Chapter 11. THE ROLE OF SEDIMENTS IN SHELF ECOSYSTEM DYNAMICS

JACK J. MIDDELBURG
KARLINE SOETAERT

The Netherlands Institute of Ecology, Yerseke

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1. Introduction

Continental shelves are characterized by an active benthic compartment in close contact and interaction with the pelagic compartment. These interactions are two-way: there is an effect of the pelagic system on the ecology and biogeochemical functioning of the benthic system and vice versa, organisms living at or in the sediments affect the pelagic system. The benthic-pelagic interactions can be direct or indirect and operate at tidal to interannual timescales. For instance, benthic suspension feeders can affect phytoplankton concentration directly by their filtering activities and indirectly by enhancing recycling of nutrients, thus supporting pelagic primary production.

Traditionally, the benthic compartment of shelf ecosystems is considered to receive detritus settling out of the water column and to return most of these materials (with some delay) in the form of dissolved inorganic carbon and nutrients and to consume significant quantities of oxygen (Soetaert et al., 2000). A small but significant fraction of the incoming organic matter is buried (Middelburg et al., 1993; Hedges and Keil, 1995). Shelf sediments are also known to transform fixed N into N_2 by denitrification either directly by nitrate uptake from the water column or indirectly by coupled nitrification-denitrification following mineralization of

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organic nitrogen (Rysgaard et al., 1994). This N_2 escapes from the shelf ecosystem and this loss of fixed N by denitrification in shelf sediments accounts for ~7 Tmol N yr^{-1} or about $^1/_3$ of total nitrogen loss from the ocean (Middelburg et al., 1996; Brandes and Devol, 2002).

Shelf ecosystems are biologically active. Estimates of primary production range from 375 to 1195 Tmol C yr^{-1} (Gattuso et al., 1998; Wollast, 1998; Alongi, Chapter 10; Longhurst et al., 1995; Ducklow and McCallister, Chapter 9) and estimates of shelf ecosystem respiration vary from ~200 to ~300 Tmol C yr^{-1} (Gattuso et al., 1998; Wollast, 1998; Alongi, Chapter 10). The difference between production and respiration is either buried in shelf sediments (~13 Tmol C yr^{-1}; Hedges and Keil, 1995) or transferred to the open ocean (by difference: 77 to 895 Tmol C yr^{-1}).

A large proportion of organic matter processing in shelf ecosystems occurs in the benthic compartment because these systems are shallow, and the proportion of benthic to total respiration depends primarily on water depth (Heip et al., 1995). The relationship reported by Heip et al. (1995) predicts the benthic contribution to respiration to vary from about 40 % at shallow depths to a few % at a 100 m. Middelburg et al. (2004) reported a global respiration rate of shelf sediment of about 166 Tmol yr^{-1}, consistent with the 160 Tmol yr^{-1} of Jørgensen (1983). Wollast (1998) reported global shelf production and respiration rates of 500 and 300 Tmol yr^{-1} with sediments accounting for 150 Tmol yr^{-1} or about 1/2 of shelf respiration (range 65 to 333 Tmol yr^{-1}). Similarly, Rabouille et al. (2001) reported that sediments accounted for about 40 % of total respiration in the distal zone of the coastal ocean (mean depth of 130 m). Alongi (Chapter 10) reported a total shelf respiration of 307 Tmol yr^{-1} with 54 % occurring in the sediments.

Notwithstanding the prominent position of sediments in the nutrient and carbon cycling of shelf ecosystems, many studies only consider the pelagic compartment. On the basis of this incomplete, biased picture, inferences are made about the balance between autotrophic and heterotrophic processes and the export of organic matter to the open ocean. This transport of organic matter from the shelf to the open sea amounts to about (77 to 895 Tmol C yr^{-1}) and fuels the inferred open-ocean heterotrophic status (del Giorgio and Duarte, 2002).

In this chapter we will use numerical, coupled benthic-pelagic biogeochemical models to study the flow of organic matter and nutrients through shelf ecosystems. We have chosen nitrogen as our model currency and will give special attention to nitrogen dynamics of the shelf ecosystem as a function of water depth, and of sediment type. In section 11.2 we will first summarize the basic ecological and biogeochemical characteristics of shelf sediments; Jahnke (2004) provides a more detailed treatment. In section 11.3 we derive some simple parameterization of shelf-specific biogeochemical processes. In the next section we provide a short description of our modeling platform (Soetaert et al. 2001, 2000), before discussing simulations on shelf nitrogen cycling in full detail (section 11.5). In section 11.6 we address the potential importance of benthic primary producers, benthic suspension feeders and advective flow through permeable, sandy sediments for shelf biogeochemistry. In the final section, we summarize our conclusions and identify a few outstanding, pressing questions.

2. Characteristics of shelf sediments

During the last glacial advance, sea level dropped more than 150 m, and the majority of shelves were exposed and subject to erosion. At present, sediments cover most continental shelf systems. The type of sediment on the continental shelf is governed by the tectonic setting, the availability and river input of sediment and transport by waves and currents. Seasonal, storm-driven events are also important on many shelves. The inner continental shelf (< 65 m) are covered mainly with muds (37 %) and sands (47 %), the remainder is covered by corals (6%), shell debris (4%) and rocks/gravel (6%) (Hall, 2002).

These differences in sediment characteristics have a direct influence on the density, biomass, distribution and diversity of benthic communities (Heip and Craeymeersch, 1995) and on sediment biogeochemistry (Dauwe and Middelburg, 1998; Jahnke, 2004). There exists duality in the way biogeochemists and ecologists perceive and investigate benthic-pelagic coupling (Soetaert et al., 2002). While benthic ecologists have studied both the muddy and sandy substrates, most biogeochemists and microbial ecologists studying carbon and elemental cycling have focused on muddy and silty sediments. Traditionally, ecologists are mainly interested in the transfer of organic matter (food) from the water column to the benthic organisms and its cascading within the benthic food web. Both the role of bacteria and remineralization of nutrients are given only modest attention. The impact of biota on benthic-pelagic coupling is studied from the point of view of the higher organisms (Thomsen and Flach, 1997).

In contrast, biogeochemists traditionally view the seafloor as passively receiving detritus from the overlying water. Heterotrophic bacteria then mineralize this deposited organic matter, and the dissolved inorganic substances diffuse back to the water column (with some delay). These regenerated nutrients support primary production in the water column, and the nutrient cycle is closed. There are several reasons why this traditional, biogeochemical view of the role of sediment in shelf ecosystem functioning requires revision (Boudreau et al., 2001; Jahnke, 2004).

First of all, in the more shallow parts of shelf systems with clear waters, light may reach the bottom, and populations of benthic microalgae may proliferate. Cahoon (1999) and Jahnke (2004) have summarized the few data available, indicating that benthic microalgal production may approach that of phytoplankton in oligotrophic, clear water systems such as the Georgia continental shelf (Jahnke et al., 2000). The global rate of benthic microalgal production (28 Tmol yr^{-1}) reported by Charpy-Roubaud and Sournia (1990) is almost an order of magnitude lower than estimates of shelf phytoplankton production (~375 Tmol yr^{-1}; Gattuso et al., 1998; 575 Tmol yr^{-1}, Alongi, Chapter 10). However, the data set at hand is too sparse too allow derivation of a robust estimate of global shelf benthic primary production. Benthic microalgae have important consequences for the functioning of the shelf ecosystem because they (1) affect the exchange of nutrients and oxygen across the sediment-water interface, (2) constitute a major food resource for heterotrophic organisms and moderate benthic carbon flows and (3) may affect sediment stability (Paterson and Black, 1999; Middelburg et al., 2000).

Secondly, benthic suspension feeders have relative high biomass on the shelf (Heip and Craeymeers, 1995; Bryant et al., 1995) and these animals actively filter algae from the lower layer of the water column, the benthic boundary layer. This clearance of algae from the water can be a major term in benthic-pelagic exchange, by its effects on both algal loss and nutrient recycling. Benthic suspension feeders often dominate benthic-pelagic exchange and algal consumption in shallow ecosystems. This has been well documented for tidal inlets and other more enclosed basins (Herman et al. 1999; Heip et al., 1995).

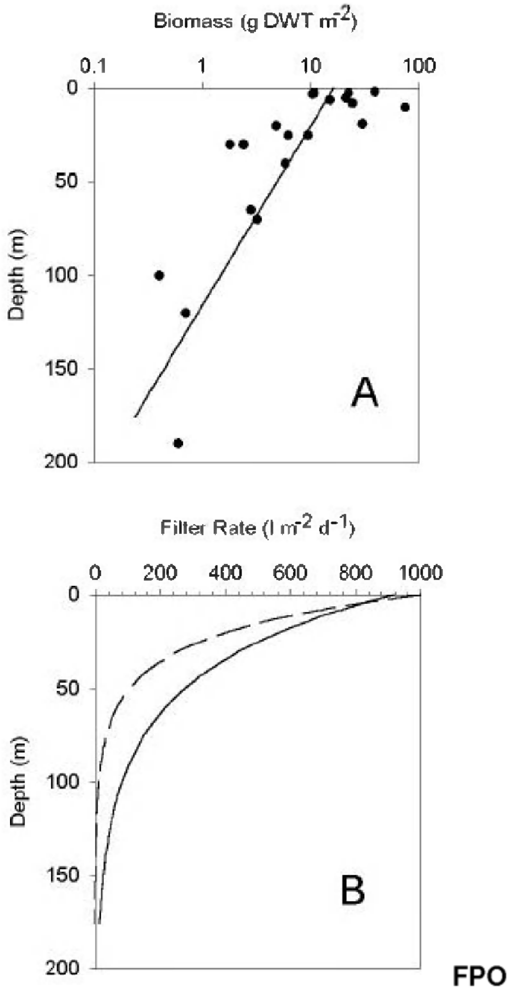

Figure 11.1 A. The depth dependence of benthic suspension-feeder biomass (data from Heip et al. 1995 and Bryant et al., 1995)
B. The depth dependence of filtering rates by benthic suspension feeders (solid line) and permeable beds (dashed line)

Thirdly, sandy sediments dominate continental shelves (de Haas et al., 2002). These sandy sediments have been subject to repeated cycles of deposition and erosion, resulting in well-sorted, permeable deposits. Their high permeability in combination with high current velocities and wave activities (another characteristic of coastal systems) results in advection through these permeable beds and enhanced dispersion (Huettel and Webster, 2001; Jahnke, 2004). Bedform topography, whether resulting from physical or biological processes, causes additional exchange of water between sediments and water column (Huettel et al., 1996; Precht and Huettel, 2003). These non-diffusive processes enhance exchange of solutes between the sediments and overlying water, relieving or eliminating diffusive limitations on oxygen and nitrate fluxes and mineralization product effluxes. This permeability-related exchange of water parcels between the water column and the sediments also results in the transfer of small particles from the water column to the sediment where they may be trapped depending on the relative sizes of pore spaces and the particles, and the energy of transport processes (Huettel and Rusch, 2001; Fries and Trowbridge, 2003). The overall effect is enhanced input of particles from the benthic boundary layer to the sediments and increased influxes of oxidants.

3. Quantifying enhanced exchange rates and primary production in shelf sea sediments.

The potential for filtration and primary production, and additional characteristics of shelf ecosystems contribute to the complexities of benthic-pelagic coupling in these regions. We are not yet able to include most of these processes as mechanistic equations in a shelf ecosystem model. However, we may describe their effect on ecosystem behavior using approximate dependencies and assuming steady-state conditions (i.e. change in biomass of neither benthic primary producers nor filter feeders).

The enhanced exchanges between water and sediment induced by filter-feeding animals or by physical advection through sands can be quantified in terms of the number of liters of water, with its dissolved and particulate contents, that is exchanged per unit area and time. These enhanced exchange rates can also be compared with filtration rates of ~10 l m^{-2} d^{-1} for diffusive exchange (Precht and Huettel, 2003). Heip et al. (1995) reported filter-feeder biomasses ranging between 9 and 74 g ash-free dry weight (ADWT, about 50% is C) for water depths shallower than 25 m. Bryant et al. (1995) tabulated values of 0.2 and 3 g C m^{-2} in the North Sea, at depths between 20-180 m. These data can be fitted with an exponential decay as a function of water depth (Figure. 11.1A). A filter feeder of 1 g AFDWT can filter on average some 57 l d^{-1} of water (Heip et al., 1995). Using this clearance rate and the above-derived biomass-depth relationship, we obtain a potential filtering of about 950 l m^{-2} d^{-1} at 0 m water depth, rapidly declining to 285 l m^{-2} d^{-1} at 50 m depth (Figure 11.1B). The best-fit function, relating filtration rate (l m^{-2} d^{-1}) to water depth (z, m) is:

$$FilterFeederRate = 945.e^{-0.024 \cdot Z} \tag{1}$$

Precht and Huettel (2003) calculated that filtering rate in beaches was about 1000 l m^{2} d^{-1}, whereas at 50 m depth on the continental shelf near the Eel River the filter rate was 103 l m^{-2} d . Fitting these points, we obtain the following regression, expressing the filtration rate through sands (l m^{-2} d^{-1}) as a function of water depth (z, m):

$$SandFilterRate = 1000.e^{-0.045 \cdot Z} \tag{2}$$

Although based on only 2 (!) points, the depth-decay coefficient for filtering by sands (0.045 m^{-1}) falls well within decay coefficients of 0.15 m^{-1} to 0.03 m^{-1} as estimated from exchange rates reported by Riedl et al. (1972) for wave periodicities varying from < 6 to > 13 s.

Based on this first-order estimate, it is clear that the potential filtering activity of biota and sands is of comparable importance, although the latter attenuates faster with water depth (Figure. 11.1B). However, there are also more subtle differences. Benthic suspension feeders have a preference for algae and often utilize only a small amount of detritus as food (Heip et al., 1995). Such particle selection is probably less pronounced in permeable beds, but data on this subject are scarce (Fries and Trowbridge, 2003). In addition, there is a feedback between algal clearance and the rate of benthic suspension feeding via biomass changes, which may not be the case for permeable bed filtration. However, clogging of permeable sediments may occur until the next sediment transport event.

Benthic primary production can be described using data from the Georgia continental shelf (Jahnke et al., 2000). We fitted a semi-mechanistic formulation that relates benthic primary production (BPROD, mmol C m^{-2} d^{-1}) to photosynthetically active irradiation at the sediment surface (I, μmol m^{-2} s^{-1}; Figure. 11.2):

$$BPROD = P\max\cdot(1 - e^{-\alpha \cdot I} - r) \tag{3}$$

where Pmax, the maximal photosynthetic rate equals 100 mmol C m^{-2} d^{-1}; α, the photosynthetic efficiency = 0.018 $(\mu mol\ m^{-2}\ s^{-1})^{-1}$ and r, the activity respiration fraction = 0.27. Both the values of α and activity respiration are within ranges observed for pelagic phytoplankton.

In what follows we will use a set of coupled physical-biogeochemical, mathematical models to exemplify the role of benthic-pelagic exchanges in shelf nitrogen dynamics. We will first deal with the nature of benthic-pelagic coupling in a setting patterned on a turbid, temperate shelf at 50 m water depth (section 11.5). We then use the model as a tool to isolate the effect of benthic primary production, benthic suspension feeders and permeable sediments on shelf ecosystem dynamics along a depth transect from 2 to 150 m (section 11.6). Although equations 1-3 only provide only a rough estimate of the potential for filtration and benthic primary production, it suffices for our exploratory modeling. We will not address the role of deposition-erosion cycles in shelf ecosystem dynamics. These intense, repeated cycles of sedimentation-resuspension interact with residual currents and result in strong lateral gradients of organic matter delivery, mineralization and burial (Dauwe and Middelburg, 1998; de Haas et al., 2002). Some parts of the shelf may act as depocenters, while other parts are net exporters. This lateral transfer causes a decoupling between local pelagic production and benthic response. We will also do not cover the regional or local groundwater input to shelf ecosystems and their ecological consequences (Moore, 1999). Moreover, we will focus our modeling efforts on biogeochemical dynamics and will use simple parameterizations for the dynamics of zooplankton.

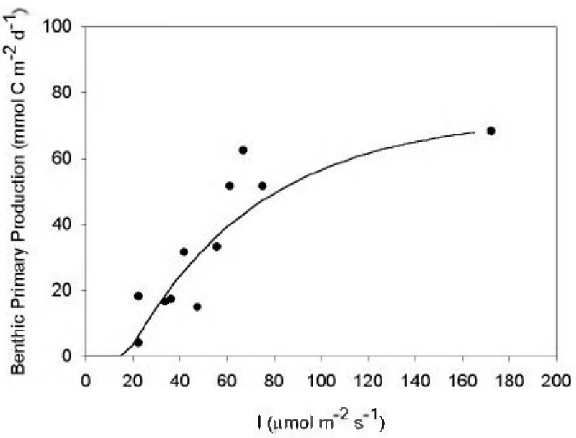

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Figure 11.2 Benthic primary production versus irradiation. Data are from Jahnke et al. (2000). The solid line corresponds to eq. 3.

4. Model description

Models, and in particular biogeochemical models, are a simplified representation of the complexity found in nature. With respect to benthic-pelagic coupling, the main task of the pelagic model is to provide upper boundary conditions to the sediment model, i.e. the solute concentrations (nutrients and oxygen) of the water overlying the sediment and the deposition of particles on the sediment surface. These properties are then used to update the corresponding sediment state variables (if appropriate). In return, the sediment model calculates the exchange of various solutes across the sediment-water interface, and these fluxes are used to update the respective pelagic state variables.

Soetaert et al.(2000) have proposed a hierarchical classification of the formulation of benthic-pelagic exchanges in biogeochemical models ranging from the simplest models where the bottom is plainly ignored to the most complex ones in which a depth-resolving pelagic model is coupled on-line with a depth-resolving diagenetic model (Boudreau, 1997). At intermediate levels of complexity one finds mass-conserving models that either consider a depth-integrated benthic model, or assume immediate equilibrium between particle deposition from the water column and the return flux of dissolved constituents from the sediment. Other, very simple descriptions where the return flux of solutes is imposed fail to conserve mass and are not suitable to represent benthic-pelagic coupling. It was argued that the computationally efficient zero-dimensional benthic models capture much of the dynamics inherent in benthic-pelagic coupling (Soetaert et al., 2000), so we will use this type of model when we calculate the effect of active filtering or benthic primary production in a water depth gradient. However, it is also instructive to examine how the variability in pelagic properties propagates towards and is smoothed by the sediments and this examination requires a fully resolved diagenetic model. Inclusion of such a generic diagenetic model also allows assessment of denitrification and partitioning of nitrogen regeneration and nitrification between the sediment and the water column. Moreover, simulations with this complete model can be used as a benchmark solution for the exploratory modeling.

The basic modeling framework was extensively described in Soetaert et al. (2000, 2001). In its most complex form it couples a Nutrient-Phytoplankton-Zooplankton-Detritus (NPZD) model for water-column biogeochemistry, a turbulence-closure and aggregate formulation for the physical part and a fully resolved diagenetic model in a 1-D setting (Figure 11.3 model 1, Table I). In short, the pelagic model is based on the algal model and detritus dynamics as propagated by Tett and Droop (1988) and Smith and Tett (2000), but including an explicit description of zooplankton dynamics. The algal model is a so-called unbalanced growth model, which explicitly describes the uncoupling of C and N assimilation through the build-up and consumption of an intracellular nitrogen pool (Droop, 1973). Turbulence intensity and temperature, the physical variables of the water column, were generated using a turbulence-closure formulation as described by Gaspar et al. (1990). In contrast to the previous modeling, sinking of detrital matter was made somewhat more realistic by taking into account aggregate formation (Kriest and Evans, 1999). The model is patterned on turbid shelf regions. Initial average nitrogen concentrations in the water column were 10.5 mmol N m^{-3}. The background extinction coefficient (m^{-1}) was made a function of total water depth and decreased from 0.1 at 5 m to 0.05 at the 150 m. While the pelagic compartment formulations are identical in all simulations, different sedimentary biogeochemical processes were included. In section 11.5 the full diagenetic model of Soetaert et al., (1996) is coupled, which essentially describes the C, N, and O cycle in the sediment (Figure 11.3 model 1). The effect of reduced species other than ammonium is lumped by describing the amount of oxygen that is needed to reoxidise them (so-called 'oxygen demand units' sensu Soetaert et al., 1996).

The exploratory model simulations in section 11.6 are based on simplified representations of the benthic compartment (Figure 11.3 model 2, Tables 9.1, 9.2). Briefly, it involves a vertically integrated dynamic sediment model in which the temporal evolution of one organic carbon and nitrogen pool is resolved and where sediment-water exchanges of constituents are parameterized (see Soetaert et al., 2000, 2002 for details). The effect of active filtration was included via the simple empirical relations derived in section 11.3: i.e. equation 1 and 2 for suspension-feeder and permeable bed filtration respectively. Sand filtering rates add to the sinking (advection) of particulate detritus and algae to the sediment surface, while suspension-feeding rates add only to algal removal from the water column. The pelagic model includes a light conservation equation (Soetaert et al., 2001), and calculates the light reaching the bottom. This fuels the net benthic primary production, modeled using eq. 3. To prevent benthic primary production from continuing to rise in the absence of nutrients, a nutrient-limitation term is added. Primary production adds organic matter to the sediment detritus pools and removes nitrate and ammonium from the overlying water column. All simulations presented include at least two full annual cycles, but our discussion focuses on only the annually integrated or averaged rates.

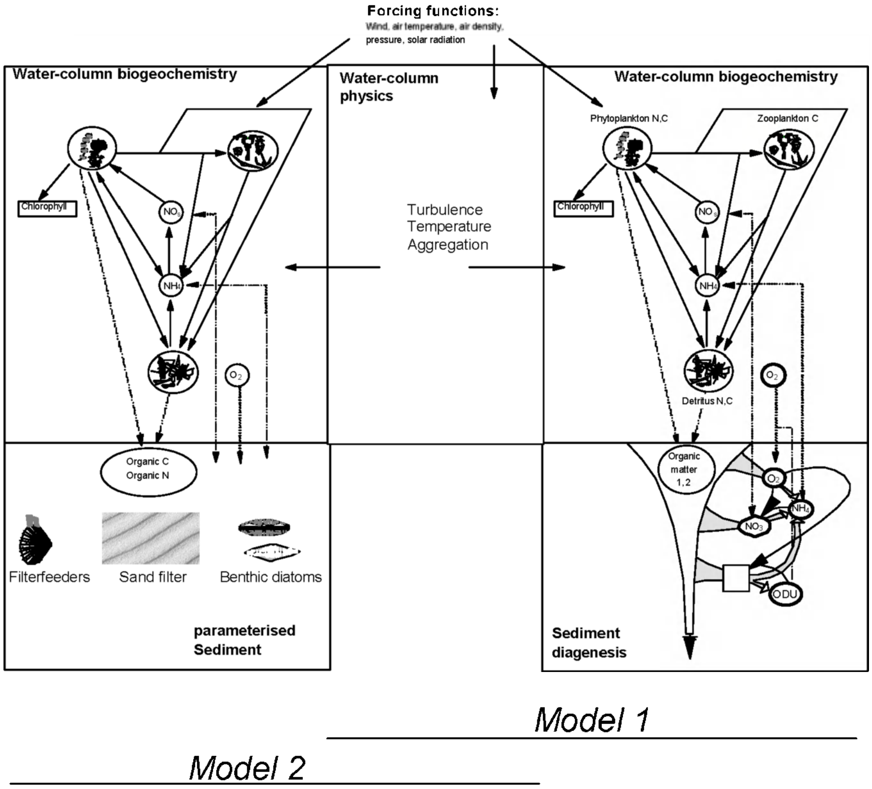

Figure 11.3 The structure of the two models, both encompassing the same physical and pelagic biogeochemical submodels, but differing in their benthic models. Model 1 (section 5) includes a vertically resolved diagenetic model, whereas model 2 (section 6) employs some simple parameterisation for benthic filter activities and benthic primary production

5. Nitrogen dynamics of continental shelf ecosystems

Nitrogen is an essential nutrient for autotrophic and heterotrophic organisms and is involved in a number of microbiological transformations including assimilation, regeneration, nitrification and denitrification. To assess its cycling in shelf ecosystems we have modeled in detail the major nitrogen flows for a 50-m deep station in a temperate shelf with depositional, silty/muddy sediments and relatively high total pelagic nitrogen content (> 7 mmol N m^{-3}). The parameter settings from the 50-m deep station were taken in accordance to the relationships derived by Soetaert et al. (1996), with a net sedimentation rate of 1 cm yr^{-1}, a bioturbation rate of 15 cm^2 yr^{-1} and diffusion enhancement by irrigation by a factor of 3 (Figures. 11.4-11.6). To prevent nitrogen loss due to sedimentary denitrification from draining the water column of nitrogen, we assumed that the N_2 flux was directly compensated by a nitrate flux towards the deepest water box. Previous tests have shown that the actual mechanism by or depth range at which this nitrogen is returned to the water column is not important (Soetaert et al., 2000).

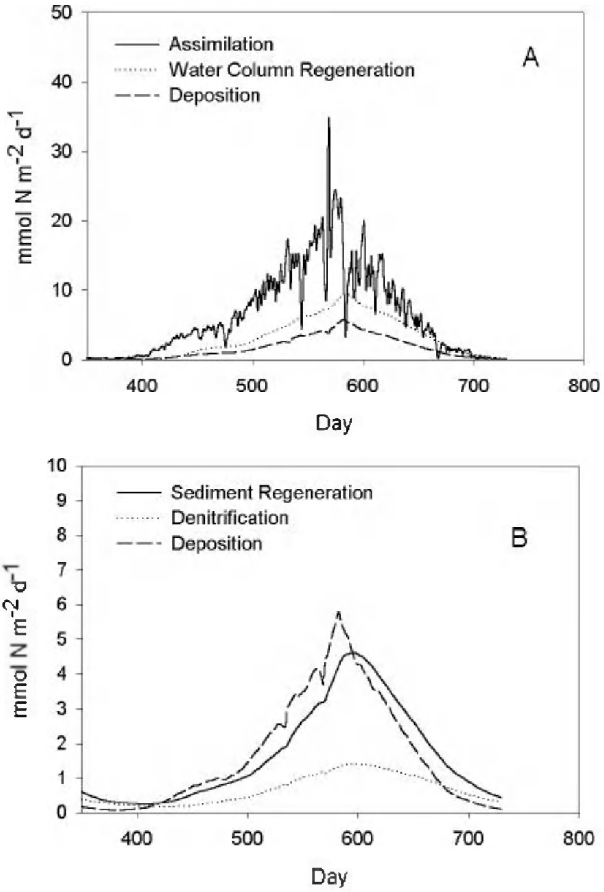

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Figure 11.4 A.) Simulated rate of water-column N-assimilation, microbial regeneration and N deposition. B.) Simulated rate of N-deposition, sedimentary N-mineralisation and denitrification.

The physical model is forced with weather and as a consequence primary production and nitrogen assimilation by phytoplankton show not only seasonal variability, but also short-term variability due to wind events (Figure 11.4A). Simulated microbial nitrogen regeneration from the detrital pool in the water column and delivery of particulate nitrogen (algae and detritus) to the sediments show much less short-term variability, and there is some delay in maximum activity (Figure 11.4A). This attenuation and delay is due to redistribution among and transfer to various members of the pelagic food web (phytoplankton, zooplankton and detritus with associated bacteria). The simulated sediment properties display far less short-term variability than the pelagic system (Figure 11.4B). Pulsed delivery of organic N to the sediments (as algae and detritus) induces a sedimentary response that is attenuated and delayed (Figure 11.5, Plate). All labile organic N delivered to the sediments is eventually regenerated, and annual integrated rates of N deposition and sediment mineralization are equal, but the seasonality in sedimentary N mineralization is smoother and has a lower amplitude. Over the year oxygen fluxes and penetration depths vary from 2.5 to 23 mmol m^{-2} d^{-1} and from 0.5 to 3.5 cm, respectively (Figure 11.5, Plate). Similarly, nitrate and ammonium effluxes vary from 0.16 to 1.6 and 0.02 to 1.4 mmol m^{-2} d^{-1}, respectively. Sedimentary denitrification varies from 0.17 to 1.4 mmol m^{-2} d^{-1} (Figure 11.4B) and contributes between 6 and 15 % to mineralization.

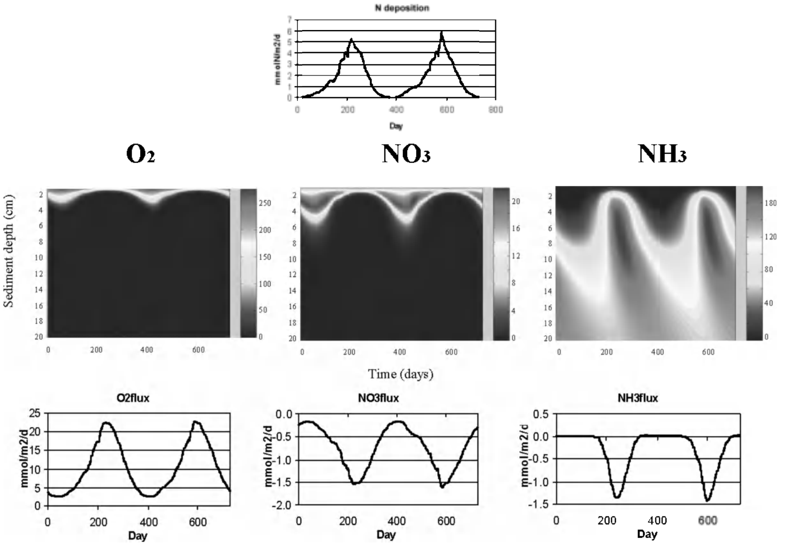

Figure 11.5 Spatio-temporal plots of oxygen, nitrate and ammonium in the sediment and time-series of nitrogen delivery to sediments and sediment-water exchange fluxes of oxygen, nitrate and ammonium.

The model predicts (Figure. 11.6) that each year phytoplankton assimilates ~ 2404 mmol N m^{-2}, 33% (791 mmol N m^{-2}) in the form of nitrate and 67% (1613 mmol N m^{-2}) as ammonium. The average phytoplankton stock (47.7 mmol N m^{-2}, corresponding to an average *Chl* of 1.83 mg m^{-3}) is turned over about 50 times per year. This rapid recycling is due to phytoplankton losses by settling (~7%, 165 mmol N m^{-2}), mortality (~ 15%, 351 mmol N m^{-2}) and grazing by metazoans (78%, 1889 mmol N m^{-2}). In the model, zooplankton (inventory of 8 mmol N m^{-2}) graze on phytoplankton only, 33% (619 mmol N m^{-2}) of the food is not assimilated and enters the detrital pool, another part of the food is respired (25%, 472 mmol N m^{-2}) and the remaining 42% (798 mmol N m^{-2}) is assimilated.

The detritus pool (46.5 mmol N m^{-2}) comprises dead organic nitrogen as well as microbial nitrogen and each year 1620 mmol N m^{-2} flows through this pool: this pool is turned over 35 times per year. Detritus is produced from algal mortality (22%, 351 mmol N m^{-2}), zooplankton mortality (40%, 650 mmol N m^{-2}) and by sloppy zooplankton grazing (38%, 619 mmol N m^{-2}). Part of the detritus (29%, 464 mmol N m^{-2}) settles to the sediment, another part is mineralized to ammonium (71%, 1157 mmol N m^{-2}). Ammonium is rapidly recycled (average turnover time of about 4 d) because its stock (22 mmol N m^{-2} or 0.44 mmol l^{-1}) is rather low compared to its total regeneration of 1886 mmol N m^{-2}: 61% (1157 mmol N m^{-2}) from detritus, 33% (622 mmol N m^{-2}) from zooplankton and 6% (107 mmol N m^{-2}) from the sediments. The majority (85%, 1613 mmol N m^{-2}) of ammonium is taken up by phytoplankton; the remaining 15% (273 mmol N m^{-2}) is nitrified. In the model universe, each year algae assimilate about 791 mmol N m^{-2} of nitrate and the nitrate stock (277 mmol N m-2 or 5.5 mmol l^{-1}) is refueled by the sediments (34%, 270 mmol N m^{-2}), by nitrification (35%, 273 mmol N m^{-2}) and by lateral advection (31%, 245 mmol N m^{-2}). The phytoplankton (165 mmol N m^{-2}, 26%) and detritus (464 mmol N m^{-2}, 74%) delivered to the sediment surface are added to the pool of sedimentary organic matter and are mineralized to ammonium (620 mmol N m^{-2}), the majority (83 %, 514 mmol N m^{-2}) of which is nitrified, the rest is buried (9 mmol N m^{-2}) or fluxes out of the sediment (107 mmol N m^{-2}). The nitrate produced either fluxes out of the sediment (53 %, 270 mmol N m^{-2}) or is denitrified (47 %, 245 mmol N m^{-2}).

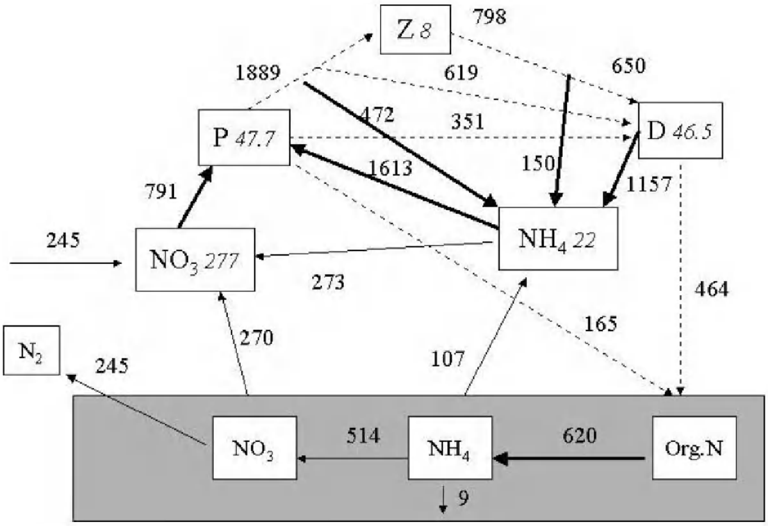

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Figure 11.6 Annual nitrogen budget for a 50-m deep shelf system. Italic numbers in boxes refer to inventories (mmol N m^{-2}). Fluxes are given in mmol N m^{-2} yr^{-1}; organic to inorganic transformation are in bold; organic-to-organic transformations are dashed and inorganic-to-organic transformations are solid arrows.

Oceanographers are increasingly studying the continental shelf because of its high primary production and important role in the oceanic biological pump (Ducklow and McCallister, Chapter 9). Net and recycled production on the continental shelf are often analyzed using approaches that have shown to be useful in the open ocean. However, the prominent role of sediment in shelf ecosystem dynamics complicates the application of some of these approaches. Primary production is often partitioned into net and regenerated production based on nitrogen substrate use and ^{15}N uptake measurement can be used to quantify this in terms of an f-ratio (Dugdale and Goering, 1967). Nitrogen isotope-based f-ratios for continental shelf systems are typically ~ 0.4 (Chen, 2003), consistent with our simulation (~ 0.33, Figure 11.6). However, a significant fraction of the nitrate is recycled within the water column (nitrification) or comes from the sediments and therefore cannot be considered as an external input. The nitrate that is denitrified in shelf sediments is truly removed from the system and provides a better estimate of new nitrate required for steady state. The rationale is as follows: denitrification in shelf sediments is mainly fuelled by nitrification (Middelburg et al., 1996), hence eventually by organic nitrogen input to the sediment. The organic nitrogen input to sediments is largely returned in a fixed form (Figure 11.6), but a small fraction is lost by denitrification and must be resupplied externally to keep the system running. Our simulations indicate that the ratio of external nitrate (245 mmol N m^{-2}) to total nitrogen assimilation (2404 mmol N m^{-2}) corresponds to an export ratio of ~ 0.1 (Figure 11.6), more in line with carbon budget estimates (Chen, 2003).

The importance of sediments to shelf ecosystem functioning is clear from the nitrogen budget. Denitrification is restricted to shelf sediments and about 65% of nitrification and 26% of nitrogen regeneration occur in the benthic compartment (Figure. 11.7). Although there is pronounced seasonality in shelf sediment nitrogen cycling and sediment-water exchange fluxes, the short-term variability found in water-column properties is attenuated in the sediment. Thus the sediment provides some memory to shelf ecosystems. One of the main factors governing the relative importance of water-column and sedimentary processes is the water depth, and we will therefore address this question in the next section.

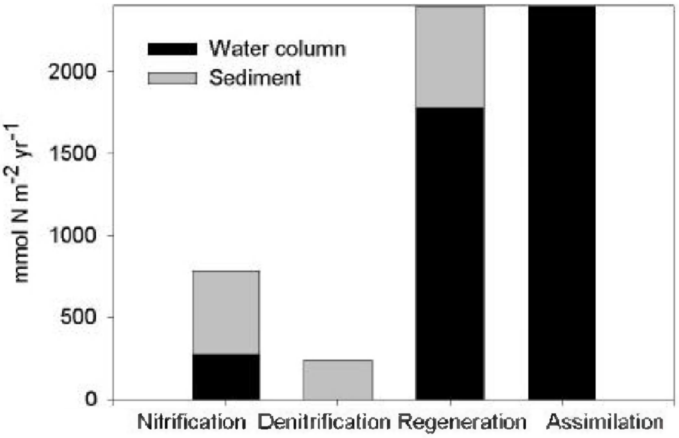

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Figure 11.7 Partitioning of nitrification, denitrification, N-regeneration and assimilation between water column and sediment for a 50-m deep shelf.

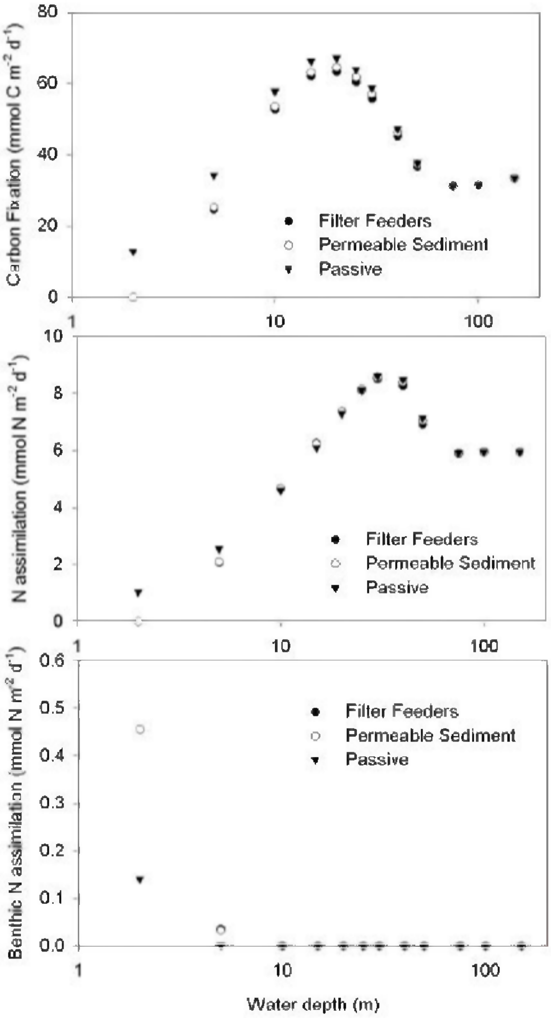
6. Dynamics of a coupled benthic-pelagic ecosystem with an active benthic compartment

In order to assess how ecosystem behavior is modulated by the action of filter feeders, physical filtering through sands and benthic primary production, the same coupled model, excluding and including the effect of these processes but with simplified benthic-pelagic exchange (Table I, II) was applied along a shelf depth gradient (2-150 m; Figures. 11.8-11.10). In the absence of benthic filtering activity (Figure 11.8 A, B), pelagic integrated photosynthesis peaks at 20 m (67.1 mmol C m^{-2} d^{-1}), while phytoplankton N-assimilation is maximal at 30 m water depth (8.6 mmol N m^{-2} d^{-1}). Both decrease with increasing station depth to about 31.5 mmol C m^{-2} d^{-1} and 6 mmol N m^{-2} d^{-1} at 100 m depth and also decrease toward the 2-m deep station (12.9 mmol C m^{-2} d^{-1}, 1 mmol N m^{-2} d^{-1}).

Integrated water-column production is a function of the total N-content of the water, the standing stock of algae and the light regime experienced by the algae, which depends on the depth of the euphotic zone and the mixed layer. With decreasing water depth, the average light regime improves, hence their capacity for biosynthesis and photosynthesis, but the total nitrogen load decreases, which lowers the total amount of nitrogen that can be converted into their biomass. Conversely, with increasing water depth, the euphotic zone becomes smaller than the mixed layer and the integrated amount of light received by algae decreases while the total nitrogen load increases. As a consequence of these opposing trends in light and N availability there is an optimum for phytoplankton assimilation around 20 to 40 m. The optimum for C fixation is shallower than that of N assimilation (Figure 11.8A,B), because the former more closely tracks the light regime than the latter.This spatial separation of optimum C and N assimilation can be compared to the uncoupling of C fixation and N assimilation observed in open-ocean, mixed-layer vertical profiles showing maximum N assimilation at greater depths than C fixation.

Simulated benthic primary production was limited to depths < 5 m and does not play a role of significance except for the shallowest station at 2 m, where it accounts for about 7% of all primary produced matter (Figure 11.8C). This limited role of benthic primary production in the absence of benthic filtration is consistent with observations in turbid, temperate estuaries and is a direct consequence of our model parameters, i.e. a relatively high background attenuation coefficient and high N concentrations in the water column: > 7 mmol m^{-3}. This large N-content allows the development of substantial phytoplankton biomass with accompanying shading.

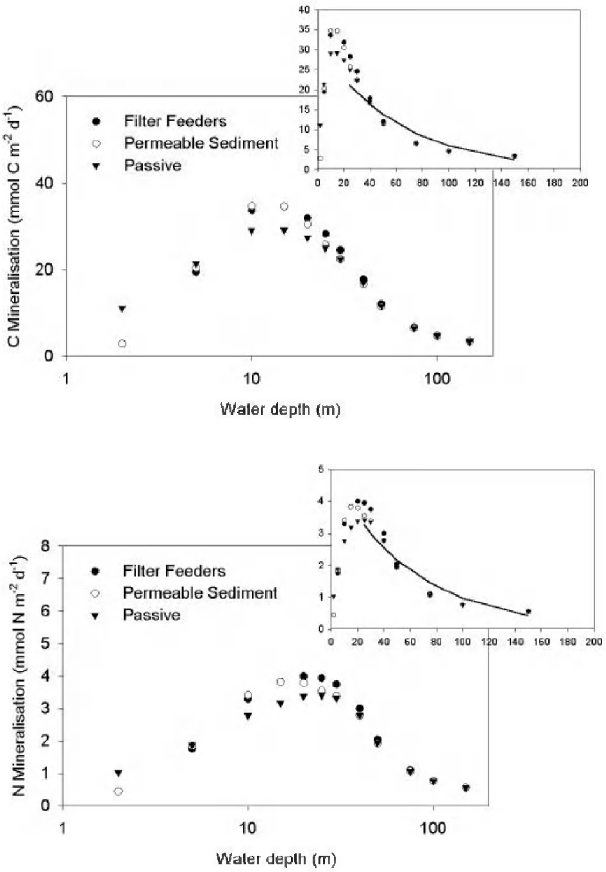
With increasing water depth, a decreasing fraction of the net assimilated carbon and nitrogen is mineralized in the sediment, 80% and 88% at 2 m, 15% and 13% at 100 m depth for carbon and nitrogen, respectively. Total benthic mineralization rates (Figure 11.9) peak at 15 m for C (29.2 mmol C m^{-2} d^{-1}) and at 25 m for N (3.4 mmol N m^{-2} d^{-1}). This difference in depth of maximum sedimentary mineralization of C and N is due to difference in the depth-integrated assimilation of C and N (Figure 11.8). The depth of maximum sediment mineralization is shallower than the depth of maximum C and N assimilation because a larger proportion of assimilated C and N is mineralized in the water column with increasing depth.



FPO

Figure 11.8 A) Simulated phytoplankton carbon fixation as a function of water depth for impermeable, passive sediments, permeable sands and sediments with benthic suspension feeders. B) Simulated phytoplankton nitrogen assimilation as a function of water depth for impermeable, passive sediments, permeable sands and sediments with benthic suspension feeders. C)Simulated nitrogen assimilation by benthic algae a function of water depth for impermeable, passive sediments, permeable sands and sediments with benthic suspension feeders.

The simulated depth dependence of sedimentary C and N mineralization (at depths more than 25 m) can be described by exponential relationships (Figure 11.9 insets) with depth attenuation coefficients of -0.017 and -0.016 m^{-1} for C and N, respectively. These attenuation coefficients based on our modeling exercises are very similar to those based on compilations of experimental results for estuarine systems (-0.015 m^{-1}: Heip et al., 1995) and shelf ecosystems (-0.018±0.006 m^{-1}: Middelburg et al., 2004). This similarity is not inherited from a common database because the settling velocity of particulate matter in our simulations is modeled with a particle aggregation module.



FPO

Figure 11.9 A) Simulated sedimentary carbon mineralization as a function of water depth for impermeable, passive sediments, permeable sands and sediments with benthic suspension feeders. The inset shows an exponential fit to sediment mineralization for depths ≥ 25 m. B) Simulated sedimentary nitrogen mineralisation as a function of water depth for non-permeable, passive sediments, permeable sands and sediments with benthic suspension feeders. The inset shows an exponential fit to sediment mineralisation for depths ≥ 25 m.

The effect of benthic filtering activity, whether biotic or abiotic is discernible only for those stations where the water column is shallower than 50 m (Figure. 11.8, 11.9). The effect of filter feeders or filtering through sands is largely similar, so we will discuss them together. While the direct effect of detrital fall and algal filtering is an increase of material transfer from the pelagic to benthic system, there are indirect effects via their impacts on the functioning of the pelagic systems that may result in lower benthic mineralization rates. Simulated benthic filtration reduces phytoplankton concentrations and as a result integrated carbon assimilation rates in the water column are depressed to 73% at 5 m depth, 92% at 10 m depth and then slowly attain 100% at 100 m. For the 2-m deep water column, filtering rates are sufficient to annihilate pelagic production, whilst increasing benthic production from 0.91 mmol C m^{-2} d^{-1} and 0.14 mmol N m^{-2} d^{-1} in the absence of filtration to 2.9 mmol C m^{-2} d^{-1} and 0.46 mmol N m^{-2} d^{-1} in the presence of filtration (Figure 11.8, 11.9). The effect on phytoplankton nitrogen assimilation rates is different, as here filtering not only reduces algal biomass, but also relaxes the nitrogen limitation via increased benthic mineralization rates. Consequently, phytoplankton nitrogen assimilation is depressed only at 2 and 5 m depth, to 0% and 80% of its value in the absence of filtering activity.

At water depths > 50 m, filtering of pelagic systems by benthic animals and/or sandy, permeable beds has minor effect on the functioning of the ecosystem (Figure 11.8–11.10). At these larger depths, most of the phytoplankton production is grazed by metazoans (~ 80%) or ends up in the microbial food chain after mortality (~ 15-19%) with little settling of algal material following aggregation (Figure 11.10A). Shoaling of the water column results in an increase in the proportion of algal settling to the sediment (~ 54% at 5 m) at the expense of zooplankton grazing (~ 35% at 5 m) and algal mortality (~ 11% at 5 m). However, the fate of phytoplankton production depends not only on water depth, but also on the nature of the benthic compartment. Filtering of the water column augments these differences between shallow and deep shelf ecosystems and at 5 m ~72% of the algal reach the bottom, ~ 22% is grazed and only 6% of phytoplankton losses can be attributed to mortality (Figure 11.10B).

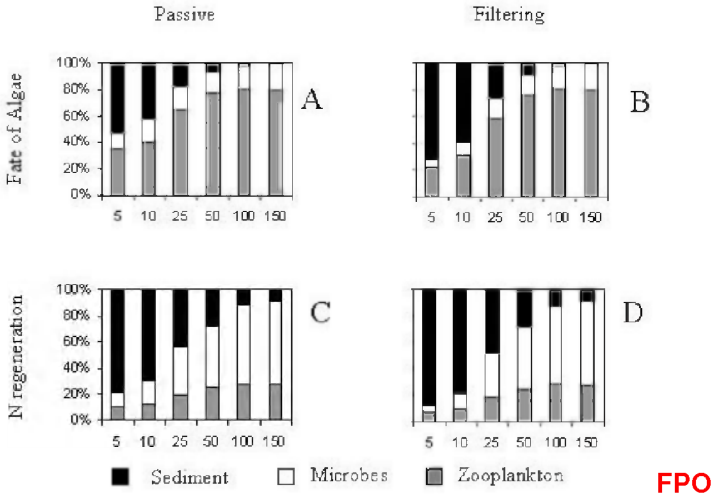


Figure 11.10 A) The fate of phytoplankton production as a function of water depth in the absence of benthic filtering activity: grazing, settling to the sediment and mortality. B) The fate of phytoplankton production as a function of water depth in the presence of benthic filtering activity: grazing, filtering and settling to the sediment and mortality. C) The partitioning of the nitrogen regeneration among sediments, zooplankton and heterotrophic microorganisms for passive sediments. D) The partitioning of the nitrogen regeneration among sediments, zooplankton and heterotrophic microorganisms with benthic filtering activity.

Similar conclusions regarding depth dependence and the role of filtering are reached when nitrogen regeneration is analyzed (Figure 11.10 C, D). At 150 m water depth, ~ 28% of the regeneration is due to zooplankton, 63 % is due to pelagic bacteria and only 9 % of the regeneration can be attributed to sediments. At 5 m depth and in the absence of filtering activities, zooplankton and pelagic bacteria each account for about 10% of the nitrogen regeneration with sediment mineralization contributing about 80% (Figure 11.10C). Active filtering of the water column by benthic animals or permeable beds further increases the share of sediment to 88% (Figure 11.10D).

7. Conclusions

The presence of a benthic compartment in direct contact with the pelagic compartment has major consequences for shelf ecosystem functioning. We are the first to admit that our computational approach has severe limitations in reproducing actual rates because of the many simplifications underlying the model. Moreover, model parameterization is based on a rather turbid, nutrient-rich shelf in the temperate zone. As a consequence we might have underestimated the role of benthic microalgae for clear-water, nutrient-poor shelf systems (e.g. Blackford, 2002; Jahnke et al., 2000). Nevertheless it will be clear that the benthos is an essential part of shelf ecosystem functioning. Respiration and N regeneration in sediments account for > 80 % of total system activity in shallow sediments to about 10 % at the shelf-break and can not be ignored in studies and budgets of the continental shelf. Moreover, some processes are limited to the sediment because they depend on suboxic or anoxic conditions, e.g. denitrification. Regeneration of material in the sediment also results in an attenuation and delay of the response of shelf ecosystems to short-term pulses of primary production (Figures 11.4, 11.5).

Biogeochemists traditionally focus on clays and silts that passively receive detritus from the overlying water (Boudreau et al., 2001). However, sandy sediments are dominant in continental shelves and act as filter beds that remove particles from the water column (Jahnke, Chapter 6). Our simulations were based on a very simple parameterization of benthic filtering activity (because of a lack of basic data) and should be considered as exploratory exercises rather than as quantitative reproductions. These simulations suggest that the effect of the benthic filter is insignificant if the water depth is > 50 m. However, at shallower depths, both the benthic and pelagic compartments are affected by filtering.

Pelagic ecosystem dynamics is influenced directly by removal of algal biomass by benthic filtering and may result in a lower phytoplankton biomass and production. At shallow depths (< 10 m), this effect is more important than the increased efficiency of input to the sediment and leads to lower supply of material to the sediments. At intermediate depths (10-50 m), the presence of a benthic filter has a smaller effect on algal mortality but significantly increases the net flux of organic matter to the sediment. We hope that we have conveyed that, in order to further understanding, a continental-shelf ecosystem study should explicitly consider the benthos. Since the median shelf depth is about 60-70 m, it is also clear that benthic filtering due to suspension feeders or permeable beds requires further study because of its consequences for ecosystem functioning and stability.

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