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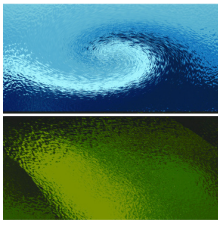

RESEARCH ARTICLE

Nutrient dynamics and primary production in the eutrophic Berre Lagoon (Mediterranean, France)

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Abstract

1 - The brackish Berre Lagoon is one of the largest Mediterranean coastal lagoons (155 km²). Since 1966, it has been influenced by a large freshwater discharge from a hydroelectric power plant, which has led to strong changes in the ecosystem structure and functioning.

2 - During 2005 and 2006, we monitored physico-chemical variables, primary production, nitrogen assimilation and regeneration in the water column using the dual-isotopic $^{15}N/^{13}C$ technique.

3 - Significant seasonal variations were observed for salinity, however summer values were similar to those observed in the lagoon before the power plant opened (30). Nitrate concentrations (NO_3^-) varied, yielding very low values in the summer to values of 220 µg $N\text{-}NO_3^-.l^{-1}$ in winter. Ammonium (NH_4^-) and phosphate (PO_4^{3-}) were observed in significant concentrations throughout the year (>7 µg $N\text{-}NH_4^+.l^{-1}$ and 3 µg $P\text{-}PO_4^{3-}.l^{-1}$ respectively). Total chlorophyll increased slightly from February 2005 to June 2006, never exceeding 17 $\mu g.l^{-1}$ until summer 2006, which was marked by a large accumulation of biomass (> 30 $\mu g.l^{-1}$) maintained until the end of the year.

4 - Mean primary production rates ranged from 50 to 1 600 $\mu gC.l^{-1}.d^{-1}$, giving a total annual production of 507 $gC.m^{-2}.yr^{-1}$ in 2005 and 742 $gC.m^{-2}.yr^{-1}$ in 2006. This production is based on the assimilation of 15 000 and 24 000 tons of dissolved inorganic nitrogen (DIN) in 2005 and 2006 respectively (uptake rates ranging from 3 to 77 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$ and from 1 to 63 µg $N\text{-}NO_3^-.l^{-1}.d^{-1}$). Regeneration processes were very active: 15 to 85 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$ were regenerated in the water column and sustained at least 60% of ammonium uptake.

5 - 95% of the measured annual primary production was regenerated production. These budgets need to be analysed with caution as biological processes are characterized by high interannual and seasonal variabilities. Regeneration processes in the water column certainly fed by other processes (acting in the sediments) are the basis of eutrophication maintenance in the Berre Lagoon.

Keywords: primary production, nitrogen uptake, regeneration, phytoplankton, nutrients, eutrophication, Berre Lagoon, Mediterranean.

Introduction

Lagoons are subject to natural constraints due to their location, acting as an interface between land and sea, and their shallow depth. Climatic, direct (wind) and indirect (rain through river flows) and marine (tide) influences cause large fluctuations and rapid changes in the physical and chemical characteristics of lagoons (Trousselier and Gattuso, 2006). Lagoon communities and ecosystems are resilient to environmental changes and are able to buffer against external stresses (Aliaume *et al*., 2007; de Wit *et al*., 2001). However, the impact of human activity on the variability of a lagoon is considerable and usually leads to the deterioration and loss of marine resources, standing stocks and coastal landscapes (Viaroli *et al*., 2007). As they receive freshwater inputs from watersheds, lagoons receive pollutants, organic and mineral nutrients from heavily exploited catchments from the surrounding urban and industrial settlements. The excess nutrients lead to massive development of macroalgae and phytoplankton with a loss of diversity in both benthic and planktonic communities and the appearance of nuisance algal blooms. The organic matter produced is consumed by heterotrophic organisms, especially towards the bottom of the water mass and this can induce oxygen deficit, the so-called "malaïgue" in Mediterranean lagoons (Caumette and Baleux, 1980). Eutrophication is thus a consequence of excess nutrients, high external loading and also nutrient feedback by regeneration processes (Howarth and Marino, 2006). The understanding and control of eutrophication, and consequently the control of production, is one of the major problems faced by those responsible for the management of these sensitive ecosystems. Dissolved inorganic nitrogen is the most studied nutrient because it is often considered to be a limiting factor of primary production (Howarth and Marino, 2006).

The Berre lagoon is a natural brackish water body. Since 1966, its ecological characteristics have undergone far reaching changes due to the large freshwater discharges from a power plant (the equivalent of 7 times the lagoon's volume per year, in 1977). The Berre Lagoon became a particularly unstable lagoon, exhibiting considerable variations in salinity (2 to 30) (Minas, 1974, Nerini *et al*., 2000, Arfi, 1989), water column stratification, and substantial nutrient inputs (from the power plant and the tributary rivers). As a consequence the waters of the lagoon became hyper-eutrophic (frequently coloured waters with the development of macroalgae), and the frequent anoxic periods (Minas, 1976) led to the disappearance of the benthos (Stora, 1983). Changes were also observed in *Zostera sp*. meadows (Bernard *et al*., 2007).
In 2004, the European Court of Justice condemned the French State for not respecting the Athens protocol (advocating Mediterranean protection against telluric pollution) and demanded new management strategies. Harsher annual restrictions were imposed: a maximum freshwater discharge of 1.2×10^9 $m^3.yr^{-1}$ equivalent to 1.3 times the lagoon's volume for 2006. The directives also required the regional government to establish and implement action programmes to reduce the impact of freshwater and nutrient inputs in order to minimise the adverse effects on the environment. Since then, regular monitoring ensures that any restrictive measures are effective.
Although nutrient inputs into the Berre lagoon have decreased over the last few years, in relation to freshwater discharge restrictions, sewage treatment and drier climate (aridity) (Gouze *et al*., 2008), there is a remarkable lack of understanding concerning the fate of nutrients in the pelagic system. In this context, hydrological properties, inorganic and organic nutrients and chlorophyll have been monitored monthly over 2 years

(2005 and 2006). Quantification of primary production and biological fluxes of nitrogen (uptake and regeneration) have been assessed and described in the water column. The final aim of this study is to understand which part of dissolved inorganic nitrogen (DIN) pool, needed by the pelagic community, are provided by continental loadings and regenerating processes ; and thus gain an understanding of the processes at the root of eutrophication in the Berre Lagoon.

Methods

Study area

The Berre lagoon is situated near Marseilles, SE France, (figure 1), at the eastern border of the Gulf of Lion (43°30'N and 5°10'E). It is a shallow semi-confined ecosystem with a mean depth of 6.5 m (depths > 8 m being restricted to the central and southern parts) extending over 155 km², it contains 980 millions m³ of brackish water. It is connected to the Mediterranean Sea via the Caronte channel to the Southwest (6 km long, 60 to 100 m wide and 9 m deep) and to the hyper-eutrophic Bolmon pond to the south-east. The channel of the hydroelectric power plant is situated to the north of the lagoon and is fed by freshwater from the Durance mountain river, which flows in from the north and is partly diverted by a dugout channel, which is used to drive plant turbines. The lagoon also receives freshwater from two natural tributaries to the North: the Arc and the Touloubre. The catchment basins of these rivers cover a surface area of 1 130 km² (730 and 400 km² respectively), i.e. 70% of the Berre Lagoon's total natural catchment area. The remaining 30% represents the immediate catchment basin of the lagoon. Within this area are 600 000 inhabitants and large industrial and commercial parks (oil refineries, petrochemistry and aeronautics industries), supporting the main economic activities of this region.

Due to imposed legislation, the freshwater discharge released from the hydroelectric power plant was restricted to 2.1 x10^9

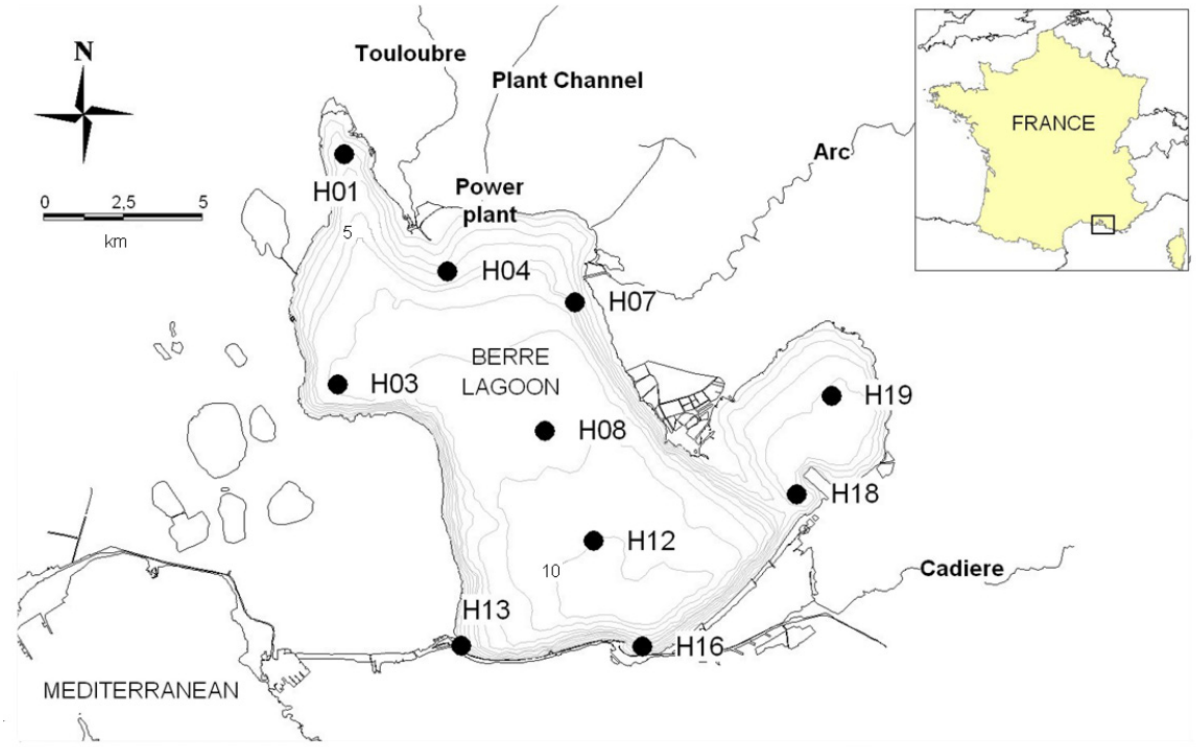

Figure 1: Location of the Berre Lagoon, and sampling stations.

$m^3.yr^{-1}$ (1994), 1.6 $x10^9$ $m^3.yr^{-1}$ (2005) and 1.2 $x10^9$ $m^3.yr^{-1}$ (2006), but even so, remains the principle tributary of the lagoon (representing around 85% of the total annual freshwater discharge) (Minas, 1974; Gouze *et al*., 2008).

Sampling programme

Following the imposed legislation, the GIPREB (Groupement d'Intérêt Public pour la Réhabilitation de l'Etang de Berre) was made responsible for collecting past and current physico-chemical data from the Berre Lagoon, and also financed and sorted out the logistics of for this study.

Water samples were collected monthly at 10 stations in the Berre lagoon (figure 1) from January 2005 to December 2006. Vertical profiles of temperature, salinity, and dissolved oxygen were measured at each station by deploying a CTD YSI multi-probe from the surface down to the bottom. Water was collected at the surface (0-1m) and near the bottom using a Niskin bottle, to measure nutrient concentrations, total matter (organic and mineral) and chlorophyll. In parallel, primary production and nitrogen assimilation and regeneration fluxes were quantified using the dual isotopic $^{13}C/^{15}N$ procedure.

Water analysis

One litre of water was sampled from the surface and bottom of the lagoon at each of the stations. This was then collected into polyethylene bottles, and stored in cool boxes ready for processing in the laboratory.

Total chlorophyll was measured by filtering 100 ml of water onto Whatman® GF/C filters, which were stored at -20°C until analysis. Chlorophyll was extracted with methanol and determined using a Turner Design 10 AU fluorometer (Raimbault *et al*., 2004). Filtered water was collected into 20 ml polyethylene flasks and frozen for nutrient analyses. Nitrate (NO_3^-), nitrite (NO_2^-) and phosphate (PO_4^{3-}) analyses were undertaken using a Technicon Autonanalyser® (Treguer & Lecorre, 1975). Detection limits (and analytical precision) were 0.8 (± 0.6) µg $N\text{-}NO_3^-.l^{-1}$, 0.1 (± 0.4) µg $N\text{-}NO_2^-.l^{-1}$, and 0.5 (± 0.3) µg $P\text{-}PO_4^{3-}.l^{-1}$, respectively. Samples for ammonium (NH_4^+) determination were collected into 50 ml Schott® flasks (following 3 washes with lagoon water) and fixed immediately after sampling, according to Koroleff (1970). Absorbance readings were taken in the laboratory within 24 hours. Detection limits (and analytical precision) were 0.3 (± 0.1) µg $N\text{-}NH_4^+.l^{-1}$. Turbidity blanks determined at 750 nm were negligible.

Suspended matter was determined by filtering 100 ml of water onto pre-combusted Whatman® GF/C filters (4h at 450°C). The filters were then rinsed with DIW, dried and weighed, then acidified (100 µl H_2SO_4 0.5N) and analyzed using high temperature combustion to determine particulate organic nitrogen and carbon. GF/C filters were used rather than GF/F in order to be comparable with the historical data. Test of comparison between GF/C and GF/F filters was assessed, and no significant difference was found to measure chlorophyll as well carbon and nitrogen concentrations.

^{13}Carbon/^{15}Nitrogen tracer experiments

Dissolved inorganic nitrogen uptake (NO_3^-, NH_4^+, NO_2^- and dinitrogen N_2), carbon fixation (primary production), and nitrogen regeneration processes (regeneration of NH_4^+ and nitrification) were measured simultaneously using the dual isotopic $^{13}C/^{15}N$ technique. Surface samples were collected at each station, while deep samples were collected at 5 stations only (H01, H04, H08, H12 and H19 only in 2006), into Niskin bottles. Water samples (300 to 600 ml) were collected in triplicate into acid-cleaned polycarbonate flasks. Each station was monitored by 3 experiments: a 2.4% solution of $NaH^{13}CO_3$ (99.9 atom%^{13}C) tracer was added to all flasks inducing a ^{13}C enrichment

of around 20% (1 ml into 300 ml of water). Then a 1 µmoles.ml^{-1} solution of $K^{15}NO_3$ (0.4 to 0.8 ml in 300 ml of water,) and a 1 µmoles. ml^{-1} solution of $^{15}NH_4Cl$ (0.3 to 0.6 ml in 300 ml of water,) was added to two series of water samples. $Na^{15}NO_2$ (0.08 ml in 300 ml of water, at 1 µg.ml^{-1}) or $^{15}N_2$ (injection of 1ml of gas for 300 ml of water, through a septum cap, according to Montoya *et al.*, 1996) were added to the third series of water samples. Initial ^{15}N enrichments generally ranged between 5 and 40%, except during summer where nitrate depletion sometimes led to an excess enrichment close to 100%. Following the addition of tracer, flasks were incubated *in situ* from solar midday to sunset, i.e. during half a diurnal period. Incubation times ranged from 5 to 7 hours according to the season.

Following incubation, NH_4^+ final concentrations were measured from the $^{15}NH_4^+$ incubation flasks. Samples were filtered (< 100 mm Hg) onto 25 mm pre-combusted (4h at 450°C) Whatman® GF/F filters. Subsequent to filtration, filters were dried at 60°C. 300 ml filtrates were recovered from the Duran Schott® flasks. These filtrates were poisoned with 1 ml (300 µl for 100 ml subsamples) of $HgCl_2$ (6.g l^{-1}) in order to prevent bacterial activity during conservation. Filtrates from the $^{15}NH_4^+$ incubations were used to measure the final ^{15}N enrichment in the DIN pool, as outlined by Slawyk and Raimbault (1995). In this procedure, all forms of DIN are removed from the sample as $(NH_4)_2SO_4$, by successive diffusion and reduction processes. In the first diffusion step, the final ^{15}N enrichment of the DIN pool is quantified, in order to estimate the isotope dilution of the tracer due to ammonium regeneration. During the second diffusion step, the oxidation of ammonium to nitrate (nitrification) is estimated through the ^{15}N enrichment of the nitrate pool in the $^{15}NH_4^+$ filtrates (Raimbault *et al.*, 1999b). The third diffusion step, following wet-oxidation enables the ^{15}N enrichment in the dissolved organic nitrogen (DON) pool and the particulate organic nitrogen (PON) pool, for organisms smaller than GF/F (< 0.7 µm), to be quantified.

^{15}N and ^{13}C enrichments were determined by mass spectrometry, using a C-N Integra mass spectrometer.

The transport rate of ^{13}C from the DIC (Dissolved Inorganic Carbon) pool to the POC (Particulate Organic Carbon) pool, *i.e.* primary production (PP in µg.l^{-1}.d^{-1} *i.e.* per diurnal period) was computed according to Dugdale and Wilkerson (1986):

$$PP = \frac{R_{POC}}{R_{0\,DIC}} \times [POC] \times \frac{1}{T} \qquad (1)$$

Where: R_{POC} and $R_{0\,DIC}$ represent the ^{13}C atom% excess enrichment in the final POC and initial DIC pool (following tracer addition). [POC] is the final POC concentration and T is the incubation time (half a day).

The transport rate of ^{15}N from the DIN pool to the PON (Particulate Organic Nitrogen) pool, *i.e.* the net DIN uptake (ρ_{DIN} in µg.l^{-1}.d^{-1}) was also computed according to Dugdale and Wilkerson (1986):

$$\rho_{DIN} = \frac{R_{PON}}{\overline{R_{DIN}}} \times [PON] \times \frac{1}{T} \qquad (2)$$

Where: R_{PON} and $\overline{R_{DIN}}$ represent the ^{15}N atom% excess enrichment in the final PON and DIN pools. [PON] represents the final PON concentration. In the ammonium experiments, $\overline{R_{DIN}}$ is the mean between initial and final ammonium enrichments, taking into account effects of isotopic dilution by the regeneration process.

Ammonium regeneration rates (r_{NH4} in µg.l^{-1}.d^{-1}) were estimated according to Laws (1984):

$$r_{NH_4} = \frac{\left[NH_4^+\right]_I + \left[NH_4^+\right]_F}{2} \times Ln\left(\frac{R_{0\,NH_4^+}}{R_{f\,NH_4^+}}\right) \times \frac{1}{T} \quad (3)$$

Where: $[NH_4^+]_I$ and $[NH_I^+]_F$ represent initial and final concentrations of ammonium during the incubation experiment. $R_{O\,NH_4^+}$ and $R_{f\,NH_4^+}$ are the initial and final excess enrichments in $^{15}NH_4^+$ for the incubation period.

Nitrification rates (ρ_{NIT} in µg.l^{-1}.d^{-1}) were computed according to Raimbault *et al.* (1999b):

$$\rho_{NIT} = \frac{R_{NO_3^-}}{R_{NH_4^+}} \times \left[NO_3^-\right] \times \frac{1}{T} \quad (4)$$

Where: $R_{NO_3^-}$ is the ^{15}N atom% excess enrichment in the (NO_3^- + NO_2^-) pool, $R_{NH_4^+}$ is the mean ^{15}N atom% excess enrichment of the ammonium pool, and [NO_3^-] is the final nitrate concentration in the filtrate.

Ammonium uptake by organisms smaller than GF/F, was estimated using the following equation (Slawyk *et al.*, 1998):

$$\rho_{<GF/F} = \frac{R_{<GF/F}}{\overline{R_{NH_4^+}}} \times \left[PON_{<GF/F}\right] \times \frac{1}{T} \quad (5)$$

Where: $R_{<GF/F}$ is the ^{15}N atom % excess enrichment of PON in organisms smaller than the GF/F pool, $\overline{R_{NH_4^+}}$ is the ^{15}N atom % excess enrichment of the ammonium pool and is the mean of initial and final ammonium enrichments. [$PON_{<GF/F}$] is the final extracellular PON concentration of organisms smaller than GF/F.

Integrated rates over the water column were calculated from 5 stations where deep samples had been collected for $^{15}N/^{13}C$ experiments. These results enabled relationships to be established between surface and integrated values (Table 1). These relationships were used to calculate integrated rates at stations where deep rates were not measured. However, no relationship was found between surface and integrated values of nitrification.

Table 1: Relationships between surface ($_s$) and integrated ($_i$) values of primary production (PP in mg.m$^{-3\ or\ -2}$.t^{-1}), ammonium uptake (ρNH4 in µg.m$^{-3\ or\ -2}$.t^{-1}), nitrate uptake (ρNO3 in µg.m$^{-3\ or\ -2}$.t^{-1}) and ammonium regeneration (rNH4 µg.m$^{-3\ or\ -2}$.t^{-1}) (t is incubation length).

	r²	n
$PP_i = 4.17 \times PP_s$	0.91	42
$\rho NH4_i = 10.1 \times \rho NH4_s$	0.63	42
$\rho NO3_i = 3.67 \times \rho NO3_s$	0.87	42
$rNH4_i = 10.79 \times rNH4_s$	0.41	42

Results

Freshwater discharge

Freshwater inputs by the power plant into the Berre Lagoon showed monthly variations (figure 2a). Early in the year, monthly water discharges ranged between 50×10^6 and 180×10^6 m^3, corresponding directly with the electricity demand. In 2005, massive winter freshwater discharges over a 4 month period, 410×10^6 m^3 from January to April, i.e. represented 62% of the total annual discharge. In 2006, 600×10^6 m^3 of freshwater discharge entered the lagoon over a six month period, from January to June, *i.e.* 85% of the annual discharge. During summer, the power plant load was small (<10 ×10^6 m^3 per month) or ceased altogether, as during June and July 2005. Freshwater discharge increased again during autumn, more drastically in 2005 than in 2006. Respecting the imposed restrictions (1.2 ×10^9 m^3·yr^{-1}), annual freshwater discharges from the powerplant in 2005 and 2006 were the lowest (0.66 and 0.71 ×10^9 m^3·yr^{-1} respectively) observed since the plant came into operation. However, the plant channel remained the main tributary of the Berre Lagoon representing 85% of the annual freshwater discharge (Gouze *et al.*, 2008).

Annual evolution of salinity

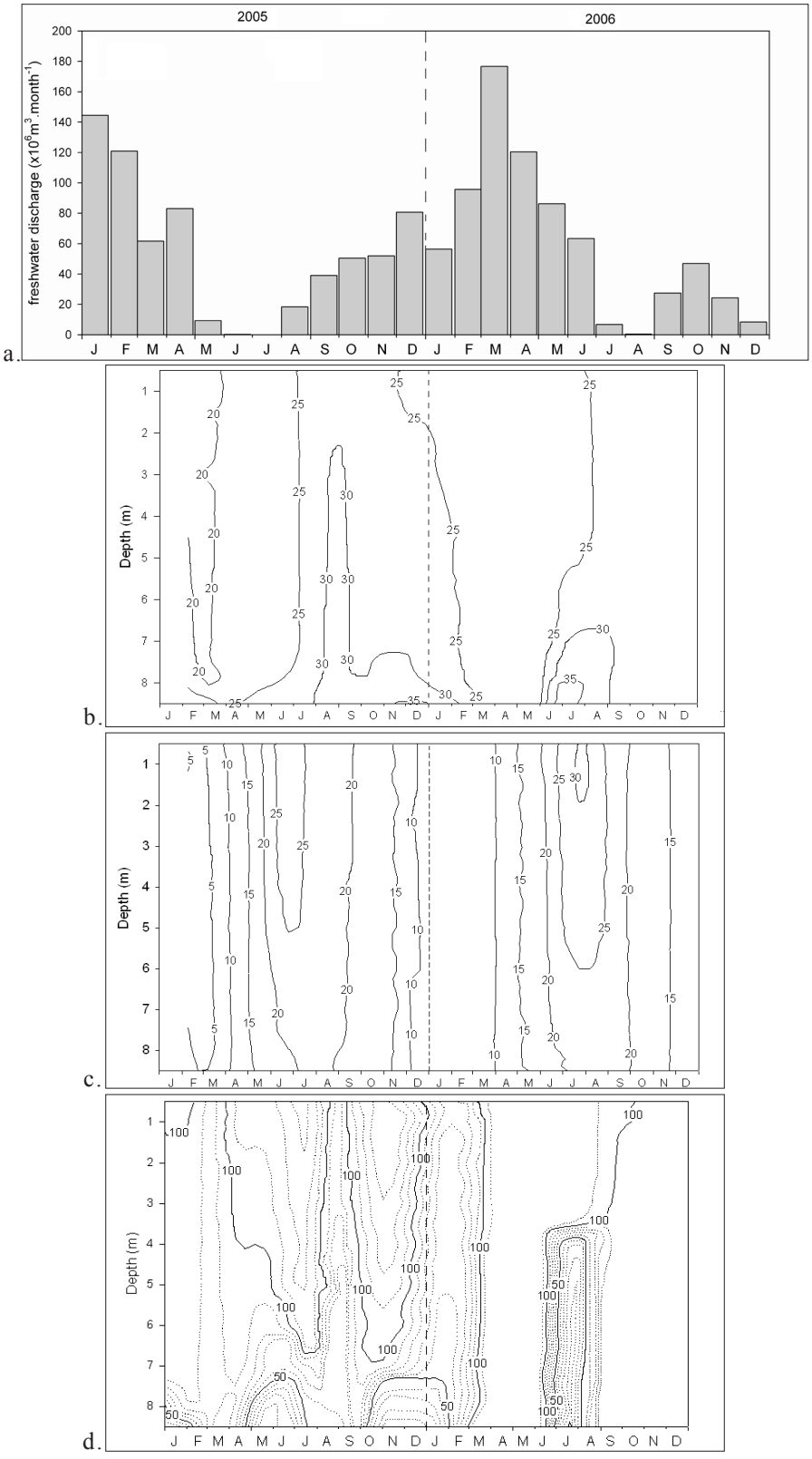

Figure 2: Monthly freshwater discharge from the power plant in the Berre Lagoon in 2005 and 2006 (a). Evolution of vertical profiles of salinity (b.), temperature (°C) (c.), and dissolved oxygen saturation (%) (d.) at the central station H08.

The seasonal variations in salinity were the same for all 10 stations. Salinity values were homogeneous throughout the water column in the shallower stations (depth <6 m). However, a haline stratification could be observed in the deep stations, close to 7 m deep (figure 2b). Figure 2b, shows salinity values from the central station H08, which is representative of the mean salinity values found in the lagoon.

In 2005, salinity was minimal during winter, with values close to 20 over the water column (figure 2b). This could be related to high freshwater discharge by the power plant and strong winds that reduced stratification. However, the difference of surface winter salinity between the northern stations (e.g. H01, H03, H04, H07, under the direct influence of freshwater inputs from the power plant and the rivers) and the southern stations (e.g. H12, H13 close to the Caronte channel and marine water entrance), could reach 7. Salinity values increased progressively during spring, reaching 25 in June and up to 30 in the water column in August, following 2 months of power plant shut down. The north-south haline gradient was reduced during summer when the freshwater inputs were minimal: the difference of surface salinity between the north and the south was less than 3.

Salinity tended to decrease at the beginning of autumn with the resumption of the freshwater discharge, but remained higher than 25 late in 2005 and higher than 23 during the first 6 months of 2006 in spite of large freshwater inputs. July 2006 was marked by a straight stratification (7 meters deep) in the southern "deep area": we measured 23 in the surface and close to 35 at the bottom. Salinity then increased, and reached 29 at the end of September. Although freshwater inputs were reduced during autumn 2006, salinity was never higher than 30 as observed in 2005. This could be related to a relatively shorter period of power plant summer shutdown. Salinity then gently decreased to 28 over the whole water column up to the beginning of winter.

Annual evolution of temperature

Temperature also showed seasonal variability (figure 2c): lower temperatures (< 6°C) were observed in winter, and values remained lower than 15°C until the end of April. Maximal values were observed at the surface during summer, reaching up to 30°C at the end of July 2006. This temperature is the highest observed since the beginning of hydrological monitoring, twelve years ago (GIPREB, unpublished data). The difference in surface temperatures between two stations never exceeded 2°C.

Dissolved oxygen saturation

The water column was well oxygenated in the first five meters, saturation rates being higher than 90% for most part of the year (figure 2d). In the southern deep area, hypoxic periods could be observed in summer and in winter, coinciding with haline and/or thermal stratification. During these periods, the stability of the water column prevented any mixing or exchange between the surface and the bottom, so preventing gas diffusion. Two short hypoxic spells were observed in the southern bottom area: 7% in May 2005 and 2% in July 2006. It's important to note that the bottom anoxia of July 2006 was spread throughout the bottom of the whole lagoon and could be caused by the thermal stratification of the water column.

Nutrient concentrations

Mean surface concentrations of nitrate varied from 0 µg $N\text{-}NO_3^-.l^{-1}$ (August 2006) to 220 µg $N\text{-}NO_3^-.l^{-1}$ (February 2005) (figure 3a.). Maximum values were observed during winter, as a consequence of the high freshwater discharge from the power plant. During this period, highest values were observed to the North-West of the lagoon: nitrate concentrations measured at stations

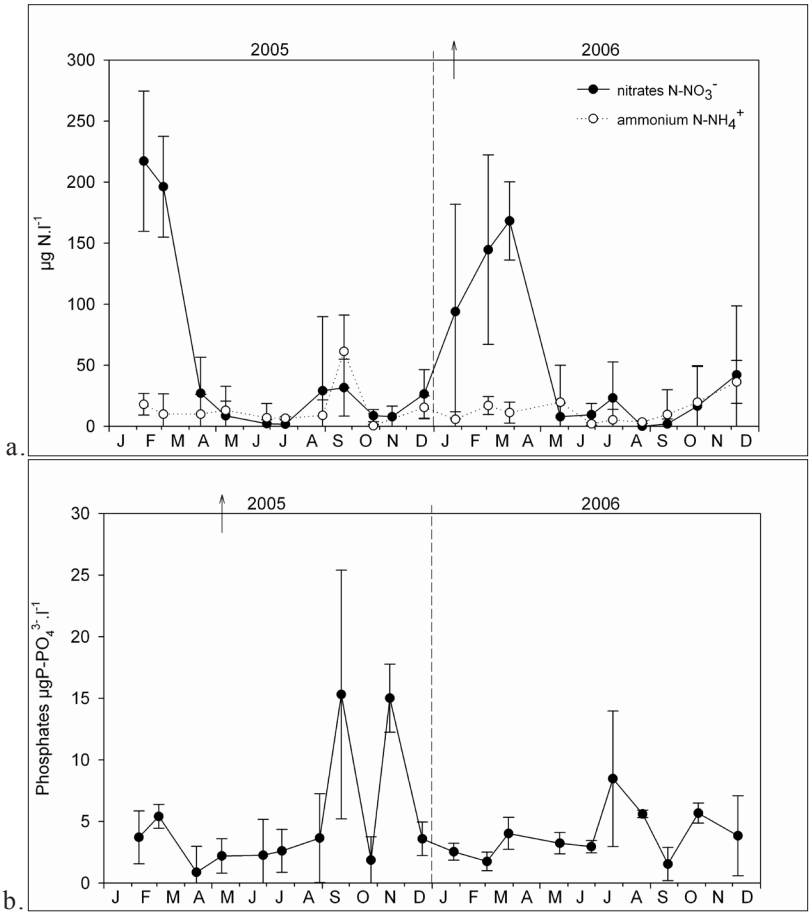

Figure 3: Evolution of surface mean concentrations of nitrate and ammonium (a.) and phosphate (b.). Arrows point to the isolated extreme values at station H13, excluded in the mean and the standard deviation calculations (370 µg $N\text{-}NH_4^+.l^{-1}$ in January 2006 ; 83 µg $P\text{-}PO_4^{3-}.l^{-1}$ and May 2005).

H01, H03, H04 and H07 were up to 200 µg $N\text{-}NO_3^-.l^{-1}$ higher than those measured in the North-Eastern area. This could be related to power plant activity, but also to the flooding of the two rivers (the Arc and the Touloubre) (Gouze *et al*., 2008) flowing into the North of the lagoon. A sharp decline in nitrate was evident from April to June at all sites, co-inciding with the start of the productive period. Other maximum were noted during September 2005 and December 2006, when the power plant resumed activity, although mean concentrations were less than 70 µg $N\text{-}NO_3^-.l^{-1}$.

Deep nitrate concentrations (data not shown) were similar to surface values, except during winter (January to March) when surface values were 40 µg $N\text{-}NO_3^-.l^{-1}$ higher than those of the bottom waters, co-inciding with the lighter and richer freshwater inputs.

Mean concentrations of nitrite (data not shown) revealed a similar pattern to nitrate, although maximum values were always much lower, ranging from 0 µg $N\text{-}NO_2^-.l^{-1}$ to 10 µg $N\text{-}NO_2^-.l^{-1}$. Secondary peaks of nitrite (in autumn 2005 and beginning of winter 2006) are in the same order of magnitude as the main winter values. There was no difference between surface and bottom concentrations.

Ammonium was observed at significant concentrations (> 7 µg $N\text{-}NH_4^+.l^{-1}$) most of the year (figure 3a.). Minimum levels were observed in October 2005 (mean of 0.4 µg $N\text{-}NH_4^+.l^{-1}$) and in the summer of 2006 (mean

of ~ 3.5 µg $N\text{-}NH_4^+.l^{-1}$). The maximum mean concentration was observed at the end of September 2005 (62 µg $N\text{-}NH_4^+.l^{-1}$), and could relate to punctual massive development of ctenophores. During the study, the highest measurements were recorded at stations H01 and H13 (e.g. 370 µg $N\text{-}NH_4^+.l^{-1}$ in January 2006 at H13), both influenced by inputs from sewage treatment plants. Bottom values were generally higher than the surface values and were never lower than 8 µg $N\text{-}NH_4^+.l^{-1}$. Maximal deep mean concentrations (≥ 40 µg $N\text{-}NH_4^+.l^{-1}$) were observed at the beginning of autumn 2005, and in summer 2006, but no permanently nutrient rich station could be determined.

Phosphate was never entirely depleted (figure 3b.) and concentrations presented a more or less constant pattern (ranging between 3 µg $P\text{-}PO_4^{3-}.l^{-1}$ and 6 µg $P\text{-}PO_4^{3-}.l^{-1}$) over the year with a relatively homogeneous spatial distribution. Only two significant peaks of phosphate were observed during November 2005 and July 2006 (mean of 16 µg $P\text{-}PO_4^{3-}.l^{-1}$ and 9 µg $P\text{-}PO_4^{3-}.l^{-1}$ respectively). During September 2005, high spatial heterogeneity was noted all over the lagoon: values were higher than 16 µg $P\text{-}PO_4^{3-}.l^{-1}$ at half the stations. The discrepancy between DIN and phosphate time evolution led to large variations in the DIN/ phosphate massic ratio ranging from 0 in summer to 216 in winter.

Time-evolution of total chlorophyll and particulate matter

As shown in figure 4, chlorophyll did not show any clear seasonal pattern. A slight increase of mean concentrations can be noted from February 2005 (1.8 µg.l^{-1}) to June 2006 (10.4 µg.l^{-1}). Only a peak was noted in October 2005 (mean of 17 µg.l^{-1}), mainly due to only one high value at station H16 (42 µg.l^{-1}). This station is strongly influenced by the Bolmon pond and has the highest concentrations of chlorophyll more particularly during winter (from 30 µg.l^{-1} to 70 µg.l^{-1}, whereas concentrations were less than 20 µg.l^{-1} on the whole lagoon in February, March, and November 2006).

A large accumulation was then noted during the entire summer 2006 period, higher than 30 µg.l^{-1} from July to September. Highest concentrations (up to 144 µg.l^{-1}) were measured to the north of the lagoon (stations

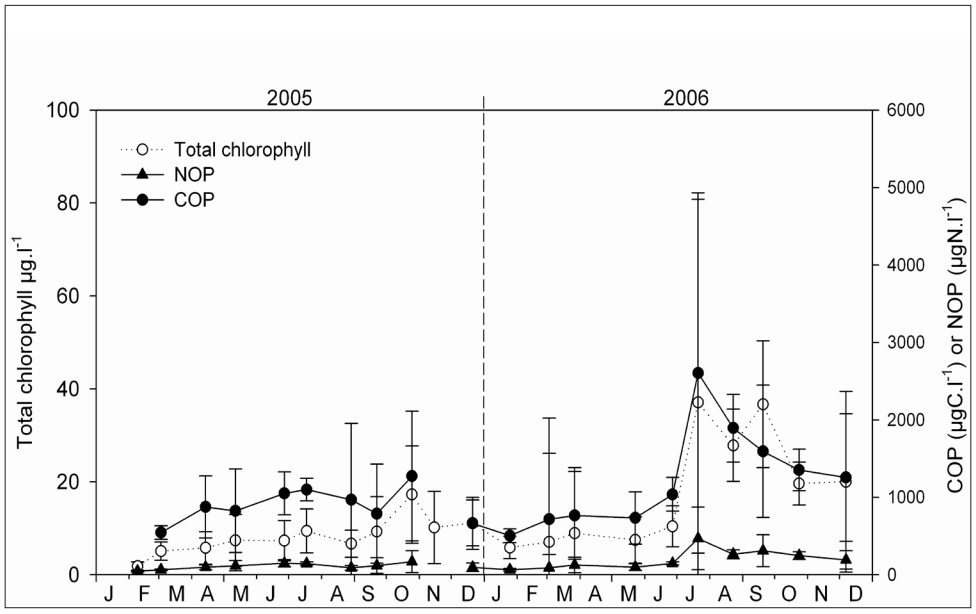

Figure 4: Surface mean concentrations of total chlorophyll (µg.l^{-1}) and particulate organic carbon and nitrogen (POC and PON in µgC.l^{-1} and µgN.l^{-1}).

H01 and H07) at the start of the bloom period. Concentrations of chlorophyll were still very high in November and December (mean of 20 $\mu g.l^{-1}$) especially in the centre and the south of the lagoon, where values up to 71 $\mu g.l^{-1}$ were measured at station H16.

Particulate Organic Nitrogen (PON) followed the same evolution as chlorophyll (figure 4), leading to a strong relationship between the two variables: PON = 8.9Chl + 36.3 ($r^2 = 0.86$ with n = 184). In 2005, mean values were closed to 40 $\mu gN.l^{-1}$ in winter and spring, and showed an accumulation during the summer and autumn (170 $\mu gN.l^{-1}$). In 2006, the winter levels were observed until June, where a strong increase was observed throughout summer, with mean concentrations reaching 460 $\mu gN.l^{-1}$.

Patterns for particulate organic carbon (POC) showed the same seasonal evolution (figure 4), leading to the following relationship: POC = 49.6Chl + 393.6 ($r^2 = 0.79$ with n = 184). Winter and spring mean concentrations ranged between 500 $\mu gC.l^{-1}$ and 1 000 $\mu gC.l^{-1}$. POC accumulation (mean greater than 1 200 $\mu gC.l^{-1}$) was observed in autumn 2005 and 2006 and summer 2006, but large standard deviations revealed a great spatial heterogeneity of POC concentrations in the lagoon.

POC/PON ratios generally ranged between 5 and 9 (figure 9). There was low variability between the 10 stations.

Primary production

A seasonal pattern for primary production at the lagoon surface could be detected with highest rates being observed during summer and autumn (figure 5). Winter rates were very low over the whole lagoon, lower than 150 $\mu gC.l^{-1}.d^{-1}$. However, station H16 was again the exception, where primary production rates reached between 500 $\mu gC.l^{-1}.d^{-1}$ and 1 300 $\mu gC.l^{-1}.d^{-1}$ right up to the end of winter. Primary production then increased progressively during spring, reaching a summer maximum in July: mean rates of 650 $\mu gC.l^{-1}.d^{-1}$ and 1 560 $\mu gC.l^{-1}.d^{-1}$ in 2005 and 2006 respectively. During these summer periods, we observed a higher variability between the stations: highest values were observed at the North of the lagoon at stations H01, H03, H04 and H07, stations that are under the direct influence of the tributaries inputs. In 2006, the very high productivity was, in part, due to the high values observed at stations H01, H04 and H07 (2 100 $\mu gC.l^{-1}.d^{-1}$ to 4 350 $\mu gC.l^{-1}.d^{-1}$), and were characterized by very high chlorophyll concentrations (> 80 $\mu g\ l^{-1}$) ; whereas at other stations, primary production was close to 750 $\mu gC.l^{-1}.d^{-1}$. During both years of study, we

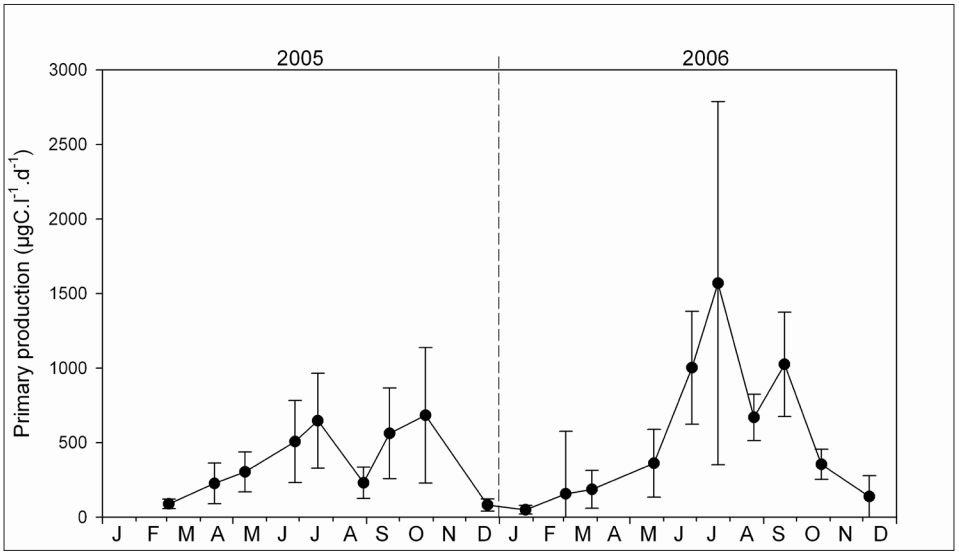

Figure 5: Mean primary production measured at the surface of the Berre Lagoon (carbon uptake: $\mu gC.l^{-1}.d^{-1}$).

observed a decrease in primary production in August (to 230 µgC.l^{-1}.d^{-1} in 2005 and 650 µgC.l^{-1}.d^{-1} in 2006), followed by a second primary production maximum during autumn, equivalent to the first summer bloom , which could be linked to the power plant resuming activity during the autumn. Primary production then progressively decreased to winter values.

On pooling all the data, carbon fixation was not clearly correlated to chlorophyll, suggesting important seasonal changes in phytoplanktonic populations or in physiological status.

Nitrogen uptake

Both nitrate and ammonium uptake rates were significant throughout the year, but this pattern did not follow those of inorganic nutrient concentrations.

Ammonium uptake (figure 6a) was generally higher than nitrate uptake (figure 6b), with

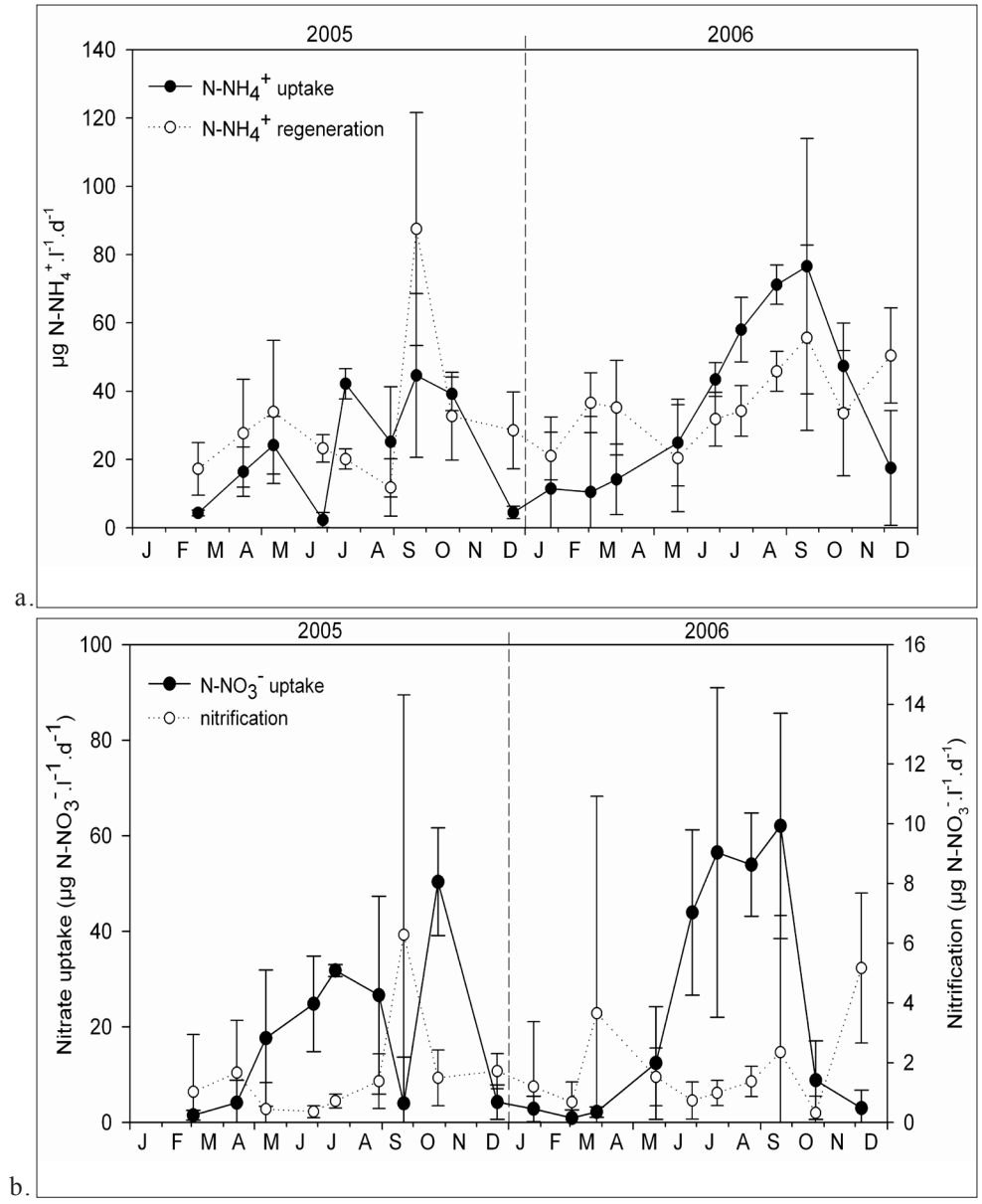

Figure 6: Fluxes of nitrogen uptake and regeneration (µg N.l^{-1}.d^{-1}) at the surface of the Berre Lagoon (a. Ammonium, b. Nitrate).

rates ranging between 2 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$ to 77 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$. The seasonal evolution of this biological process was not evident during 2005: a progressive increase of ammonium uptake was observed from winter to spring (from 4.2 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$ to 23.8 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$), then in June, values dropped to 2.8 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$ at all stations. Maximum ammonium uptake was observed over the summer, until the end of October (between 28 and 42 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$), and dropped again to winter low values. During winter, ammonium uptake rates ranged between 2 to 14 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$ over the entire lagoon, except at stations H16 and H13 where values could reach 40 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$ to 74 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$. In 2006, rates increased progressively from early spring to reach very high values at the end of summer: maximum means of 77 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$ in September, highest values being observed at stations H13 and H16 (114 and 158 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$ respectively). The slow progressive increase from April to the summer maximum, and the persistence of high assimilation rates throughout the summer, were similar to the pattern of carbon fixation for most of the stations.

The fraction of ammonium assimilated by organisms < 0.7 µm (< GF/F fraction) was generally low (figure 7), representing less than 20% of total ammonium uptake. The highest percentages were observed when total ammonium uptake rates were low, suggesting a small underestimation of ammonium utilization by using rates calculated with particulate matter on GF/F filters.

Nitrate uptake rates ranged between 1.4 µg $N\text{-}NO_3^-.l^{-1}.d^{-1}$ and 63.0 µg $N\text{-}NO_3^-.l^{-1}.d^{-1}$ (figure 6b). Changes in nitrate uptake followed a seasonal trend, with very low rates in winter (less than 7 µg $N\text{-}NO_3^-.l^{-1}.d^{-1}$), progressive increase in spring, and maximum values at the end of summer. However in 2005, we observed a drop in nitrate uptake in September, and the annual maximum one month later (50.4 µg $N\text{-}NO_3^-.l^{-1}.d^{-1}$ in October 2006). This seasonal pattern was similar to that of primary production. There was a high spatial variability for nitrate uptake rates during summer 2006: highest values were observed at the north of the lagoon (close to 100 µg $N\text{-}NO_3^-.l^{-1}.d^{-1}$), whereas minimal values (close to 5 µg $N\text{-}NO_3^-.l^{-1}.d^{-1}$) were observed at stations H13 and H16. The nitrate uptake rates obtained at some stations during summer, where nitrate concentrations were less than 7 µg $N\text{-}NO_3^-.l^{-1}$ have to be considered as potential rates since large ^{15}N enrichment (70 to 100%) could induce uptake activation.

Some data obtained on nitrite uptake and dinitrogen fixation clearly showed that these processes were low compared to nitrate and ammonium uptake (figure 8). Nitrite uptake rates ranged between 0.1 µg $N\text{-}NO_2^-.l^{-1}.d^{-1}$ and 5.6 µg $N\text{-}NO_2^-.l^{-1}.d^{-1}$, representing between 1% and 11% of the total nitrogen uptake. Evolution of nitrite uptake throughout 2005 was similar to the pattern of nitrate uptake, with the maximum value observed in October. Dinitrogen fixation rates ranged between 1.8 µg $N\text{-}N_2.l^{-1}.d^{-1}$ and

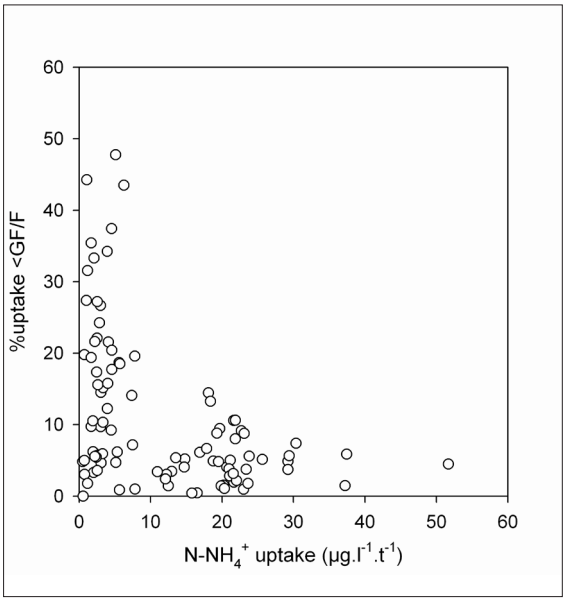

Figure 7: Ammonium assimilated by <GF/F fraction, compared with ammonium uptake rates measured by the particular fraction.

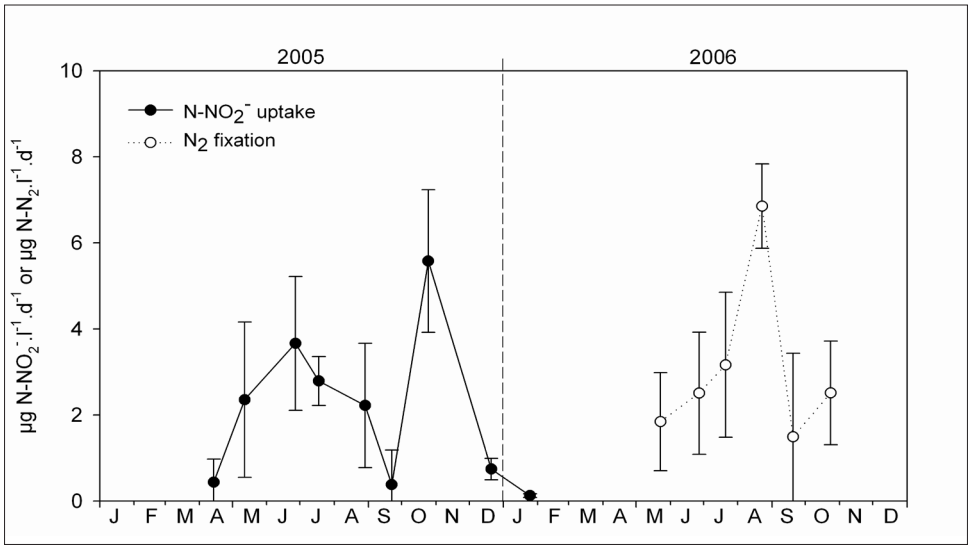

Figure 8: Mean nitrite uptake and dinitrogen fixation (in µg $N\text{-}NO_2^-.l^{-1}.d^{-1}$ and µg $N\text{-}N_2.l^{-1}.d^{-1}$) at the surface of the Berre Lagoon.

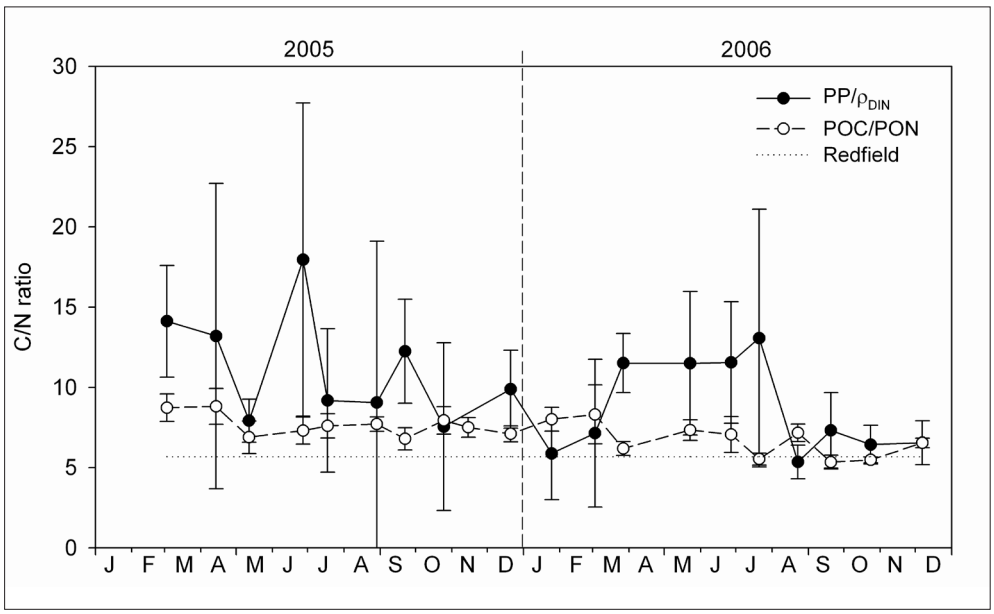

Figure 9: Evolution of the C/N ratio in particulate organic matter, and the ratio of carbon uptake to the sum of nitrate and ammonium taken up (PP/ρ_{DIN}). Comparison with Redfield C/N ratio.

6.9 µg $N\text{-}N_2.l^{-1}.d^{-1}$, representing between 1% and 7% of total nitrogen uptake. Maximum dinitrogen fixation was observed in August, when uptake of other nitrogen forms was at a maximum.

The ratio of carbon uptake to the sum of nitrate and ammonium taken up ($PP:\rho_{DIN}$) was generally higher than the Redfield ratio C:N = 5.7 at the surface of the lagoon (range between 5 and 18) (figure 9). The highest values were observed in spring and beginning of summer (> 10). Winter values were weaker, with the $PP:\rho_{DIN}$ ratio lower than 8.

Nitrogen regeneration

Ammonium regeneration ranged between 10 to 50 µg $N\text{-}NH_4^+.l^{-1}.d^{-1}$ and did not show

any significant trend in space or time, or any significant correlation with ammonium uptake (figure 6a). There is no relationship between regeneration and ambient ammonium levels, except in September 2005 and late 2006. Ammonium regeneration rates were generally equivalent to, or higher than the ammonium demand, except during summer when regeneration was between 60 and 77% of the uptake. These observations suggest that remineralization of photosynthetic products would be an important source of ammonium production in surface waters.

Nitrification ranged between 0.3 to 6.3 µg $N\text{-}NO_3^-.l^{-1}.d^{-1}$ and did not show a seasonal variation (figure 6b), but an important spatial variability was observed. Rates were generally one order of magnitude lower than the biological demand, except in winter when uptake and regeneration of nitrate were close to 1.5 to 3.0 µg $N\text{-}NO_3^-.l^{-1}.d^{-1}$. In this instance, regeneration of nitrate could sustain the entire nitrate uptake in winter, but only 1 to 40% during summer and autumn.

Discussion

During 2005 and 2006 the entire region was subjected to very dry/arid conditions. This coincided with the lowest recorded annual freshwater discharges from the power plant, since its commission in 1966. As a result of these combined factors salinity values were the highest measured, although seasonal and spatial heterogeneity were less marked. Since monitoring began in 1994, seasonal variations in salinity have ranged between 5 and 26.5 at the surface, and between 9 and 29 at the bottom (GIPREB, unpublished data). Summer salinities were close to the mean values observed before 1966, and powerplant operation (31 ± 2) (i.e. Minas, 1974; Blanc *et al.*, 1967). In 2005 and 2006, values increased to between 17.5 and 29.5 at the surface, and 20 to 31 at the bottom. The increasing surface salinities led to the attenuation of haline stratification and helped reduce isolation of the bottom layer, particularly in the central and southern deep areas of the lagoon.

The main characteristics for seasonal evolution were as follows:

- From November to March: salinity was minimal and nutrient loadings were significant in relation to intense powerplant activity. The low temperatures, low light levels and strong winds were not favourable to primary production (Arfi, 1989), but minimal activity could be observed, especially in terms of ammonium regeneration.
- From March to July: the activity of the power plant decreased. Salinity increased and nutrients inputs were reduced. Phytoplankton activity started: chlorophyll biomass increased and used up all the available nitrate pool.
- From July to October: continental inflows were very weak. Surface salinity was at a maximum. Nitrate was completely depleted due to intense biological activity. However ammonium and phosphate were still present at significant concentrations associated with regeneration processes. In the case of summer 2006 (July), haline stratification and nutrient inputs were maintained to the north by freshwater loads from the power plant and exceptional flooding of the tributaries (Gouze *et al.*, 2008). This along with high surface temperatures could have provisionally led to thermal stratification and thus bottom isolation and anoxia. Concentrations of chlorophyll were significant: we observed a biomass accumulation greater than 30 $\mu g.l^{-1}$, associated with high primary production.

The seasonal evolution of nitrate has remained unchanged since monitoring began twelve years ago, winter peaks generally reaching 250 µg $N\text{-}NO_3^-.l^{-1}$ to 500 µg $N\text{-}NO_3^-.l^{-1}$. Winter peaks lower than 250 µg $N\text{-}NO_3^-.l^{-1}$ have been observed over the last 4 years (including 2005 and 2006). These values could be related to power plant activity: Gouze (2008) showed that instantaneous nitrate concentrations were related to the freshwater volume brought in

from the 33 previous days.

These two years of monitoring clearly showed that the Berre Lagoon was a particularly productive ecosystem with high phytoplanktonic biomass: chlorophyll concentrations were one or two orders of magnitude higher than the adjacent marine water (Mediterranean). However, chlorophyll concentrations have clearly decreased since the 1990's when mean values reached 50 $\mu g.l^{-1}$ to 150 $\mu g.l^{-1}$ in spring and summer (GIPREB, unpublished data). Seasonal variations have also been less evident since 2000: values were less than 20 $\mu g.l^{-1}$, although they were higher than 30 $\mu g.l^{-1}$ during 2003 and 2006, both periods marked by a summer heatwave.

Primary production was greater than 200 $\mu g\ C.l^{-1}.d^{-1}$ over the main part of the year, reaching 650 $\mu g\ C.l^{-1}.d^{-1}$ in summer 2005 and 1 560 $\mu g\ C.l^{-1}.d^{-1}$ in the summer of 2006. These values were higher than those observed in previous studies: before the power plant, primary production rates ranged between 50 $\mu g\ C.l^{-1}.d^{-1}$ and 120 $\mu g\ C.l^{-1}.d^{-1}$ peaking (300 $\mu g\ C.l^{-1}.d^{-1}$) in October 1965 (Minas, 1976). Towards the end of the 1960's, despite intense power plant discharges, primary production remained unchanged for most of the year, reaching 500 $\mu g\ C.l^{-1}.d^{-1}$ to 1 000 $\mu g\ C.l^{-1}.d^{-1}$ in the summer. The maximum value observed was 1 500 $\mu g\ C.l^{-1}.d^{-1}$ at the north of the lagoon, in July 1968 (Minas, 1976).

In 2005 and 2006, 78 514 tons and 114 957 tons of organic particulate carbon were produced (equivalent to 507 $gC.m^{-2}.yr^{-1}$ and 742 $gC.m^{-2}.yr^{-1}$ respectively) (Table 2). Before the power plant was commissioned, integrated organic carbon produced by phytoplankton was 29 760 tons for the whole lagoon, corresponding to 192 $gC.m^{-2}.yr^{-1}$ in 1965 (Minas, 1976) (Table 2): this historical value was 2.5 to 4 times lower than those measured in the present study. Four years after the power plant started operating, Minas (1976) observed strong variations from one year to the next, alternating between years of little and years of high production (from 102 $gC.m^{-2}.yr^{-1}$ to 384 $gC.m^{-2}.yr^{-1}$) (Minas, 1976; Kim, 1983). Our study, extending over two consecutive years, confirmed the interannual variability of primary production. Although there was a similar evolution of nutrients during 2005 and 2006, 2006 was marked by an intense biomass accumulation during summer. Nixon (1982) considers that, for the most part, lagoons and other coastal waters appear to fix between 200 $gC.m^{-2}.yr^{-1}$ and 400 $gC.m^{-2}.yr^{-1}$. Thus, these observed values

Table 2: Summary table of historical data from the Berre Lagoon: primary production (PP); nutrient discharges into the lagoon by the tributaries (the Arc, the Touloubre and the power plant channel) and new primary production, calculated using the Redfield ratio or mean PP/ρDIN ratio calculated here.

Year	Measured PP	DIP tributaries	Estimated new PP		DIN tributaries	Estimated new PP				References
						Redfield		$PP/\rho_{DIN} = 9.9$		
	$tonsC.yr^{-1}$ ($gC.m^{-2}.yr^{-1}$)	inputs $tonsP.yr^{-1}$	$tonsC.yr^{-1}$	%	inputs $tonsN.yr^{-1}$	$tonsC.yr^{-1}$	%	$tonsC.yr^{-1}$	%	
1965	29 760 (192)	22	903	3						Minas (1976)
1966	47 740 (308)	169	6 934	15						Minas (1976)
1967	24 025 (155)	132	5 416	23						Minas (1976)
1968	59 520 (384)	230	9 437	16						Minas (1976)
1969	15 810 (102)	325	13 335	84						Minas (1976)
1978	45 000 (290)	345	14 155	31	4 622	26 330	58	45 573	101	Kim (1983), Kim and Travers (1997), Travers and Kim
1985		257	10 545		2 832	16 157		27 924		Arfi (1989)
2005	78 514 (507)	75	3 077	4	537	3 252	4	5 295	7	this study, Gouze et al. (2008)
2006	114 957 (742)	42	1 723	1.5	619	3 634	3	6 103	5	this study, Gouze et al. (2008)

put the Berre Lagoon amongst the most productive ecosystems (Table 3), e.g. the mouth of the Hudson River estuary off New York city, with strong nutrient inputs from urban sewage (O'reilly *et al*., 1976), or the Gulf of Cariaco, where intense upwelling along the Venezuela coast sustains an important production (Margalef, 1971).

The big difference between primary production rates measured in this study, and those found in the historical data, cannot be explained by the sampling strategy. In our study, 10 stations with very different characteristics were sampled: for example stations H01 and H03 had a relatively weak hydrodynamism, which could favour phytoplankton development. Minas (1976) and Kim (1983) only observed two stations (equivalent to stations H04 and H12). We could be led to believe that mean primary production rates, although more realistic, could be elevated by punctual high values at some of the stations. Thus, if we assess a carbon budget from stations H04 and H12 only, in order to compare with

Table 3: Summary table of primary production rates in lagoons, saline lakes, coastal marine areas and estuaries ($gC.m^{-2}.d^{-1}$ or $gC.m^{-2}.yr^{-1}$)

	Daily PP g C .m^{-2}.d^{-1}	Annual PP g C .m^{-2}.yr^{-1}	References
Berre Lagoon	0.20 - 6.55	507 to 742	this study
Lagoons			
Thau Lagoon (France, Mediterranean coast)		204	Vaulot & Frisoni (1986)
		400	Chapelle et al. (2000)
Biguglia Lagoon (Corsica)		289	Vaulot & Frisoni (1986)
Urbino Lagoon (Corsica)		297	Vaulot & Frisoni (1986)
Arcachon (France, Atlantic coast)		23	Castel et al. (1996)
Ebrié Lagoon (Ivory Coast)	0.2 - 5		Pagès et al. (1981)
Saline Lakes			
Lake Mariut (Egypt)		2601	Aleem & Samaan (1969)
Humboldt (Canada)		613	Haynes & Hammer (1978)
Little Manitou (Canada)		70	Haynes & Hammer (1978)
Soap (USA)		391	Walker (1975)
Coastal marine areas			
North Western Mediterranean	0.1 - 1.3		Garcia et al. (2006)
mouth of Hudson river estuary		700-900	O'reilly et al. (1976)
Marennes-Oléron Bay, France		185	Struski & Bacher (2006)
Narragansett Bay, USA		323	Oviatt et al. (2002)
San Francisco Bay, USA		6 - 418	Cole and Cloern (1984)
Chesapeake Bay, USA		570	Harding et al. (2002)
Gulf of Cariaco (upwelling Venezuela)		800	Margalef (1971)
World estuaries			
Amazon	0.10 - 1.00		Cadee (1975)
Changjiang	0.01 - 1.54		Xiuren et al. (1988)
Danube	0.20 - 4.40		Humborg (1997)
St Lawrence	0.01 - 0.80		Sinclair (1978)
Westerschelde, Netherlands		100 - 300	Kromkamp & Peene (1995)
Delaware estuary, USA		307	Pennock & Sharp (1986)

previous studies, the annual organic carbon produced, although smaller than that found taking values from all the stations, is still in the same order of magnitude and still much higher than historical data (476 $gC.m^{-2}.yr^{-1}$ and 646 $gC.m^{-2}.yr^{-1}$ in 2005 and 2006 respectively).

However it should be noted that some of our primary production measurements could be overestimated due to a significant addition of ^{15}N-tracer in nitrogen depleted samples, especially during summer when nitrate concentrations were often close to the detection limit. Our experiments with $^{15}N\text{-}N_2$ enrichments can be used as controls: we observe that, for all the months where comparison is possible, $PP_{DIN} = 0.95\ PP_{N2}$ ($r^2 = 0.75$, $n = 19$). Thus, DIN addition did not appear to promote primary production in these short-term experiments.

The high primary production rates measured in this study compared to historical data, could be explained by a number of factors:

- decreasing freshwater discharge led to increasing salinity and reduced dilution of autotrophic cells (Minas, 1976)
- decreasing turbidity. The mean annual discharge of suspended matter from the power plant at the beginning of its commission was 520 000 tons per year from 1966-1993. In 2005 as in 2006, following progressive restrictions and the building of a clarifying basin upstream from the power plant turbines (in the 1980's), the annual discharge of suspended matter from the power plant has dropped to 42 000 tons per year.
- increasing temperature. High primary production measured in 2006, and most particularly in July could be due to the exceptional surface temperature (>30°C). Photosynthetic rates (as assimilation number in grams of carbon/grams of chlorophyll *a* per time) increase with increasing temperature (Eppley, 1972).
- increasing water residence time in the lagoon, due to the decrease of freshwater inputs from the power plant, which are favourable to phytoplanktonic development.
- progressive accumulation of N and P in the lagoon over the years, in particular at the bottom and in the sediments. This increasing nutrient pool can subsequently supply the autotrophic demand via regeneration processes.

Primary production measured in the Berre Lagoon was simultaneously observed with an annual uptake of 14 903 tons of DIN in 2005 (3 517 tons of $N\text{-}NO_3^-$ and 11 386 tons of $N\text{-}NH_4^+$), and 24 245 tons of DIN in 2006 (4 424 tons of $N\text{-}NO_3^-$ and 19 821 tons of $N\text{-}NH_4^+$).

The Berre lagoon received 537 tons and 619 tons of DIN ($N\text{-}NO_3^-$ and $N\text{-}NH_4^+$) from its tributaries (rivers and plant channel) in 2005 and 2006 respectively (Gouze *et al.*, 2008). These exogenous nitrogen inputs were therefore insufficient, providing less than 5% of the nitrogen demand (figure 10).

The historical implications of the exogenous nutrient inputs for primary production could be assessed (table 3). New primary production, based on tributary inputs could be estimated from the Redfield ratio (C:N = 5.7 and C:P = 41.0), or from the $PP{:}\rho_{DIN}$ ratio (mean of 9.9) measured during this study. Using these calculation methods, we determined that 1 to 7% of the measured annual primary production was derived from the tributary inputs during 2005 and 2006. Interestingly, most of the primary production (93 to 99%) was sustained by *in situ* nutrient regeneration processes, as observed before the power plant opened (97% of the primary production was regenerated production in 1965) (table 3). It should be noted that, during periods of non-restricted high freshwater and nutrient discharge (1969-1985), regenerated production ranged from 0 to 85%: in 1978, during maximum powerplant activity, the nitrogen continental inputs could be responsible for all the primary production, according to this calculation method.

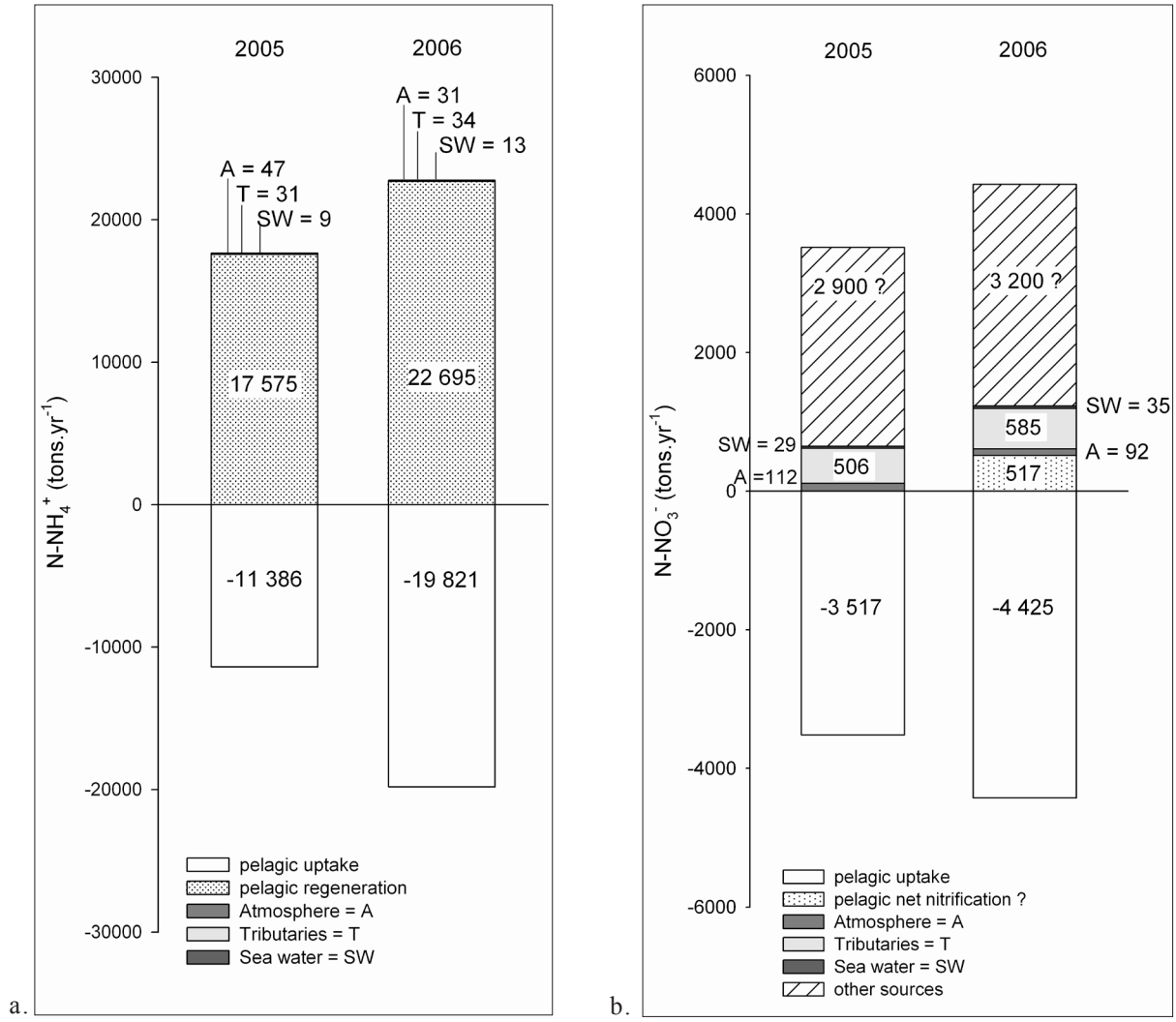

Figure 10: Ammonium N-NH_4^+ (a.) and nitrate N-NO_3^- (b.) budget in 2005 and 2006: pelagic uptake and regeneration were measured in this study (tons N.yr^{-1}). Tributaries and atmospheric nitrogen inputs were estimated with Gouze *et al*. (2008), Sandroni (2000) and Sandroni *et al*. (2007). Annual integrated nitrification could be assessed only in 2006. Other sources of N-NO_3^- were estimated to compensate at least N-NO_3^- pelagic uptake. These other assumed unknown nitrogen sources (sediment) are not represented.

Nitrogen regeneration appears to be an important process in the biogeochemical functioning of the Berre Lagoon. In the annual budget, 17 575 and 22 695 tons of *N-NH_4^+* were regenerated in the water column in 2005 and 2006 respectively. Thus, this regeneration process was able to sustain the entire annual ammonium uptake (figure 10). On a monthly scale, pelagic *N-NH_4^+* regeneration was sufficient for the low winter demand. However, from the end of spring to the beginning of autumn, this process assumed 60 to 90% of the mensual demand, suggesting the existence of additional ammonium sources.

The potential significance of "regenerated" nitrate in the euphotic zone has been acknowledged for some time (Dugdale & Goering, 1967, Ward *et al*. 1989, Bianchi *et al*. 1997, Diaz & Raimbault 2000, Ward 2000) and there is little information regarding the inhibiting effect of light on nitrification in

marine environments (Ward 1985, Horrigan & Springer 1990). Whether it is because of the difficulty in measuring *in situ* rates or because of its presumed small contribution to total nitrate assimilation, nitrification measurements in the field are far from being a routine variable in field work. Nitrification rates in the water column, presented here, were in the range of previous observations from oceanic waters (for example Ward & Zafiriou, 1988, Bianchi *et al*. 1994), and thus represents a small part of the biologic demand.

Regeneration of 517 tons of $N\text{-}NO_3^-$ was calculated in 2006 from integrated values, and this could explain 12 % of the annual $N\text{-}NO_3^-$ uptake (figure 10). On a seasonal scale, 100 % of the weak winter nitrate demand could be assumed by nitrification. But during summer and autumn, less than 5 % of the high nitrate uptake was supported by pelagic nitrification.

Other sources of nitrogen were thus expected to sustain the pelagic demand (figure 10). Actually, other sources of nitrogen were not assessed in this study:

- *exogeneous sources*:

- atmospheric wet and dry deposits at the surface of the lagoon. Mean annual input of 102 tons $N\text{-}NO_3^-$ and 39 tons $N\text{-}NH_4^+$ was estimated during the study, representing less than 3 % of the annual uptake of nitrogen (calculated from Guieu, 1991 ; Sandroni, 2000 ; Sandroni *et al*., 2001).

- marine water entering the lagoon from the Mediterranean. We assessed an "entering" annual flux of 32 tons of $N\text{-}NO_3^-$ and 11 tons of $N\text{-}NH_4^+$, both making up less than 1 % of the nitrogen pelagic demand (calculated from direct measurements of watermass exchanges through the Caronte channel, Martin, 2006 ; and nutrient concentrations in the Mediterranean, RNO, unpublished data).

- water streaming in the catchment basin and non-pointed sources: we can assume these were weak during this study, because of the dry conditions.

- *endogeneous sources*:

- nitrate regeneration versus uptake could be underestimated since this process goes on through the night. By considering similar nocturnal nitrification rates, this source would also be insufficient to provide the nitrate summer and autumn demand.

- The nitrification flux could have been underestimated. During this experiment, both bacteria and phytoplankton were present in the flask. Nitrate produced by nitrification could be instantaneously taken up by the phytoplankton in such a dynamic ecosystem, so that the endogeneous source of nitrate could not be observed at the end of the incubation. The measured flux could then be net nitrification (nitrification minus nitrate uptake), not gross nitrification (nitrification alone).

- regenerated nitrogen from intense grazing and excretion of zooplankton and macrofauna like mussels and punctual development of the ctenophore *Nemiopsis sp.* (Botha, personal communication).

- benthos and macrofauna death and degradation during generalised summer anoxia.

- nitrogen regeneration from the organic matter in the sediment. Organic matter produced in the water column and nutrients (organic, inorganic, particular, and dissolved) accumulated in the sediments, between 1 mg and 2 mg of total nitrogen per gram of sediment (Delmas, 1980).

All these sources of nitrogen could be of the cause of massive macroalgae development and could explain the accumulation of $N\text{-}NH_4^+$ at the bottom and explain why $N\text{-}NH_4^+$ was never depleted.

Conclusion

Due to the arid conditions in this area and government legislation, annual freshwater discharge by tributaries (rivers and power plant) into the lagoon during this study were

the lowest observed, since the power plant was commissioned in 1966. As a consequence, salinity tended to increase with summer values similar to the ones observed in the lagoon before the power plan was built.

The Berre lagoon is a very productive ecosystem. Moreover, primary production measured in this study was higher than those measured 30-40 years ago despite reduced nutrient inputs. Close to 95% of the primary production was from regenerated production, sustained by internal nitrogen sources. Ammonium regeneration in the water column meets the major requirements of the pelagic demand. Other regeneration processes, in the sediment were active due to the large accumulation of organic matter at the bottom, which occurred during the years of non-restricted discharge to the lagoon. The Berre Lagoon is, at the same time, a "sink" and a "source" of nutrients. Because of intense regeneration processes and the increase of water time residence in the lagoon, eutrophication and associated nuisances are maintained despite clean up efforts on catchment basin.

A study of the water/sediment interface should be carried out to determine the nutrient fluxes into the water column and would complete this data set.

Nutrient exchanges with the Mediterranean could be assessed and complete the measurements of water mass exchanges in the Caronte Channel (Martin, 2006). The ability of the lagoon to "autopurify" and to loose its nutrient load to the Mediterranean in a context of progressive freshwater and nutrient input reduction is a key process in understanding eutrophication.

This study could be part of a global subsequent strategy which would take into account modelling of hydrodynamism and matter fluxes in the water column and in sediments.

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References

Aleem AA, Samaan AA 1969. Productivity of Lake Mariut, Egypt. Part II. Primary production. Internationale Revue Der Gesamten Hydrobiologie 54: 491-527.

Aliaume C, Do Chi T, Viaroli P, Zaldivar JM 2007. Coastal lagoons of Southern Europe: recent changes and future scenarios. Transitional Waters Monographs 1: 1-12.

Arfi R 1989. Annual Cycles and Budget of Nutrients in Berre Lagoon (Mediterranean-Sea, France). Internationale Revue Der Gesamten Hydrobiologie 74: 29-49.

Bernard G, Boudouresque CF, Picon P 2007. Long term changes in Zostera meadows in the Berre Lagoon (Provence, Mediterranean Sea). Estuarine Coastal and Shelf Science 73: 617-629.

Bianchi M, Bonin P, Feliatra F 1994. Bacterial nitrification and denitrification rates in the Rhône river plume (Northwestern Mediterranean Sea). Marine Ecology-Progress Series 103: 197-202.

Bianchi M, Feliatra F, Treguer P, Vincendeau M, Morvan J 1997. Nitrification rates, ammonium and nitrate distribution in upper layers of the water column and in sediments of the Indian sector of the Southern Ocean. Deep-Sea Research II 44: 1017-1032.

Blanc F, Coste B, Minas HJ, Szekielda KH 1967. Distribution et corrélations des principaux facteurs hydrobiologiques dans un milieu de forte production organique (Etang de Berre). Marine Biology 1: 43-55.

Cadee GC 1975. Primary production off the Guyana Coast. Netherland Journal of Sea Research 9: 128-143.

Castel J, Caumette P, Herbert R 1996. Eutrophication gradients in coastal lagoons as exemplified by the Bassin d'Arcachon and the Etang du Prévost. Hydrobiologia 329: ix-xxiii.

Caumette P, Baleux P 1980. Etude des eaux rouges dues à la prolifération des bactéries photosynthétiques sulfo-oxydantes dans l'étang du Prévost, lagune saumâtre méditerranéenne. Marine Biology 56: 183-194.

Chapelle A, Ménesguen A, Deslous-Paoli JM, Souchu P, Mazouni N, Vaquer A, Millet B 2000. Modelling nitrogen, primary production and oxygen in a Mediterranean lagoon. Impact of oysters farming and inputs from the watershed. Ecological Modelling 127: 161-181.

Cole BE, Cloern JE 1984. Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay. Marine Ecology-Progress Series 17: 15-24.

Delmas D 1980. Minéralisation de la matière organique et échanges ioniques à l'interface eau-sédiment de l'étang de Berre, Méditerranée. Oceanologica acta 3: 347-356.

De Wit R, Stal LJ, Lomstein BA, Herbert RA, Van Gemerden H, Viaroli P, Ceccherelli VU, Radriguez-Valera F, Bartoli M, Giordani G, Azzoni R, Schaub B, Welsh DT, Donnelly A, Cifuentes A, Anton J, Finster K, Nielsen LB, Underlien Pedersen A-E, Turi Neubauer A, Colangelo M, Heijs SK, 2001. ROBUST: the role of buffering capacities in stabilising coastal lagoon ecosystems. Continental Shelf Research 21: 2021-2041.

Diaz F, Raimbault P 2000. Nitrogen regeneration and dissolved organic nitrogen release during spring in a NW Mediterranean coastal zone (Gulf of Lions): implications for the estimation of new production. Marine Ecology-Progress Series 197: 51-65.

Dugdale RC, Goering JJ 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnology and Oceanography 12: 196-206.

Dugdale RC, Wilkerson FP 1986. The Use of N-15 to Measure Nitrogen Uptake in Eutrophic Oceans - Experimental Considerations. Limnology and Oceanography 31: 673-689.

Eppley RW 1972. Temperature and phytoplankton growth in the sea. Fishery Bulletin 70: 1063-1085.

Garcia N, Raimbault P, Gouze E, Sandroni V 2006. Nitrogen fixation and primary production in Western Mediterranean. Comptes Rendus Biologies 329: 742-750.

Gouze E 2008. Bilan de matière de l'Etang de Berre. Influence des apports des tributaires et des processus de régénération dans le maintien de l'eutrophisation. Tesis of the University Aix-Marseille II.

Gouze E, Raimbault P, Garcia N, Bernard G, Picon P 2008. Nutrients and suspended matter discharge by tributaries to the Berre Lagoon (France): floods contribution to matter budget. Comptes Rendus Geoscience 340: 233-244.

Guieu C 1991. Apports atmosphériques à la Méditerranée Nord-Occidentale.

Tesis of the University of Paris. 225p.

Harding Jr. L, Mallonee M, Perry E 2002. Toward a predictive understanding of primary productivity in a temperate, partially stratified estuary. Estuarine Coastal and Shelf Science 55: 437-463.

Haynes RC, Hammer UT 1978. The saline lakes of Saskatchewan. IV. Primary production of phytoplankton in selected saline ecosystems. Internationale Revue Der Gesamten Hydrobiologie 63: 337-351.

Horrigan S, Springer AL 1990. Oceanic and estuarine ammonium oxidation, effects of light. Limnology and Oceanography 35: 479-482.

Howarth RW, Marino R 2006. Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: evolving views over three decades. Limnology and Oceanography 51: 364-376.

Humborg C 1997. Primary productivity regime and nutrient removal in the Danube estuary. Estuarine Coastal and Shelf Science 45: 579-589.

Kim KT 1983. Primary Pelagic Production of the Etang-De-Berre in 1977-1978 - Comparison with the Marine-Environment (Northwest Mediterranean). Marine Biology 73: 325-341.

Kim KT, Travers M 1997. Les nutriments dans l'Etang de Berre et des milieux aquatiques contigus (eaux douces, saumâtres et marines, Méditerranée NW)-2: les nitrates. Marine Nature 5: 21-34.

Koroleff F 1970. Direct determination of ammonia in natural waters as indophenol blue. ICES Information on techniques and methods for sea analysis, an interlaboratory report 3: 19-22.

Kromkamp J, Peene J 1995. Possibility of net phytoplankton primary production in the turbid Schelde estuary (SW Netherlands). Marine Ecology-Progress Series 121: 249-259.

Laws E 1984. Isotope dilution models and the mystery of the vanishing 15N Limnology and Oceanography 29: 379-386.

Loye-Pilot MD, Klein C, Martin JM, 1993. Major inorganic elements in north western Mediterranean aerosols. In: EROS 2000 fourth workshop on the North-West Mediterranean Sea. Martin JM and Barth H ed., Water Pollution Research Reports 30: 271-277.

Margalef R 1971. The pelagic ecosystem of the Carribean Sea. In UNESCO (eds), Symposium Investigations and Resources of the Caribbean Sea and adjacent regions: 483-498.

Martin LS 2006. Courantologie dans le Canal de Caronte en fonction de la marée, du vent et du turbinage à Saint Chamas ; modélisation tridimensionnelle des courants et de la salinité de l'Etang de Berre à l'aide du logiciel Telemac-3D. EDF R&D report nb: H-P76-2006-03511-FR. LNHE 29/08/06, Paris-Chatou.

Minas M 1974. Distribution, circulation and evolution of nutrients, inorganic phosphorus particularly, in Lake Etang de Berre. Influence of river Durance waters. Internationale Revue Der Gesamten Hydrobiologie 59: 509-542.

Minas M 1976. Primary Organic Production in a Brackish Eutrophic Environment (Etang De Berre) - Effects of Strong Dilution (Diversion of Waters of Durance). Marine Biology 35: 13-29.

Montoya JP, Voss M, Kahler P, Capone DG 1996. A simple, high-precision, high-sensitivity tracer assay for N-2 fixation. Applied and Environmental Microbiology 62: 986-993.

Nerini D, Durbec JP, Mante C, Garcia F, Ghattas B 2000. Forecasting physicochemical variables by a Classification Tree method. Application to the Berre Lagoon (South France). Acta Biotheoretica 48: 181-196.

Nixon SW 1982. Nutrient dynamics, primary production and fisheries yields of lagoons. Oceanologica acta 5: 357-371.

O'reilly JE, Thomas JP, Evans C 1976. Annual primary production (nanoplankton, netplankton, dissolved organic matter) in the lower New York Bay. In H. R. E. S. W. H. Mc Keon & G. J. Lauer, Inc, New York (eds), Fourth Symposium Hudson River Ecology.

Oviatt C, Keller A, Reed L 2002. Annual primary production in Narragansett Bay with no bay-wide winter-spring phytoplankton bloom. Estuarine Coastal and Shelf Science 54: 1013-1026.

Pagès J, Lemasson L, Dufour P 1981. Primary production measurement in a brackish tropical lagoon, effect of light, as studied at some stations by the 14C method. Revue Hydrobiologie tropicale 14: 3-15.

Pennock, JR, Sharp JH 1986. Phytoplankton production in the Delaware Estuary : temporal and spatial variability. Marine Ecology-Progress Series 34: 143-155.

Raimbault P, Pouvesle W, Diaz F, Garcia N, Sempere R 1999a. Wet-oxidation and automated colorimetry for simultaneous determination of organic carbon,

nitrogen and phosphorus dissolved in seawater. Marine Chemistry 66: 161-169.

Raimbault P, Slawyk G, Boudjellal B, Coatanoan C, Conan P, Coste B, Garcia N, Moutin T, Pujo-Pay M 1999b. Carbon and nitrogen uptake and export in the equatorial Pacific at 150°W: Evidence of an efficient regenerated production cycle. Journal of geophysical research 104: 3341-3356.

Raimbault P, Lantoine F, Neveux J 2004. Dosage rapide de la chlorophylle a et des phéopigments a par fluorimétrie après extraction au méthanol. Comparaison avec la méthode classique d'extraction à l'acétone. Océanis 30: 189-205.

Sandroni V 2000. Apports atmosphériques en Mer de Ligure : modes de dépôt, impact sur la couche marine de surface, implication dans les flux marins. Tesis of the University of Corsica.

Sandroni V, Raimbault P, Migon C, Garcia N, Gouze E 2007. Dry atmospheric deposition and diazotrophy as sources of new nitrogen to northwestern Mediterranean oligotrophic surface waters. Deep Sea Research Part I: Oceanographic Research Papers 54: 1859-1870.

Sinclair M 1978. Summer phytoplankton variability in the lower St. Lawrence Estuary. Journal of fishery research board Canada 35: 1171-1185.

Slawyk G, Raimbault P 1995. Simple Procedure for Simultaneous Recovery of Dissolved Inorganic and Organic Nitrogen in N-15-Tracer Experiments and Improving the Isotopic Mass-Balance. Marine Ecology-Progress Series 124: 289-299.

Slawyk G, Raimbault P, Garcia N 1998. Measuring gross uptake of N-15-labeled nitrogen by marine phytoplankton without particulate matter collection: Evidence of low N-15 losses to the dissolved organic nitrogen pool. Limnology and Oceanography 43: 1734-1739.

Stora G, Arnoux A 1983. Effects of Large Fresh-Water Diversions on Benthos of a Mediterranean Lagoon. Estuaries 6: 115-125.

Struski C, Bacher C 2006. Preliminary estimate of primary production by phytoplankton in Marennes-Oléron Bay, France. Estuarine Coastal and Shelf Science 66: 323-334.

Travers M, Kim KT 1997. Les nutriments de l'étang de Berre et des milieux aquatiques contigus (eaux douces, saumâtres et marines ; Méditerranée NW)-1: les phosphates. Marine Nature 5: 21-34.

Treguer P, Lecorre P 1975. Manuel d'analyses des sels nutritifs dans l'eau de mer (Utilisation de l'Autoanalyser II) Laboratoire de Chimie Marine, Université de Bretagne Occidentale, Brest.

Trousselier M, Gattuso JP 2006. Coastal lagoon. In Cutler J. Cleveland (eds), Encyclopedia of Earth. Environmental Information Coalition, National Council for Science and the Environment, Washington DC.

Vaulot D, Frisoni GF 1986. Phytoplanktonic productivity and nutrients in 5 Mediterranean Lagoons. Oceanologica acta 9: 57-63.

Viaroli, P, Lasserre P, Campostrini P 2007. Preface - Lagoons and coastal wetlands. Hydrobiologia 577: 1-3.

Walker KF 1975. The seasonal phytoplankton cycles for two saline lakes in central Washington. Limnology and Oceanography 20: 40-53.

Ward BB 1985. Light and substrate concentrations relationships with marine ammonium assimilation and oxidation rates. Marine Chemistry 16: 301-316.

Ward BB 2000. Nitrification and the marine nitrogen cycle. In K. DL (eds), Microbial ecology of the oceans: 427-454.

Ward BB, Kilpatrick KA, Renger EH, Eppley RW 1989. Biological nitrogen cycling in the nitracline. Limnology and Oceanography 34: 493-513.

Ward BB, Zafiriou OC 1988. Nitrification and nitric oxide in the oxygen minimum of the eastern tropical North Pacific. Deep-Sea Research 35: 1127-1142.

Xiuren N, Vaulot D, Zhensheng L, Zilin Z 1988. Standing stock and production of phytoplankton in the estuary of the Chanjiang (Yangtse River) and the adjacent East China Sea. Marine Ecology-Progress Series 49: 141-150.

