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Response of coastal phytoplankton to ammonium and nitrate pulses: seasonal variations of nitrogen uptake and regeneration

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Abstract

Seasonal variation in uptake and regeneration of ammonium and nitrate in a coastal lagoon was studied using ^{15}N incorporation in particulate matter and by measuring changes in particulate nitrogen. Uptake and regeneration rates were two orders of magnitude lower in winter than in summer. Summer uptake values were 2.8 and 2.2 μmol $N.l^{-1}.d^{-1}$ for ammonium and nitrate, respectively. Regeneration rates were 2.9 and 2.1 μmol $N.l^{-1}.d^{-1}$ for ammonium and nitrate respectively. Regeneration/uptake ratios were often below one, indicating that water column processes were not sufficient to satisfy the phytoplankton nitrogen demand. This implies a role of other sources of nitrogen, such as macrofauna (oysters and epibionts) and sediment. Phytoplankton was well adapted to the seasonal variations in resources, with mixotrophic dinoflagellates dominant in winter, and fast growing diatoms in summer. In winter and spring, ammonium was clearly preferred to nitrate as a nitrogen source, but nitrate was an important nitrogen source in summer because of high nitrification rates. Despite low nutrient levels, the high rates of nitrogen regeneration in summer as well as the simultaneous uptake of nitrate and ammonium allow high phytoplankton growth rates which in turn enable high oyster production.

Introduction

Coastal lagoons are subjected to nutrient inputs of various origin. Nitrogen from watersheds, mainly as nitrate, can lead to high concentrations (Nixon and Lee 1981; Smith et al. 1989; Picot et al. 1990) and blooms of diatoms (Vaquer et al. 1996; Collos et al. 1997). Ammonium inputs from the sediment can be important seasonally (Nixon 1980; Sornin et al. 1990; Souchu et al. 1998) and serve as main source of nitrogen for phytoplankton. In the case of lagoons dedicated to aquaculture (e.g., oyster farming), ammonium pulses can occur due to excretion by these bivalve molluscs and their epibionts (Robert et al. 1982; Vincendeau and Robert 1987; Dame et al. 1989). Under Mediterranean conditions, watershed inputs of nitrate are sudden and intense. Ammonium pulses can also be due to short anoxia periods (Souchu et al. 1998). In order to simulate those pulses of nitrate or ammonium and to study the response of natural communities of phytoplankton in the Thau lagoon (S. France), we carried out additions of ^{15}N labelled compounds and followed label incorporation in the particulate matter as well as the changes in phytoplankton biomass (as chl a) and particulate nitrogen (PN) for up to 24 hours under *in situ* conditions. This approach also allowed the estimation of regeneration rates for ammonium and nitrate.

Materials and methods

The study was carried out in the Etang de Thau, a Mediterranean coastal lagoon, located in Southern France, and dedicated mostly to oyster farming (Figure 1). Water samples were taken from the surface

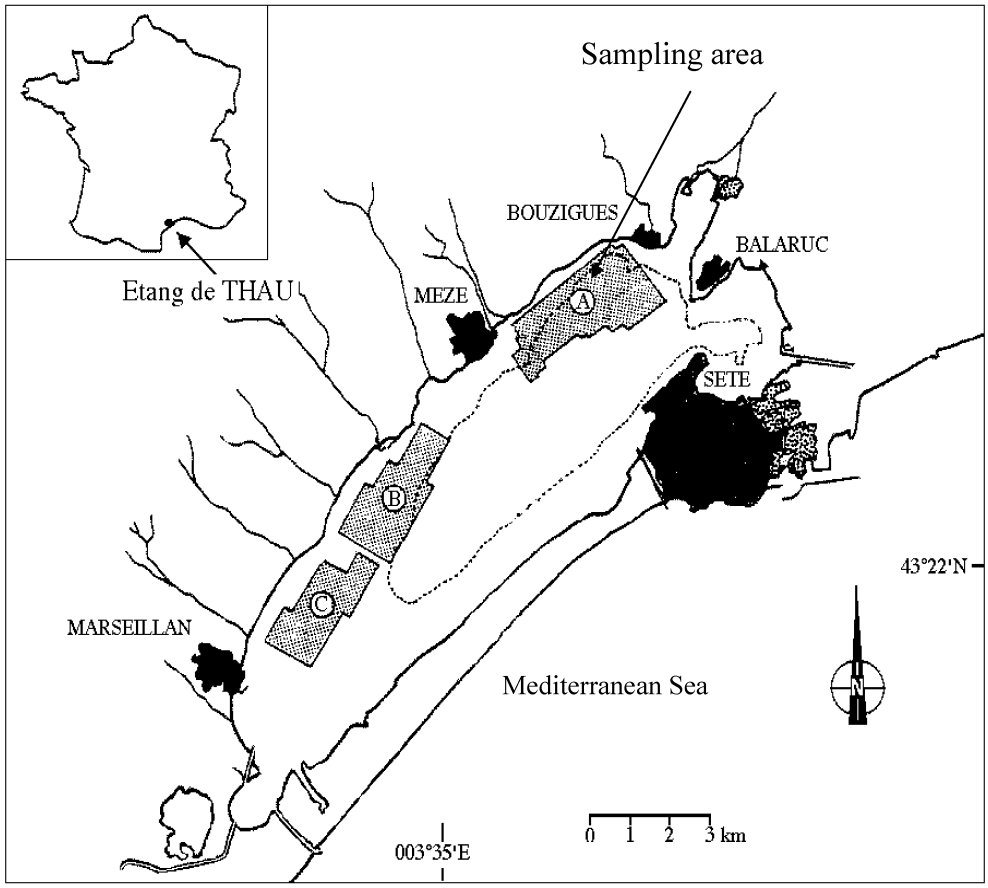

Figure 1. Map of Thau lagoon showing sampling site. Grey and black areas denote respectively the shellfish farming and urban zones.

near oyster culture racks in January, April, June and October 1993, and in February 1994.

Surface irradiance was measured with a LI-COR (Model LI-190SA) quantum sensor and employment of a LI-1000 data logger. Underwater irradiance was measured at 50 cm intervals with a LI-COR (Model 193SA) spherical quantum sensor.

In the water samples, ammonium was fixed immediately after collection in the field according to Aminot (1983). Samples for analysis of other nutrients were filtered over GF/F membranes and frozen within one hour after sampling. Nitrate, nitrite and soluble reactive phosphorus (SRP) were measured by segmented flow analysis according to Tréguer and Le Corre (1975). Phytoplankton samples were fixed with formaldehyde (2% final concentration) and examined with an inverted microscope using the Utermöhl method (Utermöhl 1958).

For the measurement of growth dynamics and primary production, 20 l polycarbonate bottles were used as sampling bottles, after cleaning by soaking in 10% HCl and rinsing with deionized water (0.06 µS conductance). Four seawater samples were collected by immersing the bottles 10 cm below the surface. In a shore laboratory, the samples were pooled in a 100 l polyethylene container from which three (one control, one enriched with ammonium, one enriched with nitrate) 20 l polycarbonate bottles were filled. The container was checked to be non toxic. One 20 l bottle was used as control. One bottle was enriched with 10 µmolN.l^{-1} ammonium, and the third bottle was enriched with 10 µmolN.l^{-1} nitrate, both labelled with ^{15}N (9.5% enrichment). The bottles were incubated *in situ* just below the surface. The nitrogen additions were not necessarily saturating (Collos et al. 1997), but were sufficient to prevent nutrient exhaustion over a 24 h period. Incubations were started in the morning and terminated 24 h later. Samples were taken at 2 h intervals during 10 or 12 h, and one final sample after 24 h. For chlorophyll a (chl a) measurements,

samples of 50 ml were immediately filtered on GF/F membranes and the filters kept on ice in the dark. Upon return to the laboratory, the filters were stored at −20 °C. Chl a samples were ground and extracted in 90% acetone for 24 h in the dark at 4 °C and analyzed fluorometrically (Holm-Hansen et al. 1965).

For ^{15}N analyses, samples were filtered using GF/F membranes, dried at 60 °C for 24 h and stored desiccated. Particulate nitrogen (PN) and isotopic analyses were carried out according to Owens and Rees (1989) with a Roboprep/Tracermass instrumentation. Uptake rates were calculated with Equation 4 in Collos (1987) which yields uptake rates unbiased by other nitrogen (N) sources and is appropriate in cases where PN changes significantly with time.

$$Rho = PNf(Cp - Co)/(Cd - Co)T$$

Where

- PNf = particulate nitrogen at the end of incubation
- Cp = atom % of the particulate nitrogen
- Cd = atom % of the label
- Co = natural abundance of ^{15}N (atom %)
- T = incubation duration (hours)

This calculation, however, does not take into account regeneration processes. The latter were estimated indirectly from mass balances following Laws (1985). Changes in PN integrate both net uptake (U) and regeneration (R) processes so that:

$$\Delta PN = U - R \tag{1}$$

As we have already observed significant decreases in PN at short time scales during incubations in this kind of shallow environment (Collos et al. 1989a, 1997), we assume that nitrogen (N) cycling in the Etang de Thau can be described by the model of Laws (1985). Rearrangement of Equation 1 leads to:

$$R = U - \Delta PN \tag{2}$$

This approach can be used in very dynamic systems where changes in PN can be detected at short time scales. Note that Equations (1) and (2) are valid in the case of one source of nitrogen only. In order to correct for changes in PN due to a N source other than the added one, we use the difference between the change in PN in the sample enriched with a given N compound (PNs) and that of the control (PNc):

$$R = U - (\Delta PNs - \Delta PNc) \tag{3}$$

Note that the difference between ΔPNs and ΔPNc depends on net uptake only and is independent of regeneration processes as demonstrated below:

$$\Delta PNs = Us - R \quad \text{and} \quad \Delta PNc = Uc - R \tag{4}$$

where Uc is net uptake of the control and Us is net uptake of the experimental bottle, and assuming that regeneration is not influenced by nutrient additions. Therefore,

$$\Delta PNs - \Delta PNc = (Us - R) - (Uc - R) = Us - Uc \tag{5}$$

The uptake values are corrected for isotope dilution due to regeneration processes according to Kanda et al. (1987). Preliminary surveys showed that, with exception of events such as rainfall pulses in fall or winter or bottom anoxia in summer, dissolved inorganic N concentrations did not change appreciably *in situ* over the 24 h time scale. This implies a regeneration-uptake ratio of about 1 which is used here. Correction for substrate enhancement was made according to Mac Isaac and Dugdale (1969) using half-saturation constants for nitrate from the same study site (Collos et al. 1997) and an average value of 1.3 $\mu molN.l^{-1}$ for ammonium as determined for eutrophic areas by Mac Isaac and Dugdale (1969).

Inorganic carbon uptake was measured by the ^{14}C-technique (Steemann Nielsen 1952). At time zero, a one liter subsample from each 20 l bottle (control, + ammonium, + nitrate) was transferred in 1 l polycarbonate bottles and inoculated with a trace addition of 2.1 MBq of ^{14}C bicarbonate (Amersham, 1.95 GBq $mmol^{-1}$ specific activity). At each sampling time, a 40 ml subsample was collected from the bottles, fixed with formalin (1% final concentration) according to Riemann and Jensen (1991), and gently filtered through 25 mm Millipore HAWP cellulose nitrate membranes. Filters were air dried and acidified with 100 µl 1 N HCl, placed in 4 ml of scintillation cocktail (Packard Instagel) and measured with a Packard Tricarb 300 liquid scintillation counter.

Net growth rates were calculated from changes in chl a or PN (Guillard 1973) and expressed as $\mu = (\ln (X_1/X_0))/(t_2 - t_1)$ in units of time (10 or 24 h; see Table 2), with X = biomass indicator (Chl a or PN).

Table 1. Initial nutrient concentrations, microalgal biomass and particulate matter levels. Chl a: chlorophyll a; PAR: mean photosynthetically available radiation; PN: particulate nitrogen; N.A.: not available.

Date	PAR ($\mu mol.m^{-2}.s^{-1}$)	T °C	Nitrate ($\mu mol.l^{-1}$)	Ammonium ($\mu mol.l^{-1}$)	Chl a ($\mu g.l^{-1}$)	PN ($\mu mol.l^{-1}$)
20 January 93	458	5.5	4.43	2.3	0.4	1.3
15 April 93	881	14.4	0.17	0.43	1.7	3.3
23 June 93	890	23.8	0.20	0.60	1.0	1.3
21 October 93	N.A.	16.8	3.30	1.2	1.0	1.4
10 February 94	527	7.4	1.80	1.7	1.0	1.5

Table 2. Seasonal variations in PN and Chl a based net community growth rates (μ) measured over 10 light hours and 24 hours *in situ*. N.A.: not available. Chla/PN: range of values over the incubation period.

Date	Treatment	μPN ($10\ h^{-1}$)	μChl a ($10\ h^{-1}$)	μPN ($24\ h^{-1}$)	μChl a ($24\ h^{-1}$)	Chla/PN (g/mol)
January 93	control	0.20	0.66	N.A.	N.A.	0.31–0.89
	+ NO_3	0.19	0.56	N.A.	N.A.	0.31–0.55
	+ NH_4	0.66	0.83	N.A.	N.A.	0.31–0.48
April 93	control	0.17	0.53	0.29	0.33	0.57–0.91
	+ NO_3	0.21	0.46	0.39	0.47	0.56–0.73
	+ NH_4	0.28	0.75	0.50	0.88	0.52–0.85
June 93	control	0.37	1.10	0.58	0.77	0.62–1.43
	+ NO_3	1.21	1.64	1.94	1.65	0.50–1.25
	+ NH_4	1.31	1.80	1.92	1.81	0.63–1.43
October 93	control	0.38	0.77	1.08	1.13	0.69–1.56
	+ NO_3	0.40	0.94	0.86	1.26	0.45–1.00
	+ NH_4	0.67	0.94	1.20	1.35	1.07–1.40
February 94	control	0.14	0.03	0.34	0.41	0.71–0.55
	+ NO_3	0.25	0.03	0.44	0.43	0.71–0.40
	+ NH_4	0.11	0.05	0.46	0.40	0.71–0.56

Results

Initial conditions on the five sampling dates are shown in Table 1. Salinity varied between 28.9 and 37.9. Water temperature ranged from 5.5 °C in winter to 23.8 °C in summer. Inorganic nitrogenous nutrients (nitrate + ammonium) were less than 0.6 $\mu molN.l^{-1}$ in spring-summer and higher than 6 $\mu molN.l^{-1}$ in winter, while phytoplankton biomass estimated as chl a did not exhibit large seasonal variations (0.4 to 1.7 $\mu g.l^{-1}$). PN and chl a were correlated, except in January. An estimate of the non-phytoplankton PN was obtained from the Y intercepts of the regression. Those ranged from 34% of the total PN in October to 56–58% at the other periods.

Within the phytoplankton, picophytoplankton species represented 73 to 93% of cell counts but only 30 to 38% of the phytoplankton biomass (estimated as chlorophyll a). At the nanoplankton and microplankton level, there was an overwhelming dominance of dinoflagellates in January 1993, followed by a few rare phytoflagellates. The latter were numerically dominant in April, with a few *Chaetoceros* and dinoflagellates. *Skeletonema costatum* was dominant in June, with few other diatoms (*Pseudo-nitzschia*, *Leptocylindricus*, *Thalassionema*). In October, several *Chaetoceros* sp. were dominant, followed by *Thalassionema* and *Thalassiosira*. Finally, in February 1994, dinoflagellates were again dominant, along with a few phytoflagellate, *Eutreptiella* and *Chaetoceros* species.

The daily time course of phytoplankton chl a in winter differed from that during the rest of the year. For example, in April (Figure 2), most of the increase took place during the light period (time zero was about 9–10 AM) in experimental as well as control incubation bottles. Similar trends were found in June and October, and led to higher growth rates over 10 hours (in the light) than over 24 hours (light and dark) (Table 2). In winter (Figure 3), inverse trends were observed, with most of the chl a increasing at night. This led to higher growth rates over 24 hours than over the 10 h light period alone (Table 2). In addi-

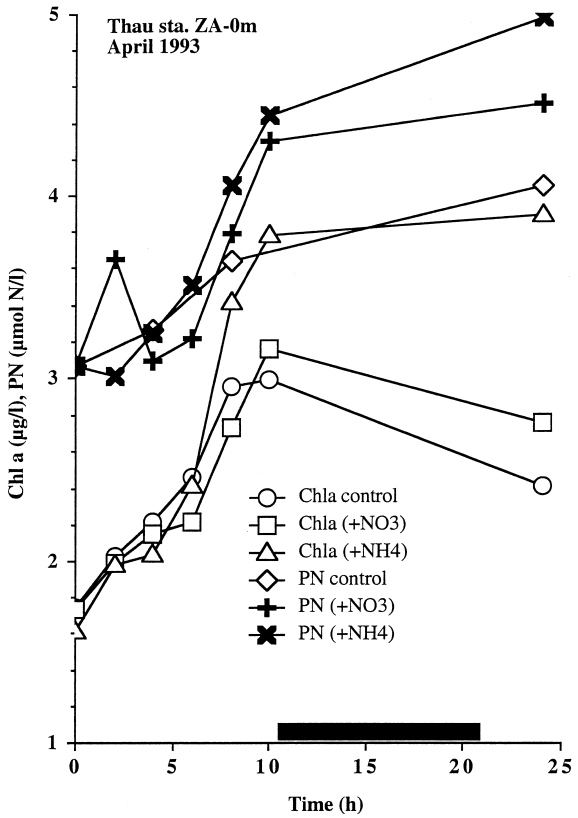

Figure 2. Changes in biomass indices during incubation: chlorophyll a (Chla) and particulate nitrogen (PN) as a function of time in April 1993 for the control and the two enrichments. The dark bar indicates the night period.

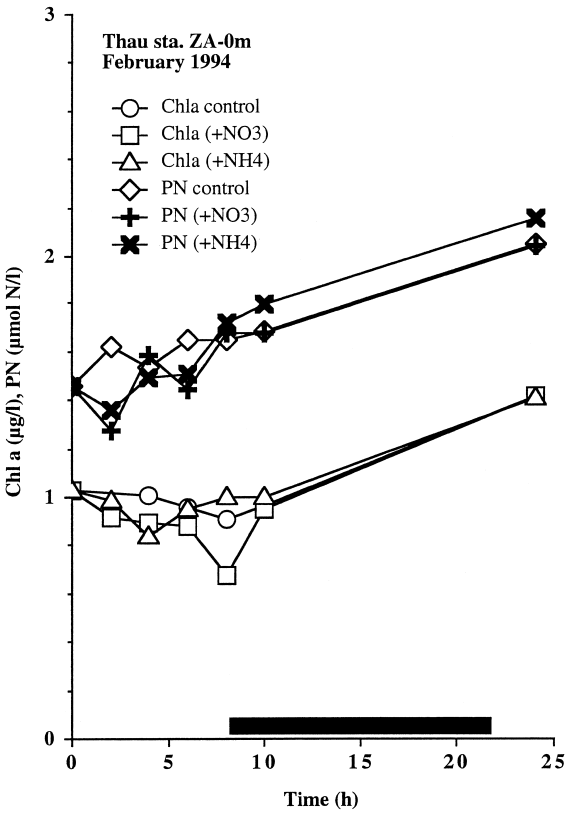

Figure 3. Changes in biomass indices during incubation: chlorophyll a (Chla) and particulate nitrogen (PN) as a function of time in February 1994 for the control and the two enrichments. The dark bar indicates the night period.

tion, increases in biomass during incubation were always lower in winter and early spring than during the rest of the year, as exemplified by the net growth rates (Table 2). In June, chl a increased by a factor of two in the controls (1 to 2 $\mu g.l^{-1}$) and a factor of six in the ammonium enriched sample (1 to 6.2 $\mu g.l^{-1}$) over 24 hours.

Changes in PN were less contrasting, as PN often increased at night just as rapidly as during the light period (February, June, October). In summer, the PN increases were large: from about 2 fold in the control (1.3 to 2.7 $\mu molN.l^{-1}$) up to about six fold in the enriched samples (1.3 to 8.5 $\mu molN.l^{-1}$).

In the controls, highest growth rates were observed in October for both indices over 24 hours (Table 2). Both rates did not appear to be different from each other. The impact of the enrichments on PN-based and chl a-based growth rates is summarized in Table 2 by comparing controls and enriched samples. Both rates were correlated, but the chl a-based growth rates were higher and lower respectively than the PN based growth rates over 10 and 24 hours. Following enrichment, the highest growth rates for both indices and both incubation durations were observed in June. The greatest stimulations were also in June (more than 2 fold for Chl a and more than 3 fold for PN over 24 hours).

Figures 4 and 5 show the cumulative uptake of ammonium and nitrate respectively on the five sampling dates, not corrected for regeneration nor substrate enhancement. The highest rates were observed in June (up to 6 $\mu molN.l^{-1}$ taken up in 24 hours for both ammonium and nitrate), and the lowest in winter (January and February), with nitrate uptake rates being extremely low in spite of the 10 $\mu molN.l^{-1}$ addition.

Uptake values corrected for regeneration and substrate enhancement are shown in Figure 6. The differences in the rate estimates between seasons were significant. The uptake values ranged over 2 orders of

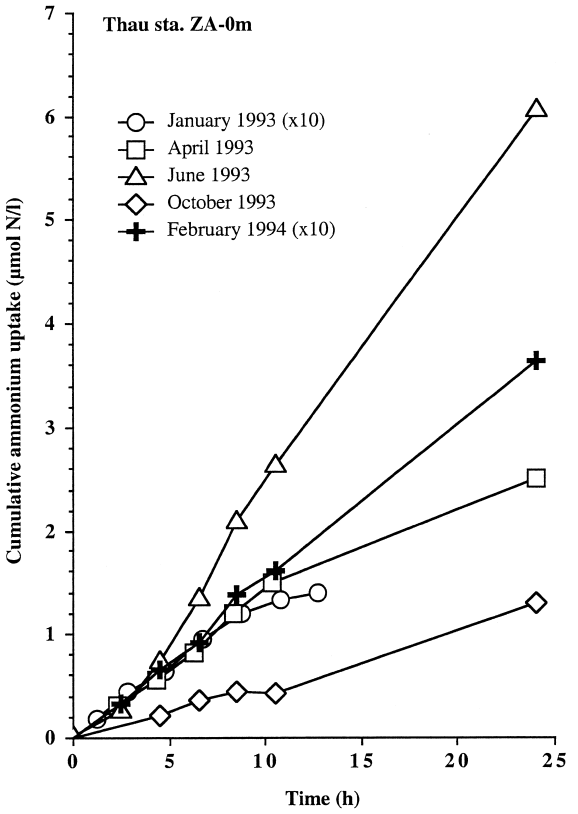

Figure 4. Cumulative ammonium uptake (uncorrected for regeneration) as a function of time of incubation at various seasons. Night period begins around T = 8 hours in winter and T = 11 h in summer. Light period begins around T = 22 h in winter and T = 19 h in summer. Values for January and February have been multiplied by ten.

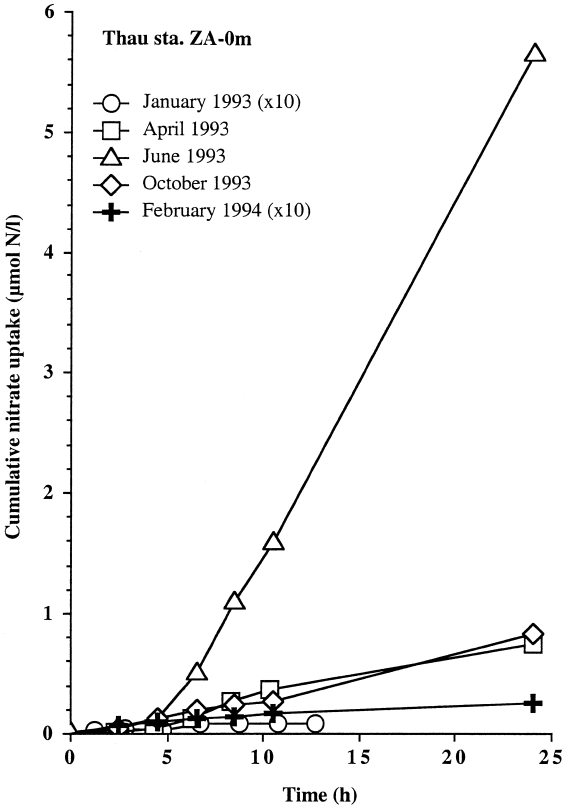

Figure 5. Cumulative nitrate uptake (uncorrected for regeneration) as a function of time of incubation at various seasons. Night period begins around T = 8 hours in winter and T = 11 h in summer. Light period begins around T = 22 h in winter and T = 19 h in summer.

magnitude between winter and summer: from 0.1 to 2.8 µmolN.l^{-1}.d^{-1} for ammonium and from 0.01 to 2.2 µmolN.l^{-1}.d^{-1} for nitrate. The same can be said about regeneration rates. Winter minima ranged from undetectable to 0.2 µmolN.l^{-1}.d^{-1} for ammonium and from undetectable to 0.01 µmolN.l^{-1}.d^{-1} for nitrate. Summer maxima were 2.9 µmolN.l^{-1}.d^{-1} for ammonium and 2.1 µmolN.l^{-1}.d^{-1} for nitrate.

Ammonium was the preferred N source (Table 3), especially in winter under low irradiances and high ammonium concentrations (Table 1). But in summer, nitrate was taken up just as fast as ammonium, even though nitrate concentrations were very low (Table 1).

Except in April and June, regeneration/uptake ratios for both ammonium and nitrate were below one (Table 3). Carbon uptake rates were generally stimulated by N additions, so both control (UC) and experimental values (UC + NH_4 and UC + NO_3) are given here as carbon/nitrogen uptake ratios. For ammonium, values ranged from 2.8 in summer to 5.6 in winter. For nitrate, the range was much greater: from 2.4 in summer to 80 in winter. This corresponds to the N uptake values corrected for regeneration but not for substrate enhancement (Vmax). In the last column of Table 3, the carbon/nitrogen values correspond to the control carbon uptake values and the N uptake values corrected to *in situ* N concentrations. These ranged from 3.3 to 6.8 by atoms.

Discussion

The coastal lagoon studied is largely dedicated to oyster culture. The assessment of its carrying capacity is important in setting limits to sustainable development of these activities. In particular, the summer situation with low to undetectable nutrient levels (Picot et al.

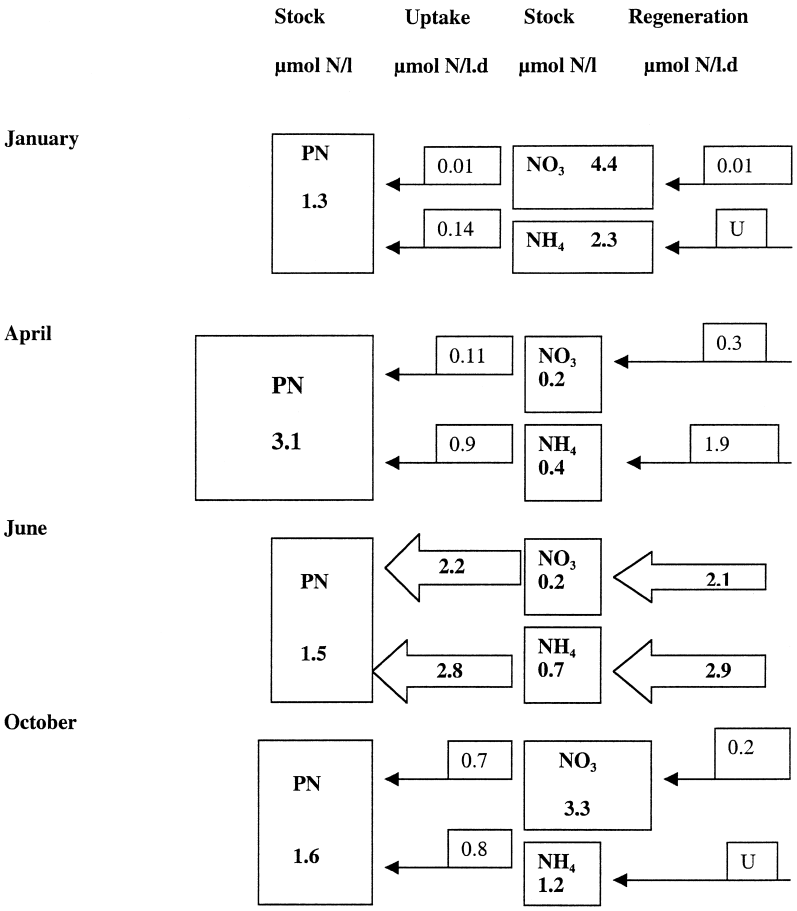

Figure 6. Summary of stocks of ammonium, nitrate and particulate nitrogen (rectangles), and fluxes of ammonium and nitrate (arrows) in the water column of Thau lagoon. Size of rectangles and arrows is roughly proportional to size of stock and flux. U: undetectable.

Table 3. Seasonal variations in ammonium/nitrate uptake (U) ratios (mol/mol), regeneration (R)/uptake ratios and carbon/nitrogen uptake ratios (mol/mol) measured over a 24 h period (except in January 1993: 12 hour incubation). N.A.: not available. Values labelled < 1 are due to undetectable regeneration rates.

Date	UNH_4/UNO_3	RNH_4/UNH_4	RNO_3/UNO_3	$(UC + NH_4)/UmaxNH_4$	$(UC + NO_3)/UmaxNO_3$	$UC/(UNH_4 + UNO_3)$
January 93	10.0	< 1	1.0	5.6	80.0	N.A.
April 93	6.5	2.7	3.0	4.1	11.9	6.8
June 93	1.3	1.0	0.95	2.8	2.4	3.3
October 93	1.0	< 1	0.3	5.4	6.7	4.9
February 94	11.5	0.8	< 1	4.6	56.7	6.4

1990; Collos et al. 1997) and simultaneous high phytoplankton biomass (Tournier et al. 1982; Vaquer et al. 1996) implies high regeneration rates of nutrients and especially inorganic N during this period. The present results confirm this by showing that both ammonium and nitrate are regenerated at high rates in summer (Figure 6).

For ammonium, the highest regeneration rate found fits in the upper range of rates reported for marine environments (Harrison 1993). The high nitrate regeneration rates are similar to those observed in a similar kind of ecosystem (Collos et al. 1988) and in other coastal environments (Helder and de Vries 1986; Lipschultz et al. 1986; Owens 1986). Such high nitrification rates allow high nitrate uptake rates by

the phytoplankton, in spite of low nitrate concentrations. The importance of nitrification in the Thau lagoon was already indicated by measurements of nitrate concentrations which were higher in the oyster farming areas than outside (Souchu et al. 2001). Our results of direct rate measurements confirm this phenomenon.

Nitrogen uptake rates are in the upper range of ammonium utilization rates reviewed by Harrison (1993), which illustrates the highly dynamic nature of the Thau lagoon ecosystem. The linearity of the cumulative uptake (Figures 4 and 5) indicates no regeneration of ^{15}N (isotope recycling) during incubation (Laws et al. 1985). For nitrate uptake, the highest values reported here are in the upper range of values reported by Paasche (1988) for coastal areas.

In summer, phytoplankton is using both nitrogen sources at equal rates. The dominant species, *Skeletonema costatum* is known to take up both N compounds simultaneously when high nitrate concentrations appear to mitigate the inhibiting effect of ammonium on nitrate uptake (Eppley et al. 1971; Maestrini et al. 1982). This allows high growth rates, enabling the characteristic explosive development of this species. During summer, regeneration rates are also highest allowing the system to sustain itself on regenerated production (both ammonium and nitrate). In winter, the preference for ammonium relative to nitrate (Table 3) seems to be related to low irradiances or high ammonium concentrations. This is due to the lower energy requirement for ammonium assimilation (Dortch 1990). In summer, however, nitrate is used just as fast as ammonium, in agreement with previous studies in a similar environment (Collos et al. 1989b), and on a more global scale (Collos 1998).

There is some degree of uncertainty associated with the uptake rate estimates. This is due to the varying regeneration/uptake ratio which we assumed to be equal to one, but can vary between 0.5 and 2 (Kanda et al. 1987). One way to assess the validity of corrected uptake rates is to examine C/N uptake ratios. Deviations from the Redfield ratio may indicate some degree of uncoupling between C and N metabolism on short time scales (hours after N additions). On a 24 hour time scale, very high values indicate that the N source is not used, such as in January 1993 or February 1994 for nitrate (Table 3). Outside those periods, however, the C/N uptake ratio generally tended towards the Redfield value over 24 hours, indicating balanced growth. Thus, the low values in the last column of Table 3 indicate that uptake rates may have been overestimated.

Despite low nutrient levels, the high rates of N regeneration in summer as well as the simultaneous uptake of nitrate and ammonium allow high phytoplankton growth rates which in turn lead to high oyster production (Souchu et al. 2001). So, there appears to be a rather tight coupling between nutrient cycling, phytoplankton dynamics and oyster growth in this ecosystem. But there may also be a top-down regulation as suggested by the unbalance between uptake and regeneration of dissolved inorganic N on the 24 hour time scale (Figure 6, Table 3). Such unbalances were observed elsewhere by Harrison (1993) and Glibert et al. (1991), Bronk et al. (1998), and sometimes explained by large heterotrophs which were not sampled (Glibert et al. 1991) or benthic regeneration (Bronk et al. 1998). In the present case, other regeneration processes such as due to macrofauna (oysters and epibionts) are probably also responsible for the difference, at least partly.

In the sediments, summer anoxic events can lead to ammonium release (Mazouni et al. 1996; Souchu et al. 1998). However, the value of 1.7 $\mu molN.l^{-1}.d^{-1}$ mentioned in Souchu et al. (1998) for the same study site, which is lower than our estimate of ammonium regeneration in the water column during the same season (Figure 5), indicates that sediments are probably not the major ammonium source, not even during an anoxic event. The observation of higher ammonium concentrations within shellfish culture zones than outside (Picot et al. 1990; Souchu et al. 1998) indicates that oysters and epibionts are more important than the sediment for supplying this N source.

As far as the nutrient pulses are concerned, our approach indicates that the pulses supplied were not readily used by the phytoplankton in winter. This may be due to low irradiance or temperature, as well as to the presence of dinoflagellates, many of which are known to be mixotrophs. The increase in PN at night (Figures 2 and 3) in January and February tends to suggest the use of organic N as source during this period (Granéli et al. 1999). In summer and fall, the pulses were used rapidly and the phytoplankton was well adapted to this kind of nutrient regime. In contrast to other diatoms, *Skeletonema costatum* and *Chaetoceros* species, which were dominant at the time, are both known to process nutrients rapidly into new biomass (Collos 1986). These diatom blooms appear to be vital for oyster growth in summer as the

latter are not able to retain the picophytoplankton because of their small size (Dupuy et al. 2000).

Acknowledgements

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