of biota on spatial and temporal variation in sediment erodability and material flux on a tidal flat (Westerschelde estuary). *Marine Ecology Progress Series* 194, 23–37.
- Willows, R.L., Widdows, J., Wood, R.G., 1998. Influence of an infaunal bivalve on the erosion of an intertidal cohesive sediment: a flume and modelling study. *Limnology and Oceanography* 43, 1332–1342.
- Wilson, J.B., Nisbet, R.M., 1997. Cooperation and competition along smooth environmental gradients. *Ecology* 78, 20004–22017.
- Yallop, M.L., Paterson, D.M., Wellsbury, P., 2000. Interrelationships between rates of microbial production, exopolymer production, microbial biomass, and sediment stability in biofilms of intertidal sediments. *Microbial Ecology* 39, 116–127.
- Ysebaert, T., Meire, P., Herman, P.M.J., Verbeek, H., 2001. Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. *Marine Ecology Progress Series*, in press.