A comparative study of nitrogen and carbon uptake by phytoplankton in a coastal eutrophic ecosystem (Bay of Brest, France)

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ABSTRACT

Nitrogen (15N) and carbon (14C) uptake rates and hydrological, chemical and biological parameters were monitored at a single station during spring (March-April 1989) in a coastal eutrophic ecosystem of western Europe: the Bay of Brest. Before the spring growth of phytoplankton populations, total nitrogen and carbon uptake rates were low (∼0.3 µmol C.l⁻¹.h⁻¹ and ∼0.025 µmol N.l⁻¹.h⁻¹). During the spring bloom, these uptake rates reached high values (0.5 µmol C.l⁻¹.h⁻¹ and 0.28 µmol N.l⁻¹.h⁻¹); at this time, nitrate was the main source of nitrogen production, although relative preference index (RPI) values showed that ammonium was the preferred nitrogen form for phytoplankton (RPI (NO₃) < 1; RPI (NH₄) > 5). C/N assimilation ratios were higher than C/N composition ratios of the particulate matter. This difference is interpreted in terms of terrestrial detritus inputs from rivers and variation of the physiological state of phytoplankton populations.


RÉSUMÉ

Étude comparée de l'absorption de l'azote et du carbone par le phytoplancton dans un écosystème eutrophe (rade de Brest, France)

Un suivi des taux d'absorption d'azote (15N), de carbone (14C) et des paramètres hydrologiques, chimiques et biologiques a été effectué au cours du printemps (mars-avril 1989) dans un écosystème eutrophe d'Europe occidentale: la rade de Brest. En régime hivernal, les taux d'absorption du carbone et de l'azote minéral total sont faibles (∼0.3 µmol C.l⁻¹.h⁻¹ et ∼0.025 µmol N.l⁻¹.h⁻¹). Au cours du bloom printanier, les taux d'absorption atteignent des valeurs élevées (0.5 µmol C.l⁻¹.h⁻¹ et 0.28 µmol N.l⁻¹.h⁻¹); les nitrates représentent alors la principale source d'azote bien que les valeurs de l'indice de préférence relative (RPI) montrent une préférence du phytoplancton pour l'ammonium (RPI (NO₃) < 1; RPI (NH₄) > 5). L'étude des rapports d'assimilation C/N montre que ceux-ci sont supérieurs aux rapports molaires C/N de la matière particulaire. Cette différence doit être imputée aux apports fluviaux ainsi qu'aux variations de l'état physiologique des cellules phytoplanctoniques.

INTRODUCTION

Located at the most westerly point of France, the Bay of Brest (180 km²), here considered as a prototype of semi-enclosed coastal ecosystem (Delmas, 1981), is a shallow basin (average depth 8 m) which exchanges water with the adjacent marine ecosystem (Iroise). Waters are well mixed by tides (semi-diurnal and fortnightly periodicities); during spring tides, the tidal variation reaches 8 m, which represents an oscillating volume of 40% of the high tide volume.

The bay is fertilized by two rivers: the Elorn in the northwest and the Aulne in the southwest; river inputs have been estimated by Delmas (1981) in February at about 12 t N-NO₃.d⁻¹, 0.5 t N-NH₄.d⁻¹, 12 kg P-PO₄.d⁻¹, and 6 t N-NO₃.d⁻¹, 0.06 t N-NH₄.d⁻¹, 168 kg P-PO₄.d⁻¹ for the Aulne and Elorn, respectively. These natural and anthropogenic inputs exhibit large variations on both seasonal and annual scales. Thus, on an annual scale, primary production ranges from 255 to 280 g C.m⁻².year⁻¹, which classifies the Bay of Brest among eutrophic ecosystems (Quéguiner and Tréguer, 1986).

Investigations of nutrient inputs (Delmas and Tréguer, 1983), phytoplankton populations (Quéguiner and Tréguer, 1984) and phytoplankton production (Delmas et al., 1983; Quéguiner and Tréguer, 1986) have been conducted in the Bay of Brest. However, although nitrogen seems to play an important role in the functioning of this ecosystem, no direct nitrogen uptake measurements have been performed so far.

Nitrogen uptake in estuarine waters has been documented in several studies, e.g. McCarthy et al. (1977) in Chesapeake Bay, Gilbert et al. (1982) in Vineyard Sound and Carpenter and Dunham (1985) in the Carmans river estuary. These works emphasize phytoplankton preference for NH₄ relative to NO₃.

The present study was undertaken to estimate phytoplankton uptake of nitrate and ammonium, using the ¹⁵N isotopic method, and to examine the relationship of the two latter parameters with carbon uptake, as measured by the ¹⁴C method. Data are interpreted with reference to the hydrological and nutritional environments in the ecosystem. C/N assimilation ratios have been calculated and compared to C/N composition ratios of the particulate matter (POC/PON).

MATERIALS AND METHODS

Sampling strategy

Samples were collected twice a week at the routine station R3 (Fig. 1) considered as typical of the study area (Delmas and Tréguer, 1985). Sampling was performed during March and April 1989 at 3-m depth at 9:00 a.m. Water was collected with a 5-l Go/Flo bottle and distributed into a series of flasks.

For pigments, particulate organic nitrogen (PON) and particulate organic carbon (POC) measurements, 500 ml of water were filtered onto Whatmann GF/C glass fibre filters. Phytoplankton samples were preserved with acid Lugol solution. Samples for measurement of dissolved oxygen and ammonium were fixed at once on board ship. Nutrient samples were immediately frozen, except silicate samples which were placed in a refrigerator.

Methods

Air temperature and irradiance data were obtained from the Brest-Guipavas weather station, 10 km from the study site; river flow data were obtained from the Service Hydrologique Centralisateur (Nantes, France). Water temperature was measured using Richter and Wiese reversed thermometers (precision ± 0.01°C); salinity was measured by the Knudsen method according to Strickland and Parsons (1972; precision ± 0.05 PSU).

Dissolved oxygen was measured by the Winkler method according to Strickland and Parsons (1972; precision ± 0.02 ml.l⁻¹). Ammonium measurements were made according to the manual method of Koroleff (1969; precision ± 0.05 µM). Nutrients (nitrate + nitrite, phosphate and silicate) were measured by the automated method described by Tréguer and Le Corre (1975; precision ± 0.1 µM N-(NO₃+N₂O₅), ± 0.1 µM Si-Si (OH)₄, ± 0.01 µM P-PO₄).
Chlorophyll a and phaeopigments were measured using a calibrated Turner 111 fluorometer according to Hafsaoui (1984; precision ± 5 %). PON and POC measurements were performed on a modified Carlo Erba analyzer model N 1 500. Cell counts and phytoplankton species determination were made using an inverted microscope (Utermöhl, 1931).

For carbon and nitrogen uptake measurements, incubations were carried out in polycarbonate bottles over a period of four hours using non-limiting level of artificial light. The irradiance was 174 µE.m².s⁻¹ which corresponds approximatively to surface incident radiation during the sampling period (range: 115-230 µE.m².s⁻¹). Incubations were conducted in a constant-temperature room, at 10°C (close to the water temperature during March and April). For carbon uptake measurements, samples were incubated in 125 ml flasks (1 ml NaH14CO3, 148 kBq added). After incubation samples were filtered onto Whatmann GF/C glass-fibre filters. The filters were analyzed for 14C uptake by liquid scintillation counting according to Quéguiner and Tréguer (1984). Nitrogen uptake rates were measured by the 15N tracer technique (Dugdale and Goering, 1967), using two 500 ml flasks. In the first flask, 15NO3 was added (= 10 % of ambient concentration); in the second bottle, 15NH4 was added (= 20 % of ambient concentration). After incubation, samples were filtered on to precombusted Whatmann GF/C glass-fibre filters and immediately frozen until isotopic analysis. Prior to analysis, filters were dried overnight at 60°C and powdered with CaO (disscated at 900°C for 3h) and cuprox. They were then introduced into one or severa! pyrex tubes according to their nitrogen content (estimated from PON measurements) in order to obtain about 6 µg nitrogen in each tube. Tubes were then sealed off and placed in a muffle furnace during 2 h at 550°C to permit deve-lopment of the oxido-reduction reaction (modified Dumas method) during which organic nitrogen is converted to N2 gas. Isotopic ratios 15N/14N were determined by emission spectrometry (spectrometer G S 1, SOPRA) as described by Lemasson and Pages (1983).

Calculation of nitrogen uptake rates, f-ratios and relative preference index

Specific uptake rates (VN as h⁻¹) were calculated using equation (a):

$$VN = \frac{(Cp - Co) \times T}{(Cd - Cp)}$$

(a)

Transport rates (ρN as µmol N-NO3,1⁻¹.h⁻¹ or µmol N-NH4,1⁻¹.h⁻¹) were calculated using equation (b):

$$\rho_N = PON_i \times VN$$

(b)

with: - PONi: initial particulate nitrogen concentration
- Cp: concentration of the label (in atom %15N) in the particulate phase after incubation.
- Co: concentration of the label (in atom %15N) in the particulate phase at time zero.
- Cd: concentration of the label (in atom %15N) in the dissolved phase at time zero.
- T: incubation time.

Equation (a) and equation (b) are respectively similar to equations (4) and (7) quoted by Dugdale and Wilkerson (1986). The fact that we used PONi instead of PONr (final particulate nitrogen concentration) in our calculations could lead to an underestimation of transport rate which can be important when Vs is high. Ammonium uptake rates are not corrected for isotope dilution (Glibert et al., 1982), so they are likely to have been underestimated, as Glibert et al. (1985) have suggested that the atom percentage enrichment of the nutrient pool (Cd) decreases exponentially during the course of incubation rather than remaining constant. In equation (b), the introduction of Cd - Cp at the denominator would usually minimize these underestimations.

Although an underestimated transport rate could result from the use of PONi instead of PONr in equation (b), we decided to introduce it for practical reasons. Except for high Vs values, the rates are not significantly affected by this procedure. Eppley and Peterson (1979) defined the f-ratio as the ratio of new N/total inorganic N utilization:

$$f = \rhoNO_3 / (\rhoNO_3 + \rhoNH_4)$$

Herein, the relative preference indices (RPI) are calculated according to McCarthy et al. (1977):

For NO3: RPI (NO3) = \frac{f}{([NO3]/[NO3]+[NH4])}\n
For NH4: RPI (NH4) = \frac{1 - f}{([NH4]/[NO3]+[NH4])}\n
RESULTS

Trophic environment

METEOROLOGY AND RIVER REGIMES

Throughout the study period, total irradiance tends to increase, reaching 2000 J. cm⁻².d⁻¹ at the beginning of April; air temperature exhibits low fluctuations and remains fairly constant near 10°C. River flows tend to decrease during spring, despite of some peaks.

HYDROLOGICAL AND CHEMICAL PARAMETERS

The water temperature rises slowly from the beginning...
of March (10°C) to the end of April (11.5°C); salinity values frequently reaching 35 PSU appear abnormally high in comparison with the values usually measured in the Bay of Brest during the same season (range: 32–34 PSU). This is ascribed to abnormally low levels of precipitation leading to low river flows during winter 1988–1989.

During the study period, the nutrient distribution (Fig. 2) exhibits decreasing concentrations. Nitrate + nitrite concentrations decrease from 40.5 \( \mu M \) N-(NO\(_2^-\) + NO\(_3^-\)) to 1.6 \( \mu M \) N-(NO\(_2^-\) + NO\(_3^-\)), which is the minimum value observed at the end of April. Ammonium is characterized by low concentrations (below 0.6 \( \mu M \) N-NH\(_4^+\)) also decreasing throughout the study period. Nitrate then accounts for more than 90% of the total inorganic nitrogen available for phytoplankton. Silicate evolution parallels that of nitrate: concentrations vary from 13.0 \( \mu M \) Si-Si(OH)\(_4^+\) to 1.1 \( \mu M \) Si-Si(OH)\(_4^+\) throughout March–April. Phosphates remain fairly constant in early March (about 0.50 \( \mu M \) P-PO\(_4^3^-\)): their concentration is regulated through adsorption–desorption processes at the water-suspended matter interface (Delmas and Tréguer, 1983). Then phosphates decrease during the phytoplankton bloom to reach the minimum value of 0.07 \( \mu M \) P-PO\(_4^3^-\) on 24 April.

The overall decrease in nutrient concentration reflects utilization by phytoplankton and the decreasing contribution of river inputs.

During the study period, water remains constantly saturated with respect to dissolved oxygen (range: 102–124 % oxygen saturation).

**Phytoplankton populations**

During March and April 1989, microphytoplankton (linear dimension ranging between 20 and 200 \( \mu m \)) populations are clearly dominated by diatoms (Tab. 1).

<table>
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<th>Sampling date</th>
<th>Dominant species</th>
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<tr>
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<td>10.04</td>
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<td>Skeletonema costatum</td>
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<td>Thalassiosira cf. fallax</td>
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<tr>
<td>24.04</td>
<td>Chaetoceros curvisetum</td>
</tr>
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<td>26.04</td>
<td>Chaetoceros curvisetum</td>
</tr>
<tr>
<td>28.04</td>
<td>Chaetoceros curvisetum</td>
</tr>
</tbody>
</table>

Microphytoplankton and nanoplankton (linear dimension < 20 \( \mu m \)) exhibit different patterns of evolution (Fig. 3). As already shown by Quéguiner and Tréguer (1984) during the same season, nanoplankton cell concentrations are relatively high (from 2.2 \( 10^5 \) to 6.2 \( 10^5 \) cells.l\(^{-1}\)) and show few temporal fluctuations, while microphytoplankton cell concentration evolution is characterized by a succession of peaks superimposed on a general trend towards increase during spring. At the end of the study period, microphytoplankton cell concentrations remain fairly constant with high values ranging from 2 \( 10^5 \) to 4 \( 10^5 \) cells.l\(^{-1}\); this coincides with the rapid and almost complete disappearance of nutrients.
Carbon and nitrogen standing stocks and production

Before the beginning of the productive period, chlorophyll $a$ concentrations (Fig. 4) are low (= 1 $\mu$g.l$^{-1}$); they only increase at mid-April, reaching a maximum value of 6.74 $\mu$g.l$^{-1}$ on 24 April. Phaeopigment concentrations (Fig. 4) exhibit relatively slight variations and range between 0.22-1.23 $\mu$g.l$^{-1}$, the maximum value being observed at the end of the spring bloom.

PON and POC levels exhibit synchronism in fluctuations, with an average value of 10 $\mu$mol C.l$^{-1}$ and 1.5 $\mu$mol N.l$^{-1}$ until 12 April. After this date, both parameters increase and reach their respective maxima of 24.8 $\mu$mol C.l$^{-1}$ and 3.8 $\mu$mol N.l$^{-1}$ on 24 April. During March, the POC/PON molar ratio (Fig. 9) is high (≥ 7): such high values are ascribable to heavy terrigenous inputs (Tréguer and Quéguiner, 1989). During April, POC/PON molar ratios range between 6-7, i.e. the values are close to the average POC/PON molar ratio (6.7) as defined by Redfield et al. (1963). Gilbert et al. (1982) observed a comparable evolution of POC/PON molar ratio values (from 7 to 9) for the Vineyard Sound waters.

Before spring bloom development, carbon uptake rates (Fig. 5) are low, not exceeding 0.3 $\mu$mol C.l$^{-1}$h$^{-1}$ until 12 April. By mid-April, carbon uptake rates increase suddenly to reach a maximum value of 1.7 $\mu$mol C.l$^{-1}$h$^{-1}$ on 20 April and then decrease to 0.5 $\mu$mol C.l$^{-1}$h$^{-1}$ at the end of the study period.

Nitrogen uptake parallels that of carbon. At the beginning of the study period, transport rates of ammonium (Fig. 6) are about 0.015 $\mu$mol N-NH$_4$.l$^{-1}$.h$^{-1}$. After a sharp increase, values reach a maximum (0.055 $\mu$mol N-NH$_4$.l$^{-1}$.h$^{-1}$) on 20 April.

Transport rates of nitrate (Fig. 6) show the same evolution as ammonium: values are low until mid-April, almost equal to ammonium transport rates, and then increase to reach the maximum of 0.232 $\mu$mol N-NO$_3$.l$^{-1}$.h$^{-1}$ on 20 April.

As regards $f$-ratio values (Table II), these range between 0.34 and 0.94, with an average value of 0.62. During the productive period (20-28 April), $f$ ranges between 0.70 and 0.80. From these values, it can be inferred that 34 to
94% (70-80% during the bloom) of nitrogen production is new production.

Table II

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>f-ratio</th>
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<tr>
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<tr>
<td>22.03</td>
<td>0.45</td>
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<tr>
<td>30.03</td>
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</tr>
<tr>
<td>28.04</td>
<td>0.71</td>
</tr>
</tbody>
</table>

RPI values for both nitrogen forms are presented as a function of total inorganic dissolved nitrogen ($\Sigma N = \text{nitrate} + \text{nitrite} + \text{ammonium}$; Fig. 7). The RPI (NO$_3$) values are always less than 1. No clear relationship is established between RPI (NO$_3$) values and $\Sigma N$. RPI (NH$_4$) values are always superior to unity, ranging between 5-45, and increase with increasing $\Sigma N$ concentrations.

Figure 7

Evolution of RPI values [a : RPI(NH$_4$); b : RPI(NO$_3$)] as a function of total dissolved inorganic nitrogen concentrations.

Evolution des RPI [a : RPI(NH$_4$); b : RPI(NO$_3$)] en fonction des concentrations en azote minéral total dissous.

Figure 8

Evolution of RPI(NO$_3$) values as a function of ambient ammonium concentration.

Evolution du RPI(NO$_3$) en fonction des concentrations en ammonium.

Figure 9

Temporal variation of C/N molar composition and uptake ratios of particulate matter.

évolution temporelle des rapports molaires C/N de composition et d'absorption de la matière particulaire.
minimum value of 5.8 is reached (Fig. 9). C/N uptake ratios measured in the bay are generally higher than POC/PON composition ratios and almost always higher than the theoretical Redfield ratio.

DISCUSSION

Nitrogen transport rate in coastal ecosystems

Ammonium transport rates in the Bay of Brest are close to those measured in Vineyard Sound by Glibert et al. (1982; range: 0.01-0.10 μmol N-NH₄L⁻¹h⁻¹) and in Chesapeake Bay by Wheeler et al. (1982; range: 0.049-0.098 μmol N-NH₄L⁻¹h⁻¹).

On the other hand, the transport rates of nitrates we calculated exhibit a maximum much higher than that found in Vineyard Sound by Glibert et al. (1982; 0.02 μmol N-NO₃L⁻¹h⁻¹). A possible explanation of this discrepancy is that nitrate concentrations in Vineyard Sound are much more lower (range: 0.13-2.10 μM N-NO₃) than in the Bay of Brest (range: 1.6-40.5 μM N-NO₃).

According to Glibert et al. (1982) f-ratio values are close to 0.05 in oligotrophic waters, implying that 95% of nitrogen utilized is as NH₄. For coastal waters, Eppley and Peterson (1979) report f-ratio values of 0.30-0.46.

Our f-ratio values are high in comparison with those reported by Eppley and Peterson (1979); they are close to values of the fmax calculated by Harrison et al. (1987) for several coastal environments. Such high values can be related to the heavy loading of new N (nitrate) in the Bay of Brest and are consistent with the positive relationship between the f-ratio and ambient nitrate concentration found by Platt and Harrison (1985). However we cannot preclude that N-urea uptake, not measured in the present study, might represent a significant fraction of total nitrogen uptake. Urea uptake by phytoplankton has been documented in several studies. McCarthy (1972) reported that urea uptake averaged 28% of total nitrogen utilization in southern California coastal waters, and McCarthy et al. (1977) measured urea uptake rates accounting for 20.3% of total nitrogen utilization on an annual scale in Chesapeake Bay. Moreover, Probey and Painting (1985) found that urea uptake supply about 27% of the nitrogen requirement for the surface water community of the Southern Ocean during the autumn. If urea uptake occurs in the same proportions in the Bay of Brest, the denominator of the f-ratio would be larger which would lower our calculated f-ratios.

According to Glibert et al. (1982), RPI values > 1 reflect preference for the considered nutrient while RPI values < 1 indicate selection against that nutrient. RPI (NO₃) and RPI (NH₄) values we calculated are respectively always less than and superior to unity. This means that in the Bay of Brest, during spring, ammonium is used preferentially despite the fact that nitrate accounts for more than 90% of total inorganic nitrogen. This preference of phytoplankton for ammonium, even at high ambient nitrate concentrations, has been reported in several studies (Dugdale, 1976; Collos and Slawyk, 1980; McCarthy et al., 1977; 1982; Proby and Painting, 1985; Kristiansen and Lund, 1989). Eppley et al. (1969) hypothesized that phytoplankton take up ammonium preferentially because nitrate utilization requires energy for nitrate reduction, whereas ammonium assimilation does not.

Although our calculated RPI values show that phytoplankton clearly prefer ammonium, nitrate is the main source for nitrogen production in the Bay of Brest during the spring bloom. At this period, it is therefore new production which dominates although regenerated production should not be neglected (20-30% of total nitrogen production come from ammonium utilization).

Variations of C/N uptake ratios during phytoplankton growth

C/N uptake ratios (range: 5.8-19.1) are in agreement with those of Carpenter and Dunham (1985) who found uptake ratios from 6 to 30 in the Carmans river estuary; Slawyk et al. (1978) reported C/N values from 5 to 45 for the northwest African upwelling area, where new production prevails.

The high uptake ratios observed at the beginning of April are related to low nitrogen-uptake rates and it can be inferred that phytoplankton have sufficient nitrogen quota.

On 20 April, when the peak of production occurs, the C/N uptake ratio suddenly decreases to a value close to the value of the POC/PON composition ratio; this is due to an enhanced nitrogen uptake rate which occurs with the increased use of intracellular nitrogen reserves during cellular divisions occurring at this time.

At the end of the study period, the C/N uptake ratio increases, which reflects the beginning of nitrogen limitation, since ambient NO₃ concentration decreased to 1.6 μM N-NO₃ at the end of April. Note that in eutrophic systems, values of the half-saturation constant for nitrate uptake, Kt (NO₃), are usually close to 1 μM N-NO₃ (McIsaac and Dugdale, 1969; Collos and Slawyk, 1980). In nitrogen-limited environments, high C/N assimilation ratios are to be expected (Carpenter and Dunham, 1985). For example, Eppley et al. (1977) found an average uptake ratio of 22.2 in the North Pacific gyre, and McCarthy (1972) reported a ratio of 12.4 for southern California coastal waters in which nitrogen was limiting.
Other factors may explain the high C/N uptake values we measured. Carbon and nitrogen uptake were measured simultaneously under a constant irradiance level, so we did not take account of the uncoupling between nitrogen and carbon uptake, on a per day basis, due to the duration of nitrogen uptake and the interruption of carbon fixation during the dark period (Laws and Caperon, 1976). Finally, it is not surprising to find C/N uptake ratios different from POC/PON composition ratios since uptake ratios are only indicative of the cellular metabolism of the biomass present in the water at the time of sampling whereas, in the best case (when samples contain only small amounts of detrital material), POC/PON composition ratios are the time-averaged resultant of this metabolism.

CONCLUSION

The Bay of Brest constitutes a typical coastal ecosystem of western Europe, characterized by heavy nitrogen loading originating in freshwater inputs. The spring period is characterized by a decline in major nutrients superimposed on a gradual increase in phytoplankton biomass (mainly diatoms). In such conditions, nitrogen production essentially originates from new nitrogen (evidenced from high f-ratios) which constitutes the main part of total dissolved inorganic nitrogen, although there is evidence of preferential uptake of ammonia against nitrate (high RPI (NH₃) values). POC/PON composition ratios exhibit great temporal variability, reflecting both detrital matter inputs from rivers and the phytoplankton elemental composition. POC/PON composition ratios reach values close to C/N uptake ratios only when C and N productions are at their maximum. C/N uptake ratios also exhibit great temporal variability, which can be interpreted in terms of variation of the nutrient status of phytoplankton during the spring bloom.

REFERENCES


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