EUTROPHICATION AND ZOOBENTHOS DYNAMICS

Carlo Heip
Centre for Estuarine and Coastal Ecology, Netherlands Institute of Ecology,
Vierstraat 28, NL-4401 EA Yerseke, The Netherlands.

ABSTRACT

The possible effects of eutrophication on benthic dynamics are discussed based on the Pearson-Rosenberg Model that describes the effects of organic enrichment on qualitative characteristics of benthic communities. Depending on the amount of organic matter reaching the sediments, the model describes three successive states: a) slight increases in biomass and few or no changes in species composition over the "normal" situation; b) strong increases of biomass and replacement of "normal" species by opportunistic species; c) disappearance of benthic animal species and azoic sediments. In the field, increase of benthic biomass and changes in species composition on decadal scales which are attributed to eutrophication have been documented in a few cases. Mesocosm studies tend to show much more rapid (weeks to months) but often incoherent responses after experimental nutrient and organic matter additions. The few studies of the "opportunistic" species that appear adapted to become the first recolonizers of azoic sediments show that there is no simple relationship between population characteristics and ability to colonize and that food quality and food requirements have to be better understood. The impact of benthic fauna on benthic-pelagic coupling (sedimentation, particle uptake), bioturbation, benthic mineralisation, nutrient and dissolved organic matter release in shallow water appears to be considerable and disappearance of fauna due to increased organic loading and/or anoxia events is bound to exert a significant influence on shallow water energy and matter cycles.

INTRODUCTION

Eutrophication of the marine environment is usually defined as a complex set of phenomena ultimately triggered by the increase of limiting nutrients, especially nitrogen and phosphorus from terrestrial sources. In short, increase of limiting nutrients leads to increased primary production by pelagic and benthic algae. The increased amounts of organic material subsequently deposited in sediments are in turn assimilated by increased heterotrophic metabolism of bacteria and grazing and detritus-feeding animals. This may eventually lead to increases in benthic biomass but also to anoxic conditions in sediments and massive die-off of benthic animals.
Equating eutrophication to a series of effects of nutrient increase leads to a number of problems when benthos is considered. The possible effects are often not directly related to increased primary production and require a series of intermediate processes which in turn are not directly related to the nutrient increase itself. An increased primary production can result in a higher input of organic matter into benthic food chains in many different ways, including direct grazing of benthos on macroalgae, higher plants or phytoplankton. Often the increase of organic matter input into sediments is unrelated to in situ primary production and may be traced directly or indirectly to primary production elsewhere (detrital material derived from plants, faecal pellets). Even when the input is based on known primary production sources the existence of a microbial loop both in the water and in sediments renders the quantification of the processes difficult. When the origin of the organic matter input to sediments is unclear the distinction between eutrophication based on nutrient increase and direct organic matter input (e.g. by sewage) into aquatic systems becomes blurred.

Furthermore, there are many possible indirect effects of increased organic matter production, including oxygen depletion, changes in species composition and species interactions, changes in sediment characteristics etc. Since benthic metabolism is an important agent determining characteristics of sediment-water exchange, a series of additional feed-back mechanisms exists, including particle transfer, mineralisation and release of nutrients, and the production of pelagic larvae of benthic species that may graze on the phytoplankton directly in the water and therefore decrease primary production again (Fig. 1).

Benthic animals cover a much larger diversity in species, feeding types and sizes than the zooplankton. Except in very shallow water, where grazing on in situ production of plants is possible, and in some cases where chemoautotrophic processes are important, their energy source is remote and water movement is the main agent responsible for bringing in organic matter. Many characteristics of the benthos are therefore not related to primary production per se but refer to current regime, water depth and sediment type. In terms of size benthic animals vary from minute organisms only a few hundreds of microns long when adult, to typically some decimeters, or even longer. Benthos therefore spans 6-7 orders of magnitude in length. Moreover, the distribution of sizes is not unimodal and the distinction that is made between micro-, meio- and macrofauna appears to correspond to evolutionary strategies (Warwick 1984). If the number of species (typically tens to hundreds on length scales of a meter) is indicative, the diversity of particles and food items that can be managed by benthic communities must be very large and certainly much larger than our current knowledge and technology are capable of detecting.

The problem is therefore complex and in this paper I will not attempt to relate benthic dynamics to nutrient increases in a direct or quantitative way. Moreover I will restrict this paper to soft-bottom and shallow waters and will mainly draw...
EUTROPHICATION AND ZOOBENTHOS DYNAMICS 115

Fig. 1. The Pearson-Rosenberg Model showing changes in abundance (A), biomass (B) and species richness (S) of macrobenthos with changing inputs of organic material.

from experience in the North Sea and its estuaries. I will first briefly describe the Pearson-Rosenberg model and then discuss the evidence from the field and from laboratory experiments that supports the thesis of a relationship between increased nutrient concentrations and changes in benthic animal communities. I will deal with two further features of the model that describe the characteristic responses to high organic loading, the appearance of opportunistic species and eventually the development of azoic sediments.

THE PEARSON-ROSENBERG MODEL

Changes in species composition due to organic enrichment have been studied by Pearson & Rosenberg (1978) who showed that the early stages of eutrophication and organic enrichment are often characterized by increases in abundance, biomass and numbers of species. Although this model has a serious drawback in that it is purely qualitative, it is sufficiently general to be used as a conceptual framework in which further quantification is possible, at least in principle. Moreover this model is still the basic reference for the literature on effects of organic enrichment on benthic communities.

It is therefore of interest to look at the features of this model and the biological mechanisms invoked to support it, even though there may be no exact equivalence between effects of direct organic enrichment and indirect effects of increased nutrient inputs. The Pearson-Rosenberg model is based on structural characteristics of groupings of co-occurring benthic species called communities or, perhaps more properly, assemblages. The basic characteristics are weight and size of benthic individuals, and abundance, biomass and number of species of benthic communities, usually expressed per unit of surface. Changes in these
characteristics follow a typical pattern that can be described as follows (Fig. 2): when organic loading increases, species abundance and biomass initially increase, then decrease to what is called the ecotone point, followed by secondary maxima of biomass and abundance associated with a few small opportunistic species, mainly polychaetes. If enrichment continues in the end all macrofauna disappears and an azoic sediment appears. These trends may occur spatially around point sources of organic pollution or temporally in succession patterns, e.g. after a disturbance such as an anoxia event (Rhoads 1974).

Besides changes in diversity, abundance, biomass and weight there is also a marked decrease in the depth at which fauna occurs, related to shifts in the redox potential due to the organic loading. In the “equilibrium” or “normal” community from oligotrophic sediments large and deep burrowing animal species occur, whereas the opportunistic species from eutrophic sediments tend to be small and surface deposit feeders. The depth to where benthic animal life occurs is probably limited by the occurrence of sufficient food in oligotrophic sediments and by oxygen availability and sulfide concentrations in eutrophic sediments. Animals feeding at depth must have access to oxygen, either in the surface layers or from the
overlying water. When oxygen availability is limited, or when the sediment oxygen demand at the feeding depth is too large, animals are presumably no longer able to withstand this environmental stress. Since the quality of food decreases sharply with depth in the sediment and since animals are limited in their ability to process sediment and extract food from it, the yield of food per unit time must decrease with depth of feeding and preclude high rates of respiration, growth and reproduction. The slow-decaying, almost constant food source of deep-burrowing animals guarantees a more pronounced temporal stability for deep-burrowing species. Protection from predation in the sediment decreases the need for fast reproduction. These features together favour the development of large body size and general K-strategy life histories (Herman pers.comm.).

FIELD EVIDENCE FOR LONG-TERM EUTROPHICATION EFFECTS

Since most benthic metabolism depends on import of organic material produced elsewhere, eutrophication may be expected to lead to an increase in benthic biomass, even when there is no obvious increase in phytoplankton biomass. In a few well documented cases biomass increases over (but not during) long periods of time (five decennia) have been recorded and have indeed been attributed to eutrophication. These cases are from subtidal areas in the Baltic, the Kattegat and Skagerrak (including Oslofjord) and intertidal areas in the Wadden Sea.

In one of the first studies of this kind, Rosenberg & Möller (1979) found large increases in biomass, abundance and number of species in a number of stations in the Kattegat that were revisited after a period of about fifty years. However, they attributed these increases mainly to artifacts of sorting and possibly sampling, a conclusion that was later contested by Cederwall & Elmgren (1980) who considered that eutrophication is just as likely an explanation for these results.

In bottoms shallower than 70 m in the Baltic Basin the faunal biomass has increased significantly from 13 to 46 g ww.m\(^{-2}\) on average from the 1920's till the 1970's (Cederwall & Elmgren 1980). These authors resampled in 1976-1977 stations around the islands of Öland and Gotland that had been studied by Hessle in 1920 and observed a significantly higher biomass (median over four times higher) above the halocline, where anoxia does not occur. Species composition did not change appreciably, although *Macoma balthica* was replaced by *Mytilus edulis* as the dominant species. All taxa increased in abundance except the large relict isopod *Mesidothea entomon*. Since abundance increased more than biomass, the average macrofauna individual weighted less in the 1970's than in 1920. Below 70 m depth all stations showed a significant decrease in biomass, with one station even being devoid of macrofauna.

Similarly, Weigelt (1991) described the changes in benthic biomass and species composition in Kiel Bay where oxygen depletion events have increased in fre-
The study by Kröncke (1990) on the Dogger Bank in the North Sea showed increases in small polychaete species as well, which she attributed to fisheries effects, and an important extension of the ophiuroid *Amphiura filiformis*.

Very detailed comparisons have been made in the Kattegat-Skagerrak areas between stations sampled in the 1910's by Petersen (1918) and between 1980 and 1985 by several authors. Pearson et al. (1985) and Rosenberg et al. (1987) revisited stations in the Kattegat, Skagerrak and in Oslofjord that had been sampled by Petersen in 1911-12 (Kattegat) and 1914 (Skagerrak, Oslofjord) during his classical studies which were formative for benthic community research. In the Kattegat, considerable changes in biomass and species composition had occurred. Changes in biomass were both positive and negative depending on geographical location. However, over all stations the biomass was not significantly different between 1911 and 1984 (the average value decreased from 333 to 237 g ww.m$^{-2}$, but the decrease was not significant and not different in shallow (from 331 to 200 g ww.m$^{-2}$) and deep stations (from 334 to 268 g ww.m$^{-2}$)). However, stations on the eastern side of the Kattegat tended to have a higher biomass in 1984. At nearly all the stations the majority of species showed a weight decrease in 1984 when compared with 1911-1912. The characteristic echinoids of the Kattegat area, *Echinocardium cordatum* and *Brissopsis lyrifera*, had decreased whereas the large polychaetes *Polychaeta crassa* and *Pectinaria auricoma* as well as the ophiuroid *Amphiura filiformis* had the most striking increases. Many molluscs (*Nucula sulcata*, *Tiritella communis*, *Aporrhais pes-pelicani* and *Cyprina islandica*) had decreased.

The comparison between the Kattegat and the Skagerrak (including the Oslofjord) is interesting because these areas differ considerably, the Skagerrak being deeper and more strongly influenced by North Sea-Atlantic interactions. The mean total biomass in these areas had increased significantly between 1914 and 1985, from 74 to 131 g ww.m$^{-2}$, and the change occurred mainly in the deeper stations. The increase was apparent in several taxonomic groups and was significant in the echinoderms (from 30 to 60 g ww.m$^{-2}$) and “worms” (from 15 to 38 g ww.m$^{-2}$). In 1914 there was a linear decrease of biomass with depth, but this relationship had disappeared in 1985. The mean individual weight of the species found did not change. In contrast to the pattern in the Baltic but similar to the Kattegat, species differences in the Skagerrak were striking. In the shallow stations the gastropod molluscs *Aporrhais pes-pelicani* and *Tiritella communis*, which dominated in 1914, were not recorded in 1985. The bivalve *Abra nitida* had become dominant at one of the stations. In the Oslofjord there was a high biomass of the polychaetes *Polychaeta crassa* and *Scalibregma inflatum*. In the deeper stations the increased biomass was mainly due to the echinoid *Brissopsis lyrifera*; other dominants were the polychaete *Leanira tetragona* and *Abra nitida*. 
In the outer Oslofjord the biomass of worms increased at all stations and the abundance of *Amphiura filiformis* was higher at many stations. In the inner Oslofjord, where organic enrichment occurs, the polychaetes *Polyphysia crassa* and *Scalibregma inflatum* were found. In deeper parts, where periodic anoxic conditions exist, the opportunists *Capitella capitata* and *Polydora* spp. occur.

From the intertidal only a few studies covering the same time span are available. Reise et al. (1989) compared the fauna on tidal flats and in channels around the isle of Sylt in the Wadden Sea between 1923-1940 and 1980-1988. Several important changes occurred which were considered to be evidence for organic enrichment: i.e. the massive growth of green algae on sheltered tidal flats, the decline of red algae in the subtidal zone, the expansion of mussel beds along the low water line, and the increased abundance of polychaetes inhabiting intertidal and subtidal sandy bottoms. Beukema & Cadée (1986) observed similar changes in the Dutch Balgzand area. In Sylt, faunal changes in channels could also be due to increased bottom trawling, since especially reef-builders such as the polychaete *Sabellaria alveolata* and the flat oyster *Ostrea edulis* have disappeared. The possible confusion between effects of increased organic matter inputs and effects of the fisheries is an unexplored problem that requires careful consideration in a number of other areas as well.

In an interesting study, Jensen (1992) compared abundance and growth rates of benthic populations of intertidal flats of the Danish Wadden Sea between the 1930's, 1940's and 1980's. Two species (one of them being *Scrobicularia plana*) disappeared and one emerged during this period. Deposit-feeding polychaetes (*Scoloplos armiger* and capitellids) and *Nereis diversicolor* were much more abundant in the 1980's. In the case of *Nereis* the difference may be due to a high number of juveniles. There were no abundance changes in the mudsnail *Hydrobia* and the cockle *Cerastoderma edule*. Moreover, growth rates of the cockles matched perfectly between the 1930's and the 1980's. In both periods these populations had lower growth rates and higher abundances than elsewhere in the Wadden Sea. On these intertidal flats there was therefore no evidence of long-term changes due to eutrophication.

The studies discussed above show that when biomass increases, these increases are with a factor 2-5, from perhaps 1 to about 5 g C.m⁻² over periods of about 50 years. If the annual increase in biomass were linear over time, which in the Skagerrak it was probably not, it would therefore only be of the order of 0.1 g C per year, or between 2-4% of the standing stock per year. Such small increases would be very difficult to measure over short time intervals. Monitoring programmes aimed at detecting effects of eutrophication should use the appropriate decadal time scale. If we estimate that the total carbon intake of a standing stock of 1 g C.m⁻² over a year is about 20 g C.m⁻², much less than the annual input of organic matter in the sediment is consumed by macrobenthos and if this
is the case the relationship between the biomass increase and increased primary production will be very difficult to measure.

Besides being difficult to measure, these changes are also difficult to explain in a straightforward manner. Reise et al. (1989) already drew attention to the possible impact of bottom trawling, a factor that has also to be considered in the case of the Kattegat (Pearson et al. 1985). Bottom trawling affects huge areas in many shallow water bodies around Europe and may lead to disappearance of long-lived species such as *Arctica islandica* and *Aphrodite aculeata* and may favour opportunists such as small polychaetes. An increase in the amount of suspended matter, which may be a long-term change associated with erosion of the land due to deforestation or changed agricultural practice, may lead to the increase of suspension feeders such as *Amphiura filiformis* and many polychaete species. In areas where periodic anoxia occurs benthic biomass may actually decrease as a consequence of eutrophication and shifts to shorter-lived, smaller species will also occur. Anoxia events in poorly flushed basins may be natural consequences of prolonged stratification periods depending on the weather or climate, the evolution of the deep basins in the Baltic being a good example of this. Changes in species composition may be the consequence of many different kinds of perturbation or may be part of long-term natural changes that are linked to climate. Our knowledge of the effects of perturbations and the effects of long-term natural changes in ecosystems is for the moment insufficient to allow a good interpretation of the kind of observed changes described above.

**EXPERIMENTAL STUDIES ON THE RESPONSE OF BENTHOS TO NUTRIENT ENRICHMENT**

A few long-term studies have been performed in mesocosm facilities in which known amounts of nutrients were added to experimental systems with known initial conditions. Most of such studies show at least some of the expected reactions of the fauna, but there is often much variability in the results. Daily addition of nutrients (N, P and Si) from one to 32 times the natural daily input from sewage and runoff was added over a three year period to experimental tanks containing water and sediments at the MERL facilities in Rhode Island, USA. These additions did not lead to any clear patterns of meio-benthic biomass changes (Widbom & Elmgren 1988). The response was different for different meio-benthic groups, leading to changes in meio-benthic community structure. Nematodes and juvenile polychaetes increased whereas kinorhynchs, ostracods, harpacticoids and juvenile bivalves decreased. This lack of a clear response is in sharp contrast with the increasing primary production in the water column of the tanks.

In the same mesocosms Grassle et al. (1985) studied the responses of macrofauna to the addition of dried algae (*Ascoplryllum*) and nutrients and compared those to field data from Narragansett Bay. Following addition of about 103 g ash-free
dwt Ascophyllum to each tank (2.52 m² sediment surface) over about nine weeks the densities of juvenile Mediomastus ambiseta, Polydora ligni (Polychaeta) and amphipods increased significantly to levels roughly about three times higher than controls, but densities of the mollusk Nucula annulata did not change. When nutrients were added, chlorophyll levels increased followed by a sharp increase in the recruitment of several polychaete species.

In boxcosm experiments on Texel, the Netherlands, Van Duyl et al. (1992) studied the effects of the input of Phaeocystis derived organic matter supplied either in one dose of 24 g C. m⁻² or in weekly doses of 8 g C. m⁻². The tests were performed on sterilized sandy sediments inoculated with micro- and meiofauna and with individuals of several macrofaunal species. Bacterial densities and production increased after input of organic matter. When macrofauna was present, this increase was also apparent in deeper sediment layers, showing that macrofauna (in this case especially the sea urchin Echinocardium cordatum) transport organic matter to deeper sediment layers.

**THE BIOLOGY OF OPPORTUNISTIC SPECIES**

In the Pearson-Rosenberg Model the second stage in the faunal succession is characterized by the appearance of so-called opportunistic species, which appear either when azoic sediments are recolonized or after the increased organic loading has eliminated the deeper-living fauna. The classical example of opportunistic species are the polychaetes of the Capitella capitata group, which have now been well studied, but many other examples are cited in the literature with changes involving shifts between whole taxonomic groups such as from mollusks and crustaceans to polychaetes and echinoderms.

Characteristically Capitella, which rapidly colonizes azoic areas, has high population growth but rapidly declines subsequently and is replaced by other species. This is often conceptualized within the r-K life-history strategy paradigm of population biology, in which r stands for the rate of increase in the exponential population growth curve, whereas K stands for the carrying capacity of the population, both parameters being combined in the logistic equation of population growth. The r-strategy involves increased reproductive effort through early reproduction, small and numerous offspring with large dispersive capability, short life-span and small body size of adults and provides a selective advantage in unpredictable or short-lived environments. Opportunism may also be reflected in feeding behaviour and in a generalistic ecological niche.

Capitella species are often reported to have a high reproductive potential and large dispersive capabilities and are normally considered as being typical r-strategists. However, although Capitella species often produce large numbers of small eggs, some Capitella species produce small numbers of large eggs (Grassle
1980; Tsutsumi et al. 1990). Moreover, *Capitella* species have only a limited dispersal capacity and populations maintain themselves, with large fluctuations in population size, without any reliance on dispersal ability (Tsutsumi 1987, 1990). Dispersal apparently does not always play an important role in the dynamics of these populations.

The growth of *Capitella* species was studied by Tenore (1977, 1981, 1983) and by Marsh et al. (1989). Both individual growth and population growth were related to the nitrogen content of the organic material. Marsh et al. (1989) showed the growth rates of juveniles to be correlated with the concentrations of the amino acids histidine, phenylalanine, threonine and valine and the fatty acid 20:5w3. Another interesting and important observation is that juvenile *Capitella* grew on detritus collected in sediment traps in Spring but not on the same material collected in Summer. Tsutsumi et al. (1990) also showed that growth of *Capitella* populations was independent of the absolute levels of organic matter in the sediment but was correlated with additions of organic matter in the form of algal powder.

Other characteristics of r-strategists are the rapid succession of build ups and break downs of population density. The instabilities in population densities of *Capitella capitata* were ascribed to competition by Pearson & Rosenberg (1978) but later studies proved that this is not necessarily the case (Tsutsumi 1987). Even in the absence of competitors, *Capitella* populations oscillate between low and high densities and Chesney & Tenore (1985) therefore proposed the alternative hypothesis that population density is driven by food availability. In experimental situations, on constant food *Capitella* maintains a biomass plateau for as many as 8 weeks, and then gradually decreases (Grémare et al. 1989). A postulated overshoot of their carrying capacity is contradicted by the relatively long decline period (at least ten weeks) that follows the peak and is hardly compatible with the idea of a crash. Grémare et al. (1989) showed that during population decline the reproduction and secondary production were reduced but that adjustment of the energetic requirements to the food supply also occurred and that the population did not overshoot the carrying capacity. Grémare et al. (1989) postulate that succession of *Capitella* by other species may be due to its high energy requirements in conjunction with a diminution of food availability.

An important generalisation from the Pearson-Rosenberg model, that species tend to become smaller at higher organic loading, has been nuanced by Weston (1990) who showed that in an assemblage indeed dominated by smaller species in more eutrophic situations, the individuals within these smaller species were actually becoming larger under higher loading. This is in accordance with growth experiments on *Capitella*, showing dramatic increases in growth rate and adult size at high organic loading (Bridges et al. 1994). However, Weston's (1990) eutrophic stations were mainly negatively characterized by the absence of deep burrowing deposit feeders and this generally accepted feature of the Pearson-Rosenberg
EUTROPHICATION AND ZOOBENTHOS DYNAMICS

EUTROPHICATION AND ZOOBENTHOS DYNAMICS

A model was not found back by Warwick & Clarke (1994) in a statistical analysis of many different data sets. Warwick & Clarke (1994) showed that the changes in species composition under eutrophication stress were caused by a shift in dominance between phyla, but within phyla only by species shifts in the Polychaeta. Moreover, the dominance of larger species in normal situations is only apparent when expressed on a biomass basis and the number of individuals of the large deep-burrowing species is small in comparison with the total number of individuals.

These examples of studies where the biology of the classical opportunistic species *Capitella cf. capitata* has been examined in more detail show that generalizations, even for these well studied species, should be made with caution. Information on quality and quantity of food, on food requirements for reproduction, growth and maintenance, on physiological adaptations to changing food, is nearly absent for many eutrophication related species other than *Capitella*, e.g. the echinoderm *Amphiura filiformis*, the polychaetes *Heteromastus* and *Polydora*, the amphipod *Corophium volutator* to name but a few.

EFFECTS OF ANOXIA AND THE ROLE OF FAUNA IN SEDIMENT BIOGEOCHEMISTRY

Anoxic sediments in shallow water are dominated by sulfur-based metabolism. They are not necessarily azoic provided oxygen concentrations in the overlying water are sufficiently high. However, prolonged periods of anoxia lead to extinction of macro- and most of the meio- and microfauna. Disappearance of fauna from anoxic areas may change the characteristics and magnitude of processes driving benthic-pelagic coupling: catching and incorporation of particles by animals in the sediments, the stimulation by animals of mineralization processes due to changes in redox conditions, increase of active surfaces, direct grazing on microbes and subsequent exchange of dissolved organic and inorganic solutes between the sediments and the overlying water.

**Benthic-Pelagic Coupling**

In a general way the biological processes involving the benthic fauna increase the flux of particles and oxygen from the water column to the sediment and the release of dissolved substances and gases (CO₂, N₂) to the water column (Fig. 3). The particles include particulate organic matter of very different origin and nutritious quality and inorganic particles ranging from sands to clays.

The earliest model describing the relationship between pelagic primary production and benthic community metabolism, measured as oxygen uptake, was proposed by Hargrave (1973). In this model the mean annual oxygen consumption is given as:
in which $C_0$ is the carbon equivalent of sediment oxygen uptake, $C_i$ is the annual primary production and $Z_m$ is the mixing layer depth. Later, the view of carbon uptake by benthic communities as a gradual process changed drastically when it was discovered that sedimentation events may be discrete and of short duration. Graf (1992) recently reviewed the main features of benthic-pelagic coupling in two well studied areas, Kiel Bight and the Norwegian Sea. In Kiel Bay diatoms of the spring bloom settle over only a few days and the benthic response to this settling, as shown by e.g. benthic oxygen uptake, is almost immediate (Graf et al. 1982). Not only is a large part of the annual input of organic material to the sediment delivered over a short time span, but also the nutritional value of the sedimenting bloom material is higher. In boreal systems the spring phytoplankton bloom consists mainly of diatoms which settle as clumped aggregates after bloom development. They reach the surface of the sediment as intact cells providing high food quality for benthic organisms (Graf 1992). The response is very rapid but also very brief. In experiments increased oxygen consumption lasted for 4-6 days only. Such brief events can easily be missed in field studies.
The fast response is mainly due to bacteria and protozoans with an assimilation efficiency of over 50% (Graf 1987). Webb & Montagna (1993) have shown that in quiet conditions the initial burial and subsequent degradation of sedimented phytoplankton may be dominated by meiofaunal and microbial communities and is not affected by deposit-feeding macrofauna. Effects of settling blooms on higher trophic levels can be estimated indirectly. For macrofauna, Ankar (1980) showed an increased productivity and a higher growth rate of _Macoma balthica_ after feeding on a settled phytoplankton bloom and an increase in glycogen and lipid reserves. Although the response of small biota may be so fast that nothing is left for larger animals, the rapid disappearance of the increased biomass of small organisms indicates that transfers to higher trophic levels may be important. In Kiel Bay it was estimated that at least 2 g C. m\(^{-2}\) was transferred from smaller to larger organisms within four weeks after the maximum development of smaller biota (Graf 1992). Still the implication remains that much of the annual primary production is mineralised over a short period of time and that (reduced?) benthic activity over most (the rest) of the year has to be fuelled by other organic material than directly sedimenting phytodetritus. Unfortunately, there are no data to investigate whether the amount of sedimenting phytodetritus has changed over the last decades as a consequence of increased nutrient concentrations in the pelagic.

Vertical sedimentation is only part of the process of benthic-pelagic coupling and lateral advection is as important for bringing particles to sediments. Part of these particles may have been resuspended. Suspension feeders in the benthos capture particles even before they are settled on the sea floor and therefore increase the flux from the water column to the sediments, a process that is called biodeposition (Fig. 4) (Graf 1992). Whether suspension or deposit feeding dominates depends on water velocity and food quality and quantity. In most shallow-water environments strong gradients in water velocity exist. These gradients have important consequences not only for particle transfer between water and sediment (Jumars & Nowell 1984) and for chemical exchanges (Aller 1984), but also for biological processes including feeding, growth and recruitment (Butman 1987). Many infaunal species may shift from suspension to deposit feeding depending on the flow regime (Brafield & Newell 1961). At low water velocity feeding is almost exclusively on particles on the sediment surface. At higher velocities suspension feeding is favored and behavioral shift occur such as a reorientation of feeding appendages in polychaetes (Taghon & Greene 1992).

Besides water velocity also food quality is important. Macrobenthic suspension feeders will dominate the benthos where the flux of material at or just above the sediment-water interface consists primarily of high-quality, live phytoplankton. Subsurface deposit feeders receive the greatest share (and can increase this share by their bioturbation activities) where the material is relatively refractory, as is the case in places where extensive reworking of the top sediment layers and
lateral advection of organic material takes place (Herman pers. comm.). Particles of low specific gravity are generally more nutritious than particles of high specific gravity because they tend to have a higher organic content. On a unit volume basis low specific gravity particles have lower settling velocities and are more readily resuspended and transported in suspended load (Jumars & Nowell 1984). Taghon & Greene (1992), who studied switching feeding and growth rate of two spionid polychaetes, showed that when suspension feeding both species had reduced feeding rates and egestion rates and produced fewer faecal pellets than when deposit feeding. In one of the species (*Pseudopolydora kempi japonica*) the growth rate also decreased, but in the other species (*Boccardia sp.*) the growth rate actually increased when suspension feeding. These differences are difficult to understand since both species are very similar morphologically.

**Effects of benthos on decomposition of detritus**

Rice & Rhoads (1989) developed a model for the secondary production of deposit feeders under different conditions of organic loading. They distinguished two
different extremes, one where the flux of organic carbon is constant (typical of sediments in deeper waters) and one where the surface concentration of organic matter in the sediment is kept constant due to continuous reworking and lateral advection (typical of estuarine areas where the top centimeters of the sediments are often reworked by currents and waves). In the latter situation, the total concentration of metabolizable organic matter in the sediments is critically dependent on bioturbational mixing: the faster the animals work the organic matter into the sediment, the more organic matter will be present. The quality of the organic material with constant concentration at the surface of the sediment is also of great importance. For the same constant surface concentration of 4 mg C cm$^{-2}$, the total scope for benthic secondary production is 28 g C m$^{-2}$y$^{-1}$ if all this material would be fresh phytoplankton detritus (degradation constant 15 y$^{-1}$), and 5.5 g C m$^{-2}$y$^{-1}$ if it would be entirely made up of reworked sediment organic matter (degradation constant 0.6 y$^{-1}$). Of the first value, however, only 11% would be available below the top cm, whereas 65% of the low production value of 5.5 g C m$^{-2}$y$^{-1}$ would be available deeper down. Even in absolute numbers, more production would be possible below 1 cm in the case of loading with relatively refractory organic matter. From this model it can be concluded that where the magnitude of the flux is primarily determined by the reactivity of the material arriving at the sediment, low fluxes favor, in relative and even in absolute terms, animals feeding at depth (Herman pers. comm.).

The existence of two principal sources of organic matter is also reflected by the meiobenthos. Rudnick (1989) suggested that there may be two groups of meio-benthos present in sediments: one utilizing fresh phytodetritus at the sediment surface and one utilizing the large reservoir of old detritus. The first group is dominated by meio-benthic crustaceans, mainly harpacticoid copepods but also ostracods and small nematodes. The group, living deeper in the sediment, is mainly dominated by large nematodes but also contains the slender interstitial harpacticoids, turbellarians and kinorhynchs.

In areas where benthic primary production occurs, grazing by benthic animals on macroalgae, vascular plants or microphytobenthos may provide an autochthonous source of organic matter. However in most sediments the organic material is imported from elsewhere and besides phytoplankton organic matter may also be derived from macrophytes. Macrophytes which are decaying in winter may be transported over long distances. Liebezeit (1986) demonstrated that 73% of the carbohydrates in sediments of Kiel Bay was derived from macrophytes.

Kristensen et al. (1992) studied the effects of macrofauna on the degradation of a pulse of organic matter derived from the macroalgae Chondrus crispus at different temperatures. The added detritus disappeared from the sediment surface in a few days when the polychaete Nereis diversicolor was present whereas it remained on the surface in worm-free cores. In these cores white bacterial films developed
in some cases. The presence of *Nereis* stimulated oxygen uptake and carbon dioxide production by 30-70% and 20-50% more detritus was respired when *Nereis* was present, an excess that was incorporated into worm biomass. Interestingly, the bioturbation by *Nereis* affected the mineralisation of old detritus more than that of the freshly deposited detritus.

The importance of macrofauna for the decomposition of microalgae was studied by Andersen & Kristensen (1992). Mineralization rates increased by almost 50% in the presence of macrofauna in the first day but after four days the difference disappeared. Overall total CO$_2$ release was 70% higher in experiments with fauna and O$_2$ uptake was 17% higher. This indicated that anaerobic mineralization processes were stimulated more than aerobic processes and that most of the CO$_2$ flux originated from older and relatively refractory organic material already present in the sediment.

Downward particle transport by fauna in the experiments of Andersen & Kristensen (1992) was limited. This was in part due to the species involved (*Nereis diversicolor*, *Hydrobia neglecta* and *Corophium volutator*) which are surface deposit feeders, although *Nereis diversicolor* may also behave as a filter feeder. However, transport of dissolved material was more important, which may reflect the ventilation and movement of the fauna. Newly settled microalgae will be decomposed mainly at the sediment-water interface although a small transport of organic matter to deeper sediment layers exists.

**Bioturbation**

As well as moving around within sediments, the fauna builds tubes, constructs burrows and feeding pits, transports sediments and so on. When fauna disappears, as during anoxia events, the physical and chemical characteristics of the top sediment layers are greatly changed. A spectacular example of this has occurred in the Baltic. Since the 1950’s hypoxia (< 2 ml. l$^{-1}$) has existed almost continuously below 70 m in the Baltic proper. Deep-bottom fauna has been severely affected and is now strongly reduced over an area of approximately 100,000 km$^2$ (Andersin et al. 1978). The absence of bioturbation is demonstrated by the development of laminated sediment layers in deposition areas deeper than 75 m and the total area of laminated sediments is estimated as being three times larger in the late 1980’s than in 1960.

The effects of macrofaunal activity on transport of particles and solutes within sediments are now well known (Aller 1982). Benthic macrofauna may increase apparent diffusion by a factor 2-10 compared to molecular diffusion. The scale of macrofauna particle reworking is large relative to biogeochemical zonations in the sediment and they may transfer particles and solutes between different redox zones rapidly. Much less is known for the meiofauna, although bioturbation caused by the smaller fauna must also be important. One cubic centimeter of a
North Sea surficial sediment typically contains a few hundred nematodes and a few tens of harpacticoid copepods. In shallower lagoons and estuarine mud-flats these numbers can be an order of magnitude higher. Effects of the activity of these animals are not well understood. Recently, Aller & Aller (1992) have estimated that the transport of solutes in estuarine muds is increased only by a factor 1.7-2.3 in the presence of meiofauna, depending on temperature. Part of this effect was the consequence of increased porosity, especially in the fluff layer that is formed on top of the sediment when meiofauna is present. Aller & Aller (1992) argued that meiofauna play a significant role in aerobic decomposition in the uppermost sediment layer because they increase transport rates and also increase reaction rates by feeding on bacteria. Macrofaunal activity increases all reaction rates but promotes anaerobic relative to aerobic reaction pathways during the initial stages of burial (Aller 1988, 1990; Kristensen et al. 1991).

**Nutrient regeneration**

Benthic regeneration of nutrients is thought to be a major factor determining productivity of estuarine and coastal waters. Although most nutrient regeneration is due to bacterial activity, the few studies that exist tend to show that macrofaunal activity significantly increases nutrient export from the sediment to the water column. A large part of this is probably due to ventilation of tubes and feeding activities, as in the hard clam *Mercenaria mercenaria* which increased the fluxes of oxygen and silicate by 20% and 86% respectively, and probably also increased inorganic nitrogen fluxes but not those of phosphate and CO$_2$ (Doering et al. 1987). In shallow waters, the entire water column may be turned over in a few days by filter feeders such as *Mytilus edulis* in the Oosterschelde (Herman & Scholten 1990). Also *Nereis diversicolor*, traditionally viewed as an animal feeding on organic material on or in the sediment, has been shown to start filter feeding when phytoplankton is present (Vedel et al. 1994). *Nereis* populations can potentially filter 5.6 m$^3$ water per m$^2$ per day, a volume 11-55 times greater than that of the overlying water column.

Effects of deposition of organic matter on phosphorus dynamics in sandy marine sediments were studied by Slomp et al. (1993). Addition of organic matter to boxcosms resulted in an increase of porewater phosphate concentrations and an increase in phosphate release rates from the sediment by a factor 3-5. No clear effects of macrofauna on sediment-water exchange of phosphate were found although the macrofauna appeared to rework the sediment. Also the incorporation of chlorophyll from senescent cells of *Skeletonema costatum*, as studied by Webb & Montagna (1993), was not affected by macrofauna.

Davey & Watson (1995) measured increases of ammonium and silicate fluxes of up to two orders of magnitude in the presence of *Nereis diversicolor* in the Tamar (UK). Such increases could not be explained only by the increased internal sur-
face due to the burrow structure, estimated at 200-300% when density was large, but required active ventilation. Through the activity of *Nereis*, the overlying estuarine water received ammonium from the sediment in quantities 10-20 times larger than from the river and sewage. Macrofauna may thus increase the nitrogen load in the water column but may also serve in reducing it: denitrification rates of NO$_3^-$ out of the water and from nitrification within the sediment were enhanced 3- and 5-fold respectively in the presence of the tube-building amphipod *Corophium volutator* (Pedret pers. comm.) and Kristensen et al. (1991) found a threefold increase in denitrification rates in the presence of *Nereis virens*.

**Effects of fauna on benthic community metabolism**

Benthic communities are major consumers of oxygen from the near-bottom layers of the water column. Much of benthic metabolism is usually related to bacteria and effects of the fauna are considered to be indirect. Benthic community metabolism is usually determined as oxygen consumption and carbon dioxide production by the whole sediment system (e.g. Hargrave & Phillips 1981) and therefore includes all respiratory processes by the whole array of benthic biota. From such measurements a community respiratory quotient CRQ can be determined that theoretically may change between 0.7 and 1.0 for aerobic systems, depending on the type of organic matter being oxidized. The fauna may indirectly play an important role here. In anoxic sediments, when the importance of anaerobic processes becomes larger, the CRQ may become considerably higher, from 1 (Teal & Kanwisher 1961) to 4 (Andersen & Hargrave 1984), the higher values only occurring when all sulfide produced by sulfate reduction is precipitated as FeS or FeS$_2$ (Jørgensen 1977). In this case community metabolism is severely underestimated. On the other hand, the CO$_2$ produced may be taken up by chemoautotrophic bacteria or by chemical processes such as CaCO$_3$ precipitation due to pH changes, which conversely may also lead to CaCO$_3$ dissolution (Anderson 1986).

The influence of macrobenthos on benthic community metabolism in Danish estuaries was studied by Andersen & Kristensen (1988). Input of labile organic matter from benthic primary production stimulated the overall heterotrophic metabolism in sediments exposed to light. In cultures kept continuously in the dark metabolism gradually decreased, probably due to a lack of readily decomposable material. In this study an important effect of macrobenthic animals on exchange of O$_2$, CO$_2$ and DIN across the sediment-water interface was measured. The presence of the deep burrowing *Nereis virens* increased the dark fluxes between 2 and 3 times, although the worm itself only contributed 10% to this increase. One of the mechanisms of this stimulation of microbial benthic activity appears to be the elimination of toxic metabolites and the supply of electron acceptors by the burrowing and ventilation activities of the worm (Kristensen
EUTROPHICATION AND ZOOBENTHOS DYNAMICS

1988). Effects of other macrobenthic estuarine species, *Corophium volutator* and *Hydrobia* spp., were less pronounced; however, these are mainly surface deposit feeders that do not burrow as deep as *Nereis vires*. Oxygen uptake in these experiments was stimulated twice as much as either carbon dioxide or dissolved inorganic nitrogen release, showing that reoxidation of the organic or inorganic substrates takes place. High CRQ's may however be an artifact of experimental handling (Kristensen & Blackburn 1989).

Secondary production by bacteria may increase as a consequence of increased inputs of organic material into sediments. This increased production is apparently utilised mostly by micro- and meiobenthic consumers, although the extent of the grazing and the partitioning by different benthic grazers is largely unknown. Certain ciliates and nematodes were found to be the most important grazers in experiments by Epstein & Shiaris (1992), with individual rates of 126-169 (labeled) bacteria per hour, whereas other ciliates and nematodes had much lower grazing rates. Microflagellates and harpacticoid copepods generally had low rates as well. Interestingly, gastrotrichs and foraminiferans did not graze on the labeled bacteria at all. Ciliates are voracious feeders on bacteria, each individual consuming up to 600 bacteria per hour, but still the total consumption only represents a very minor part of bacterial standing stock.

Interactions between benthic macrofauna and microbial communities in sediments are mainly due to burrowing and ventilation (Kristensen 1988) and by direct feeding on detritus and microorganisms (Cammen 1980; Hanson & Tennenore 1981). Increased transport due to ventilation of burrow water usually enhances reaction rates and solute fluxes by a factor 2-5 (Kristensen 1985) whereas reworking during burrowing is responsible for displacement of organic particles. Microbial activity may also be stimulated by meiobenthic animals due to fractioning of particles and to a series of little known meiofauna-bacterial interactions, from grazing to gardening. Nematodes, but also other meiofauna groups, produce large masses of mucus (Riemann & Schrage 1978). This mucus secretion may help in strengthening burrows or attaching eggs to the substratum but is certainly also involved in feeding. Riemann & Schrage (1978) hypothesized that many (most?) marine nematodes feed by entrapping small particles, including bacteria and even macromolecules, in the mucus threads which are subsequently browsed together with the mucus. Another interesting observation is that nematodes appear to construct tubes around decomposing organic matter, in which subsequent colonization by bacteria speeds up the decomposition process. The mucus secretion may also serve as a substrate for algal and bacterial growth that may be exploited by the nematode, a phenomenon called gardening.

**CONCLUSIONS**

Eutrophication may lead to increased primary production and therefore to in-
creased inputs of high quality organic material in shallow water sediments. These increased inputs may change benthic metabolism in many different ways. Mineralisation will become more intense in the surface layers of the sediment and more organic material will be buried deeper down. Increased organic loadings will lead to upward movement of reducing conditions and anoxia in sediments and ultimately in the water column and this will shift sediments from aerobic to anaerobic pathways that may ultimately lead to the disappearance of the fauna. Before this happens many other changes may occur. An increase in sedimenting high quality organic matter does not just lead to increases of benthic biomass but apparently favours fast growing, smaller species living in surface layers of the sediment, species that are unstable and tend to disappear shortly after the increased sedimentation stops. Productivity per unit biomass will become higher during such periods but total biomass may become lower. The often observed relationship between high productivity and low diversity in ecosystems probably also holds for marine sediments.

The quantification of these changes and of the relationships with nutrient loadings from river and the atmosphere, necessary for the management of our coastal systems, can not be achieved if the quantity and especially quality of the organic material arriving at and buried in sediments cannot be better measured and modelled. This requires better understanding of sedimentation-resuspension processes as related to primary production and water movement, and of mineralisation processes in the water. Benthic biology and metabolism enter the eutrophication arena because, as argued, the presence of the fauna fundamentally changes the physical and chemical behaviour of sediments and sediment-water exchange. Both release of solutes to the water and final burial of organic matter in the sediment change when fauna is absent. Faunal characteristics will have to be related to physical models that quantify sedimentation and water movement, but also to the biochemical characterisation of organic matter and its oxidation in sediments. An important effort is required in ecological modelling in which all such aspects are taken into account, which is linked with physical models and in which some synthetic information on the fauna (feeding types, reproductive strategies) is modelled together with sediment-water exchange and diagenetic processes and the breakdown of organic material within the sediments.

Finally, more detailed work on benthic biology and on interactions between animals and bacteria in sediments is required, e.g. on stimulation of bacterial growth by feeding, excretion, burrowing and ventilation of animals. The microbiology of organic matter mineralisation in marine sediments is still full of gaps. Although the main features of the Pearson-Rosenberg model are corroborated, the spatial and temporal dynamics and the quantification are still uncertain, e.g. the relationship between sedimentation processes and benthic biology needs much further study. The consequences of the species changes for energy flow in the marine ecosystem are also relatively unstudied but of large potential
economic consequence, e.g. the questions on which organisms are exploiting the high productivity of small polychaetes and what the shift from mollusks and crustaceans to echinoderms means for demersal fish and fisheries.

**LITERATURE**


Kristensen, E., M. H. Jensen & R. C. Aller, 1991. Direct measurement of dissolved inorganic nitro-
EUTROPHICATION AND ZOOBENTHOS DYNAMICS


