Nitrogenous nutrient transfers in oyster ponds: role of sediment in deferred primary production

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ABSTRACT: The oyster pond under study has a natural sediment bottom and water is changed only once or twice every month depending on tidal height. Between successive water renewals, the pond is a closed system, equivalent to a batch culture in which sinking and biodeposition of particulate matter are the only sources of organic matter to the bottom. Particulate organic matter enrichment of the sediment in winter is followed by intensive ammonification in summer with very limited nitrification. Seasonal nitrogen budgets involving particulate and dissolved phases show that in summer during batch mode periods, ammonium enrichment from the sediment to the overlying water is an order of magnitude higher than the initial nutrient supply in the feed water. This allows a large increase of the phytoplankton biomass. We introduce the term 'deferred' primary production for this phenomenon because of the seasonal lag between particulate nitrogen deposition and dissolved nitrogen fluxes from the sediment.

INTRODUCTION

In coastal and estuarine areas, benthic organic matter mineralization and exchanges at the water/sediment interface are important processes in nutrient cycling (Nixon 1981, Balzer 1984, Hopkinson 1987). Moreover, there is now evidence that benthic nutrient flux contributes significantly to the requirements of pelagic primary producers (Boynton & Kemp 1985, Hargrave & Phillips 1986).

Along the French Atlantic coast, shallow oyster ponds (less than 1 m deep) cover several thousand hectares in marsh areas. These ponds are subjected to high nutrient pulses from feed water at spring tides. As a result of their physical characteristics (small volume, well-defined water exchanges between pond and sea), their large planktonic blooms and easy access, these ponds can be used as models to study biological rate processes.

Early studies of seasonal variations in phytoplankton abundance in such environments (Zanette 1980) showed maximal biomass during summer, when the nutrient supply by feed water was lowest. Similar observations were made by Robert (1983) who also reported a decrease in external nutrient supply and an increase in chlorophyll a values during summer.

In the present study, seasonal variations of various elements in suspended matter, as well as exchanges between water and sediment, were followed in an oyster pond in order to determine if nutrient regeneration in sediments during summer allows the development of a phytoplankton biomass which cannot be explained by the initial nutrient supply. Conversely, we also determined if, during winter, the supply of organic matter to the sediment would allow sufficient accumulation of nitrogen reserves.

Since shellfish cultures enrich the sediment through biodeposition processes (Kusuki 1981, Sornin et al. 1983) and enhance the recycling of some elements to the overlying water (Kaspar et al. 1985), we made these measurements in an oyster culture sediment area with high sedimentation rate and high organic matter content, and compared these to a control sediment area without oyster farming.

METHODS

Area description. The oyster pond selected for the present study is a closed earth pond, 50 cm deep, ca

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1500 m^2 with 5 m^2 devoted to above-ground oyster cultures of *Crassostrea gigas*. This small culture area was chosen to reduce the effect of oysters on phytoplankton consumption in relation to the total quantity available in the pond. The density was 200 oysters m^{-2}, with a mean oyster biomass ranging from 1.7 g of tissue dry weight at the beginning of farming up to 7.3 g, 1 yr later. The pond was submerged during spring tides (tidal constant above 80) which occur every 15 or 30 d. A complete water renewal occurs every month when the pond is emptied at low tide.

Sampling. At the beginning of each batch growth period (between water renewals), pond water was collected daily for 10 d for analysis of dissolved nutrients.

During batch growth, monitoring of water temperature and sampling of suspended particles were carried out weekly over the year. Particulate matter was collected by filtration through precombusted glass fiber filters (Whatman GF/C) for total and organic seston, particulate nitrogen and chlorophyll a (chl a) determination. In this study, only chl a was used to estimate phytoplankton biomass.

Once a month, during water renewal, cores were taken in the culture and in a control area in the same pond. Within 3 h of collection, each core (8 cm diameter, 10 cm long) was cut into 4 slices: 0–0.5, 0.5–1, 1–2 and 2–5 cm. Then, interstitial water was extracted by centrifugation for dissolved nutrient analysis. The sediment was then freeze-dried for total particulate nitrogen and for primary amino nitrogen (PAN, i.e. proteins and amino acids) determinations.

In order to estimate sediment accumulation and resuspension, 2 sediment trap models were used. Briefly, a plastic box, buried at the sediment surface, with a mouth protected by a honeycomb style baffle, trapped all sedimenting material (net sedimentation + local resuspension) with limited under- or overtrapping, as the cells of the baffle have a height/diameter ratio = 3 (Gardner 1980b). A smooth plastic plate, lying at the sediment surface, provided an estimate of net sedimentation assuming an equilibrium between resuspension output and input as this was the less efficient collector (Gardner 1980a).

These sediment traps were set and retrieved every month in the control area and under oyster cultures. Hence, after ignition of the collected material (4 h at 450 °C), we could estimate monthly rates of mineral sediment accumulation (raising of the sediment level) and resuspension.

Actual nutrient fluxes (DF) were measured in situ during short-term experiments (24 h) using dark incubators lying on the sediment. Water samples were taken hourly from the benthic chamber (volume = 31 l, area = 0.126 m^2) for dissolved nutrient analysis (Gouleau et al. 1986).

Analysis. Dissolved nutrients (nitrate, nitrite, ammonium and soluble reactive phosphorus) were measured on a Skalar continuous flow analyzer (Strickland & Parsons 1968). Dissolved organic nitrogen was not measured. Chl a was estimated by the fluorometric method of Holm-Hansen et al. (1965). Primary amino nitrogen was measured by fluorescence of orthophtaldialdehyde derivatives of constitutive amino acids (Petty et al. 1982) freed by acid hydrolysis (5.8 N HCl for 20 h at 105 °C). Total particulate nitrogen was determined on an Erba Science Model 1500 nitrogen analyzer with sample processing according to Hedges & Stern (1984).

Calculation. The accumulated stock (AS) of total particulate nitrogen was estimated from the rate of surface sediment accumulation and its particulate nitrogen content measured in the 0–0.5 cm slice.

Total particulate nitrogen degradation was estimated for a 2 cm thickness of sediment by difference between the theoretical stock (TS) of particulate nitrogen (initial + accumulated stock) and the measured stock. We consider that the measured stock (MS, $g\,m^{-2}$) is given by the formula:

$$MS = \sum \frac{P_j \times TPN_j \times T_j \times 10^3}{W_j + 100} \tag{1}$$

where j = sediment level; T = thickness (mm); P = wet sediment density ($g\,cm^{-3}$); TPN = total particulate nitrogen content (% of sediment dry weight); W = water content (% of sediment dry weight).

The theoretical stock is given by

$$TS = MS_i + AS \tag{2}$$

where MS_i = initial measured stock ($g\,m^{-2}$); AS = accumulated stock ($g\,m^{-2}$).

A similar calculation was carried out to estimate variations of the dissolved inorganic nitrogen stock (nitrate, nitrite and ammonium) in interstitial water. Rates of stock enrichment or depletion (in $\mu mol\,m^{-2}\,h^{-1}$) were estimated at monthly intervals during the study period (February 1985 to March 1986).

The theoretical flux (TF) of dissolved inorganic nitrogen was calculated from concentration gradients measured between the 2 levels 0–0.5 cm and 0.5–1 cm (Berner 1976):

$$TF = \phi_0\,D_0\,\frac{dC}{dx} - \frac{C_0\,F_s}{P_s}\,\frac{\phi_x}{1-\phi_x} \tag{3}$$

where TF = theoretical flux of the dissolved compound between the sediment and water, measured negatively towards the bottom ($\mu mol\,m^{-2}\,h^{-1}$); F_s = flux of solid particles towards the sediment due to accumulation ($g\,m^{-2}\,h^{-1}$); P_s = mean density of solid particles (2.65 g dry weight per cm^3 dry sediment); C_0 = dissolved

compound concentration at the sediment surface (0–0.5 cm) (μM or 10^3 μmol cm^{-3}); D_0 = diffusion coefficient at the water-sediment interface (10^{-4} cm^{-2} s^{-1} in mud; Billen 1982); ϕ_0 = porosity at the water sediment interface; and ϕ_x = porosity at a depth x below which this porosity remains constant.

When ammonium release by fluxes in each batch mode period exceeded the standing stock depletion of NH$_4$ in pore water it was assumed that the difference was due to ammonification. Therefore, the ammonification rate AR (μmol cm^{-3} h^{-1}) was roughly determined by the formula

$$AR = (DF - \Delta MS) \times 1/T \times 10^{-4} \qquad (4)$$

where DF = measured dark flux of ammonium (μmol m^{-2} h^{-1}); ΔMS = rate of change of the dissolved pore-water ammonium stock measured during batch periods (μmol m^{-2} h^{-1}); and T = thickness of the sediment slice (cm).

RESULTS

Algal biomass and nutrients in the water column

Microalgal biomass estimated from chl a in suspended particulate matter varied over an order of magnitude during the study period, and showed a regular increase from spring to summer with a maximum of 11.3 μg l^{-1} in August. Values then decreased to a minimum of 1.1 μg l^{-1} in December (Fig. 1).

Dissolved inorganic nitrogen (DIN) concentrations in feed water followed a seasonal trend which was opposite to that of chl a in pond water: concentrations were lowest in summer (6.3 μM in August) and highest in winter (66.7 μM). In the feed water, the N/P (DIN/soluble reactive phosphorus) ratio (by atoms) ranged between 1.5 in July and 26.6 in January. The lowest values occurred during summer when the water had a very low DIN content.

The DIN in feed water was used to calculate the potential production of phytoplankton [1 μg chl a produced by 1 μmol N consumed (Maestrini & Robert 1981)]. The potential chl a production could be compared to values actually measured in the pond. The difference (the equivalent amount of DIN in excess or in deficit; Table 1) showed that negative values occurred in June, July and August, i.e. in these months the observed chl a was greater than the potential chl a.

Water temperature increased regularly up to maximal values in August (over 21 °C), then decreased to 2 °C in November. A highly significant positive correlation (r = +0.83, n = 36, p < 0.01) existed with chl a but there was a negative correlation (r = −0.79, n = 10, p < 0.01) between temperature and DIN input by feed water.
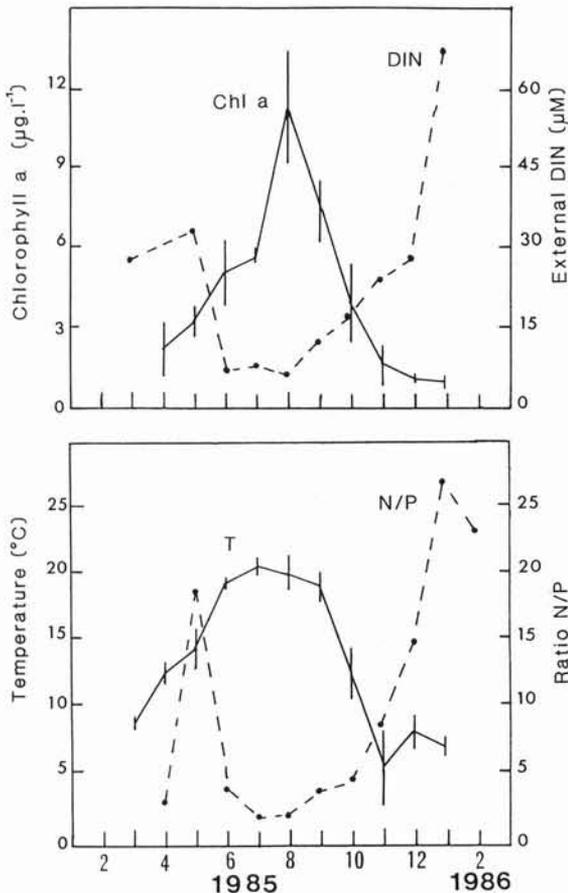

Fig. 1. Seasonal changes in dissolved inorganic nitrogen (DIN) and N/P ratio by atoms in supplies by feed water before each batch mode period; chlorophyll a (chl a) and temperature (T) in the pond water column during batch mode period

Table 1. Dissolved inorganic nitrogen balance (DIN Bal.) estimated as the difference between the amounts of chlorophyll a that could potentially be produced from feed water dissolved inorganic nitrogen (Pot. chl a) and the amounts of observed chlorophyll a (Obs. chl a), assuming that 1 μg chl a is produced by 1 μmol N consumed. Negative values correspond to DIN supplied by a source other than feed water

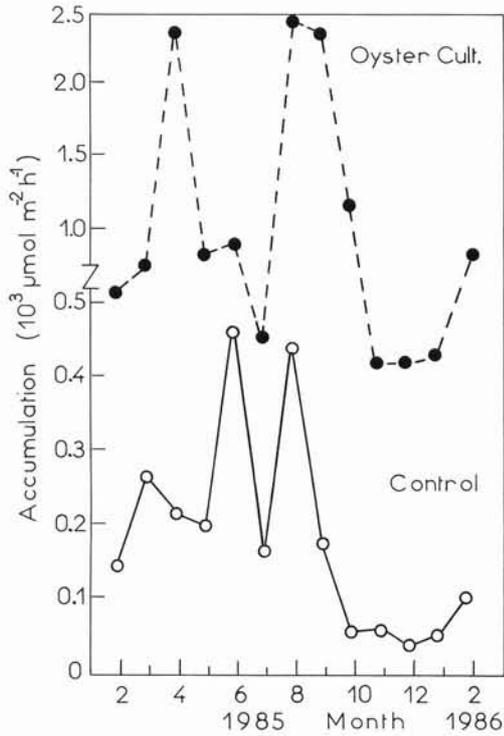| Month	Pot. chl a (μg l^{-1})	Obs. chl a (μg l^{-1})	DIN Bal. (μmol l^{-1})
Apr	6.0	3.1	2.9
May	32.5	3.5	29.0
Jun	7.2	7.3	−0.1
Jul	7.7	9.3	−1.6
Aug	6.2	15.5	−9.3
Sep	10.8	8.5	2.3
Oct	18.1	8.5	15.3
Nov	36.3	1.2	35.1
Dec	27.6	0.9	26.7
Jan	66.7	1.1	65.6

Fig. 2. Accumulation of total particulate nitrogen (TPN) in control and experimental sediments

Sediment particulate nitrogen

In both the oyster and control zones, the sediment consisted of mud, with 80 % of particles smaller than 10 μm. Accumulation rates estimated from sediment traps showed identical seasonal trends in the control and oyster culture areas: high values of total particulate nitrogen in spring and summer, and low values in fall (Fig. 2). However, in spring the accumulation under the oysters was an order of magnitude higher than in the control area.

Generally, TPN levels decreased with sediment depth in the first 5 cm. In the control sediment, maxima were observed in winter with nitrogen comprising 0.39 % of sediment dry weight in February. A notable depletion in May and June led to a decrease of TPN values (0.2 % at 1 cm depth). Under the oysters, sediments were clearly enriched in TPN; at the surface, values were up to 0.46 % in February and remained high until the beginning of summer, then decreased and exhibited rapid variations which destabilized the depth distribution of TPN. From September to January, successive enrichment and depletion periods could be observed over several centimeters. A stable depth profile reappeared only in February.

Sediment primary amino nitrogen

PAN accumulation represented between 10 and 20 % of TPN input at the sediment surface and showed the same trend as TPN.

However, in contrast to TPN, the depth distribution of PAN was maintained throughout the year in the control sediment (Fig. 3A) and in the oyster zone (Fig. 3B); values ranged between 246 and 551 μg N g^{-1} in control sediments and reached 689 μg N g^{-1} in the oyster zone. Moreover, the PAN standing stock showed a clear decrease during summer, followed by a progressive increase over the whole sediment thickness.
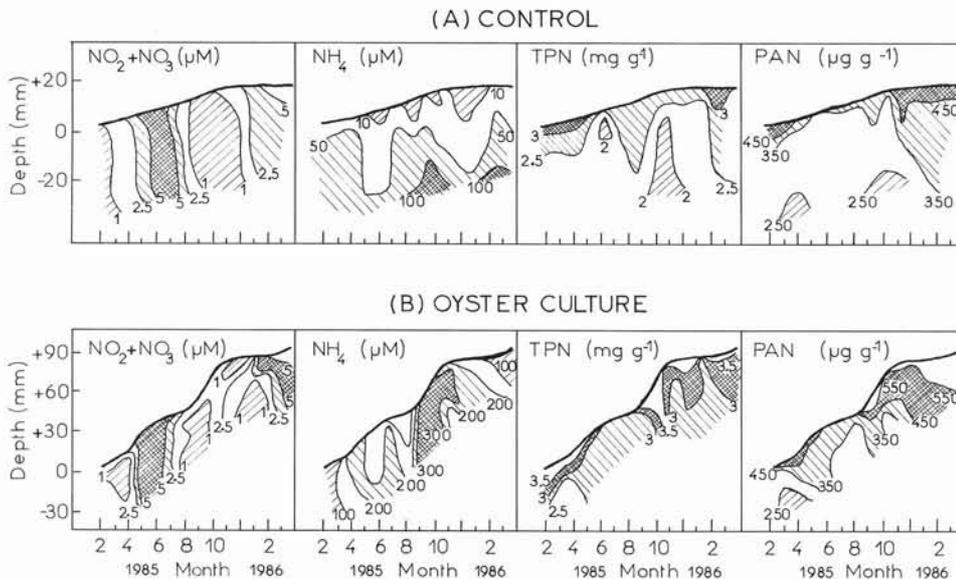

Fig. 3. Changes in nitrogenous compounds of surface sediments and interstitial water in (A) control and (B) experimental area. Positive values show the raising of the sediment interface level induced by sedimentation

Ammonium in interstitial water

In control sediments, ammonium distribution exhibited a depth profile which was the reverse of that observed for previous compounds: concentrations were low at the surface and increased with depth (Fig. 3A), varying between 3.3 and 120.2 µM. The lowest values were observed at the end of summer, rapidly followed by high values which remained so during fall. Under the oyster culture, the concentrations in the sediment were much higher (Fig. 3B) and reached 554 µM in September at 1 cm depth.

Theoretical fluxes (TF) varied drastically in the control sediment (Fig. 4) without any clear seasonal trend. They ranged from −120 (flux towards the sediment) to +200 $\mu mol\, m^{-2}\, h^{-1}$ (upward flux). In the oyster zone sediment, the range of variations was much higher (Fig. 4): −20 to +1100 $\mu mol\, m^{-2}\, h^{-1}$. A clear increase in upward flux was noted during summer and early fall.

Control sediment fluxes measured in situ in dark incubators (DF) showed little seasonal variation (Fig. 4), with values ranging from 12 (April) to 46 $\mu mol\ m^{-2}\ h^{-1}$ (September). Within the oyster zone, amplitudes were much more marked with fluxes of 953 and 77 $\mu mol\ m^{-2}\ h^{-1}$ in July and March, respectively. Generally, we found good agreement between theoretical flux estimations and in situ measurements.

Nitrate and nitrite in interstitial water

Nitrate and nitrite gradients could not be detected over the 5 first cm at any time of year in control sediments (Fig. 3A). Concentrations increased from winter to July in the entire sediment thickness to a maximum of 6.8 µM and then decreased gradually from the end of summer to December. A new enrichment was seen only in January.

Similarly, sediment concentration below the oysters increased gradually up to 7 µM in July (Fig. 3B). However, in the fall the decrease was shorter in duration, and the sediment became enriched again in November. A gradient occurred in winter with concentrations slightly higher at the surface.

These low levels, in control as well as in oyster zones, led to weak theoretical fluxes (TF) which were near zero with 2 exceptions: −115 and +65 $\mu mol\, m^{-2}\, h^{-1}$ in February and November respectively. Actual fluxes measured in situ (DF) were not detectable. In these sediments, nitrate and nitrite standing stocks as well as their fluxes were of little importance compared to ammonium.

Nitrogen budget

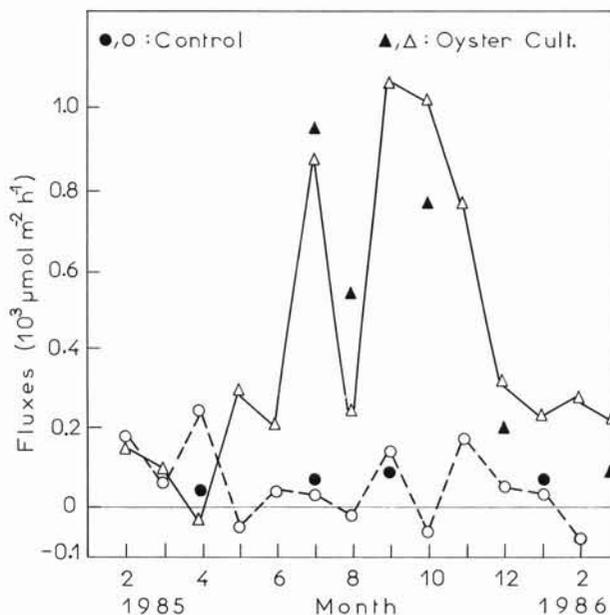Calculations described above made it possible to establish budgets for the different nitrogenous forms

Fig. 4. Seasonal variations in ammonium fluxes. Open symbols: fluxes calculated from concentration gradients between 0–0.5 cm and 0.5–1 cm; closed symbols: fluxes measured in dark bell jars in situ. Positive values represent upward fluxes

for each season as well as the enrichment or depletion rates of standing stocks (Fig. 5). As dissolved organic nitrogen (DON) was not measured, complete mass balance calculations were not possible. Few studies have considered DON flux across the sediment-water interface. DON flux has been reported to be either relatively unimportant (Nixon 1981, Hopkinson 1987) or to approximate NH_4 flux following a similar seasonal time course (Boucher & Boucher-Rodoni 1988). Thus, we can expect that the general trends were not significantly affected.

Seasonal variations of particulate supply and dissolved inorganic nitrogen release indicated an enrichment in winter with a mean of +140 $\mu mol\ m^{-2}\ h^{-1}$ in the control area and about 4 times higher under oysters (+587 $\mu mol\ m^{-2}\ h^{-1}$). Conversely, depletion of particulate nitrogen standing stock took place from spring to fall in control sediments (−174 and −79 $\mu mol\ m^{-2}\ h^{-1}$ respectively), and only in the fall in the oyster zone (−148 $\mu mol\ m^{-2}\ h^{-1}$).

In interstitial water, seasonal enrichment or depletion rates of DIN stocks were relatively small: about +1 $\mu mol\ m^{-2}\ h^{-1}$ in control sediments and +11 µmol $m^{-2}\ h^{-1}$ in summer under oysters. These were essentially due to ammonium since variations in nitrate stocks were very limited.

Approximate total ammonification rates in the 0–0.5 cm slice ranged between 0.5×10^{-3} and 40.3×10^{-3} $\mu mol\ cm^{-3}\ h^{-1}$ in the control zone and 18.0×10^{-3} to 220.0×10^{-3} $\mu mol\ cm^{-3}\ h^{-1}$ in the oyster zone.
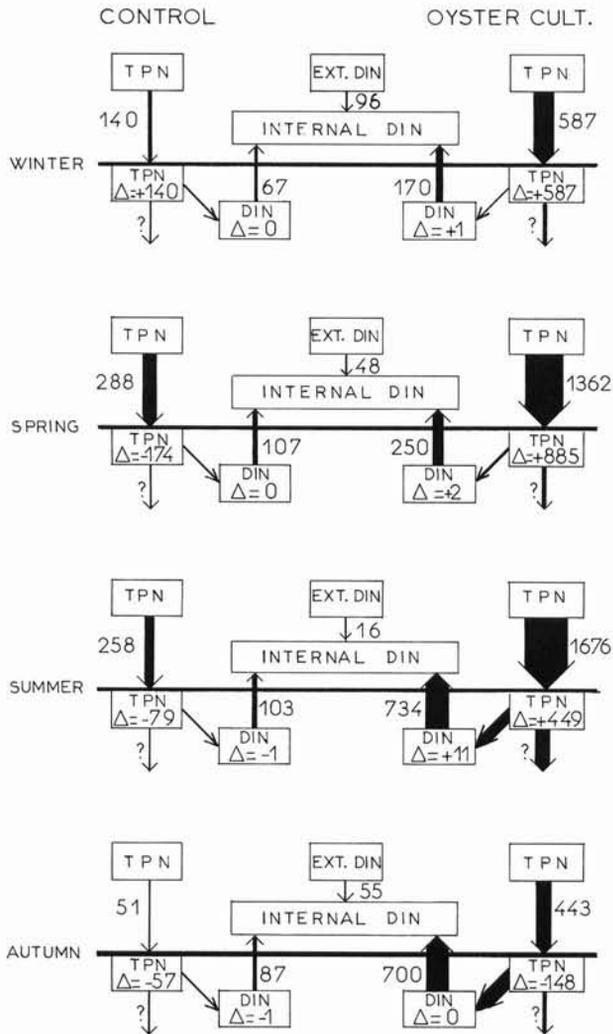
Fig. 5. Mean rates of seasonal exchanges inside (boxes) and between (arrows) the different nitrogen stocks actually measured in the oyster pond (μmol m^{-2} h^{-1}). Seasonal values are averages of 3 monthly measurements between February 1985 and March 1986. TPN: total particulate nitrogen; DIN: dissolved inorganic nitrogen; EXT. DIN: external feed water dissolved inorganic nitrogen

DISCUSSION

In an oyster pond, phytoplankton standing stocks are related to the carrying capacity of the environment and grazing by oysters. In summer, grazing accounts for only 2 % of the phytoplankton standing stock (Sornin et al. 1987). Obviously, nutrients are the main controlling factor. Variations in phytoplankton biomass in the pond are inversely related to the amount of nutrients supplied by feed water (Fig. 1). In winter, coastal waters are strongly enriched by drainage from agricultural areas. On the other hand, in summer, rainfall is reduced and drainage does not affect nutrient levels in coastal waters. Moreover, phytoplankton blooms in

coastal areas lead to nutrient depletion in feed water. Therefore, between June and September, the difference between maximal chl a observed and the potential level of chl a estimated from DIN levels (Table 1) gives a nitrogen deficit. This is accompanied by a feed water N/P ratio below 5 (Fig. 1) which should lead to nitrogen (N) limitation of primary production if we assume an N/P uptake ratio of 16 by phytoplankton (Redfield et al. 1963, Robert et al. 1982). The discrepancy between these trends illustrates the need for an alternate N source besides that in external feed water brought in during a tide.

As the oyster pond under study is a closed system between water renewals, the only 2 major sources of nutrients are sediment and oysters. Concerning the latter, we have assumed a steady state between growth of phytoplankton and grazing by oysters and other organisms. This assumption is based on the observation (Fig. 6) that, in bottles containing water from the pond (thereby removing the phytoplankton from grazing pressure) and incubated in situ, chl a increased rapidly, while at the level of the whole pond, there is no change in phytoplankton standing stock in the water on short time scales (order of a day). Moreover, oysters are not net producers of DIN as their uptake of particulate nitrogen exceeds their release in dissolved form.

On a seasonal time scale, the observed increase in phytoplankton biomass must, therefore, be attributed to the nutrient supply from the sediment. This probably originates from organic matter degradation and mineralization taking place in summer (Billen 1977, Jørgensen & Sørensen 1985). This phenomenon leads to a decrease in sediment N compounds, which is particularly notable for the PAN. These amino compounds are more easily degraded than other common
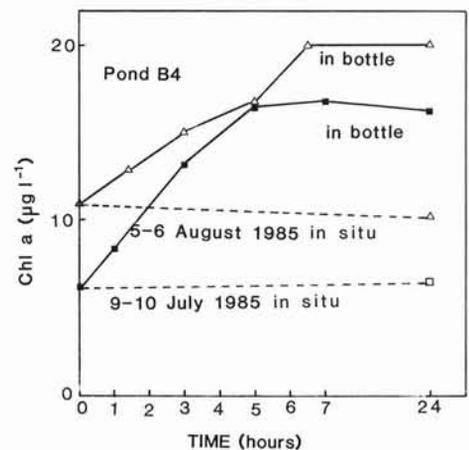

Fig. 6. Short-term changes in chlorophyll a in suspended matter. (----) in situ: whole water sample; (——) in bottle: 1.5 l sample incubated in a 2 l polycarbonate bottle floating at the pond's surface

N-containing macromolecules (Christensen et al. 1983).

Conversely, in winter, organic matter degradation is low while TPN supply is high, leading to sediment enrichment in particulate organic matter. The level of organic matter (nitrogen, PAN) is clearly higher in sediments below oysters (Kusuki 1981, Sornin et al. 1983, Feuillet-Girard et al. 1988). In the pond studied here, the sediment richness under oysters was due to particulate organic supplies by sedimentation plus supplies by biodeposition which can increase the deposited quantities by a factor of 20 (Sornin et al. 1987).

Mineralization periods, mainly leading to seasonal release of ammonium, were particularly marked in sediments enriched by the large organic supplies of biodeposits in spring and summer (above 1000 µmol N $m^{-2} h^{-1}$). These led to a lowering of the redox potential which became less than +50 mV at the 0–0.5 cm sediment depth, and negative below that (results not shown). These oxidoreduction conditions do not allow nitrification to proceed when the pH is near 7 (Billen 1977), and explain the low levels of nitrate in interstitial waters. Maximal rates of ammonification correspond to periods of high bacterial activity: during spring in control sediment, and late summer and fall in sediments under oysters. These rates are of the same order of magnitude as those found by Billen (1977): between 0.7 and 10.8×10^{-3} µmol $cm^{-3} h^{-1}$, by Blackburn (1980): 11.9×10^{-3} µmol $cm^{-3} h^{-1}$ and by Henricksen et al. (1984): 46.8×10^{-3} µmol $cm^{-3} h^{-1}$.

The time lag observed in the different stocks indicates that sediments are a nutrient reservoir. Thus, the TPN stock is enriched in winter and supplies N which is mineralized and liberated in summer in the water column. Such seasonal lags have been described for oxygen uptake (Hargrave 1978) and for organic carbon and nitrogen mineralization (Kemp & Boynton 1984, Rudnick & Oviatt 1986). This phenomenon allows a 'deferred' primary production in summer. The seasonal trends depicted above are related to the increase in surface irradiance and subsequent temperature changes in spring and summer which has 2 effects: an increase in biological activity such as DIN consumption by phytoplankton (Collos et al. 1988), ammonification by bacteria, bioirrigation by meio- and macro-fauna, and a greater diffusion rate for dissolved compounds in interstitial waters (Krom & Berner 1980).

In summer, when the nutrient deficit is most noticeable, the control sediment can provide (TF) up to 100 µmol $m^{-2} h^{-1}$ of NH_4 (Fig. 4). However, after uptake by microphytobenthos at the interface, the ammonium flux reaching the water column is about 40 µmol $m^{-2} h^{-1}$. These fluxes are about the same order of magnitude as those estimated or cited by Hopkinson (1987): between 8 and 300 µmol $m^{-2} h^{-1}$. Theoretical

Table 2. Contribution of feed water and benthic fluxes to the DIN budget in the water column for 14 d of batch mode growth

Season	Feed water (µmol l^{-1})	Sediment (µmol l^{-1})	Total (µmol l^{-1})	Sediment (% total)
Spring	32	73.0	105.0	70
Summer	11	72.5	83.5	87
Autumn	37	61.6	98.6	62
Winter	65	45.8	110.8	41

fluxes from sediment under oysters can reach 1100 µmol $m^{-2} h^{-1}$, and are in good agreement with fluxes measured at the interface (950 µmol $m^{-2} h^{-1}$). As the water depth does not exceed 1 m, the regulation of primary production by the sediment flux is much more important in our study site than in other coastal or estuarine areas (Table 2).

Taking into account the respective areas for the 2 types of sediments in the pond under study, the water column enrichment in nitrogen by fluxes coming from the sediment is about 0.2 µmol $l^{-1} h^{-1}$, or 4.8 µmol l^{-1} d^{-1}. In summer, the *daily* nutrient supply from the sediment is therefore equivalent to the *total* monthly supply by external feed water (6.5 µmol l^{-1}). For a budget over 14 d of batch mode growth, the sediment supplies 10 times more DIN than the feed water, and allows the phytoplankton development observed at this time when the maximal metabolic demand occurs.

In conclusion, environments such as the one studied are subjected to 2 modes of nutrient supplies: a continuous one from the sediment, over which is superimposed a discontinuous one. The latter results from water renewal, whose frequency was monthly in the present case, but can also be variable. This change in nutrient regime also corresponds to a change in the N source, with mainly ammonium coming from the sediment, and nitrate from the feed water (Collos et al. 1988). As in this (Robert et al. 1986) and other (Glibert et al. 1982) kinds of environments, microalgal succession may be regulated by the nature of the N nutrients.

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