

## CHAPTER 14

# *Modelling Benthic Nitrogen Cycling in Temperate Coastal Ecosystems*

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### 14.1 INTRODUCTION

This chapter describes the ecological processes of the inshore regions of the continental shelf in temperate latitudes. In many of these areas, particularly those of the North Atlantic shelf, the high turbulence due to tides and winds ensures good vertical homogeneity of a rather shallow water column. Under such circumstances, sediments play a prominent part in the overall working of the ecosystems, and are in close interaction with the planktonic phase (Paasche; Blackburn, this volume).

Besides being the starting point of the benthic trophic chain, of considerable economical importance in coastal regions, sediments play two key roles with respect to the plankton system:

1. They act as *regenerators* of mineral nutrients for the water column. Direct comparison between benthic nitrogen release and planktonic primary production shows that sediments often supply 30–70% of nitrogen requirements by phytoplankton (Table 14.1).
2. Sediments are often the only site in coastal marine ecosystems where anaerobic conditions exist. They are therefore the site of denitrification, a process which can result in the elimination of up to 25% of nitrogen mineralized in the benthos (Table 14.1).

In shallow systems, sediments constitute by far the most important reservoir of nitrogen. Owing to the buffering effect of this large stock, benthic nutrient regeneration is more steady than most water column remineralization processes, and is also more constant than exchange through thermoclines, which are often of intermittent nature. We will see that the seasonal variations of planktonic processes in temperate coastal ecosystems are largely dependent on the

Table 14.1. Selection of data on benthic nitrogen recycling processes in coastal environments

Environments	N flux across sediment-water interface (mg N m <sup>-2</sup> d <sup>-1</sup> )			Denitrification (mg N m <sup>-2</sup> d <sup>-1</sup> )		N requirements of primary production (g N m <sup>-2</sup> y <sup>-1</sup> )		References
	NH <sub>4</sub> <sup>+</sup>	NO <sub>3</sub> <sup>-</sup>	Total		Percentage total N mineralization		Percentage supplied by benthic mineralization	
La Jolla Bight (CA, USA)	12	2	14	—	—	77	7	Hartwig 1974
Loch Turnaig (UK)	13	0	13	—	—	29	17	Davies, 1975
Buzzard Bay (MA, USA)	18	1	19	—	—	10	70	Rowe <i>et al.</i> , 1975
Cap Blanc (Africa)	78	58	136	—	—	128	39	Rowe <i>et al.</i> , 1977
Belgian coastal zone	25	32	57	17	23	27	78	Billen, 1978
Southern Bight of the North Sea	13	17	30	5	15	28	38	Billen, 1978
Narraganset Bay	34	4	38	33	16	—	—	Seitzinger <i>et al.</i> , 1980
South River (NC, USA)	38	0.5	38.5	—	—	48	29	Fisher <i>et al.</i> , 1982
Neurse River estuary (NC, USA)	76	1	77	—	—	107	26	Fisher <i>et al.</i> , 1982
Georgia Bight (USA)	55	3	59	—	—	132	16	Hopkinson and Wetzel 1982
Great Belt (DK)	10	7	17	49	16	17	36	Blackburn and Henriksen 1983
W. Kattegat (DK)	13	5	18	69	22	15	42	Blackburn and Henriksen, 1983
E. Kattegat (DK)	20	5	25	28	8	17	53	Blackburn and Henriksen, 1983
Limfjord (DK)	25	13	38	188	26	26	55	Blackburn and Henriksen, 1983

behaviour of the large pools of organic material deposited in the sediments.

For understanding the role of benthos in nutrient cycling at the ecosystem level, and for relating this role to the basic microbiological and physicochemical processes occurring in the sedimentary environment, mathematical modelling can be a very powerful tool.

A model can be defined as a simplified representation of reality, relating processes at a certain level of complexity to processes at a lower level. In this sense models are very close to what is generally considered to be a scientific explanation, and do not necessarily involve mathematics. Mathematical formulation of models is, however, often the simplest way to achieve quantitative predictions.

Mathematical models can be used at different stages of an ecological investigation. The current practice is to consider modelling as the final step of the study, as a way of summarizing all observational and experimental data collected, and checking their coherence. Models can also constitute the final aim of the study, because models are often urgently required as a management tool, allowing optimization of human action for altering or restoring the working of ecosystems in a desired direction.

But modelling can also be practised at an earlier stage of ecological investigations, and in a more interactive way with respect to experimental and observational work. In this way it can help in planning field work and in identifying the processes which are worth a more detailed study. Results of mathematical simulation, by aid of roughly idealized models, suggest experiments and observations, which in turn allow us to reconsider and refine the model.

It is an implicit ambition of the present review to illustrate these different ways of practicing mathematical modelling in ecological investigations. Our aim is not to present *the* final model of nitrogen recycling in sediments, which would be in any case quite presumptuous! Instead, we shall begin with deliberately oversimplified models of nitrogen transfer in coastal marine ecosystems which will help in understanding the basic roles of sediments in the dynamics of planktonic processes. In the light of these models we shall then examine, in much more detail, the data available in the literature concerning the control mechanisms of those sedimentary processes, identified as important by the preceding discussion. This will allow us to develop a more realistic model of benthic nitrogen cycling, the results of which will be compared to observations reported in the literature.

#### 14.2 IDEALIZED MODELS OF SEASONAL VARIATIONS OF NITROGEN CYCLING

Marked seasonal variation in the stocks and fluxes of planktonic compartments is a characteristic of shallow and neritic zones as compared with the oceanic

systems (Heinrich, 1962). In temperate coastal zones the prominent feature of this variation is the occurrence of a spring phytoplankton bloom lasting 1–2 months (accompanied, after only a few days delay, by a peak of heterotrophic bacteria) which results in the exhaustion of nutrients (see e.g. Lancelot and Billen, 1984; Peinert *et al.*, 1982). In the summer, primary production and phytoplankton biomass reach a lower, more steady level, as is also the case for nutrient concentrations and heterotrophic bacterial activity. Primary production drops during the winter and high levels of dissolved nutrients are regenerated.

The beginning of the spring phytoplankton bloom is explained by the rise of light intensity and photoperiod above a critical level, required for the net growth of phytoplankton in the whole water column (Sverdrup, 1953; Gieskes and Kraay, 1975). The wane of the bloom was classically explained by an increasing pressure of zooplankton grazing. The presence of overwintering zooplankton species was also put forward as the explanation for the absence of a distinct spring phytoplankton bloom in North Atlantic waters (Heinrich, 1962). However, recent data show that net zooplankton grazing in coastal ecosystems does not play dominant role in the dynamics of phytoplankton and is not responsible for the wane of the spring phytoplankton bloom (see e.g. Fransz and Gieskes, 1982; Joiris *et al.*, 1982; Lancelot and Billen, 1985).

The purpose of the present discussion is to assess the role of sediments on the pattern and intensity of planktonic processes.

#### 14.2.1 Closed system—three-compartment model

Very simple models of nutrient transfers between the first trophic levels of aquatic ecosystems are able to simulate adequately the general trends of the seasonal variations of nutrients and phytoplankton biomass summarized above, without making explicit reference to zooplankton.

Let us first consider the basic model described in Figure 14.1 which includes a classical representation of light, temperature and nutrient control of primary production, a first-order loss rate of phytoplankton and a first-order decay of a single detritus compartment (made of dissolved, as well as particulate, non-living organic matter).

As seen in Figure 14.2, this model predicts the occurrence of a distinct phytoplankton spring bloom provided that the turnover time of the detritus compartment is longer than about 1 month. With shorter residence time of the detritus pool no nutrient limitation occurs, and high phytoplanktonic biomasses are maintained during summer.

In the scope of this model the occurrence of a distinct spring bloom, followed by a summer steady state with lower biomasses, depends on the storage of a significant part of the nutrients in a reservoir not directly available to primary production, with a residence time longer than the life time of phytoplankton cells.

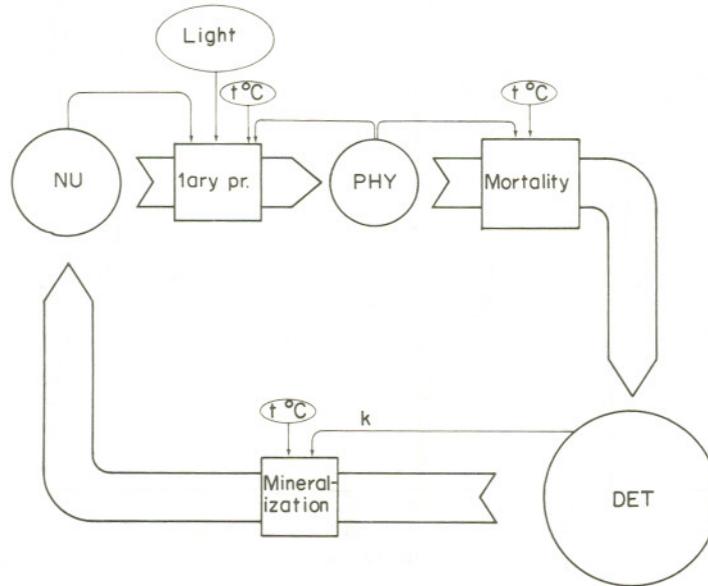


Figure 14.1. Closed system—three-compartment model of nitrogen transfers in marine ecosystems.

NU = inorganic nitrogen

PHY = phytoplankton biomass

DET = total pool of detritus (dissolved and particulate, in the planktonic as well as in the benthic phase).

The transfers between the three compartments are assumed to obey the following kinetics:

$$\text{Primary production: } \mu_{\text{max}} \cdot f_{\text{Mich}}(\text{NU}) \cdot f_{\text{Vol1}}(I) \cdot f_{\text{Arrh}}(T) \cdot \text{PHY}$$

$$\text{Phytoplankton mortality: } k_{\text{PHY}} \cdot f_{\text{Arrh}}(T) \cdot \text{PHY}$$

$$\text{Detritus mineralization: } k_{\text{DET}} \cdot f_{\text{Arrh}}(T) \cdot \text{DET}$$

$$\text{with: } f_{\text{Mich}}(\text{NU}) = \text{NU} / (\text{NU} + k_{\text{NU}})$$

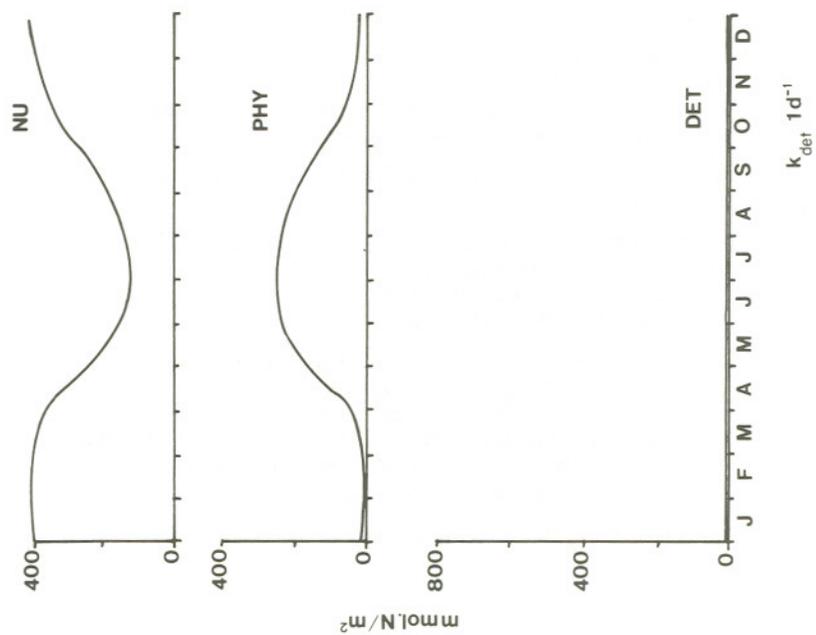
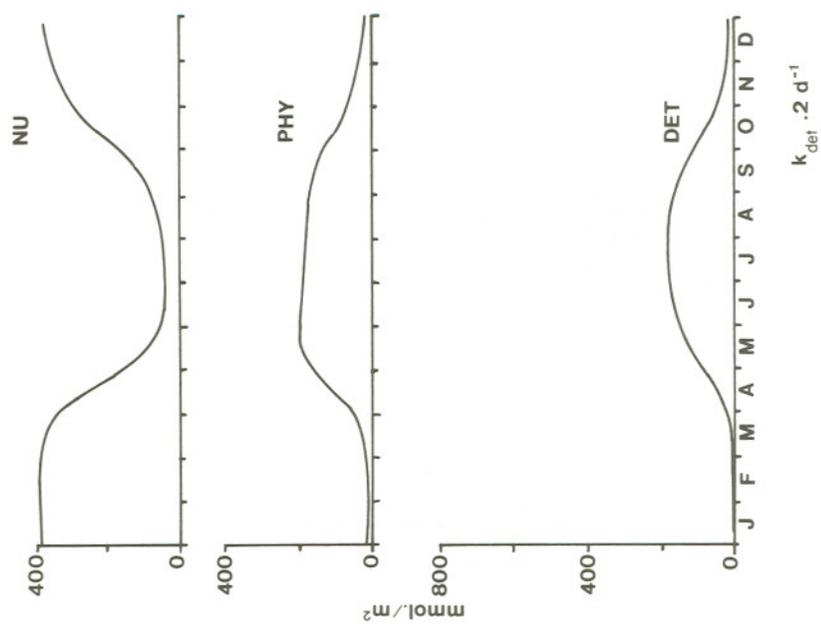
$$f_{\text{Vol1}}(I) = \frac{1}{\eta \cdot z} \frac{I/k}{\sqrt{1 + (I/2.6Ik)^2}} \quad (\text{Vollenweider, 1965})$$

where:  $I$  = the hourly incident light intensity

$\eta$  = the extinction coefficient of the water including the effect of self shading by the phytoplankton biomass

$z$  = the depth of the water column

$$f_{\text{Arrh}}(T) = 2^{(T-20)/10} \quad \text{where } T \text{ is temperature}$$



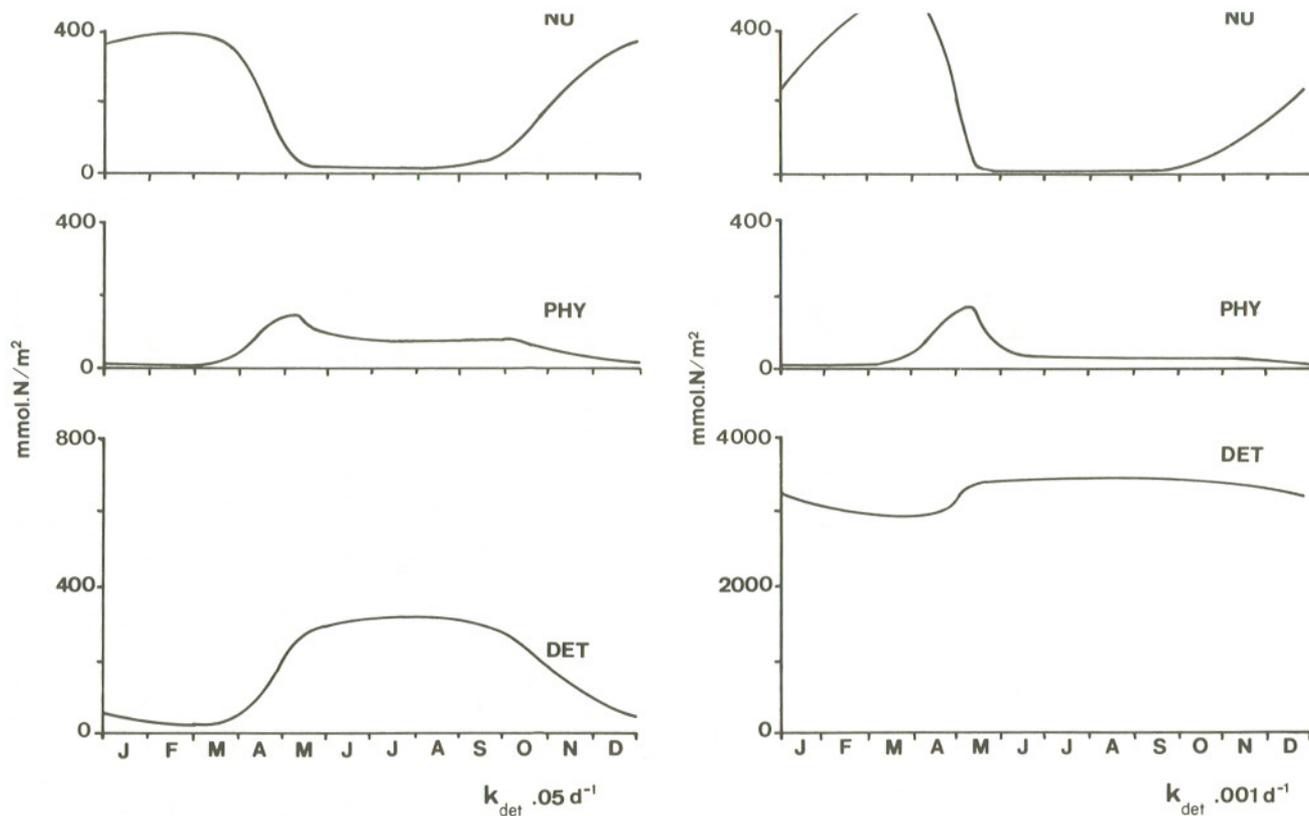


Figure 14.2. Seasonal variations of mineral nitrogen, phytoplankton biomass and total detritus simulated by the model described in Figure 14.1 for increasing values of the first-order constant of detritus mineralization ( $k_{det}$ ). The variations of  $I$  and  $T$  are those observed in coastal North Sea. The values of the other parameters are as follows:

$$\begin{aligned} \mu_{max} &= 5/\text{day} \\ k_{NU} &= 1 \mu\text{M} \\ \eta(/m) &= 0.2 + 0.07 \text{ PHY} \\ z &= 20 \text{ m} \\ k_{PHY} &= 0.2/\text{day} \end{aligned}$$

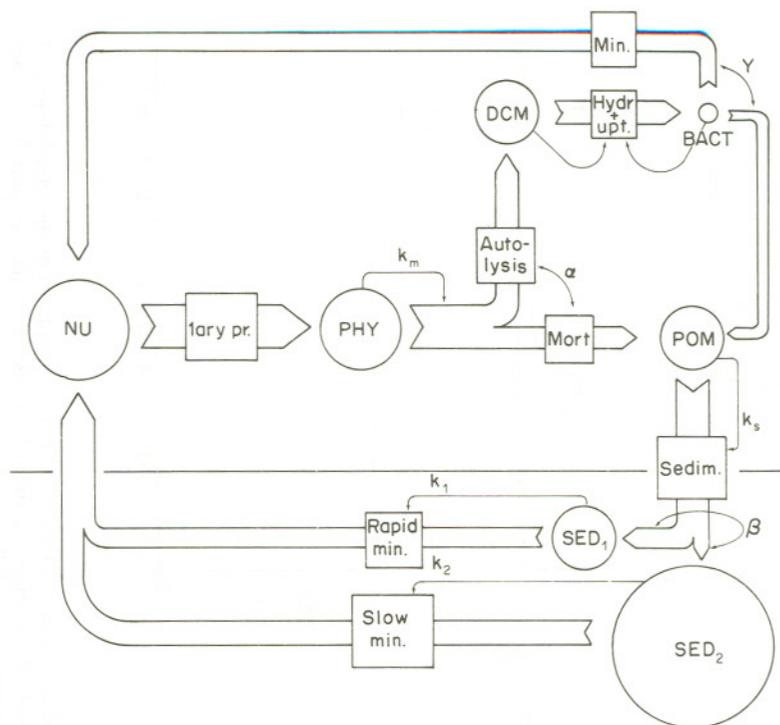


Figure 14.3. Closed system—seven-compartment model of nitrogen transfers in marine ecosystems.

NU = inorganic nitrogen

PHY = phytoplankton biomass

DOM = dissolved organic nitrogen

BACT = bacterial biomass

POM = suspended particulate organic nitrogen

SED1 = rapidly biodegradable organic nitrogen deposited on the sediments

SED2 = slowly biodegradable organic nitrogen deposited on the sediments.

The transfers between the seven compartments are assumed to obey the following kinetics:

*Primary production:* as in Figure 14.1.

*Phytoplankton mortality:* as in Figure 14.1, with the release of DOM and POM in the proportions  $\alpha$ ;  $1 - \alpha$

*Bacterial utilization of DOM:*  $e_{\max} \cdot f_{\text{Mich}}(\text{DOM}) \cdot f_{\text{Arrh}}(T) \cdot \text{BACT}$ . A fraction  $1 - Y$  is mineralized as NU, the rest forms bacterial biomass.

*Bacterial mortality:*  $k_{\text{BACT}} \cdot f_{\text{Arrh}}(T) \cdot \text{BACT}$ . This process is assumed to form DOM.

*Sedimentation of POM:*  $k_{\text{sink}} \cdot \text{POM}$ . No degradation of POM is assumed to occur in the water column. POM is supposed to be made of SED1 and SED2 in the ratio  $\beta$ ;  $1 - \beta$ .

*Benthic mineralization of SED1 and SED2:*  $k_{\text{sed1,2}} \cdot f_{\text{Arrh}}(T) \cdot \text{SED}_{1,2}$

#### 14.2.2 Closed system—seven-compartment model

In stratified ecosystems the stock of nutrients accumulated in the lower layer can constitute such a reservoir. However, no such reservoir exists in the water column of well-mixed coastal ecosystems. Several authors described an increase in dissolved organic carbon following phytoplankton bloom and lasting for the whole summer (Duursma, 1965; Banoub and Williams, 1973). Such an increase was not as evident for dissolved organic nitrogen. When a peak of dissolved nitrogen was observed it was generally short-lived (Riley and Segar, 1970; Wafar *et al.*, 1984). Similarly, a particulate nitrogen detritus peak appeared just a few days after the phytoplankton bloom, and disappeared rapidly (Lancelot-Van Beveren, 1980; Joiris *et al.*, 1982).

Nutrient recycling by planktonic organisms appears, therefore, as an efficient and rapidly adjusting mechanism. In particular, planktonic bacteria are able to follow phytoplanktonic growth closely, with only a few days delay, even during the first outburst of the spring bloom (Lancelot and Billen, 1984).

In the sediments, on the other hand, the residence time of at least a part of the organic matter is much longer. Estimates of the mean residence time, relative to microbial degradation of plankton-derived organic matter in bottom sediments, are generally in the range 0.5–2 years (Turekian *et al.*, 1980; Berner, 1980; Billen, 1982a). There are only a few reports in the literature of the seasonal variations of the rates of nutrient recycling in coastal sediments (Davies, 1975; Graf *et al.*, 1982; Wassmann, 1984). They all show a rapid response to the increasing deposition of fresh planktonic material during, or at the end of, the spring bloom, superimposed to a much steadier level of activity, remaining significant even during the winter.

These observations (and others which will be discussed below) complicate our closed-ecosystem model as indicated in Figure 14.3.

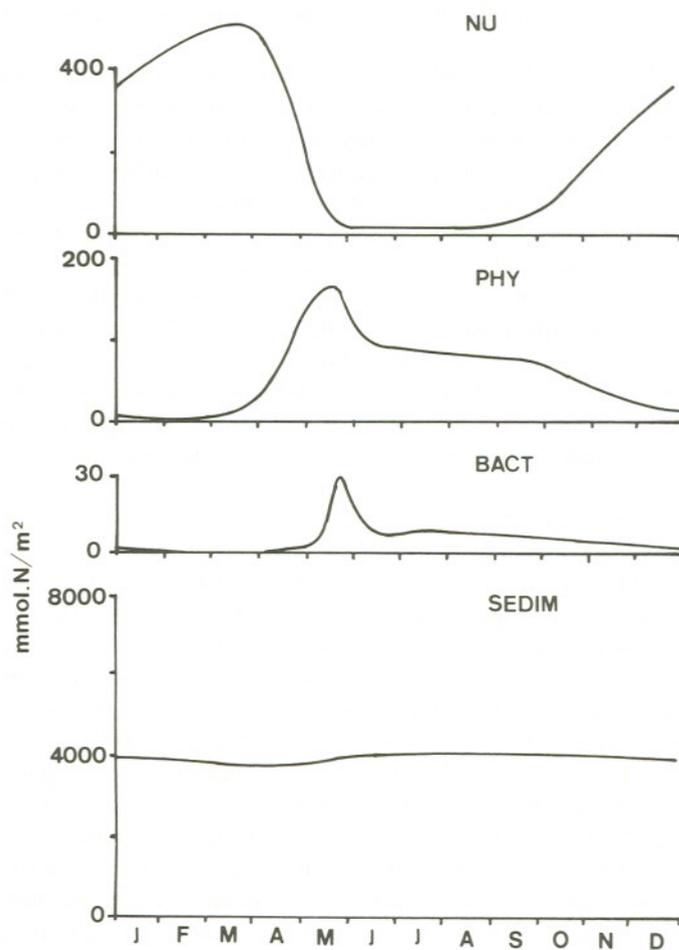
Phytoplankton cells lyse or disrupt according to first-order kinetics, producing dissolved organic nitrogen and particulate detritus in the ratio  $\alpha:1-\alpha$ . The former is used by planktonic bacteria, according to Michaelis–Menten kinetics. The latter sinks to the sediments. This material is considered to be made of two classes of biodegradability, deposited in the ratio  $\beta:1-\beta$ , each mineralized according to first order kinetics, with its own rate constant.

Figure 14.4 shows the simulation of the seasonal variations of planktonic and benthic variables obtained by this model, for a few sets of the parameters. Increasing the proportion of the slowly degradable fraction of the material deposited (decreasing  $\beta$ ) results in a higher standing stock of nitrogen in the sediments and tends to decrease the level of biomass during the summer steady state. The opposite effects result from an increase in the proportion of phytoplankton mineralized in the water column (increasing  $\alpha$ ) or from an increase of the rate constant of degradation of the more labile fraction of deposited phytoplanktonic material (increase of  $k_1$ ). Variations in the rate of sedimentation

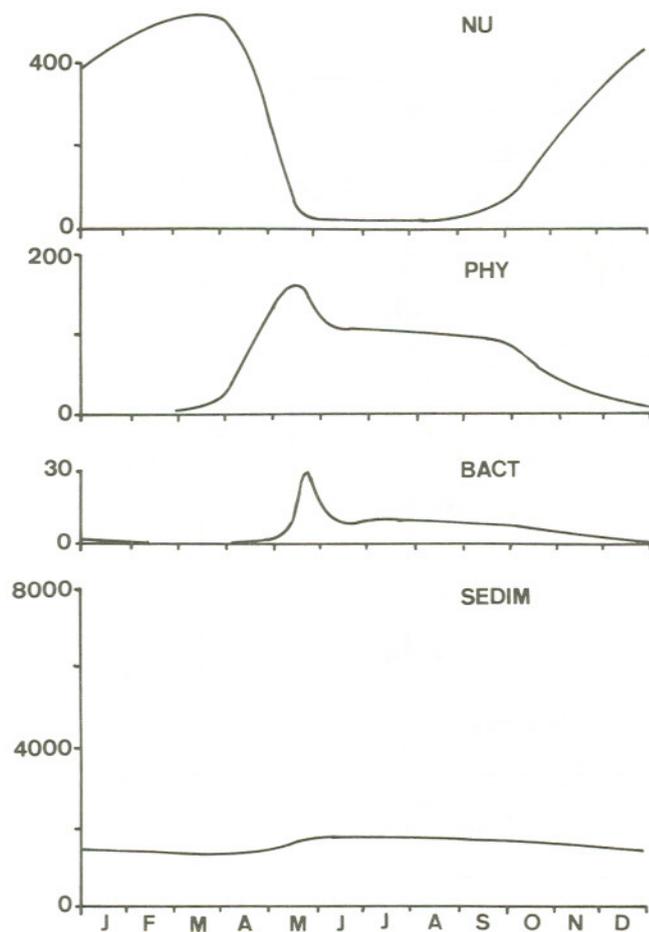
do not significantly affect the simulation, apart from the level of suspended material in the water column.

Clearly the slowly biodegradable organic material accumulated in the benthos is responsible for the increase in nutrient concentration during the winter, and hence to the main part of phytoplanktonic primary production during the outbursts of the spring bloom.

On the other hand, the rapid recycling of organic nitrogen in the water column, along with that of the rapidly biodegradable material deposited in the sediments, mainly sustains primary production during the summer steady state.



(a)



(b)

Figure 14.4. Seasonal variations of inorganic nitrogen, phytoplankton biomass, bacterial biomass and total organic nitrogen in the sediments simulated by the model described in Figure 14.3. Values of the parameters as in Figure 14.2 with, in addition:

$$\begin{aligned}
 \alpha &= 0.2 \\
 k_{\text{DOM}} &= 5 \mu\text{M} \\
 e_{\text{max}} &= 2.5/\text{day} \\
 Y &= 0.5 \\
 k_{\text{sink}} &= 0.1/\text{day} \\
 \beta &= 0.6 \text{ (a)}, 0.9 \text{ (b)} \\
 k_{\text{SED1}} &= 0.05/\text{day} \\
 k_{\text{SED2}} &= 0.001/\text{day}
 \end{aligned}$$

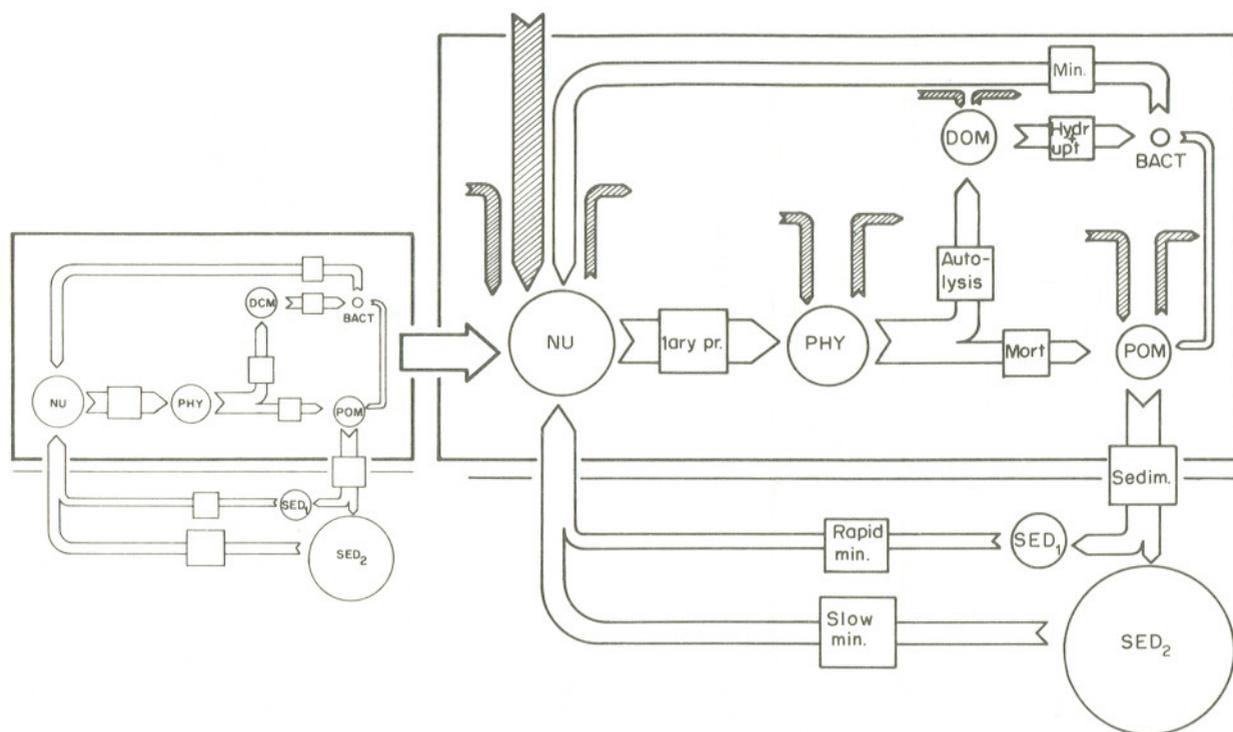


Figure 14.5. Open system model of nitrogen transfers in coastal marine ecosystems. The structure is exactly the same as in the model described in Figure 14.3, except that an input of inorganic nitrogen from terrestrial origin and exchanges with the planktonic phase of adjacent, systems with different characteristics are taken into account

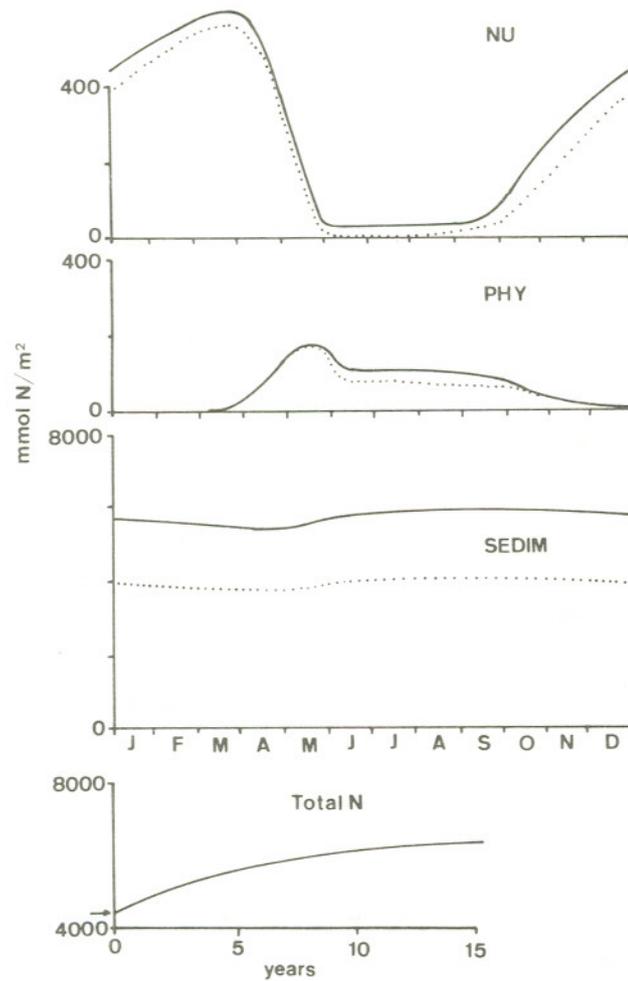


Figure 14.6. Seasonal variations of inorganic nitrogen, phytoplankton biomass and total organic nitrogen in the sediments simulated by the model described in Figure 14.5. The residence time of the water masses in the coastal zone ( $1000 \text{ km}^2$  area) is 30 days. The coastal zone considered differs only from the adjacent offshore zone in that a higher rate of sedimentation exists in the former ( $k_{\text{sink}} = 0.1/\text{day}$ ) than in the latter ( $k_{\text{sink}} = 0.05/\text{day}$ ). No input of mineral nitrogen from terrestrial origin is taken into account. The seasonal variations of all planktonic compartments in the offshore zone simulated according to the model of Figure 14.3 (dotted line) is taken as the limit and initial conditions for the simulation of the coastal zone. A steady state is reached only after about 10 years.

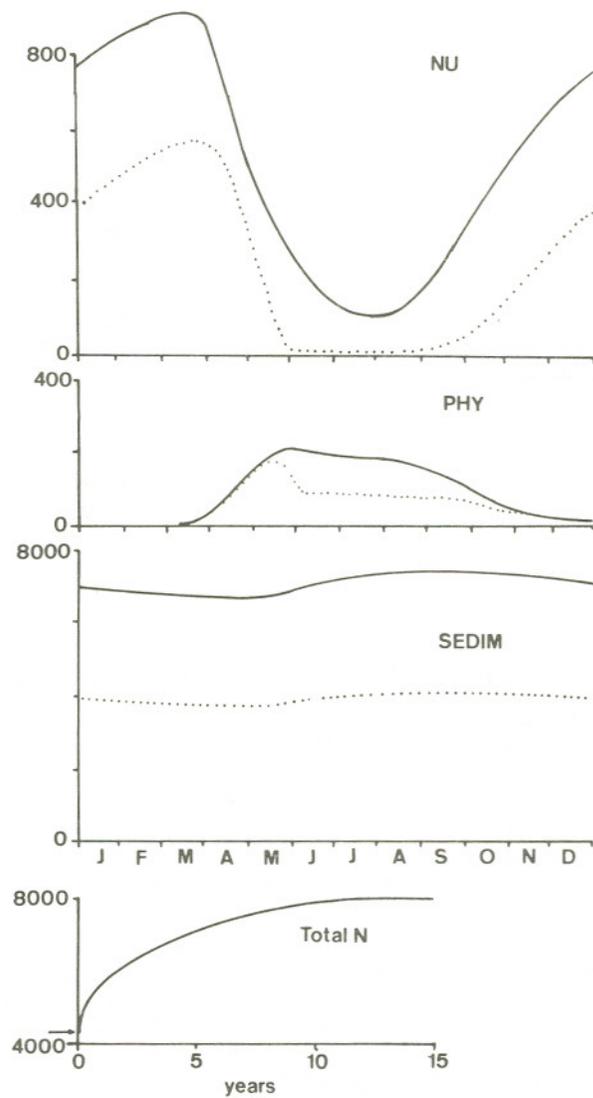


Figure 14.7. Same simulation as in Figure 14.6 but with an additional input of inorganic nitrogen from terrestrial origin of 150 T nitrogen/day

### 14.2.3 Open system model

The preceding closed system models can only be considered as acceptable approximations of real situation for the case of marine areas surrounded by similar ecosystems and receiving no terrestrial inputs. This is not the case with many coastal ecosystems, which have significant exchanges both with adjacent offshore areas, of differing characteristics and with terrestrial ecosystems.

The model described in Figure 14.5 takes these exchanges into account. For the rest it is quite similar to the model of Figure 14.3.

Figure 14.6 shows the simulation with this model of the situation where a coastal zone is characterized by a higher sedimentation rate than the adjacent offshore areas: a regular increase of total nitrogen in the coastal ecosystem is observed, due to the accumulation in the sediments of slowly degraded organic material trapped from the adjacent zone.

Figure 14.7 shows the simulation of an additional constant terrestrial input of nitrogen. As seen, the main effect of this enrichment is to increase the stock of nitrogen in the sediments, and to increase the level of biomass during the summer steady state.

## 14.3 KINETICS OF SEDIMENTARY PROCESSES

The idealized models developed in the preceding section have identified a few sedimentary processes which are of particular importance for the overall working of coastal ecosystems.

Because of the different rates of planktonic and benthic remineralization, and of the trapping effect that enhanced sedimentation, in some coastal areas, can play with respect to adjacent ecosystems, the *mechanisms of organic matter deposition* are important to understand. The *rate of organic matter decomposition* in the benthos determines the residence time of nitrogen in the benthos, and hence the importance of the spring bloom with respect to total annual primary production. Lastly, the *processes of nitrification and denitrification* can result in the elimination of a significant amount of nitrogen, thus counteracting to a certain extent the effect of nitrogen enrichment of coastal system.

The present section will review the data available in the literature concerning the kinetics and the control mechanisms of these processes.

### 14.3.1 Input of organic matter to coastal sediments

Although a simple relationship between the fraction of primary production deposited on the sediments and the depth of the water column, as observed in deep-water environments (Suess and Muller, 1980; Hargrave, 1984) does not hold for shallow coastal system, it is well documented that a large part of primary production in most of these systems is recycled in the benthos (see Table 14.1).

This is particularly true during the spring phytoplankton bloom: in the Kiel Bight, Peinert *et al.* (1982) observed the deposition of 65% of spring primary production, while Forsskåhl, H. L. *et al.* (1982) reported values of 40% in a Finnish Fjord.

In these studies, as well as in other similar ones (Zeitschel, 1965; Smetacek, 1980) it was clearly shown that faecal pellets by no means constitute the bulk of the material reaching the sediments (as often postulated in the past—Steele, 1974), but that direct sedimentation of phytoplankton occurs.

In some cases the input of organic matter to the benthos is higher than primary production in the overlying water column, showing the importance of imports from adjacent areas (Graf *et al.*, 1982).

Understanding the overall process of phytoplankton sedimentation requires a separate examination of sinking and deposition, i.e. of the processes occurring within the water column and those occurring at the sediment—water interface.

#### 14.3.1.1 Sinking of phytoplankton

In the above idealized models, dealing with well-mixed water column, sinking is treated as a first-order process, i.e. the flux of material to the sediments ( $F_{\text{sed}}$ ) is considered to be proportional to the amount of particulate material in the water column ( $P$ ):

$$F_{\text{sed}}(ML^{-2}T^{-1}) = k_{\text{sink}} P(ML^{-2}) \quad (1)$$

The sedimentation constant  $k_{\text{sink}}$  has the dimension ( $T^{-1}$ ) and can be viewed as

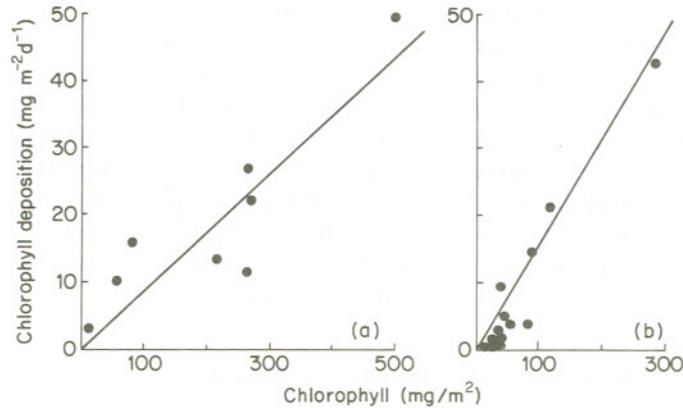


Figure 14.8. Empirical relationship observed between the flux of phytoplankton material deposited on the sediments and the biomass of phytoplankton in the water column, for two shallow aquatic environments: (a) storage basin of Merys/Oise (France) (data from Billen *et al.*, 1968); (b) Kiel Bight (data from Peinert *et al.*, 1982)

Table 14.2. Estimates of the apparent sinking rate of phytoplankton in shallow turbulent aquatic systems

Environment	Dominant phytoplankton population	Depth (m)	$k_{\text{sink}}$ ( $\text{d}^{-1}$ )	$v_{\text{sink}}$ ( $\text{m h}^{-1}$ )	References
Kiel Bight	Small diatoms	20	0.15	0.125	Peinert <i>et al.</i> , 1982 <sup>a</sup>
Norwegian Fjord Storage basin of Mery	— Large diatoms	60 9	— 0.084	0.04–0.08 0.030	Wassman, 1984 Billen <i>et al.</i> , 1986*

<sup>a</sup> See Figure 14.8.

the ratio between a characteristic velocity  $v_{\text{sink}}$  ( $LT^{-1}$ ) and the depth of the water column  $Z(L)$ .

In turbulent waters, however,  $v_{\text{sink}}$  represents a residual rate of sedimentation, depending not only on the buoyancy of the particle, but also on the hydrodynamics of the area. Jewson *et al.* (1981) clearly showed the importance of both physical and physiological factors in controlling phytoplankton sinking. When turbulent conditions prevail there is a slow, steady loss of cells by settling, while during calm-weather periods, cells fall out much more rapidly, particularly under conditions of nutrient limitation which induce a change in buoyancy (Titman and Kilham, 1976; Anderson and Sweeney, 1977; Bienfang, 1981; Bienfang *et al.*, 1982).

In spite of the variability of these factors in a given environment a good correlation is often observed between the flux of phytoplankton to the sediments and its concentration in the water column, giving experimental support to relation (1). Two examples are shown in Figure 14.8. Table 14.2 gathers a few estimates of the apparent sedimentation velocities of phytoplanktonic material in shallow turbulent aquatic systems. These values, in the range 0.03–0.12 m/h, compare well with, and are even higher than, published data of sinking rates measured on pure cultures of phytoplankton under conditions of active metabolism in the absence of turbulence, from 0.005 m/h for nanoplanktonic organisms, upto 0.07 m/h for large diatoms (Bienfang and Harrison, 1984).

#### 14.3.1.2 Deposition

The hydrodynamic conditions required for deposition of fine material have been the subject of several empirical and theoretical studies.

An example of empirical study is provided by the work of Postma (1967) and Creutzberg and Postma (1979), who defined a critical current velocity above which no deposition of a given particle type can occur. The work of Adam *et al.*

(1981) offers an example of a more theoretical approach, where the condition for deposition is defined in terms of minimum erosion energy and converging distribution of erosion stress. However, recent observations by Jenness and Duineveld (1985) showed that considerable amounts of phytoplanktonic material are incorporated into the sandy sediments, in places where the above criteria would predict no deposition. A mechanism involving transient surface deposition during period of slack current, followed by burial to at least 5 cm through the process of ripple formation during ebb current periods, has been proposed.

#### 14.3.2 Nitrogen mineralization in sediments

Microbial degradation of organic matter in sediments results from a succession of basic enzymatic processes involving exoenzymatic hydrolysis of macromolecules, microbial uptake of the resulting monomeric substrates, respiration and biosynthesis of microbial biomass and degradation of this biomass by lysis or grazing by meiofauna. Significant progress have been accomplished during the past few years in developing methods of measuring these basic processes in sediments: exoenzymatic activities (Meyer-Reil, 1981), direct substrate uptake at *in situ* concentration (Meyer-Reil, 1978; Ansbaek and Blackburn, 1980; Christensen and Blackburn, 1980), bacterial production (Moriarty and Pollard, 1981), bacterial grazing (Montagna, 1984). In spite of these recent efforts, which have to overcome considerable technical difficulties, the kinetics of organic matter degradation in sediments remain much less well understood than in the water column.

Therefore, although rather unsatisfactory from a microbiologist's point of view, the geochemical approach, consisting in the assumption of first-order kinetics for the overall process of organic matter degradation, must still be adopted in modelling nutrient mineralization in sediments. In order to account for the different susceptibilities to bacterial attack of different classes of compounds making up the overall organic matter ( $G$ ), some authors (Jørgensen, 1978; Berner, 1980; Westrich and Berner, 1984) have suggested the use of 'multi  $G$ s—first-order kinetics':

$$G = \sum_i G_i$$

$$\frac{dG_i}{dt} = -k_i G_i$$

where  $G_i$  is the concentration of fraction  $i$  of the total organic material  $G$ , and  $k_i$  its first-order degradation constant which is temperature-dependent. Westrich (1983) generalized this approach and suggested that organic material from natural origin can be viewed as made of eight different classes with first-order

constant differing from one another by roughly one order of magnitude (quantum  $G$  model).

Table 14.3 shows the values of the first-order degradation constants found by various authors for the degradation of phytoplankton during laboratory decomposition experiments in aerobic conditions, and estimated from *in situ* measurements in sediments.

In laboratory experiments using freeze-dried phytoplankton, a rapid autolysis of the material is first observed, liberating about 30% of the original material as

Table 14.3. First-order constant for the degradation of organic carbon and nitrogen measured during decomposition experiments with marine (mar) and freshwater (frw) phytoplankton at 20 °C in aerobiosis, or deduced from direct measurements in marine or freshwater sediments

**Laboratory decomposition experiments (20 °C)**

Material	References	$k_{0i}$ ( $d^{-1}$ )	$k_1$ ( $d^{-1}$ )	$k_2$ ( $d^{-1}$ )
mar org N	Von Brand <i>et al.</i> , 1937			0.038–0.056
mar org N	Grill and Richards, 1964		0.038	0.0087
frw org C	Jewell and McCarthy, 1968		0.19–0.06	
frw org N	Otsuki and Hanya, 1972		0.056	0.005
frw org C	Fallon and Brock, 1979		0.041	
mar org C	Newell <i>et al.</i> , 1981		0.06	
mar org C	Skopintsev, 1981		0.088	
mar org N	Skopintsev, 1981		0.085	
mar org C	Westrich, 1983		0.066	0.003
mar org N	Garber, 1984	0.15–0.26	0.018–0.012	

**Shallow water sediments (mean temperature 10 °C)**

Location	Sediment type	References	$k_0$ ( $d^{-1}$ )	$k_1$ ( $d^{-1}$ )	$k_2$ ( $d^{-1}$ )
Long Island Sound	mud 0–5 org C	Turekian <i>et al.</i> , 1980			0.0012
Long Island Sound	mud 0–5 org C	Berner, 1980			0.0016
Coastal North Sea	sand 0–10 org N	Billen, 1982a			0.0013–0.005
Storage basin of Mery (frw)	mud 0–10 org N	Billen <i>et al.</i> , 1986		0.013	0.0005
Long Island Sound	mud 2–5 org C	Westrich and Berner, 1984		0.019–0.024	0.0023–0.0027

dissolved organic matter (Otsuki and Hanya, 1972; Newell *et al.*, 1981; Garber, 1984). Most authors, following the subsequent degradation of the residual particulate material over a time span of several months, found a first-order constant of about 0.05/day at 20 °C for a fraction of about 60% of the total. Another fraction (about 20–25%) was decomposed more slowly with a first-order constant of 0.005/day. A third fraction (about 20–25%) was found refractory to bacterial attack within the time scale of the experiment. Only Garber (1984), observed a very rapid degradation at the beginning of the experiment, with rate constants of about 0.2/day. This phase of the degradation, if it exists, can be difficult to distinguish from the autolysis phase, and could have escaped observation by other authors.

Most values reported for the apparent first-order constant of the bulk of sedimentary organic matter, are representative of the more resistant fraction of phytoplanktonic material, as measured in laboratory experiments (see Table 14.3). Only the very careful experiments of Westrich and Berner (1984) with Long Island Sound sediments, and the observations of Billen *et al.* (1986) in the basin of Mery s/Oise with a sedimentation rate as high as 1 cm/month, directly revealed the presence in the sediments of an organic carbon and nitrogen fraction corresponding to the most labile fraction of phytoplankton, with first-order degradation constant of 0.013/day. Further evidence for the presence and the degradation of this kind of labile organic material in shallow-water sediments comes from the observation of the seasonal variations of benthic microbiological activities. As already mentioned above, a rapid response of microbial activities to sedimentation of planktonic material was observed by Graf *et al.* (1982) (microcalorimetry and ETS activity), Wassman (1984) (oxygen consumption), and Billen *et al.* (in press) (nitrogen flux across the water–sediment interface).

Comparison of the data of Table 14.3 with the sedimentation constants of Table 14.2 shows that, except for the most labile fraction of phytoplankton susceptible to autolysis, the residence time of particulate organic matter in the water column of shallow ecosystem is short, with respect to the time necessary for its degradation. Particulate organic matter degradation can be considered, in good approximation, to be essentially a benthic process, while planktonic bacteria live mostly on dissolved organic matter produced by excretion and lysis of phytoplankton.

From the data of Table 14.3, no systematic differences can be observed between the decomposition rate of organic carbon and nitrogen. However, many authors (Holm-Hansen *et al.*, 1966; Gordon, 1971; Lee and Cronin, 1982) have postulated a preferential bacterial utilization of organic nitrogen relative to carbon for explaining the variations of C:N ratio in the sediments. Thus Blackburn and Henriksen (1983) observed that the C:N ratio in top layers of sediments increases from 6.5 to 17 with increasing depth of the water column in Danish waters. The organic matter reaching deep-sea sediments has C:N ratio in the range 10–13 (Williams *et al.*, 1980). Walsh *et al.* (1981) showed that area of

low C:N (6–8) in shelf bottom sediments reflect deposition of 'fresh' marine material from region of nutrient enrichment. The C:N ratio in top layers of sediments also varies seasonally, being lower during periods following phytoplankton blooms, when a massive input of fresh material is deposited on the bottom, and increasing during subsequent degradation (Blackburn and Henriksen, 1983; Graf *et al.*, 1982). Similarly, an increase of the C:N ratio of the organic matter up to 15–17 is often observed as a function of depth within the sedimentary column (Rosenfeld, 1981). All these observations, however, are better explained by assuming that the more labile fractions of organic material deposited in the sediments have a lower C:N ratio than the more resistant ones.

It is unclear whether the refractory fraction of organic matter present in the deeper layer of the sediments represents a residual fraction pre-existing in the original deposited material or whether it has been formed during decomposition. Condensation reactions between reactive carbohydrates and phenol, produced during organic matter microbial decomposition, with polypeptides and amino acids have been suggested as the source of nitrogenous geopolymers or marine humic substances (Duursma, 1965; Gagosian and Lee, 1981; Rice, 1982). Extracellular production of mucopolysaccharides by microorganisms could also contribute to the formation of refractory organic compounds (Hobbie and Lee, 1980).

### 14.3.3 Nitrification and nitrate reduction in sediments

The fate of mineral nitrogen, once produced by organic matter mineralization in sediments, is manifold: it can be released to the water column as ammonium or can be oxidized to nitrite and nitrate. These oxidized forms of nitrogen can in turn either diffuse across the sediment-water interface or be reduced to either ammonium or gaseous nitrogen species (mostly  $N_2$ ). The kinetics and control mechanisms of these processes is reviewed in this section.

#### 14.3.3.1 Nitrification

Nitrification, as an obligate aerobic process, is restricted to the zone of sediments where oxygen from the water column can penetrate. Although the walls of polychaete tubes penetrating anoxic sediments constitute microniches with intense nitrification (Sørensen, 1984), it is a good approximation to identify the site of nitrification in sediments to the oxygenated upper layer of sediments (Vanderborgh and Billen, 1975; Billen, 1976; Henriksen *et al.*, 1981).

The depth of this layer varies considerably, according to the organic matter content of the sediments and the mixing processes they undergo. Direct measurements in coastal sediments reported in the literature range from more than 40 cm in organically poor sands (Kepkay and Novitsky, 1980) to a few millimetres in organic-rich muds (Revsbech *et al.*, 1980a,b). The depth of the

oxygenated layer can be theoretically related to the flux of organic matter deposited on the bottom, the biodegradability of this organic matter and the physical properties controlling the dispersive oxygen transport within the sediments (Lancelot and Billen, 1985). Figure 14.9 shows the theoretical relationship expected from the model of Lancelot and Billen for different set of parameters values, representative of coastal sediments. The range of oxygen

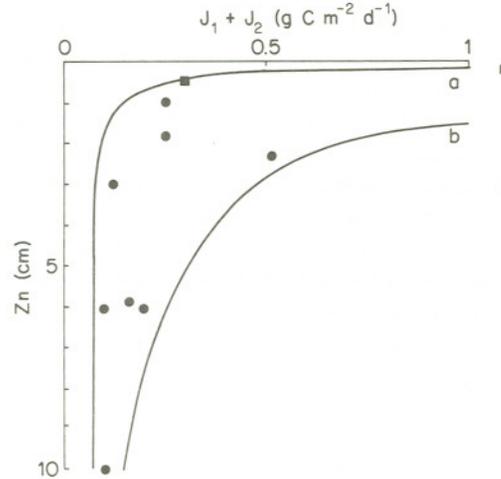


Figure 14.9. Theoretical relationship between the depth of the oxygenated layer and the total flux of organic matter sedimentation expected from the model of Lancelot and Billen (1985) for different conditions of sedimentary mixing processes representative of cohesive muds with low bioturbation (a) and of perturbed sands (b)

Values of the parameters		(a)	(b)
$D_i$	mixing coefficient of the interstitial water ( $\text{m}^2/\text{h}$ )	$3.6 \times 10^{-6}$	$3.6 \times 10^{-5}$
$D_s$	mixing coefficient of the solid phase ( $\text{m}^2/\text{h}$ )	$7.2 \times 10^{-9}$	$3.6 \times 10^{-7}$
$K_{\text{sed}_1}$	rate constant of degradation of the rapidly biodegradable fraction of sedimentary organic matter ( $\text{h}^{-1}$ )	$2 \times 10^{-3}$	$2 \times 10^{-3}$
$K_{\text{sed}_2}$	rate constant of degradation of the slowly biodegradable fraction of sedimentary organic matter ( $\text{h}^{-1}$ )	$2 \times 10^{-4}$	$5 \times 10^{-5}$
$\beta$	ratio between rapidly and slowly biodegradable fraction of sedimentary organic matter	60/40	60/40

For comparison, selected data of observed values of the depth of the oxygenated layer are also shown: ■ muds from Danish waters (Hansen *et al.*, 1981); ● sands from coastal North Sea (Billen, 1978)

penetration depth observed in various coastal environments is also shown.

The rate of nitrification in the oxygenated layer was measured by different techniques (N-serve inhibited [ $^{14}\text{C}$ ]bicarbonate incorporation (Billen, 1976); potential rate of  $\text{NO}_3$  production (Henriksen *et al.*, 1981);  $^{15}\text{N}$ -isotopic tracer technique (Koike *et al.*, 1984)). Billen (1982a) observed that the nitrification rate in sandy sediments from the North Sea was closely related to ammonium production rate in the same layer, amounting to 80% of it. This relationship is not valid for Danish muddy sediments (Henriksen *et al.*, 1981; Blackburn and Henriksen, 1982) where nitrification is restricted to the top few millimetres, and consumes significant amounts of ammonium diffusing from the lower layers.

Because the thickness of the nitrification layer and the intensity of nitrification in this layer are negatively correlated with each other (owing to their opposite dependence on organic richness of the sediment), the total nitrification per unit area in coastal sediments does not vary a lot, neither seasonally (see e.g. Hansen *et al.*, 1981) nor geographically. Most values cited in the literature fall in the range 2–20 nmol/cm<sup>2</sup>·h (Koike *et al.*, 1984; Henriksen *et al.*, 1981; Billen, 1978).

#### 14.3.3.2 Nitrate reduction

The rate of nitrate reduction in sediments is controlled both by nitrate concentration and by organic matter availability. Although it results from the activity of several different groups of bacteria, the overall process of nitrate reduction closely obeys a Michaelis–Menten kinetics with respect to nitrate concentration, with apparent  $K_m$  around 25–50  $\mu\text{M}$  or higher (Billen, 1978; Oren and Blackburn, 1979; Esteves, 1984; Koike and Sørensen, this volume). For simplicity, and because nitrate concentration is often lower than this range, a first-order kinetics has been assumed by most authors (Vanderborgh and Billen, 1975; Jahnke *et al.*, 1982; Goloway and Bender, 1982).

The first-order kinetic constant  $k_{\text{den}}$  further depends on the size of the nitrate-reducing population, which adjusts itself in response to the availability of biodegradable organic matter. Lancelot and Billen (1985) have proposed a model relating the value of  $k_{\text{den}}$  to the flux of organic matter to the sediments. The predictions of this model are consistent with the observed range of  $k_{\text{den}}$  values in coastal sediments ( $1\text{--}50 \times 10^{-3}/\text{h}$ ) (Billen, 1978). Pheffer Madsen (1979) reported seasonal variations of  $k_{\text{den}}$  in lake sediments, which clearly reflected more the variations of the input of fresh organic material to the bottom than the variations of water temperature or nitrate concentration.

The products of nitrate reduction can be either  $\text{N}_2$  or  $\text{N}_2\text{O}$  (denitrification) which are lost from the ecosystem, or  $\text{NH}_4^+$  which can be nitrified or reassimilated. The former process usually represents 60% or more of total nitrate reduction (Koike *et al.*, 1984; Sørensen, 1978; Nedwell, 1982; Kaspar *et al.*, 1982), but the latter can be significant at high organic matter content and low nitrate concentration (Tiedje *et al.*, 1982).

It has been emphasized by several authors (Kaspar, 1982; Tiedje *et al.*, 1982; Jenkins and Kemp, 1984) that the capacity for denitrification in sediments often exceeds the *in situ* rate of the process, because of the low nitrate concentrations prevailing in sediments. For this reason the total rate of denitrification in sediments is strongly enhanced by high nitrate concentration in the water column. This explains the importance of denitrification in river sediments, where nitrate concentrations are much higher than in marine systems. For instance, Billen *et al.* (1986) showed that about 50% of the total inputs of nitrogen in the hydrographic net of the Scheldt watershed is eliminated in river sediments, and does not reach the sea.

When nitrate concentration in the overlying water is low, nitrification in the upper oxygenated layer of the sediments is the only source of nitrate for denitrification. The separation of these two processes into distinct vertical strata is, however, a serious limitation for the rate of denitrification. For this reason the existence of anaerobic microniches in the upper oxidized layer (Jenkins and Kemp, 1984) or of region of enhanced oxygen penetration within the lower reduced layer (Sørensen, 1984) can have a significant effect on the overall rate of denitrification. Jenkins and Kemp (1984) provide evidence that a close coupling between nitrification and denitrification within the oxygenated upper layer can exist in certain sediments.

#### 14.4 MODELLING BENTHIC NITROGEN RECYCLING

Most mechanisms discussed in the preceding section concerning sedimentation of organic material, microbial mineralization of this material, nitrification and denitrification are taken into account in the idealized model of nitrogen recycling proposed by Lancelot and Billen (1985). This model was itself evolved from those published by Vanderborgh and Billen (1975), Jahnke *et al.* (1982), Goloway and Bender (1982) and Billen (1982b). It relates the release of inorganic nitrogen as nitrate and ammonium, and the rate of denitrification in the sedimentary column, to the input of organic matter to the bottom, for given values of nitrate concentration in the overlying water and provided that  $D_i$  and  $D_s$ , the mixing coefficient of the sediment interstitial and solid phases, are known (see Billen, 1982a).

The structure of the model is diagrammatically represented in Figure 14.10. The organic material deposited on the sediments is considered to comprise two fractions, differing in their first-order degradation constant and C:N ratio. Nitrification is considered as proportional at each depth to ammonification, but is restricted to the oxygenated layer ( $z < z_n$ ). Denitrification, restricted to the lower anoxic layers ( $z > z_n$ ), is considered as first-order with respect to nitrate concentration, with  $k_{den}$  defined in such a way that denitrification, at saturating nitrate concentration, would be responsible for all organic matter degradation at depth  $z_n$ .

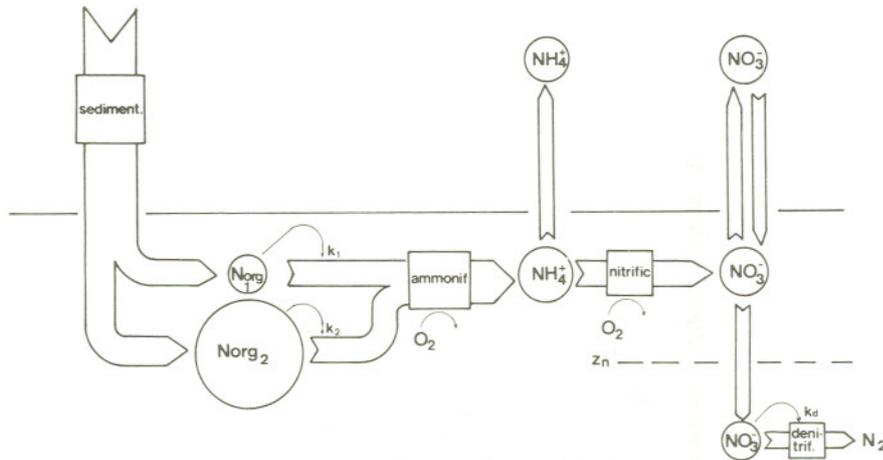


Figure 14. Diagenetic model of nitrogen mineralization in sediments. (After Lancelot and Billen, 1985.)

This model can be applied to many sedimentary situations. Some general results are illustrated in Figure 14.11. This figure shows that the contribution of nitrate to the total inorganic nitrogen flux decreases with increasing organic matter input to the bottom. Denitrification is zero for low organic matter inputs to the sediments, and increases with increasing inputs. It is strongly enhanced by high nitrate concentrations in the overlying water.

The results are not very sensitive to change in the values of the parameters  $D_i$ ,  $D_s$  and the ratio between rapidly and slowly biodegradable organic matter.

Two examples of more specific applications of this model will be discussed below.

The main limitation of the model is that it does not take into account the important role of benthic infauna in organic matter degradation and nutrient recycling. Only its role in bioturbation of the sediment is taken implicitly into account through the values of  $\bar{D}_s$  and  $D_i$ .

#### 14.4.1 Seasonal variations of denitrification

There are few reports of the seasonal variations of actual denitrification rates in marine sediments. The data of Sørensen (1984) from the Kysing Fjord, however, offer a complete set of measurements performed over an annual cycle. The most striking feature in these data is the existence of a sharp peak of denitrification in April–May preceded and followed by very low denitrification rates all the rest of the year. This pattern of seasonal variations contrasts with those of oxygen consumption and sulphate reduction, which show a more distinct

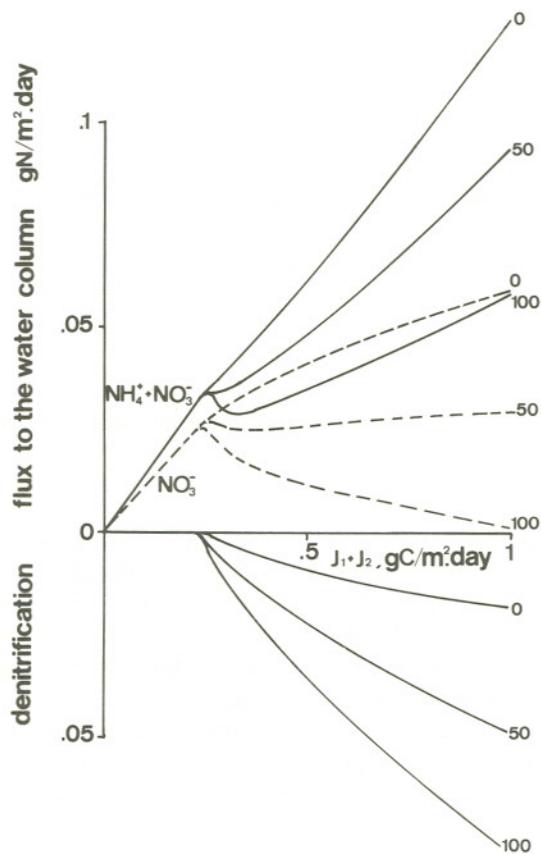


Figure 14.11. Ammonium and nitrate fluxes to the overlying water and total denitrification rate, as a function of total organic carbon input to the sediments, calculated with the model described in Figure 14.10 for the following values of the parameters:

$$\begin{aligned}
 D_i &= 3.6 \times 10^{-5} \text{ m}^2/\text{h} \\
 D_s &= 7.2 \times 10^{-8} \\
 k_1 &= 2 \times 10^{-3} \text{ h}^{-1} \quad (\text{C:N})_1 = 7 \\
 k_2 &= 2 \times 10^{-4} \text{ h}^{-1} \quad (\text{C:N})_2 = 7 \\
 \beta &= 0.5 \\
 [\text{NO}_3]_0 &= 0 \text{ (a); } 50 \mu\text{M (b); } 100 \mu\text{M (c).}
 \end{aligned}$$

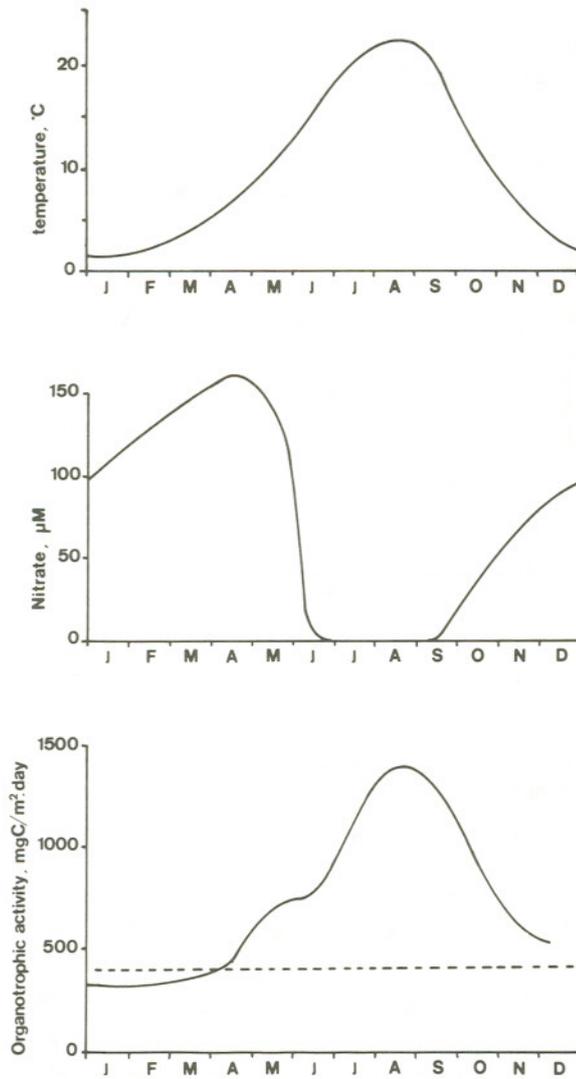


Figure 14.12(a). Observed seasonal variations of temperature, nitrate concentration in the overlying water and total organotrophic activity in the sediments (calculated from measurements of total oxidants consumption) of Kysing Fjord, 1983. (Smoothed from data of Sørensen, 1984.)

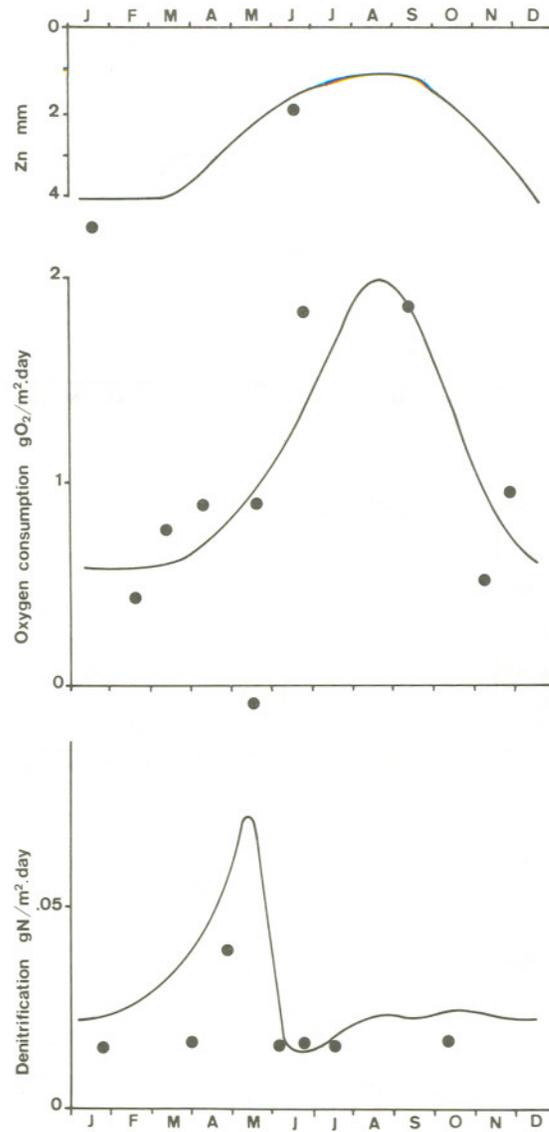


Figure 14.12(b). Seasonal variations of the depth of the oxygenated layer, the rate of oxygen consumption and the rate of denitrification in Kysing Fjord. Dots are observed values reported by Sørensen (1984). The solid line shows the predicted variations according to the model described in Figure 14.10 with the control variables shown in Figure 14.12a, and the following values of the parameters:

$$\begin{aligned}
 D_i &= 3.6 \times 10^{-6} \text{ m}^2/\text{h} \\
 D_s &= 7.2 \times 10^{-9} \text{ m}^2/\text{h} \\
 k_{\text{sed}1} &= 2 \times 10^{-3} \text{ h}^{-1} \quad (\text{C:N})_1 = 5 \\
 k_{\text{sed}2} &= 2 \times 10^{-4} \text{ h}^{-1} \quad (\text{C:N})_2 = 10
 \end{aligned}$$

correlation with temperature. The model discussed above easily explains these observations.

To our knowledge no data are available concerning organic matter sedimentation in Kysing Fjord. However, the data on oxygen and sulphate reduction in the sediments (Sørensen, 1984) show a rather constant, low rate of heterotrophic activity during the summer. In the scope of our model this can be interpreted as resulting from the slow decomposition of a refractory pool of organic matter, showing no important seasonal variations, and the rapid degradation of labile organic matter, deposited only from May to October (Figure 14.12a). The fluxes of organic matter of two classes of biodegradability were calculated according to this hypothesis. These fluxes, nitrate concentrations in the overlying water and temperatures reported by Sørensen (1984), constitute the three control variables of the model which calculates the seasonal variations of oxygen consumption by the sediments, the depth of the oxygenated layer and the integrated rate of denitrification. The results are shown in Figure 14.12b and compared with the observed data reported by Sørensen (1984) and Hansen *et al.* (1981). The agreement is striking.

The very peculiar seasonal pattern of denitrification in Kysing Fjord results from nitrate limitation: nitrate is only present in high concentration in the overlying water during the winter, when the input of fresh organic matter to the sediments is low. During the summer it is depleted from the water and the very thin oxic layer prevailing at that time prevents a significant nitrification from occurring in the sediments. Therefore high denitrification rates are only possible during a few weeks in the spring.

The data of Kaplan *et al.* (1979) offer quite a different picture of the seasonal variations of denitrification in the sediments of a saltmarsh ecosystem. In this system nitrate is supplied in abundance all year, both by groundwater imports and by an intense nitrification occurring down to 10 cm depth in the sediments. Accordingly, much higher denitrification is observed and its seasonal variations closely follow that of temperature.

#### 14.4.2 Long-term variations of nitrogen diagenesis

In the preceding applications of the model it was assumed that steady-state conditions are established, either with respect to annual mean conditions or with respect to instantaneous conditions. This assumption does not allow for long-term effects, such as those discussed in the first section (coastal zone enrichment). The observations of Billen *et al.* (in press) on the long-term variations of nitrogen mineralization in the fresh water sediments of the storage basin of Mery s/Oise offer an interesting model of what happens, at quite another time scale, in coastal zones with preferential sedimentation.

The storage basin of Mery s/Oise is an artificial basin of 9 m average depth, fed with water from the river Oise at a rate corresponding to a mean residence time of

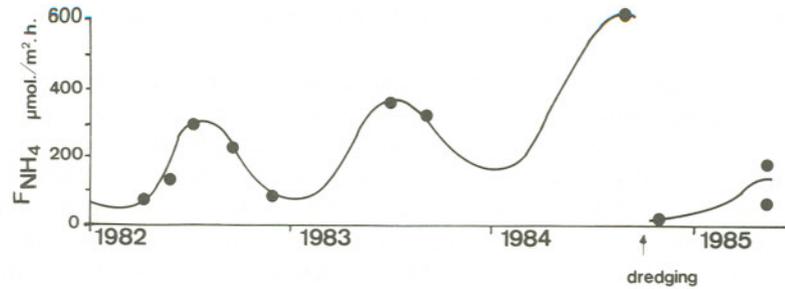


Figure 14.13. Observed long-term evolution of the flux of ammonium across the sediment-water interface of the storage basin of Mery s/Oise. The basin was flooded in July 1980. The sediments were dredged away in September 1984

4 days. Sedimentation rate is about 0.7 cm/month. Organic matter deposited on the bottom is composed of two fractions with different biodegradabilities. The first fraction is fresh phytoplanktonic material, degraded with a first-order constant of 0.013/day and deposited in direct ratio to chlorophyll content in the overlying water. The second fraction is detrital organic matter, less biodegradable ( $k = 0.0005/\text{day}$ ) and deposited at a constant flux.

Measurement of the fluxes of oxygen, nitrate and ammonium across the sediment-water interface have been performed for 4 years, after the flooding of the basin. The results clearly show both the recurrent seasonal variations and a long-term increasing trend of the ammonium flux (Figure 14.13). Four years after the flooding the sediments were dredged away and low values of the fluxes were again observed.

The model described above was applied to this situation, taking into account these factors. The results are shown in Figure 14.14 for a 2-year period following the flooding. During the first 40 days, the sedimentary column is entirely oxic, and the oxygen flux to the sediment increases with the depth of the accumulated sediments. Later an anoxic layer develops and the oxygen flux displays only recurrent seasonal changes in response to the variations of temperature and input of fresh phytoplanktonic material. During the period of time when the whole sedimentary column is oxic, no denitrification occurs, and the flux of nitrate is directed to the water column as a result of nitrification (Figure 14.14a). As soon as the anoxic layer develops, denitrification rapidly dominates, reducing not only all nitrate produced by nitrification in the oxic layer, but also an important amount of nitrate from the water column. The resulting inversion of the nitrate flux across the sediment-water interface is a quite remarkable event at the end of the first period after flooding.

The flux of ammonium to the water column is rather low during this first period, because most ammonium produced is oxidized by nitrification (Figure 14.14a). It increases considerably when the anoxic layer develops. For more than

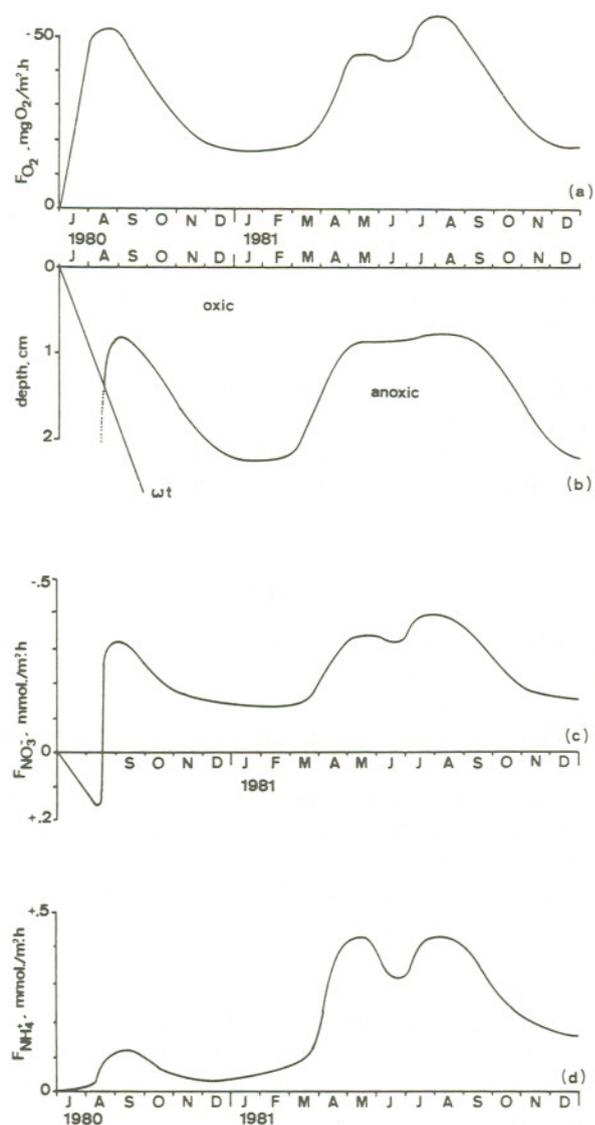


Figure 14.14(a). Calculated variations of the flux of oxygen, the depth of the oxygenated layer, the flux of nitrate and of ammonium in the storage basin of Mery s/Oise, during 18 months after flooding, according to the model described in Figure 14.10

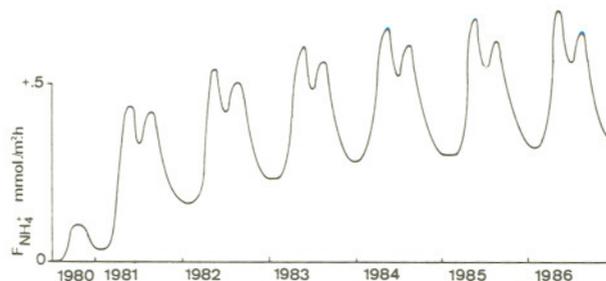


Figure 14.14(b). Long-term variations of the flux of ammonium across the sediment–water interface, calculated with the model

10 years after the flooding it displays seasonal variations, superimposed to a long-term increasing trend (Figure 14.14b). This long-term increase is due to the increasing contribution to the total ammonification rate of the slow degradation of detritic organic matter accumulated in the deeper and deeper sedimentary column.

#### 14.5 CONCLUSIONS

The conclusion to be drawn from the models developed in this chapter concerns mainly the role sediments play with respect to primary production and enrichment of coastal ecosystems.

Dudgale and Goering (1967) introduced the now widely used distinction between 'new' and 'regenerated' primary production based on the source of N supply. New production is defined as that part of primary production sustained by nitrogen inputs from upwelling benthic mineralization or terrestrial runoff. The fact that, in open ocean and upwelling areas those inputs are in general mostly made of nitrate-nitrogen, while photic zone regeneration only releases reduced forms of nitrogen, justifies an operational distinction between new and regenerated primary production based on the form of N uptake by phytoplankton (Eppley and Peterson, 1979; Probyn, 1985).

The sources of N supply for shallow well-mixed coastal systems are listed in Table 14.4. In accordance with the discussions presented in this chapter, a distinction has been introduced between the degradation of rapidly used organic matter and of more refractory organic matter, which indeed dominates the total organic pools in the sediments. The form under which nitrogen is supplied from these processes varies a lot, and the fact that ammonium often represents a significant part of nitrogen released by shallow sediments (see Table 14.1) deprives the operational distinction between new and regenerated production based on nitrate vs. (ammonium + urea) uptake of its usefulness.

On the other hand, because of the close coupling existing between benthic

Table 14.4. Characteristics of the different sources of N supply in shallow coastal areas

Nitrogen supply	Form		Coupling with primary production	
	$\text{NO}_3^-$	$\text{NH}_4^+$		
Planktonic mineralization	dominates at low $J_1 + J_2$	mainly dominates at high $J_1 + J_2$ high $[\text{NO}_3^-]_0$	close } close } long-term response } none }	
Sediment mineralization from rapidly degradable organic matter		} regenerated		
from slowly degradable organic matter				'new'?
Terrestrial input	mainly	sometimes		

mineralization of rapidly degradable organic matter and planktonic primary production, it seems rather illogical to consider all benthic mineralization as supporting 'new' primary production. This term should be restricted to the part of primary production sustained by nitrogen supply processes which are not under direct control by primary production.

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