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Ecology of Estuarine Macrobenthos

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I. SUMMARY

Macrobenthos is an important component of estuarine ecosystems. Based on a cross-system comparison, we show that estuarine macrobenthos may directly process a significant portion of the system-wide primary production, and that estuarine macrobenthic biomass may be predicted from primary production data. At large scales, food may be the prime limiting factor for benthic biomass. Depending on the characteristics of the system, grazing by benthic suspension feeders may be the most important factor determining system dynamics.

The detailed spatial patterns and dynamics resulting from feeding interactions are discussed separately for suspension feeders and deposit feeders. The theory on local seston depletion and its consequences for spatial distribution of suspension feeders is compared critically with observed patterns of spatial distribution. It is concluded that additional non-linear interactions between

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biomass of the benthos and water currents must exist to explain the observed patterns.

The relation between organic matter deposition fluxes and benthic community structure is discussed in the framework of the classical Pearson–Rosenberg paradigm. The importance of organic matter quality, in addition to quantity, is stressed. A simple model framework to investigate the relation between community structure and quantity of organic flux is proposed.

Internal dynamics of benthic food webs are characterized by a high degree of omnivory (feeding on different trophic levels). This feature is contrasted with published data on food webs in other systems. It is hypothesized that the high quality of marine detritus (compared with terrestrial detritus) is the prime factor explaining the differences. Since theoretical studies suggest that omnivory destabilizes food webs, a number of stabilizing mechanisms in benthic food webs are discussed. Problems and mechanisms that could be explored fruitfully in theoretical studies and field comparisons are identified.

II. INTRODUCTION

Estuaries, in general, are shallow, open and dynamic systems. The small volume of water per square metre of sediment surface, the presence of intertidal flats and very shallow subtidal areas, and the generally well-mixed nature of the water column are physical conditions that intensify the exchange of matter and energy between the water column and the sediment system. In deep, stratified marine systems, the benthos essentially receives the deposits of the pelagic export production and returns nutrients to the deeper water layers. It may take years before these nutrients can be utilized by photoautotrophs again. In estuarine systems, however, pelagic–benthic links are not only quantitatively more important, but also qualitatively different, since the benthos can be responsible for direct grazing on live phytoplankton, recycling of nutrients occurs within a growing season, and there is important *in situ* benthic primary production. Moreover, it is not possible to understand the dynamics, spatial distribution or trophic composition of the benthos without taking into account the general patterns of energy and matter flow in estuarine systems.

According to their size, benthic organisms are classified as microbenthos, meiobenthos and macrobenthos. Microbenthos ($< 32\ \mu m$) is composed of bacteria and Protista. Many bacterial species are simultaneously present in sediments, in guilds that are metabolically dependent on one another. Total bacterial density is typically in the order of 10^9 cells per ml of sediment. The meiofauna (from $32\ \mu m$ to 1 mm) is usually dominated by Nematoda, with densities in the order $10^6\ m^{-2}$ (Heip *et al.*, 1995). Further dominant groups are Copepoda, Ostracoda, Turbellaria and Foraminifera. The macrofauna (> 1 mm) is composed of Mollusca, Polychaeta, Echinodermata, Crustacea and other groups. In estuaries typical densities are in the order of $10^4\ m^{-2}$, and biomass is usually in the range 1–100 g AFDW m^{-2} (AFDW = ash-free dry weight) (Heip *et al.*, 1995). Variability in macrofauna biomass of two to three orders of magnitude is typically found within most estuarine systems.

Extensive research has been conducted on the feeding habits of many macrofaunal species. Classifications of macrofaunal species into feeding groups have been made (e.g. Fauchald and Jumars, 1979) but considerable debate remains about these classifications. For many species, sufficient autoecological information is lacking. However, the accumulation of autoecological information for some species has rendered proper feeding group classification an even more difficult task. In this review, we will argue that the qualitative composition of the food of benthic animals fosters omnivory and generalism as a general strategy, precluding the use of a too narrow feeding group classification. We will, however, make a general distinction between two major feeding types: (1) *suspension feeders*, which filter their food directly from the water column, and (2) *deposit feeders*, which depend on the physical deposition of food particles on to the sediment surface, and (for "deep-deposit feeders") the subsequent incorporation of the food particles into the sediment matrix. Water and sediment have dramatically different properties for animals that want to extract food particles from them, and because of this we expect different processes to regulate the occurrence and dynamics of both groups. Again, individual species may show varying degrees of generalism, as is the case for "interface feeding" spionid polychaetes (Dauer *et al.*, 1981; Taghon and Greene, 1992).

In this review, we argue that the benthos is responsible for a large and predictable part of total system metabolism in estuaries, and that food is an important limiting and structuring factor in benthic communities. The particular characteristics of the sediment surface as a boundary layer and of the sediment as a habitat have consequences for the dynamics and spatial distribution of benthic communities, which we try to generalize. Our hope is that increased insight into the physical, geochemical and biological processes controlling benthic communities will facilitate the interpretation of community characteristics, spatial distribution and temporal evolution of benthic communities.

Macrofauna is an important food resource for epibenthic crustaceans, fish and birds. Humans also harvest many species of shellfish and crustaceans. Evaluation of the consequences of anthropogenically induced changes in a system will likely include the possible responses of the benthos. Moreover, the benthos is often monitored as an indicator of possible changes in the system. Being fixed in place and relatively long lived, the benthos integrates environmental influences at a particular place over a relatively long timespan. For the purposes of predictive modelling, and also for the *post hoc* interpretation of changed patterns of occurrence and altered community composition in monitoring studies, insight into the processes governing the temporal and spatial dynamics of benthic populations is needed. For this insight, we believe a consideration of the dynamics of the interaction between the benthos and its food is essential.

A. The Importance of System Dynamics for Macrobenthos

Heip *et al.* (1995), extending previous data compilations by Nixon (1981), 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 mineralized in the sediment. The relation is given by the equation

$$\log_{10}(F) = 1.6 - 0.0146H \qquad (1)$$

where F is the percentage of the system mineralized 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 time^{-1}). An estimate of the latter, taking degradability constants around 20 year^{-1} for fresh phytoplanktonic material (Westrich and Berner, 1984; Middelburg, 1989), is in the order or 2–3 m day^{-1}. This is an estimate for net effective sinking speed, taking into account the effects of resuspension cycles.

Drawing on the relation of eqn.(1), an order-of-magnitude estimate for sediment mineralization in shallow estuaries can be made. The fraction mineralized in shallow systems (approximately 10 m) is around 60% of the total primary production. Taking an estimate for yearly primary production of about 200 g C m^{-2} year^{-1}, one would arrive at approximately 120 g C m^{-2} year^{-1} for sediment mineralization. Direct observations on benthic mineralization rates show considerable variability. Heip *et al.* (1995) summarized values for 14 estuarine systems, estimated either from CO$_2$ production rates or O$_2$ consumption rates. Excluding the deep St Lawrence estuary, these values vary between 31 and 392 g C m^{-2} year^{-1}, with a median of 120 g C m^{-2} year^{-1}. Adding recently published values (Kristensen, 1993; Roden *et al.*, 1995; Middelburg *et al.*, 1996; Caffrey *et al.*, 1998; Rocha, 1998) and our own unpublished data for CO$_2$ production on a tidal flat in the Westerschelde, we obtain a total of 33 sites, with the frequency distribution shown in Figure 1A. The median value for this data set, which is probably biased by intertidal Westerschelde sediments, is 181 g C m^{-2} year^{-1}. The higher values in the data set typically come from estuaries (e.g. Westerschelde) with high exogenous carbon input.

It is difficult to establish which fraction of the carbon mineralized 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 from a representative sampling of the different strata in the system. From the median figures on macrobenthic biomass and benthic mineralization it can, however, be qualitatively deduced that this fraction is not insignificant. Taking a median biomass of 15 g AFDW m^{-2} (Figure 1B), a carbon : AFDW ratio of 0.5, an annual production/biomass ratio (P/B) of 2 year^{-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 25 g C m^{-2} year^{-1}, which constitutes around 15–20% of the median total respiration of the sediment. This estimate at the system scale is very similar to that based on concurrent biomass and sediment respiration data from single stations (Dauwe *et al.*, 1999b).

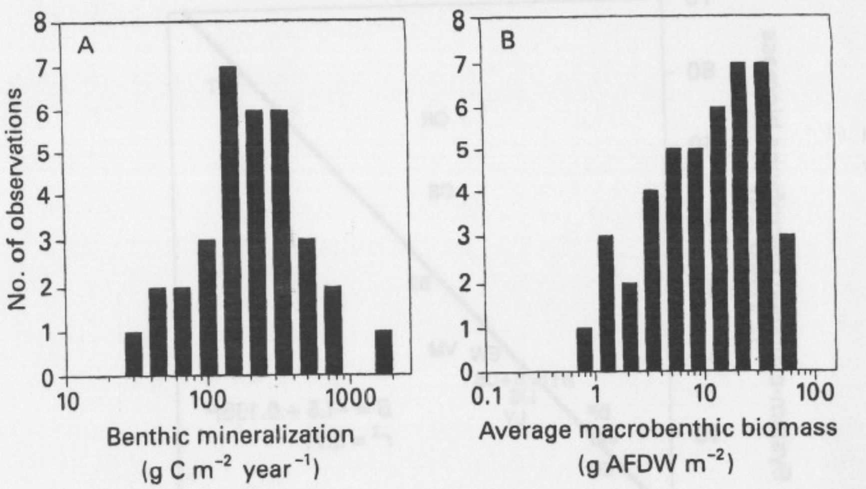

Fig. 1. Frequency distribution of observations of (A) total sediment mineralization (measured as either total inorganic carbon production or oxygen consumption) and (B) system-averaged benthic biomass. Most observations are listed in Tables 23 and 29 of Heip *et al.* (1995); for (A) additional data have been taken into account (see text).

Parsons *et al.* (1977) showed a dependence of system-averaged benthic biomass on the magnitude of the spring phytoplankton bloom. This relation strongly suggests dependence between benthic biomass and pelagic primary productivity. In Figure 2 we assemble data on benthic biomass and system productivity. For the systems in the SW Netherlands (Westerschelde, Grevelingen, Oosterschelde and Veerse Meer; see Heip (1989) and Nienhuis (1992) for a description of the systems), benthic biomass was averaged from the large database available at the Netherlands Institute of Ecology. For other systems we relied on published estimates. Both our own data and the published results are not necessarily true system biomass averages, because

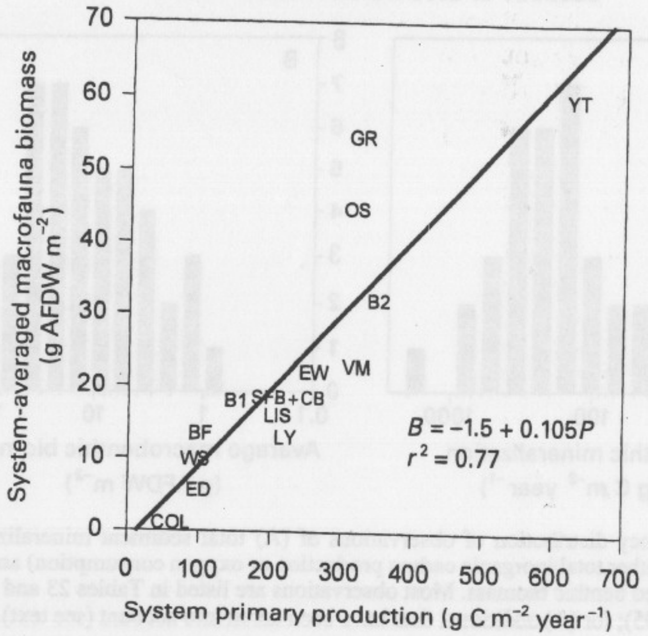

Fig. 2. Relation between system-averaged macrobenthic biomass and primary productivity of shallow well-mixed estuarine systems. Data points are indicated by the abbreviation of the name of the system. The regression line is a predictive linear least-squares line. System abbreviations and sources are: YT, Ythan estuary (Baird and Milne, 1981); GR, Grevelingen (benthic data from the authors' own database; primary production from de Vries, 1984); OS, Oosterschelde (benthic data from the authors' own database; primary production from Wetsteyn and Kromkamp, 1994); B1, Balgzand (Dutch Wadden Sea) in the 1970s (Beukema and Cadée, 1997); B2, Balgzand (Dutch Wadden Sea) in the 1980s (Beukema and Cadée, 1997); VM, Veerse Meer (benthic data from the authors' own database; primary production from Nienhuis, 1992); EW, Ems estuary near the Wadden Sea (benthic biomass from Meire *et al.*, 1991; primary production from Baretta and Ruardij, 1988); ED, Ems estuary, inner part ("Dollard") (benthic biomass from Meire *et al.*, 1991; primary production from Baretta and Ruardij, 1988); SFB, San Francisco Bay (benthic biomass from Nichols, 1977; primary production from Cole and Cloern, 1984); LY, Lynher estuary (Warwick and Price, 1975); WS, Westerschelde (benthic data from the authors' own database; primary production from Soetaert *et al.*, 1994); BF, Bay of Fundy (Wildish *et al.*, 1986); COL, Columbia River estuary (Small *et al.*, 1990); LIS, Long Island Sound (benthic biomass from Parsons *et al.*, 1977; primary production from Riley, 1956, cited in Sun *et al.*, 1994); CB, Chesapeake Bay (benthic biomass from Dauer, 1993; primary production from Harding *et al.*, 1986).

of bias in the sampling scheme. The same may be true for the primary production data, which in principle are net annual primary production figures including microphytobenthos and macrophytobenthos production, but in practice may more or less deviate from this ideal, depending on the data

available. The resulting relation suggests that for these shallow estuarine systems between 5% and 25% of the annual primary production is consumed by macrobenthos respiration. On a system-averaged basis, suspension feeders are often the dominant component (with respect to biomass) of estuarine benthic assemblages. Their contribution to benthic biomass is 41%, 74%, 82% and 81% for the Westerschelde, Oosterschelde, Veerse Meer and Grevelingen data sets respectively. Suspension feeders are, both in absolute and relative terms, less dominant in the turbid Westerschelde, Ems-Dollard and Columbia River estuaries, all three of which are at the low end of the production spectrum. However, suspension feeders contribute 86% to the total benthic production in the Bay of Fundy, which is not very much more productive than the Westerschelde (Wildish *et al.*, 1986).

Suspension feeders typically occur in much higher local biomass than deposit feeders, which are much more equally spread over (generally lower) biomass classes (Figure 3). In the Oosterschelde, over 75% of the total biomass of suspension feeders was found at local biomass values of more than

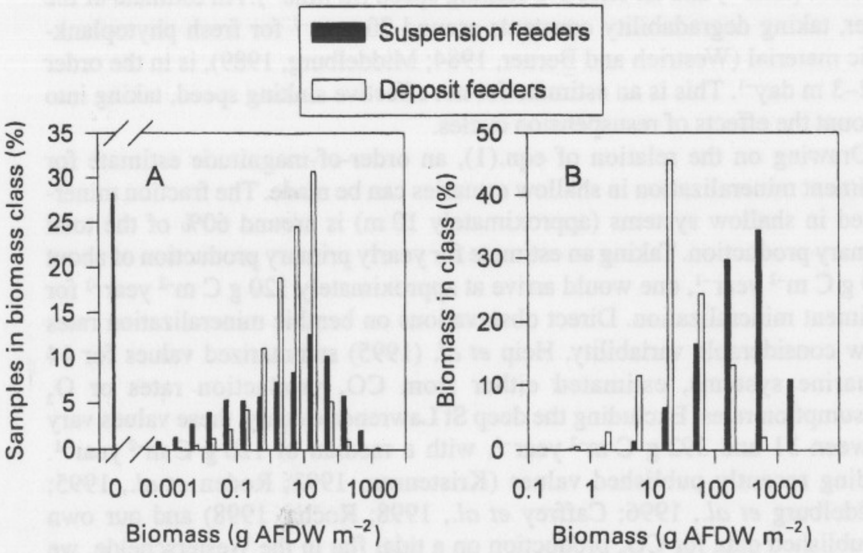

Fig. 3. (A) Frequency distribution of suspension and deposit feeder biomass in the Oosterschelde ($n = 2368$, data collected between 1990 and 1998) over logarithmic biomass classes. Suspension feeders are absent from a large number of samples and occur more frequently in very high local biomass classes. (B) Percentage of the total recorded biomass found at local biomass values in logarithmic classes. More than 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.

100 g AFDW m^{-2} (Figure 3B), whereas 53% of the samples contained less than 1 g AFDW m^{-2} of suspension feeders (Figure 3A) and 28% of the samples contained no suspension feeders at all (Figure 3A). For deposit feeders, only 15% of the system biomass was found at local biomass values of more than 100 g AFDW m^{-2} (Figure 3B) but only 20% of the samples contained less than 1 g AFDW m^{-2} of deposit feeders and there were virtually no samples without deposit feeders (Figure 3A).

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 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 Skaggerak-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.

Heip *et al.* (1995) showed a dependence of total system biomass of commercial benthic suspension feeders on the 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 *et al.* (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. However, they identified systems (Delaware Bay and Chesapeake Bay, notably) where relations based on residence time and on primary production seriously overestimate the relative importance of benthic filter feeders. As argued by Dame and Prins (1998), this may have historical reasons in overfishing or eutrophication. In detailed ecosystem models of Marennes-Oléron and Carlingford Lough, Bacher *et al.* (1998) demonstrated the importance of physical transport and advection of food into coastal bays for the carrying capacity of bivalve filter feeders. In Marennes-Oléron, which is open to the import of phytoplankton from coastal waters, the carrying capacity is far higher than in Carlingford Lough.

The general conclusions are that a substantial fraction of the carbon flow in estuarine systems passes through macrobenthic populations, and that therefore macrobenthic populations at a system level may be limited by food fluxes to the sediments.

B. The Importance of Macrobenthos for System Dynamics

Deposit feeders transport particles and fluid during feeding, burrowing, tube construction and irrigation activity (Rhoads, 1974; Aller, 1988; Aller and Aller, 1998). By enhancing transport of (labile) particulate organic carbon to deeper sediment layers, these organisms stimulate anaerobic degradation processes and so can affect the form and rate at which metabolites are returned to the water column. Bioturbation causes an upward movement of reduced components such as sulfides, as a consequence of which rates of sedimentary oxygen uptake are higher and not necessarily coupled directly to organic carbon oxidation (Aller, 1994). As a result, there may be temporal uncoupling between benthic oxygen uptake and nutrient regeneration. Enhanced exchange between overlying water and pore fluids has consequences for sedimentary oxygen uptake, the extent that aerobic processes contribute to organic matter oxidation, the efficiency of reoxidation of reduced substances and the fraction of nutrients produced that escapes the sediments (Aller, 1988; Aller and Aller, 1998). The effect of bioturbating infauna on the benthic cycling of nitrogen, in particular the coupling between nitrification and denitrification, has been studied intensively (Aller, 1988; Pelegrí *et al.*, 1994; Rysgaard *et al.*, 1995). This loss of (fixed) nitrogen from estuaries due to benthic denitrification directly influences the availability of this limiting nutrient for phytoplankton production.

The importance of macrobenthic suspension feeders for total system dynamics has been the subject of a number of model studies. Officer *et al.* (1982) used an idealized Lotka–Volterra modelling approach to show that equilibrium between benthic suspension feeders and phytoplankton is reached when the grazing time-scale (τ_g) equals the production time-scale (τ_p):

$$\tau_g = \frac{H}{RB} = \tau_p = \frac{1}{\mu_p} \qquad (2)$$

in which H is system water depth (m), R is specific clearance rate of the benthos (m^3 g^{-1} day^{-1}), B is benthic biomass (g m^{-2}), and μ_p is specific phytoplankton net growth rate (day^{-1}). For this equilibrium to be reached at low phytoplankton biomass (a few milligrams of chlorophyll per cubic metre), the system must be shallow (a few metres) and benthic biomass relatively high (in the order of 100 g total fresh weight m^{-2}). This is a realistic situation for many well-mixed tidal estuaries. Using an ecosystem simulation model, Herman and Scholten (1990) showed how grazing by benthic suspension feeders effectively controls phytoplankton in the Oosterschelde. Herman (1993) extended the argument to show that the open nature of estuarine systems is essential: when nutrients accumulate in a system without effective removal mechanisms, one would expect ever-increasing levels of phytoplankton under eutrophication, despite high grazing pressure. Koseff *et al.* (1993) modelled the conditions under which phytoplankton can develop a bloom in the presence of benthic suspension feeders. In contrast to Officer *et al.* (1982), they explicitly included vertical mixing in the water column as a critical process. In non-stratified waters the possibility for a bloom depends in a non-linear way on two non-dimensional ratios of time scales: α' and K'. α' is the ratio of the production time-scale (τ_p) to the grazing time-scale (τ_g), essentially defined as in eqn. (2), but with vertical averaging of the phytoplankton growth rate, as this model explicitly resolves the vertical dimension. K' is defined as the ratio of the production time-scale to the vertical (turbulent) mixing time-scale H^2/K, where H is water depth and K is the turbulent diffusion coefficient. The possibility for the development of a bloom depends on the details of the model versions, but is qualitatively different in only two cases: when vertical sinking velocity exceeds a certain threshold, or when stratification develops. The most general case for a non-stratified system, with a vertically variable turbulent mixing coefficient depending on tidally varying current velocity and a moderate phytoplankton sinking velocity, is illustrated in Figure 4. Benthic grazing can limit bloom development provided that both K' values are high (vigorous vertical mixing and shallow water) and grazing is sufficiently intense compared with primary production (high α').

Lucas *et al.* (1998) investigated the role of stratification for this type of model in much more detail. With respect to the influence of benthic grazing on the occurrence of phytoplankton blooms, their results are qualitatively similar to those of Koseff *et al.* (1993): as soon as even a mild form of permanent vertical stratification affects the system, benthic grazing rates are no longer a major factor to be considered for the prediction of blooms. Benthic grazing is especially important in shallow well-mixed systems, although under favourable conditions of light and stratification, it may also be significant in deeper water columns of the order of 15 m.

The mechanisms relating macrobenthic energy flow to system productivity operate on a much smaller temporal and spatial scale than the scale of the system at which the correlation is observed. How do macrobenthic animals sequester their food, how do they influence the total flux rate of organic matter to the sediment, and what determines their share of the resources? These questions require the study of spatial and temporal distributions of physical, chemical and biological variables within the system. Numerous factors potentially influence the spatial distribution of benthic animals in estuarine systems (see Dame, 1996, for an extensive review on suspension feeders). We will concentrate our discussion here on food. If food limitation sets the constraints for the system-integrated biomass of benthic animals, then a number of predictions can be made about the spatial distribution pattern of macrobenthos, based on the characteristics of the animals and of estuarine pelagic–benthic exchange.

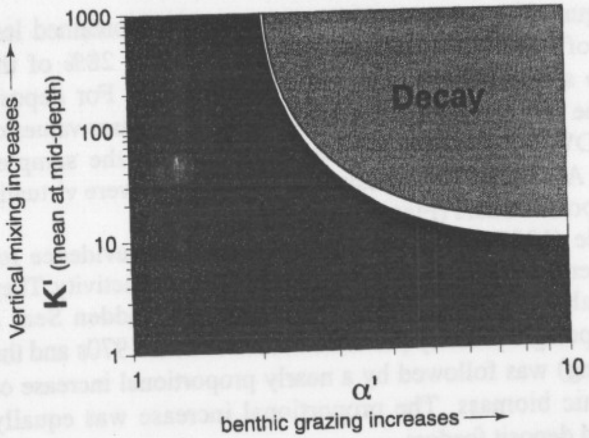

Fig. 4. Influence of (non-dimensionalized) benthic grazing and vertical mixing on the possibilities for the development of a bloom in a shallow tidal estuary. α' is the ratio of the grazing to the phytoplankton growth time scales. K' is the ratio of the production time-scale to the vertical mixing time-scale (see text for details). This figure summarizes model runs with tidally varying current velocity and vertically varying turbulent mixing. Parameter regions where blooms consistently develop are separated from regions where the phytoplankton decays by a transition zone characterized by oscillations in time. Adapted from Koseff *et al.* (1993).

In principle, the situation is different for benthic suspension feeders and deposit feeders. Suspension feeders have direct active access to pelagic production. In well-mixed estuaries, all suspension feeders are consequently to a certain extent in competition with one another (and with the pelagic herbivores), since their food resource is continuously redistributed over space, and food not taken by one animal remains available to the others. In contrast, deposit feeders are restricted to the food items deposited in a limited volume of sediment, even though they can also influence the sedimentation flux through their bioturbation (see section IV.B).

III. SPATIAL DISTRIBUTION AND DYNAMICS OF SUSPENSION FEEDERS

A. The Sediment Surface as a Boundary Layer

Due to the mixing and the general availability of the food resources, one can assume that the biomass of suspension feeders will be distributed over space according to the suitability of the sites for capturing food. The best studied aspect (see Wildish and Kristmanson, 1997, for a recent review) of suitability is the relation with water flow velocity and, linked with that, vertical turbulent mixing of the water column. The filtration capacity of suspension feeders is high (several litres per hour for a 1g AFDW animal), the animals can occur locally in high biomass (several hundreds of g AFDW m^{-2}), and they are restricted to filtering the lowermost water layers. Consequently, the probability of refiltering previously filtered water increases with increasing local biomass. This may lead to local food depletion in the lower part of the water column, an effect that is counteracted only by vertical turbulent mixing. The latter effect is current dependent, since turbulence is generated by shear near the bottom.

In one (vertical) dimension, the concentration of a substance, say food particles, in the water is governed by an advection–diffusion–reaction equation

$$\frac{\delta C}{\delta t} = \frac{\delta}{\delta z}\left(K_z \frac{\delta C}{\delta z}\right) - \frac{\delta}{\delta z}(wC) + \text{sources} - \text{sinks} \qquad (3)$$

where C is the concentration of the substance, t is time, z is the vertical coordinate, K_z is the depth-dependent turbulent mixing coefficient, w is the sinking rate, and sources and sinks are biological production or consumption reactions.

This equation can readily be extended to two (e.g. Verhagen, 1986; Fréchette *et al.*, 1989) or three dimensions, but we will concentrate here on the vertical dimension only. Eqn. (3) can be solved analytically or numerically to yield time- and depth-dependent values of the concentration, given appropriate boundary conditions and, for time-dependent solutions, initial conditions (e.g. Crank, 1986; Boudreau, 1997).

The depth-dependent values of K_z are of prime importance for the flux of food particles to benthic consumers. Mixing is generated by the generation of turbulent eddies from the shear (vertical gradient) near the bottom. The eddy diffusivity is characterized by a turbulent velocity scale and a length scale. In estuaries, the friction velocity u^* and the water depth H are used for these parameters. Using the logarithmic law velocity profile for flows with only one source of turbulence (the bottom shear), the vertical mixing coefficient for momentum and mass transport is then given by

$$K_z = \kappa u^* z\left(1 - \frac{z}{H}\right) \qquad (4)$$

where κ is the von Karman constant (approximately 0.4), H is water depth and u^* is the friction velocity. This friction velocity is given by the relation

$$u(z) = \frac{u^*}{\kappa} \ln\left(\frac{z}{z_0}\right) \qquad (5)$$

which describes the logarithmic profile of current velocity $u(z)$ as a function of distance to the bed. The parameter z_0, the roughness height, corresponds to the height above the bed where the extrapolated current velocity drops to zero. For rough turbulent flow, z_0 is determined by the height k_s of the roughness elements on the bed, with the approximate relationship $z_0 \approx k_s/30$. The friction velocity u^* is related to the bottom shear stress, a tangential force per unit area responsible (when a critical threshold is exceeded) for the movement of particles on the bed, by

$$\tau_0 = \rho(u^*)^2 \qquad (6)$$

where ρ is the density of water. Since for every height in the water column $u(z)$ is proportional to u^*, with a proportionality coefficient dependent on height z (eqn (5)), the bottom shear stress can also be expressed as a quadratic function of $u(z)$ at a particular height. Conventionally, a height of 100 cm is used, with the relation

$$\tau_0 = \rho C_{100}\,(u_{100})^2 \qquad (7)$$

where u_{100} is the velocity at 100 cm from the bed, and C_{100} is the drag coefficient at 100 cm. From the equations above, it can easily be derived that

$$C_{100} = \frac{\kappa}{\ln(100/z_0)} \qquad (4)$$

B. Seston Depletion Above Suspension Feeder Beds

Wildish and Kristmanson (1979) have solved eqn. (3), while assuming steady state, neglecting particle sinking and production/consumption terms (except for the consumption of food by the benthos at the lower boundary) and adopting an average mixing coefficient (K_z) linearly related to the free-streaming current velocity. Under these assumptions, and taking typical values for the coefficients, the vertical flux of food (NA) at the lower boundary is given by

$$NA = \gamma u_{\text{free}}\,(C_0 - C') \qquad (9)$$

where γ is a dimensionless hydrodynamic parameter related to bottom roughness, for which Wildish and Kristmanson give a value of 0.003, u_{free} is the current velocity at the top of the benthic boundary layer in m h^{-1}, C_0 is the upstream food concentration in g m^{-3} and C' is the effective food concentration at the intake in g m^{-3}.

This vertical flux of food is actually the food flux to the benthic grazers at the lower boundary of the model. It is the food that is actively filtered from the water. It can, therefore, also be expressed in terms of the suspension feeder biomass, its clearance rate and the effective food concentration

$$NA = BR\alpha C \qquad (10)$$

where NA is the food flux in g m^{-2} h^{-1}, B is the biomass of suspension feeders in g m^{-2}, R is the clearance rate per gram of biomass in m^3 g^{-1} h^{-1}, and α is the filtration efficiency (dimensionless). From eqns (9) and (10), the following equation can be derived.

$$\frac{(C_0 - C')}{C'} = \frac{BR\alpha}{\gamma u_{\text{free}}} \qquad (11)$$

in which the right-hand side is a dimensionless measure called the seston depletion index (SDI; Wildish and Kristmanson, 1997). It is the ratio of the filtration capacity to the turbulent mixing intensity. When it exceeds a certain threshold value, depletion effects can be assumed to occur.

Eqn (11) can be considered as a first-order approximation to the problem of seston depletion by suspension feeders. Verhagen (1986) and Fréchette *et al.* (1989) have presented more elaborate analytical and numerical solutions, including solutions of the two-dimensional problem. They show how the depletion effect gradually builds up as the current flows over a dense bed of suspension feeders, leading to relatively more favourable conditions at the edge of the bed. After several metres in the bed, the vertical distribution of food is reasonably described by eqn (11) (Wildish and Kristmanson, 1997).

Assuming that a minimum (fixed) value of C' is needed for growth and survival of the organisms, several conclusions can be drawn from this equation. For a fixed C' and a fixed C_0, the maximum allowable filtration capacity of the animals will increase linearly with current velocity if the roughness of the bottom is uniform. It will increase more steeply over rougher surfaces, which is important because the animals themselves may contribute considerably to the roughness (Green *et al.*, 1998; O'Riordan *et al.*, 1995). In systems with different "background" food concentrations' C_0, the maximum filtration capacity will be higher in the more productive systems. With species differing in their specific filtration capacity, those that filter more actively will be limited at a lower biomass than the less active ones.

In estuarine systems, omission of the advective term in eqn (3) (i.e. the term representing the sinking of the food particles) is not always warranted. Figure 5 illustrates the differences in sedimentation and resuspension patterns of chlorophyll between a tidal flat in the Westerschelde (total suspended matter (SPM) 80–250 mg l^{-1}) and one in the

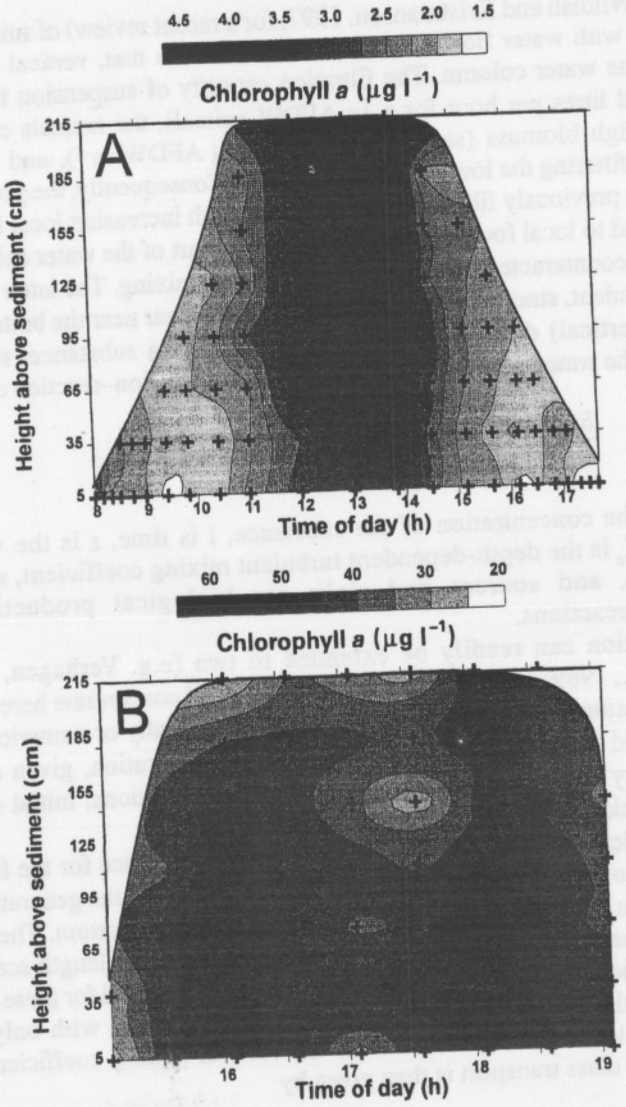

Fig. 5. Concentration contours of chlorophyll *a* in suspended matter during a tidal cycle over tidal flats in two estuaries differing in the total suspended matter concentration. Concentrations are expressed as a function of time of day (abscissa) and height above the sediment (ordinate). Crosses denote positions of samples in space and time. (A) Tidal cycle on a flat in the Oosterschelde, in the immediate vicinity of a mussel bed. (B) Tidal cycle on the Molenplaat (Westerschelde) near the centre of the flat. See text for discussion.

Oosterschelde (SPM 2–12 mg l^{-1}), which is in the vicinity of a large mussel bed. In the Westerschelde, the pattern is dominated by a pattern of resuspension and sedimentation, as shown by the maxima at flooding and ebbing tide, when the current velocity is at maximum. The vertical gradient is towards higher concentrations near the bottom, and there is a good correlation between total SPM and suspended chlorophyll *a* in the water. In the Oosterschelde, chlorophyll *a* concentration is highest at flood (when grazing pressure per unit volume of water is minimal), sedimentation–resuspension intensity is limited, concentration of chlorophyll *a* is lower near the bottom and there is no correlation between SPM and chlorophyll *a*. The pattern can be interpreted when taking into account the relatively high SPM content of the Westerschelde. With increasing SPM content of the water, a number of correlated processes might be expected to occur: (1) the productivity of the pelagic algae decreases due to light limitation; (2) as a consequence total system biomass of suspension feeders will be relatively low; (3) flocculation processes involve both inorganic and organic particles, and will tend to co-precipitate algae with SPM, thus increasing net sinking speeds of algae; (4) resuspension–resedimentation cycles will be more intense; and (5) highest above-sediment concentrations of algae may be expected at places that have the strongest sedimentation rates, i.e. those with relatively low current velocities. This pattern was indeed apparent in the Westerschelde data on the tidal flat "Molenplaat" (Figure 6). The highest biomass of suspension feeders (in fact, nearly all suspension feeders found on the flat) was in the centre of the flat, where maximum tidal current velocity was minimal, as was the maximum bottom shear stress over a tidal period.

Consideration of food depletion sets a current-dependent upper limit to the biomass of suspension feeders, as it essentially describes a negative density-dependent effect that is spatially variable. If food depletion were the major factor governing the spatial distribution of suspension feeders, they would be predicted to follow an ideal-free distribution (Sutherland, 1996), i.e. they would be distributed such that everywhere a similar C' is reached. This would lead to a linear dependence between biomass and current velocity. Food depletion theory does not describe an upper limit of current velocity for suspension feeders. Although the direct negative physiological effects of too high currents have been described (Wildish and Kristmanson, 1993), such a description is not available for many species of suspension feeders and its generality, therefore, remains to be tested. It seems logical, however, to assume that stability of the sediment bed, which becomes more vulnerable to resuspension as current velocity increases, sets the upper limit. In fact the critical parameter for the resuspension of particles is the bottom shear stress (Hall, 1994), which increases with the square of the current speed (eqn (6)).

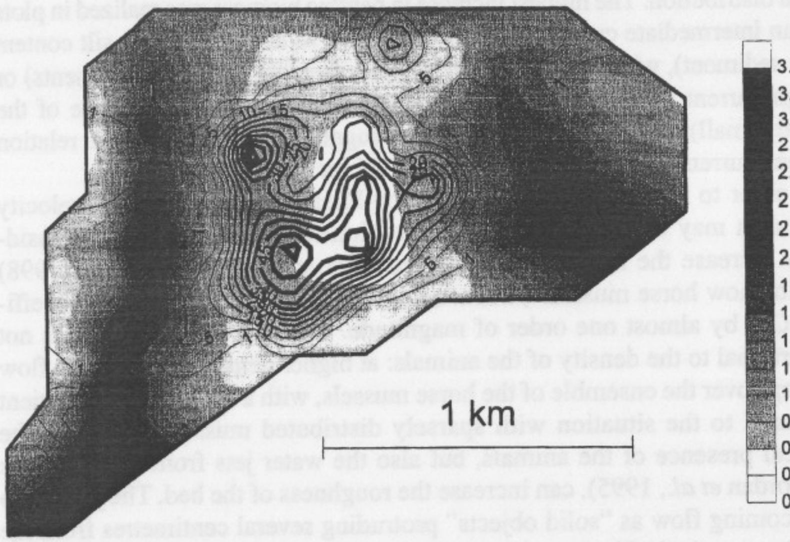

Fig. 6. Spatial distribution of suspension feeders (mainly *Cerastoderma edule* and *Mya arenaria*) on the Molenplaat, Westerschelde, as a function of bottom shear stress. Grey shades depict contours of modelled maximum bottom shear stress during a tidal cycle (Pa), isolines depict biomass (g AFDW m^{-2}) of suspension feeders. Suspension feeders are concentrated in areas of low shear stress on this flat.

C. Seston Depletion and Non-linear Density–current Relations

Is food depletion theory, combined with erosion of animals from the bed, setting an upper limit to current velocity, sufficient to predict the spatial distribution of benthic suspension feeders? Most field validations have been made on reef-building species (e.g. mussels and oysters). Extensive reviews of these studies are given in Wildish and Kristmanson (1997) and Dame (1993, 1996). These animals typically occur in dense patches, up to more than 1 kg of AFDW per square metre, which naturally leads to measurable food depletion in nature, but the occurrence of these patches is at odds with predictions from seston depletion equations. In fact, maximum density is predicted to vary linearly with average current velocity, which in estuarine systems has a range of about one order of magnitude only. This poses a serious problem of interpretation of field results. Wildish and Kristmanson (1993), for example, found an empirical relationship between the logarithm of suspension feeder production and average water column current velocity, which implies an order-of-magnitude increase of production for an increase of current velocity by only 0.2 m s^{-1}.

Beukema and Cadée (1997) showed that the increase of benthic biomass with increased primary production in the Balgzand area did not show a homogeneous spatial distribution. The highest increase in benthic biomass was realized in plots with an intermediate current velocity (measured as an intermediate silt content of the sediment), whereas in low current velocity plots (very fine sediments) or in high current velocity plots (very coarse sediments) no real increase of the (already small) biomass was recorded. This suggests a highly non-linear relation between current velocity and growth potential for the populations.

In order to resolve this problem of non-linearity of the biomass–velocity relation, it may first be noted that suspension-feeding animals may considerably increase the roughness of the sediment surface. Green *et al.* (1998) describe how horse mussels (*Atrina zelandica*) may increase the drag coefficient C_{100} by almost one order of magnitude. This increase, however, is not proportional to the density of the animals: at higher densities, skimming flow develops over the ensemble of the horse mussels, with a lower drag coefficient compared to the situation with sparsely distributed mussels. Not only the physical presence of the animals, but also the water jets from their siphons (O'Riordan *et al.*, 1995), can increase the roughness of the bed. The jets act to the incoming flow as "solid objects" protruding several centimetres from the bed. On an actively filtering mussel bed in a flume, L. van Duren (unpublished findings) measured an increase of bottom roughness of two orders of magnitude compared with a flat bed. This increase was significantly affected by filtration of the animals. Hence, these animals can significantly affect their food supply through affecting their physical environment. The spatial distribution of the animals in clumps and boulders with empty or sparse patches in between can further enhance the bottom roughness (Fréchette *et al.*, 1989). More detailed measurements and modelling should clarify the importance of these structural characteristics for vertical turbulence and hence food supply.

The disadvantages of a clumped spatial distribution for food gathering may be offset by a number of biological processes which may be advantageous or simply inevitable. Protection against (bird) predation by oversaturating predators could be such a mechanism. Several bird species foraging on benthic suspension feeders have interference mechanisms that depress their intake rate when foraging on favourable beds with high density of food (e.g. Ens and Goss-Custard, 1984). Clumped distributions will then lead to a decrease in mortality risk per prey individual. Reducing the risk of erosion by currents may also be an important factor. At least in reef-building species such as mussels or oysters, the critical value for resuspension may depend on animal density. Densely covered mussel beds with their sediment structure full of empty shells are much more resistant to erosion than sand without animals or shells. (Nehls and Thiel, 1993).

By affecting physical conditions and predation pressure, suspension feeders may induce positive feedback between enhanced suspension feeder density and enhanced survival or growth. Positive feedbacks are considered a major influence in structuring ecological communities (Wilson and Agnew, 1992). They may invoke alternative stable states (Van de Koppel *et al.*, 1997). When this concept is applied to the benthic environment, one of these states is characterized by a dense bed of suspension feeders, whereas in the other state suspension feeders are absent. Disturbance of suspension feeder density in the dense state may lead to a permanent switch to the other state, namely collapse of suspension feeder populations. This could explain the slow return rate of natural mussel banks, once they have been destroyed by fisheries (Piersma and Koolhaas, 1997).

The mechanism proposed here differs from the classical concept of "trophic group amensalism" (Rhoads and Young, 1970; see Snelgrove and Butman, 1994, for a critical discussion and review). That theory critically depends on the destabilization of the sediment by deposit feeders as a means of preventing the establishment of suspension feeders, whereas suspension feeders in turn could prevent the establishment of deposit feeders. We do not assume a very strong linkage between the two groups, and we do not predict a spatial separation of deposit-feeding and suspension-feeding communities. In fact, the data shown in Figure 2 do not suggest such a mutual exclusion, but rather the existence of mechanisms causing the absence of suspension feeders at many places, and their concentration at a few places, whereas other governing processes must be at play in deposit-feeding species.

For a number of infaunal species (notably the bivalves *Macoma balthica*, *Cerastoderma edule* and *Mya arenaria*), detailed analyses of recruitment processes have been conducted (Beukema and de Vlas, 1989; Günther, 1991, 1992; Armonies and Hellwig-Armonies, 1992; Beukema, 1993; Armonies, 1996). Primary recruitment of the pelagic larvae of these species into the sediment is dependent on: (1) availability of larvae in the water column; (2) suitable conditions for larval settlement, implying relatively low current speeds; and (3) the ability of young post-larvae to maintain themselves in the sediment once settled, (i.e. a relatively low bottom shear stress). In a transect from a gully to an intertidal flat, recruitment usually peaks at the deepest places with sufficiently calm current conditions. In the Wadden Sea this is the lower intertidal, but in a recent study in the Westerschelde this zone occurs only in the high intertidal, excluding elevation itself as a major factor (M. Duiker *et al.*, H. Bouma *et al.*, unpublished results). After this first phase of primary recruitment, several cycles of motility, transport and resettlement follow. This may lead to a substantial redistribution of the animals, but traces of the original settlement distribution may remain even after 1 year (H. Bouma *et al.*, unpublished results). In any event, the animals lose their motility before they grow to a size where their joint filtration capacity may lead to significant seston depletion problems.

In summary, the use of boundary layer physics as a framework to study and understand the spatial distribution of suspension feeders should be carefully re-evaluated by taking into consideration flocculation, enhanced sinking and fast sedimentation–erosion cycles, particularly in turbid estuaries. This framework should further be critically evaluated for its ability to explain non-linear correlations between animal density and current velocity. More study is needed of the physical maintenance of animals in currents and waves. Finally, recruitment processes and other biological interactions should be explicitly incorporated into the models of spatial distribution.

The relations described in this chapter are highly relevant for measures taken in the light of management policies for estuarine habitats. Dredging, land reclamation or sea level change may lead to changes, within an estuary, in the relative availability of areas with a particular current regime. It is predicted, for example, that further dredging in the Westerschelde estuary will lead to increased steepness of the banks of intertidal flats, and to a general increase in the sediment dynamics on these flats. The question is whether this loss of most suitable habitat will lead to increased production of benthic suspension feeders on the remaining suitable parts (so that the fraction of total system production consumed by benthos will remain constant), or whether any loss of habitat will translate into a loss of fauna, including fish and birds. From the general distribution theory based on seston depletion problems, increased production seems likely. However, more detailed studies of the biological effects related to recruitment and positive density-dependent mechanisms in dense patches are needed before these questions can be answered.

IV. SPATIAL DISTRIBUTION AND DYNAMICS OF DEPOSIT FEEDERS

The development of predictive models for the spatial distribution of deposit feeders is hampered by the lack of insight into the basic processes determining the relation of these animals to the particulate organic carbon (POC) in sediments. Both the flux of carbon into the sediment, and the availability of particulate organic carbon in the sediment, are determined by complex processes, including abiotic and biotic factors. Attempts to relate biomass of deposit feeders directly to POC concentration in the sediment have generally failed, and with respect to POC flux (as, for example, in problems of anthropogenic organic loading) there is a paradox of enrichment. The very similar "succession after disturbance series" or "distance to pollution source series" of Rhoads *et al.* (1978) and Pearson and Rosenberg (1978) founded a solid base of empirical descriptions on how benthic communities typically react to varying loading with organic wastes, and how their structure may change in time or space as the pressure is changed. This evidence has been the basis for a number of methods allowing fast assessment of anthropogenic (organic) stress on benthic communities (Heip, 1995). Due to the generally poor quantification of the organic fluxes and concomitant biogeochemical changes in the sediments, it remains problematic to use this conceptual model as a basis for a process-oriented understanding of how deposit-feeding assemblages react to enhanced POC fluxes.

A. The Sediment as a Habitat

1. *Sediment Texture*

Sediments comprise a variety of particles and interstitial water in which various components are dissolved. Porosity (ϕ), the fraction of volume occupied by water, typically ranges from 0.9 in the surface layer of muddy sediments to 0.4 in sandy sediments, and usually decreases exponentially with depth due to compaction (Berner, 1980). As a consequence, the solid volume fraction of sediments ($\phi_s = 1 - \phi$) exhibits a pronounced gradient in the upper few centimetres.

Sediments can be classified according to their grain size as clay (< 2 µm), silt (2–63 µm), sand (63–2000 µm) or gravel (> 2 mm). Sedimentary grain-size distributions are the result of sorting processes during deposition, erosion and transport (Allen, 1985). Sediment particles are transported via bedload (also known as traction load and including rolling and saltation) and in suspension. Particles may settle individually according to Stokes' law, or form aggregates due to ionic strength (salinity) changes or biofilm formation. Moreover, suspension feeders may actively remove particles from the water column to the sediments (biodeposition). The physical stability of the sediment surface layer may, in various ways, be influenced by biological processes (Paterson, this volume). Kranck *et al.* (1996a,b) have proposed a grain-size distribution-based partitioning approach that allows distinction between sediments that have settled from suspension with no subsequent reworking and those that have been reworked a number of times. The net result of numerous deposition–erosion cycles is the occurrence of gravel and cobbles in estuarine channels and the dominance of fine sands in tidal flats. The sediment grain-size distribution has important consequences for sediment permeability (a proportionality factor between water pressure gradient and water flow) because voids between larger particles may be clogged by the presence of smaller particles. It also determines the living space for micro-organisms and meiofauna which themselves are not able to displace the sedimentary particles.

2. *Sedimentary Organic Matter*

The quantity, quality and spatial distribution of particulate organic matter in sediments and the biomass, vertical distribution and composition of benthic communities are related by a number of processes. On the one hand, animals affect the carbon flux to the sediment by biodeposition and via transport from the frequently resuspended surface layer to the deeper sediment layers. On the other hand, particulate organic matter constitutes the food and may (directly or indirectly) control the number, size and diversity of benthic animals.

Sedimentary organic matter concentrations vary from less than 0.05 wt% in sandy sediments to more than 10 wt% in fine-grained sediments, the majority of the values lying between 0.1 and 5 wt% (Hedges and Oades, 1997). For ecological studies, it is more appropriate to express the amount of organic matter available on a volume or area basis because this accounts for differences in water contents and porosity. For instance, organic carbon concentrations in intertidal sediments in the Westerschelde estuary expressed on a dry weight basis varied from 4.6 wt% in the freshwater area to 1.4 wt% in the marine section. There was no such gradient when expressed on a volume or area basis (1.1–1.8 mmol cm^{-3}; Middelburg *et al.*, 1996). Similar arguments in favour of volume- or area-based numbers have been put forward for bacterial densities (Schmidt *et al.*, 1998).

Organic matter is usually concentrated in the surface mixed layer of the sediment, typically the top 10 cm (Mayer, 1993). This is due to deposition or formation of organic matter at the sediment–water interface and subsequent burial and mixing downward of organic matter while being subject to degradation. The relative surface enrichment depends mainly on the rate of mixing (due to moving animals) and the lability of the organic material. Benthic animals such as *Arenicola marina* and *Heteromastus filiformis* can also enrich the surface layer via selective ingestion of organically enriched particles at depth and defaecation at the sediment–water interface (Neira and Höpner, 1994; Grossmann and Reichardt, 1991).

Organic matter comprises living biomass (macrofauna, meiofauna and microbial components), detritus (non-living biomass and its alteration products) and black carbon, a highly condensed carbonaceous residue from incomplete combustion processes on land, e.g. charcoal and soot (Middelburg *et al.*, 1999). The contribution of living biomass to bulk sedimentary organic matter has not often been determined, but is usually less than 10%. Given a typical estuarine macrofauna biomass of 0.6 mol C m^{-2} (i.e. 15 g AFDW m^{-2}) and a typical carbon stock of 200 mol C m^{-2} (1 wt%, porosity of 0.52 and integrated over 20 cm), it is clear that macrofauna biomass contributes little (< 1%) to sedimentary carbon. Meiofauna biomass values in estuaries cluster around 1 g C m^{-2} (Heip *et al.*, 1995; approximately 0.1 mol C m^{-2}) and do not contribute significantly to sediment carbon. The number of bacteria in sediments is rather invariant at about 10^9 to 10^{10} cm^{-3} (Schallenberg and Kalf, 1993; Schmidt *et al.*, 1998). Integration over 20 cm and assuming 2×10^{-13} g C per cell (Lee and Fuhrmann, 1987), this relates to about 3–33 mol C m^{-2} (1.5–15% of the total organic carbon). This is consistent with the 5% (range 1–20%) contribution of bacterial biomass to lacustrine sedimentary organic matter reported by Schallenberg and Kalf (1993).

The majority of sedimentary organic particulate matter is strongly associated with the mineral matrix, but about 10–30% may occur as discrete low-density particles (Mayer *et al.*, 1993). These low-density particles usually have a high nutritional value and organisms may selectively feed on these particles in sandy sediments (e.g. *Callianassa;* Stamhuis *et al.*, 1998). There is a close correlation between organic matter on the one hand and grain size or surface area on the other (Mayer, 1994; Hedges and Oades, 1997), because of (1) the tight association of organic matter with mineral particles and (2) similarities in the hydrodynamic behaviour of fine particles and discrete organic matter. The nature of organic matter–mineral interactions is not well known, but ionic as well as weaker interactions due to hydrogen bonding and van der Waals forces are involved. The majority of estuarine sediments below the bioturbated zone have a fixed amount of organic carbon per unit surface area of the grains (40–80 μmol C m^{-2}; 0.5–1.0 mg C m^{-2}), the amount being equivalent to a monolayer of organic material covering mineral surfaces (Mayer, 1994). This adsorbed organic matter is in dynamic equilibrium with the porewater (Keil *et al.*, 1994, 1997) and sorption sites may compete with enzymes for labile organic matter. Sorption of organic matter to surfaces in pores smaller than 10 nm (accounting for > 50% of the total surface area) may constitute a mechanism for preservation of intrinsically labile compounds because microbial exo-enzymes are too large to enter these pores. One may speculate whether macrobenthos may perhaps profit from this sorbed material if the conditions in their digestive systems enhance desorption from these sites.

The quality of organic matter is a loosely defined proportionality factor between mineralization and food availability on the one hand and organic carbon quantity on the other. This term has been introduced to reconcile the orders of magnitude variability in mineralization rates with the invariance of sedimentary organic matter concentrations. The quality depends on the accessibility/availability and the composition of the organic material. In a simple approximation, it can be characterized by the first-order degradation rate of the organic material. This is based on the degradation model

$$\frac{dC}{dt} = -kC \qquad (12)$$

where C is the concentration of organic matter, t is time and k ($time^{-1}$) is the first-order degradation rate. The higher k is, the faster degradation proceeds, hence its use as a quality parameter.

The composition of the organic matter depends on its source and subsequent degradation history because of preferential consumption of more labile compounds and consequent selective accumulation of more refractory compounds (de Leeuw and Largeau, 1993; Cowie and Hedges, 1994; Dauwe and Middelburg, 1998). To the extent that animals are more dependent for their metabolism on the freshly arriving matter than on the matter present in the sediment (e.g. Tsutsumi *et al.*, 1990), this quality difference between flux and stock may be responsible for the lack of any apparent correlation between growth of the animals and POC present in the sediment.

Organic geochemical approaches to constrain the nutritional value of organic matter are hampered by a number of factors. First, only the fraction of organic matter that remains after extensive utilization can be analysed, not the fraction that has been respired or assimilated. Second, despite significant improvements in analytical techniques, a large fraction (> 40%) of the sedimentary organic matter remains biochemically uncharacterized (Wakeham *et al.*, 1997; Dauwe and Middelburg, 1998). Third, chemical characterization usually involves hydrolysation with strong acids (e.g. for amino acids, amino sugars and carbohydrates) or extraction with organic solvents (e.g. for fatty acids) and there is no simple straightforward relation between these chemically defined compounds and enzymatically available substrates (Mayer *et al.*, 1995; Dauwe *et al.*, 1999a). Despite these difficulties, considerable progress has been made in the use of chemical measures for organic matter quality. The ratio between chlorophyll and total organic carbon may be a useful measure (Hargrave and Phillips, 1989) of the nutritional value because chlorophyll is readily degraded ($k = 0.02–0.04\ \text{day}^{-1}$; Sun *et al.*, 1991). The contribution of amino acids to the total organic carbon (Ittekkot, 1988; Cowie and Hedges, 1994), the molecular composition of amino acids (Dauwe and Middelburg, 1998) and the enzymatically available amino acid pool (Mayer *et al.*, 1995; Dauwe *et al.*, 1999a) are also useful quality measures at time-scales relevant to estuarine sediments.

Molar C/N ratios and sedimentary nitrogen contents have also been used quite extensively because organic nitrogen is an essential and limiting nutrient in deposit feeders diets (Tenore, 1988). However, the use of C/N ratios is not straightforward because organic matter derived from different sources may have variable C/N ratios and different pathways of nitrogen mineralization. Molar C/N ratios of allochtonous marine and autochthonous estuarine material are in the range of 6–8 and increase during degradation because of preferential mineralization of nitrogen-rich material (e.g. Burdige, 1991; Rosenfeld, 1981). Molar C/N ratios of terrestrial and higher (marsh) plant-derived matter are generally higher than 12 but decrease because of nitrogen enrichment as a consequence of bacterial processing. Bacterial processing of higher plant material is a well-known requirement before heterotrophic organisms can assimilate terrestrial organic matter with a low quality (see section IV). However, nitrogen enrichment cannot always be equated with increasing nutritional value to benthic detritivores because part of the nitrogen is incorporated in recalcitrant compounds (Rice, 1982). Bacterial processing of marine and estuarine algal material also occurs, but is not obligatory because bacteria and algae are rather similar in terms of their amino acid and carbohydrate composition, and nutritional value to macrofauna (Cowie and Hedges, 1994; Dauwe and Middelburg, 1998; Dauwe *et al.*, 1999a).

3. Sediment Biogeochemistry

Early diagenesis comprises all processes occurring in the surface layers of sediments subsequent to deposition. The main factor driving these biogeochemical processes is the degradation of organic matter, which causes consumption of oxidants and production of metabolites (including nutrients and hydrogen sulfide). Recycling of nutrients is a prerequisite for production by estuarine autotrophs. The production of metabolites such as hydrogen sulfide, however, may toxify benthic fauna. In estuarine sediments, the major electron acceptors for oxidation of organic matter are oxygen, nitrate, manganese oxide, iron oxides and sulfate, and the oxygen bound in organic matter itself (Heip *et al.*, 1995). These oxidants are generally utilized sequentially with a distinct biogeochemical zonation pattern and pronounced pore-water–composition–depth gradients as a result (Aller, 1982). However, recent studies have clearly shown that many of the oxidation pathways occur in the same depth interval (e.g. Canfield and Des Marais, 1993; Canfield *et al.*, 1993), partly due to heterogeneity induced by macrobenthic activity.

Early diagenetic models, describing transport and reaction in aquatic sediments, have been used extensively to predict and understand the changes in sediments due to organic matter degradation (Berner, 1980; Soetaert *et al.*, 1996a; Boudreau, 1997). They are almost always restricted to one dimension, (but see, for example, Aller, 1980a; Boudreau and Marinelli, 1994), because the data available are usually related only to depth and because of mathematical complexity. For derivation of equations and their analytical and numerical solution the reader is referred to the excellent treatment by Boudreau (1997). Basically, partial differential equations specifying advection, diffusion and reaction are solved, given appropriate boundary and initial conditions.

Application of early diagenetic models to estuarine and intertidal sediments may require a number of adaptations to capture the salient features of these systems. In sandy and intertidal sediments the formulation of pore-water advection should include lateral water flows (in the Brinkman layer; Svensson and Rahm, 1991; Khalili *et al.*, 1997) and falling water levels during air exposure (Rocha, 1998). These flows enhance solute transport rates and may bring oxygen to much greater depth in the sediments than would be possible by diffusion alone (Hüttel and Gust, 1992; Lohse *et al.*, 1996; Boudreau and Jørgensen, 1999; Güss, 1998).

Steady-state assumptions may not be adequate since seasonal changes in temperature, bioturbation and carbon input markedly influence the system (Aller, 1980b; Klump and Martens, 1989; Soetaert *et al.*, 1996b).

Bioturbation, the mixing of sediments due to the activity of moving animals, is usually approximated as being a diffusional type of process, i.e. continuous, symmetrical and over small distances (Boudreau, 1986). The bioturbation coefficient (D_b), an eddy–diffusion-like mixing parameter, is then estimated from concentration or activity versus depth profiles of tracers with known decay rates, for example radionuclides (Berner, 1980) or chlorophyll (Sun *et al.*, 1991). However, it is clear that this diffusion approximation of sediment mixing does not apply when (1) sediment motions are not random, but directed (e.g. conveyer-belt mixing), (2) mixing occurs between two non-adjacent points, (3) mixing is intermittent and (4) higher dimensional processes must be incorporated into the one-dimensional framework (Boudreau, 1997). Non-local transport processes may then be included (Boudreau and Imboden, 1987; Soetaert *et al.*, 1996c; Boon and Duineveld, 1998). Wheatcroft *et al.* (1990) identified a number of different ways in which animals may move sediment particles; clearly many of these types of movement deviate far from random diffusion-like transport.

In the present generation of diagenetic models, macrobenthos (and meiobenthos) figure only as modulators of sediment (and solute) transport without consumption of any organic matter. This is clearly inconsistent with estimates of animal respiration (see section II.B). Moreover, the dynamics of macrobenthos are also not included.

Macrophytes (e.g. seagrasses) or algae often inhabit shallow water and intertidal sediments. These benthic producers supply significant organic matter to sediments and should therefore be included explicitly in these biogeochemical models. Moreover, they affect oxygen inputs and nutrient cycling (Risgaard-Petersen *et al.*, 1994; Risgaard-Petersen and Jensen, 1997). Specification of the upper boundary conditions in intertidal estuarine sediments requires special attention. Besides the need to include carbon production during low tide by microphytobenthos (Heip *et al.*, 1995) and enhanced solute exchange due to ripples and bioroughness (Boudreau and Jørgensen, 1999), it is also necessary to deal with the alternation between air exposure and submergence. During exposure the sediment surface acts as a reflecting boundary for solutes, while gases may pass, and this is best represented with a surface evaporation type of boundary. During submergence both solutes and gases are exchanged between water and sediments. This alternation requires dynamic diagenetic models able to resolve the tidal time-scale. Estuarine sediments are dynamic in terms of particle movement due to moving wave and current ripples (Khalili *et al.*, 1997), with a consequence that particulate organic matter becomes homogenized. In such a case it is better to specify the concentration of organic matter at the sediment–water interface than to specify the flux of organic matter to the sediments (Rice and Rhoads, 1989).

B. Deposit Feeders and their Food

The basic features of the response of benthic deposit-feeding communities to organic enrichment are (Pearson and Rosenberg, 1978): (1) large species are replaced by smaller species, even if within species individuals may grow larger near to the source of organic pollution (Weston, 1990); (2) deep-dwelling bioturbating species are replaced by surface or sub-surface deposit-feeding species; (3) average lifespan decreases and *K*-selected species are generally replaced by *r*-selected species; (4) density increases (faster than biomass) up to a certain loading, but crashes when free sulfide reaches the water column; and (6) species diversity decreases, but not in a monotonic way: intermediate high values may be found. It has been shown that many of these features can be summarized in abundance biomass curves (Warwick, 1986), which are cumulative plots of normalized density and biomass by species rank. "Stable" or "equilibrium" or "undisturbed" communities are characterized by a biomass curve well above the abundance curve, because their biomass is dominated by large, relatively rare species, whereas communities dominated by small opportunistic species tend to have their abundance curve above the biomass curve. Intersecting curves are interpreted as indicative of moderate disturbance, but the justification for this is often unclear. Over the past decade, these methods for pollution detection have had numerous new developments, but we concentrate here on the fundamental patterns of difference between benthic communities subject to different organic fluxes.

It has been pointed out by Beukema (1988) and Craeymeersch (1991) that many estuarine samples exhibit abundance biomass curves of the disturbed types, without other obvious signs of eutrophication or human disturbance. The patterns and community types described as a response to eutrophication stress also occur under natural conditions. These conditions can be rather obvious: under extreme physical stress, causing instability of the bed, only a few small, motile species can survive. However, at the other extreme of the physical disturbance scale, in quiet, extremely muddy environments with a high organic content, the benthic assemblage may also typically be composed of small surface or shallow sub-surface deposit feeders, characteristic of "high loading" or "high disturbance" pollution sites. It is an intriguing question as to which processes could be responsible for these patterns.

Dauwe *et al.* (1998) have considered the relation between the quality of the arriving organic flux and the optimal rate of bioturbation in a sediment. They used an analytical diagenetic model composed of a bioturbated top layer and a non-bioturbated layer, forced by a constant flux of organic carbon and a constant sediment accretion rate. With this model they calculated the mineralization rate (expressed as a fraction of the arriving flux) at the bottom depth of the bioturbated layer, as a function of bioturbation rate and first-order degradation rate of the organic matter.

The result is shown in Figure 7 as a contour graph in the $k - D_b$ plane. For every quality of incoming flux, there is an increase of mineralization at depth with bioturbation. However, this increase is strongly non-linear, and the bioturbation range where the steepest increase can be realized is dependent on quality. For very refractory influx ($k = 0.01$ year^{-1}) there is no real increase for varying D_b. For $k = 0.1$ year^{-1} the increase is between 1 and 20 cm^2 year^{-1}. For $k = 1$ year^{-1} it is between 20 and 100 cm^2 year^{-1}. For very high-quality material ($k = 10$–100 year^{-1}) no realistic values of D_b allow more than traces of organic matter to be brought to the depth ($x = 10$ cm) used here as a reference. Based on these model results, the most intense and deepest bioturbation would be predicted to occur in sediments receiving low to intermediate quality of organic flux. Sediments with a more refractory flux will show deep but not very intense bioturbation, and in sediments receiving more labile carbon flux, bioturbation depth will become shallower and eventually restricted to the near-surface zone only.

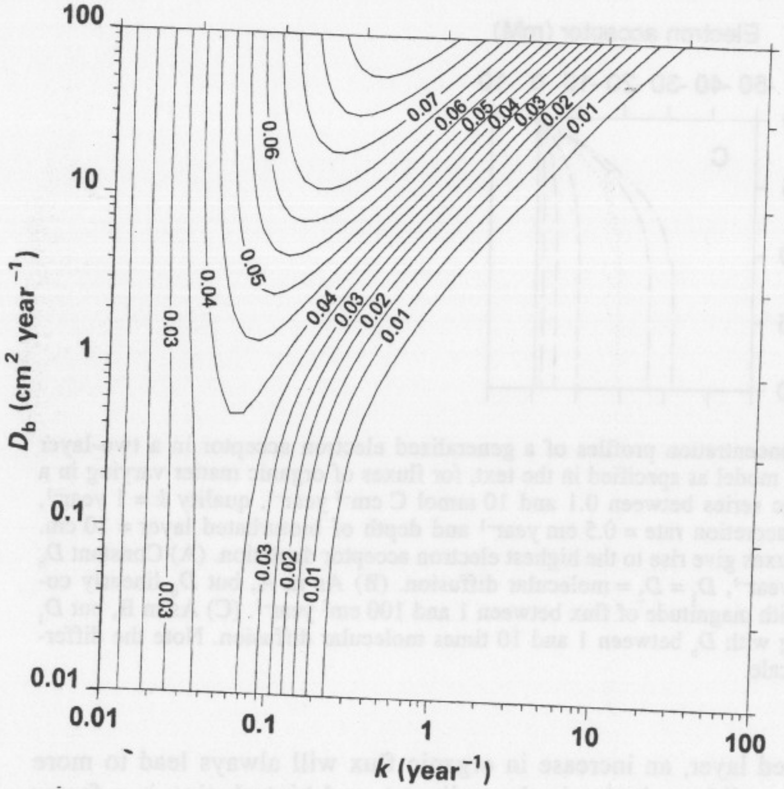

Fig. 7. Isolines of mineralization rate (first-order rate constant $k \times$ concentration of organic matter, mmol C cm^{-3} year^{-1}) at a depth of 10 cm for a two-layer model of organic matter diagenesis in sediments (Dauwe *et al.*, 1998). Parameters of the model (flux of organic matter = 1 mmol C cm^{-2} year^{-1}, depth of bioturbated layer = 10 cm year^{-1}, sediment accretion rate = 0.5 cm year^{-1}, depth of bioturbated layer = 10 cm k (first-order degradation rate of organic matter, year^{-1}) and D_b (bioturbation coefficient, cm^2 year^{-1})) were varied as shown.

Rice and Rhoads (1989) have argued that it is unrealistic to prescribe a constant-flux upper boundary for sediments in shallow water. The top layer of these sediments is continuously reworked physically, leading to a relatively constant concentration in the upper layers. This boundary specification has important consequences for the effects of bioturbation. If the concentration in the top layer is kept constant, more bioturbation will lead to an increase of the flux into the sediment, since more material is mixed down from the surface layer into the sediment. When applying this boundary condition to the model of Dauwe *et al.* (1998), the resulting graph is qualitatively similar, but quantitatively different, to the constant flux boundary condition. In particular, the influence of bioturbation on mineralization at depth is predicted to occur at slightly higher quality of the organic matter. Moreover, the influence is steeper and at generally higher bioturbation levels.

All results in this model exercise are normalized to the incoming flux or to the top concentration respectively. The disappearance of deep-deposit feeders upon organic enrichment cannot be explained by a shortage of energy at depth for the bioturbating organisms, since this will increase at least linearly with the magnitude of the flux. A theory for the paradox of benthic enrichment should therefore contain at least one extra factor. Classically, the increased production of sulfide, the shallower depth of the redox potential discontinuity (RPD) layer, depth of oxygen penetration or similar parameters related to increased mineralization in the sediments have been put forward as the main factor contributing to the disappearance of deep-burrowing animals. At least qualitatively, one could argue against these hypotheses that many deep-deposit feeders are known to survive in reasonably anoxic sediments, and that the animals can contribute to the oxygenation of the sediment by flushing the interstitial water (irrigation), which can increase the apparent diffusion coefficient for dissolved species in the interstitial water by an order of magnitude (compared to molecular diffusion).

We extended the constant carbon flux model with the dynamics of a "generic electron acceptor". Positive values of the general electron acceptor denote oxygen concentration, while negative values provide the concentration of reduced substances that can be oxidized by oxygen ("oxygen demand units"; see Soetaert *et al.*, 1996a). The model is specified as follows.

$$0 \le x \le L: \quad \frac{\delta Ox}{\delta t} = \frac{\delta}{\delta x} D_1 \frac{\delta Ox}{\delta x} - kC$$

$$x > L: \quad \frac{\delta Ox}{\delta t} = \frac{\delta}{\delta x} D_2 \frac{\delta Ox}{\delta x} - kC$$

Boundary conditions: $Ox = Ox_0$ at $x = 0$

$$D_1 \left.\frac{\delta Ox}{\delta x}\right|_{x=L}^{\text{upper}} = D_2 \left.\frac{\delta Ox}{\delta x}\right|_{x=L}^{\text{lower}}$$

$$\left.\frac{\delta Ox}{\delta x}\right|_{x=\infty} = 0 \qquad (13)$$

where Ox denotes the generalized electron acceptor concentration, x is space, t is time, L is the depth of the bioturbated layer, C is the concentration of organic matter as derived from the model of Dauwe *et al.* (1998), D_1 is the diffusion coefficient of the electron acceptor in the upper (bioturbated) layer, and D_2 is the (molecular) diffusion coefficient of the electron acceptor in the lower (non-bioturbated) layer. D_1 can be higher than D_2 if the animals' activity enhances the diffusion of the electron acceptor.

The results of this model are shown in Figure 8 for different values of the organic matter flux, with a quality (first-order degradation rate) of 1 year^{-1}, a sediment accretion rate of 0.5 cm year^{-1} and a bioturbation depth of 10 cm. When the bioturbation coefficient is held constant (Figure 8A), the concentration of the electron acceptor at depth becomes increasingly negative with the magnitude of the flux. In Figure 8B, the bioturbation coefficient D_b increased proportionally with the flux, from 1 cm^2 year^{-1} at a flux of 1 mol C m^{-2} year^{-1} to 100 cm^2 year^{-1} at a flux of 100 mol C m^{-2} year^{-1}. It can be seen that the result of increased bioturbation is a much more negative concentration of the electron acceptor. Bioturbation shifts the average depth of mineralization to greater depth, thereby making it increasingly difficult for oxygen to reach this depth. Bioturbation in itself therefore results in a shift from aerobic to anaerobic mineralization in sediments, a result also demonstrated by Heip *et al.* (in press) with the aid of the more elaborate diagenetic model of Soetaert *et al.* (1996a). When the diffusion coefficient of the electron acceptor increases with bioturbation (Figure 8C), this effect is counteracted by the increased flushing of the bioturbated layer, and the concentration of the electron acceptor at depth becomes less negative. However, this effect is not unlimited, as the animals cannot influence the diffusion coefficient of the lower layer, and the mineralization taking place there increases with the flux and with the bioturbation (the model effectively leaks organic matter to the lower layer). Thus, no matter how the animals influence the diffusion coefficient of the electron acceptor in the bioturbated layer, an increase in organic flux will always lead to more reduced conditions deeper in the sediment, and bioturbation is a factor enhancing this effect.

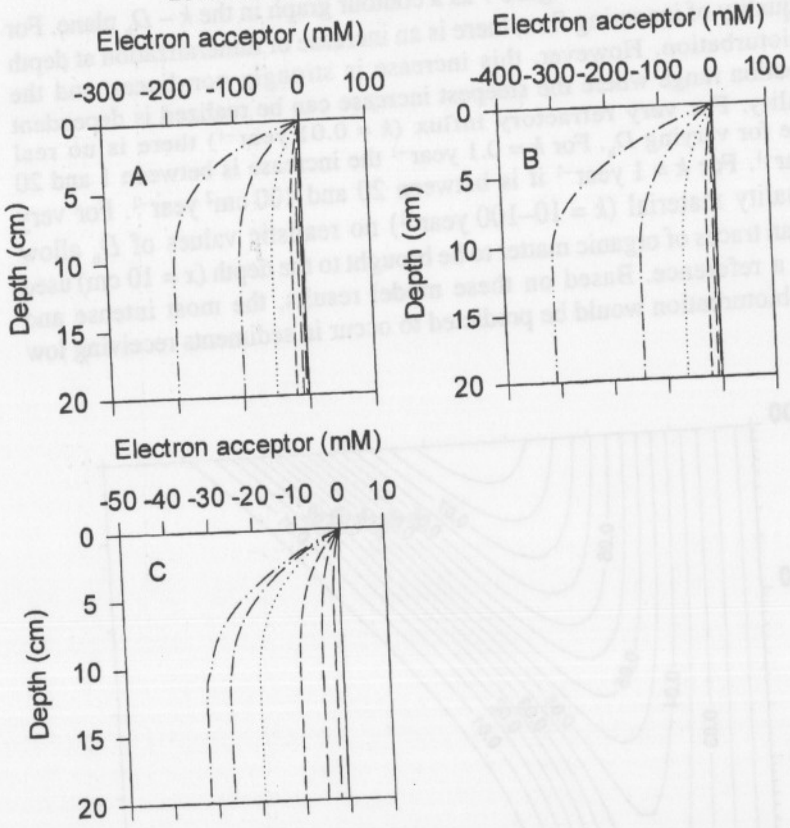

Fig. 8. Concentration profiles of a generalized electron acceptor in a two-layer diagenetic model as specified in the text, for fluxes of organic matter varying in a logarithmic series between 0.1 and 10 mmol C cm^{-2} year^{-1}, quality $k = 1$ year^{-1}, sediment accretion rate = 0.5 cm year^{-1} and depth of bioturbated layer = 10 cm. Highest fluxes give rise to the highest electron acceptor depletion. (A) Constant D_b = 10 cm^2 year^{-1}, $D_1 = D_2$ = molecular diffusion. (B) As in A, but D_b linearly co-varying with magnitude of flux between 1 and 100 cm^2 year^{-1}. (C) As in B, but D_1 co-varying with D_b between 1 and 10 times molecular diffusion. Note the differences in scale.

From these calculations three qualitative predictions may be made. First, clogging of the sediment, even with inert fine material, should decrease the diffusion enhancement and would therefore be detrimental to deep bioturbating organisms in sandy sediments. Second, the transition between a community dominated by deep bioturbators to a community dominated by surface deposit feeders should be relatively sharp: upon disappearance of the bioturbation, the diffusion enhancement should also disappear, and conditions should become reduced near the surface. Third, the large animals dominating bioturbation at depth should create a niche for a number of other species, by keeping the sediment relatively well oxygenated to considerable depth. These predictions are in line with the general observations on the effects of a broad class of organic waste dumpings on benthic communities (Valente *et al.*, 1992).

In summary, the use of a relatively simple diagenetic model illustrates how the interactions between the quality and quantity of the organic flux to sediments on the one hand, and the animal activities on the other, shape the possibilities for the occurrence of deep-deposit feeding. Even without reference to higher-order interactions between bioturbation and mineralization processes in sediments (Aller and Aller, 1998), these dynamics are highly non-linear and characterized by the presence of strong feedback loops between animals, their food and their chemical environment.

V. INTERNAL DYNAMICS OF BENTHIC COMMUNITIES

It would be an oversimplification to consider the structure and functioning of benthic communities solely as functions of external forcing, be it current regimes or organic flux into the sediment. In fact, communities are shaped by strong internal interaction links as well. Extensive effort has been put into testing the importance of predator–prey interactions in benthic communities (see review in Foreman *et al.*, 1995). Theory on predator control proved successful in explaining the dynamics of freshwater pelagic systems (Carpenter *et al.*, 1985, 1987; McQueen *et al.*, 1986; Brönmark *et al.*, 1992; Strong, 1992). Predatory effects in benthic communities were found to be more complex (Wissinger and McGrady, 1993; Lodge *et al.*, 1994). The discrepancies between the theory of predator control and the results from experimental studies in benthic systems may be due to a high incidence of omnivory (feeding at more than one trophic level) (Ambrose, 1984; Committo and Ambrose, 1985; Polis *et al.*, 1989; Posey and Hines, 1991; Menge *et al.*, 1996). Epibenthic predators such as birds, crabs and fish prey not only on non-predatory infauna, but also on predatory infauna (Ambrose, 1984; Committo and Ambrose, 1985). Most deposit feeders ingest a broad spectrum of potential food sources including detritus, algae, bacteria and protozoa (Lopez and Levinton, 1987; Retraubun *et al.*, 1996). As a consequence, prey in benthic systems may experience not only the direct negative effects of predation by omnivores, but also indirect positive effects because of reduced predation by the omnivores' other prey.

The high incidence of omnivory in benthic marine compared with, for example, terrestrial above-ground communities may be the consequence of physiological difficulties in feeding on different trophic levels (Yodzis, 1984; Pimm *et al.*, 1991). These difficulties are related to the quality and accessibility of food sources. Consuming terrestrial plants requires a specialized morphology and digestive tract adapted to handling low-quality plant tissues, excluding the adaptations needed to capture often elusive prey. This specialization may explain the low occurrence of omnivory in terrestrial above-ground communities. The requirements needed to catch benthic prey seem less stringent. Most epibenthic predators are able to handle a broad variety of benthic preys (Ambrose, 1984). Many deposit feeders are bulk feeders that ingest both dead organic materials and the micro-organisms that are attached to it (Lopez and Levinton, 1987). It appears that feeding on multiple trophic levels is relatively easy in benthic systems. In fact, it may even be hard to avoid.

Physiological limitations may not be the only factor determining the occurrence of omnivorous links in food webs. Theoretical studies suggest that a high incidence of omnivory is destabilizing to food webs, and therefore that omnivory should be rare in natural communities (Pimm and Lawton, 1978; Pimm, 1982). Early studies on the properties of real food webs indicated that omnivorous interactions are indeed less common than expected by chance alone (Pimm and Lawton, 1978; Pimm *et al.*, 1991), but these findings have been heavily criticized recently by, among others, benthic ecologists. These authors have claimed that omnivory is more common in real, well-documented food webs than in the earlier incomplete food webs analysed (Hall and Raffaelli, 1991, 1993; Polis, 1991). Studies of food web structure in freshwater and desert ecosystems seem to support this view (Vadas, 1990; Polis, 1991). Holt and Polis (1997) made a detailed mathematical study of the dynamics of a system with omnivores. They analysed a three-species system of two predators and a prey, in which one of the predators also preys on the other. Their model predicts that such systems are vulnerable to losing the intermediate predator, especially when production of the bottom prey is high (Figure 9). In benthic communities, however, omnivores seem to be encountered most frequently in more productive environments (Persson *et al.*, 1988, 1996). The discrepancy between theoretical and empirical studies reflects our limited insight in the nature of omnivorous interactions in benthic communities.

To improve insight into the trophic structure of communities, it is important to understand the extent to which predators and omnivores affect their prey and are controlled by their predators (Hairston and Hairston, 1993). If predatory interactions between omnivores and prey on the adjacent trophic level are of only minor importance to their dynamics, it may be more appropriate to regard both species as competitors. If, at the other extreme, prey on the lowest trophic position are only a minor constituent of the food consumed by the omnivore, the system can probably be better regarded as a food chain.

Deposit feeders consume a broad range of potential food sources of which detritus and micro-organisms are the main constituents (Lopez and Levinton, 1987). Deposit feeders can efficiently remove and assimilate

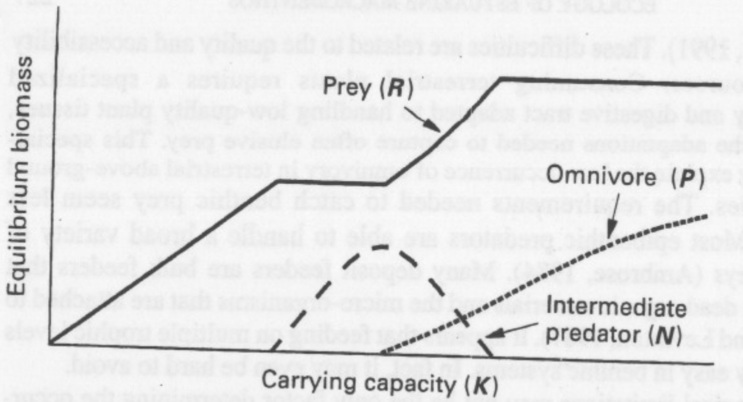

Fig. 9. Relation between prey-carrying capacity (assumed to reflect productivity of the system) on equilibrium biomass of a three-species system of two predators and a prey, in which one of the predators (the omnivore *P*) also preys on the other predator (*N*). The dynamics of the system are given by (following Holt and Polis, 1997): $dR/dt = R[r(1 - R/K) - aN - a'P]$; $dN/dt = N(abR - m - \alpha P)$; and $dP/dt = P(b'a'R + \beta\alpha N - m')$. See Holt and Polis (1997) for details. Note that the intermediate predator is lost from the system at high carrying capacity *K* because of competition and predation by the omnivore.

micro-organisms from the sediment, whereas detritus is in most cases more refractory. The relative importance of detritus and bacteria as a food source for deposit feeders differs among systems. In most marine non-vegetated sediments, bacterial densities seem insufficient to be an important carbon source to the resident stocks of deposit feeders (Kemp, 1987). In mangrove-dominated systems, however, bacteria form a much more important source of carbon for deposit feeders (Odum and Heald, 1975). Mangrove sediments have among the highest recorded bacterial densities in marine systems (Schmidt *et al.*, 1998). In some freshwater sediments bacteria constitute up to 79% of the organic matter consumed by the benthos (Schallenberg and Kalf, 1993), and this is attributed by these authors to the fact that macrophyte-derived material is often the prime carbon source in lake sediments. The differences between these findings are most likely related to the quality and lability of organic matter. Macrophyte- or mangrove-dominated systems are characterized by low-quality organic matter with high C/N ratios (Giddins *et al.*, 1986; Robertson, 1988). Digestive constraints may limit carbon uptake from detritus by deposit feeders (Alongi and Christoffersen, 1992), and hence deposit feeders rely more strongly on microbial food sources. Despite the high carbon loading of mangrove sediments, deposit feeder densities are generally found to be low (Alongi and Christoffersen, 1992; Sheridan, 1997). This suggests that only a limited part of detrital carbon is eventually incorporated into the production of these animals

(Odum and Heald, 1975; Robertson *et al.*, 1992), which is consistent with the hypothesis that in these systems an additional trophic link (over bacteria) mediates the transfer from detrital carbon to the organisms.

Most marine non-vegetated sediments or sandy beaches obtain detritus from marine algal sources, which provide relatively high-quality organic matter with C/N ratios of about 6–8 (see section IV.A.2). Furthermore, bacterial densities in marine sediments are around 10^9 ml^{-1} (Alongi and Sasekumar, 1992; Schmidt *et al.*, 1998), values that are too low to meet the energy demands of macrofauna (Kemp, 1990). Hence, bacteria are unlikely to be an important food source for macrofaunal detrivores in marine sediments (Kemp, 1987; Lopez and Levinton, 1987). It is furthermore unlikely that deposit feeders remove more than 10–15% of bacterial production in most sediments (Kemp, 1990), unless both bacterial production and deposit feeding are focused in the surface layer. In most non-vegetated marine sediments, the strength of interaction between bacteria and macrofauna is probably weak, and detritus is considered to be the main food source for deposit feeders (Tenore *et al.*, 1982).

Holt and Polis (1997) showed that the intermediate predator in a three-component system with omnivory may be unstable in productive environments. The detritus–bacteria–deposit feeder system may therefore be considered as intrinsically unstable. In benthic soft-bottom communities, however, a number of mechanisms are likely to have a positive influence on the persistence and hence on the stability of omnivorous interactions. Habitat complexity may protect a part of the intermediate predator population by providing a refuge against predation (Diehl, 1992). Some benthic prey may seek refuge under dense root-mats (Peterson, 1982) or by retreating to a depth within the sediment at which predation by epibenthic predators is reduced. Deposit feeders, consuming both detritus and micro-organisms, may depend on micro-organisms as a source of nutrients (Lopez and Levinton, 1987). In mangrove-dominated systems, detritus is a poor source of nutrients such as nitrogen or phosphorous. Most mangrove detrivores prefer ingesting food that is aged and colonized by bacteria and fungi (Alongi, 1998). Furthermore, bacteria may provide an essential source of certain amino acids or vitamins (Lopez and Levinton, 1987). Any deposit-feeding organism that depletes the standing stocks of such micro-organisms may deprive itself from valuable nutrients. Hence, food shortage would effectively prevent deposit-feeding organisms from overexploiting their bacterial food supply, and eliminating omnivorous interactions. This may explain the high densities of micro-organisms found in sediments dominated by low-quality mangrove detritus.

A number of stabilizing factors are typical to benthic environments. Diffusion in aquatic sediments may limit the availability of oxygen to benthic organisms. Many benthic omnivores not only interact directly with their prey, but also have indirect effects on prey by changing environmental conditions. Deposit feeders often disturb the sediment, causing enhanced mixing and transportation of sediment and solutes to deeper layers or to the surface. Enhanced pore-water irrigation due to the activity of deposit feeders results in higher oxygen penetration into the sediment, which may stimulate the growth of micro-organisms (Van de Bund *et al.*, 1994). While the microbial contribution to the decay of labile organic matter was reduced, deposit feeders were found to stimulate bacterial decomposition of relatively refractory organic matter (Anderson and Kristensen, 1992; Kristensen *et al.*, 1992). Some deposit feeders may stimulate the growth of bacteria in their burrow systems, a process called microbial gardening (Hylleberg, 1975; Grossmann and Reichardt, 1991). Growth of micro-organisms may furthermore be facilitated by concentration of organic matter in faecal pellets (Neira and Höpner, 1994). Stimulation of the growth of micro-organisms may compensate for losses due to predation, and prevent deposit feeders from significantly depleting micro-organism densities. When one of the prey species, rather than the top predator, is a deposit-feeding species, predation may decrease pore-water irrigation. In such systems oxygen availability is likely to decrease as predation on the prey species becomes more severe. Studies on the effects of low oxygen availability have shown that benthic predators may become ineffective in low-oxygen environments (Kolar and Rahel, 1993; Sandberg, 1994, 1997). This would prevent the top predator from depleting prey stocks, and hence promote persistence in benthic communities.

A better understanding of the interaction strength between omnivores and their food sources on various trophic levels will be crucial in expanding insight into the dynamics of benthic communities. Recent research has shown that the strength of interaction between organisms is an important determinant of the stability of food webs (De Ruiter *et al.*, 1995; McCann *et al.*, 1998). Little is known about how omnivores such as deposit feeders depend on their prey or influence prey dynamics, and how this interaction is influenced by system-specific properties such as the quantity and quality of the organic supply. Second, the dynamic implications of indirect effects of omnivores on prey, especially effects mediated by the environment, are virtually unknown. The effects of pore-water irrigation on the chemical properties of sediments were illustrated in section IV.B. The ecological consequences of this feedback, however, have mainly been ignored. Incorporating feedback relations between benthic species and their environment into models of species interactions and food webs will significantly improve the predictive power of theory on predator control in benthic environments.

VI. CONCLUSIONS

In shallow, well-mixed estuaries, the coupling between benthic and pelagic systems is intense. Productivity of the system is an important factor limiting average benthic biomass. Respiration rates of benthic animals account for a substantial fraction of the primary production. Within the total sediment metabolism, animal respiration also represents a significant fraction. The dynamics of macrobenthic populations is important to understand estuarine system dynamics.

There are strongly non-linear two-way interactions between macrobenthic animals and their physical and chemical environment, as shown for suspension feeders and flow, and for deposit feeders and the chemistry of the sediment. Moreover, as shown for the deposit-feeding community, food and food quality is determining the type of interactions between the species, and thereby the dynamics of the community. It is not possible to describe macrobenthic populations as passively undergoing the influence of extrinsic factors. The feedback mechanisms by which the animals change their own environment offer a challenging scope for further study of estuarine benthos in the context of the system. As shown by the deposit-feeding community interactions, the macrobenthos does not comply to simple theoretical predictions based on terrestrial and pelagic aquatic environments. The identification of peculiar characteristics of benthic systems leading to this discrepancy can offer more insight into the processes and mechanisms shaping these communities. Eventually, it may also contribute to better and more general concepts in ecology.

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Integrated Coastal Management: Sustaining Estuarine Natural Resources

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I. SUMMARY

Many countries are now recognizing the ecological and economic importance of the resources in their coastal zones. Coastal ecosystems carry out a wide range of processes and functions which the wider environment and human society benefit from and are reliant on. These ecosystems are, however, under mounting severe stress from the associated pressures of rapid human population expansion and climate change-induced sea-level rise. In large part, loss and

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