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Contributions of benthic and planktonic primary producers to nitrate and ammonium uptake fluxes in a nutrient-poor shallow coastal area (Corsica, NW Mediterranean)

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Abstract

By using the stable isotope ^{15}N, we have measured in situ the uptake of nitrate and ammonium by the seagrass *Posidonia oceanica,* its leaf epiphyte community, the brown macroalgae *Halopteris scoparia* and the suspended particulate organic matter (SPOM). In Revellata Bay (Gulf of Calvi, Western Corsica), which is a very nutrient-poor region, the specific uptake rates *(V)* ($\mu g\ N\ g\ N^{-1}\ h^{-1}$) of SPOM measured at ambient concentrations are 10-1000 higher than those of benthic primary producers. Macroalgae have intermediary *V,* between the seagrass leaf and leaf epiphytes. *V* are quite variable and the reasons for this variability remain unclear.

Despite the difference of specific uptake rates found between benthic and pelagic primary producers, when integrating the uptake fluxes for a water column of 10 m depth, the contribution of benthic primary producers to N uptake fluxes ($g\ N\ m^{-2}\ h^{-1}$) is significant, corresponding on average to 40% of total uptake flux. This results from the dominance in terms of N biomass of benthic primary producers in this shallow nutrient-poor area. When reported for the entire volume of the Revellata Bay, the contribution of benthic primary producers is reduced to 5-10% of total N uptake flux.

Although this contribution could appear relatively low, it results in a significant direct transfer of inorganic nitrogen from the water column to the benthic compartment. By this transfer, the benthic plants act as a biological pump incorporating the pelagic N into the benthic compartment for a time longer than the characteristic time of phytoplankton dynamics (month-years vs. day-week).

Keywords*:* Macroalgae; ^{15}N tracer; Nitrogen uptake; NW Mediterranean; Phytoplankton; Seagrass

1. Introduction

Coastal regions play a major role in global oceanic element cycles (e.g., Herbert, 1999; Frankignoulle and Borges, 2001) and marine primary production (e.g., Charpy-Robaud and Sournia, 1990). Metabolism of open ocean is primarily determined by phytoplank-tonic primary production (Gattuso et al., 1998). However, in coastal zones where the photic depth reaches the seafloor, benthic flora develops and interacts with the pelagic compartment (Valiela et al., 1997) to influence the nutrient and carbon dynamics of the coastal ecosystems (e.g., Herbert, 1999; MacGlathery et al., 2001). Plant communities in shallow coastal areas are composed of a large number of species representing various growth strategies and life forms (Pedersen and Borum, 1997). In nutrient-poor areas, slow-growing macroalgae and phanerogams are often dominant species in the benthic community (e.g., Cloern, 2001; Duarte, 1995; Pedersen and Borum, 1996, 1997; Valiela et al., 1997).

The impact of benthic primary producers on the nutrient dynamics of very nutrient-poor coastal zones is not well known, as many studies have focused on one type of primary producer or have been conducted in eutrophied areas (Sfriso et al., 1992; Viaroli et al., 1996), in estuaries (Pedersen and Borum, 1996; Valiela et al., 1997) or in mesotrophic environments (e.g., Dudley et al., 2001).

The aim of this study is to determine the relative contributions of benthic and planktonic primary producers (phytoplankton, macroalgae, seagrass and their leaf epiphytes) to inorganic nitrogen uptake fluxes in a very nutrient-poor and shallow coastal area (Revellata Bay, West Corsica, NW Mediterranean).

We addressed the problem in situ by measuring the uptake of NH_4 and NO_3 by the different primary producers, using the ^{15}N tracer method. Although this method has been known since the 1960s (e.g., Dugdale and Goering, 1967), N tracers are mainly used for phytoplankton studies, less so in benthic plant studies (e.g., Dudley et al., 2001; Stapel et al., 2001; Marba et al., 2002) and are particularly rare in studies integrating both pelagic and

benthic compartments. The use of ^{15}N method allows to simultaneously measure the uptake of benthic and planktonic producers at ambient substrate concentrations and, therefore, to assess the N uptake dynamics in a nutrient-poor ecosystem where pelagic and benthic primary producers have strong interactions.

2. Materials and methods

2.1. Area description

All sampling and measurements were performed in Revellata Bay (Gulf of Calvi, Western Corsica, France), near the marine research station STARESO (42°35'N, 8°43'E) (Fig. 1). This bay, which is open to the northwest, has a surface of 245 ha and a mean depth of ~ 30 m (maximum ~ 60 m). The rocky shore is carboniferous granite and is colonised by photophilous algae from a few cm under the mean sea level to 25 m depth (Hoffmann et al., 1992). The seafloor slope is progressive (2%) from south to northwest. Residence time of waters in the bay varies from 5 days (in winter) to 10 days (in summer) (Norro, 1995). Land nutrient supplies in the bay are limited due to low river and sewage discharges. Precipitation in this area is also very low and characteristic of the Mediterranean climate. The main external source of new nutrients for the bay is the open sea (Goffart et al., 2002). Skliris et al. (2000, 2001) have shown that entrance of deep and nutrient-rich waters is very seasonal (mainly winter and early spring) and strongly linked to the occurrence of N-NE winds. Winds from the SW are more frequent and drive nutrient-poor surface water from the open sea into the bay.

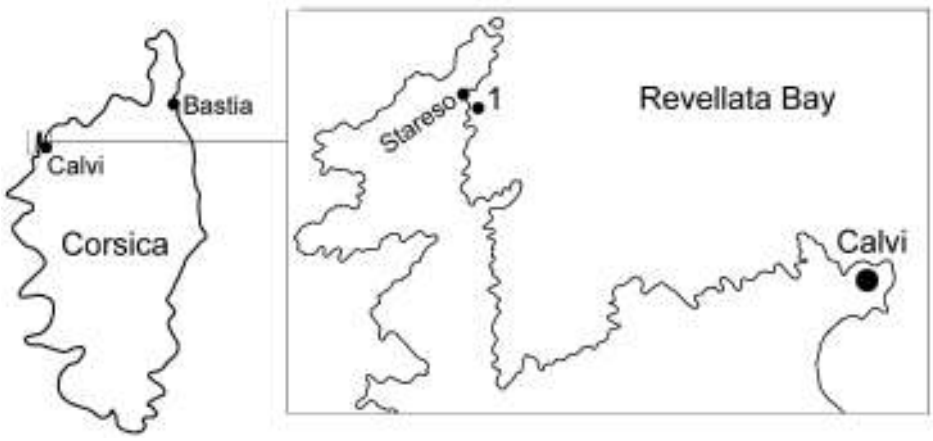
The water column is very clear due to generally low phytoplankton biomass and the absence of important river discharges (light attenuation coefficient $k < 0.2$ m^{-1}) (Bay, 1984).

Phytoplankton biomasses are low (maximum bloom: 1 mg Chl *a* m^{-3}). The occurrence and intensity of phytoplanktonic bloom in Revellata Bay are variable (Goffart et al., 2002). Primary production is considered to be related to NH_4 regeneration most of the year, except during the bloom (Velimirov and Walenta-Simon, 1992). A dense and continuous *Posidonia oceanica* seagrass meadow grows to 40 m depth, which is close to the deepest limit recorded for this species in the Western Mediterranean (Gobert et al., 2003). This meadow, which is one of the most productive *P. oceanica* beds of the NW Mediterranean (Pergent-Martini et al., 1994), covers 70% of the seafloor of the Revellata Bay (Bay, 1984). On the rocks, at our sampling site, the brown algae *Halopteris scoparia* was the dominant species of the photophilous settlement, constituting between 40% and 90% of the algal biomass (personal observations).

2.2. Experimental design

All experiments were conducted in situ at 10 m depth in the seagrass meadow or on rocks. Nitrate and ammonium uptake were measured for suspended particulate organic matter (SPOM), brown algae *H. scoparia, Posidonia* leaves and their epiphytes. Experiments were performed in 1997 and 1998 during the months of February, June and October, and in 1999, from February to June. Data for the *P. oceanica* leaves are presented in detail in another paper focusing on the nitrogen budget of this species (Lepoint et al., 2002b).

Fig. 1*. Location of the Revellata Bay and experimental sites (1) in the Gulf of Calvi along the Corsican coast.*



2.3. Experimental device

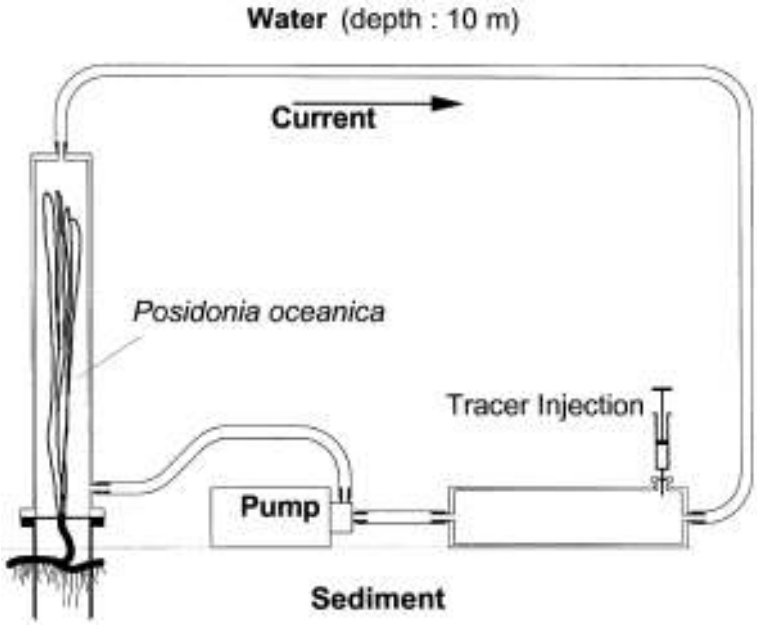
The experimental device was composed of two transparent Plexiglas cylinders and a submerged pump to ensure the homogenisation of the cylinder water content (about 8 1). During the experiment, the submerged pump creates a water current in the cylinder of about 5 cm s^{-1} which is in the order of the ambient water velocity.

For macroalgae, the two cylinders were placed horizontally on rocks. Two specimens of *H. scoparia* were placed in one cylinder at the start of the experiment.

For seagrass leaves, a PVC base was driven in the sediment (25 cm depth) 24 h before the experiment, isolating one shoot of *P. oceanica* (Fig. 2). A Plexiglas cylinder was placed vertically on the PVC base. A rubber membrane separated the cylinder and the PVC base, isolating a leaf and a root chamber. The second cylinder was placed horizontally in the meadow and connected to the pump and to the first cylinder.

In both types of experiments, the second cylinder is used for SPOM collection (see below).

Fig. 2. *Experimental device used to measure at 10 m depth in Revellata Bay the uptake of $^{15}NO_3$ and $^{15}NH_3$ by P. oceanica leaves, their epiphytes and suspended particulate organic matter.*



2.4. Experimental protocol

All experiments had a duration of 1 h. A shorter time would lead to surge uptake effect and longer time to substrate exhaustion effects, due to the low concentration of substrate. The ^{15}N tracers were solutions of ammonium sulphate (99.0% ^{15}N) or sodium nitrate (99.0% ^{15}N) (Eurisotop, France). Water samplings were made in the cylinder before and 5 min after the tracer addition and at the end of experiment for nutrient concentration measurements. Tracer addition represented about 10-20% of the ambient N concentrations or 0.05 and 0.1 μM for NO_3 and NH_4, respectively, when the ambient concentrations were close to the analytical limit.

At the end of the experiment, benthic primary producers were collected in the first cylinder and the second cylinder was closed and taken up. The water in this cylinder was filtered under low pressure on pre-combusted GF/F filters (450 °C, 48 h) (Whatman) to collect SPOM.

2.5. Sample treatment and measurements

To remove the adsorbed ^{15}N tracer, the filters were rinsed with 100 ml of filtered oligotrophic seawater (GF/F) and then oven-dried 48 h at 60 °C. Macroalgae were also briefly rinsed, oven-dried at 60 °C during 48 h and weighed. *Posidonia* leaves were scraped with a razor blade to remove epiphytes. Leaves were briefly rinsed,

oven-dried at 60 °C during 48 h and weighed. After a first drying, leaf epiphytes were acidified with HC1 (0.1 N) for decalcification, briefly rinsed and oven-dried at 60 °C. They were weighed before and after decalcification. Mean carbonate content of epiphytes was about 65%.

All samples, except filters, were finely ground for spectrometric and elemental analysis. Measurements were performed in triplicate with an isotopic ratio mass spectrometer (Optima, Micromass, UK) coupled to a C-N-S elemental analyser (Carlo Erba, Italy). Elemental results are expressed in percentage of the considered element relative to the total dry weight (%dw) (before acidification in the case of epiphytes).

Nitrate and ammonium concentrations in water samples were measured with an analytical automated chain (Technicon, USA or Skalar, Netherlands). Analytical precision was 0.01 and 0.03 μM for nitrate and ammonium, respectively. Detection limit was estimated to be 0.02 and 0.05 μM for nitrate and ammonium, respectively.

With the aim to compare results of benthic and planktonic primary producers, planktonic biomass was expressed in terms of nitrogen, rather than in terms of chlorophyll *a.* This N biomass was measured at the end of the experiment on the filter used for SPOM uptake rate calculation, using filtered volume and elemental data (Collos, 1987). For seagrass and macroalgae, standing crops (g_{dw} m^{-2}) were measured during each campaign in 1997 and 1998 and monthly between February and June 1999. *Posidonia* leaf standing crop was calculated using the average shoot density and the shoot dry weight. The density was counted during each campaign using a circle with a diameter of 40 cm randomly launched in the meadow. We observed no significant seasonal change of density during this study (n = 259, 402 ± 140 shoot m^{-2}). Dry weights of the shoots and leaf epiphytes were measured during each campaign (and monthly in 1999), using 10 shoots randomly collected plus the experimental shoots.

For *Halopteris* biomass measurements, we entirely scrapped an area of 400 cm^2 in the *Halopteris* settlement (7-10 m depth), using an underwater sucking device (Bussers et al., 1983). Three samplings were randomly taken at each campaign (and monthly in 1999). *Halopteris* specimens were separated from other algae species before drying and weighing. Conversions of field dry weight biomass in terms of N biomass were done using elemental data of experimental samples.

2.6. Calculations

Specific uptake rates *(V)* (μg N g N^{-1} h^{-1}) and uptake fluxes (ρ) (μg N m^{-2} h^{-1}) were calculated according to (adapted from Collos, 1987):

$$V = \frac{A_f - A_0}{A_d \times t} = \frac{\rho}{\text{Biomass N}} \qquad (1)$$

where A_f *is* the final ^{15}N abundance measured in the plant, A_0 is the initial (= natural) ^{15}N abundance in the plant, A_d is the ^{15}N abundance in the dissolved phase at the beginning of the experiment, and t is the duration of the experiment. Biomass N is the biomass measured in the field in terms of nitrogen. The conversion of field biomasses in terms of dry weight in biomass N was done using averaged N measurements of experimental material. The natural abundance *(A_0)* of ^{15}N in the different producers was determined during another study (Lepoint et al., 2000). For example, in *Posidonia* shoots, this natural abundance was 0.3673 ± 0.0005% ^{15}N (i.e. + 2.6 ‰ in δ notation) and did not show a clear seasonal pattern (Lepoint et al., 2000). Variation of the ^{15}N natural abundance for other producers was within the same range. The experimental particulate material is considered as enriched in N relative to N natural abundance when $A_f - A_0$ was >0.001% ^{15}N.

A_d was considered to be constant during the experiment duration (1 h) and was calculated according to the isotopic mixing equation:

$$C_d \times A_d = A_{d0} \times C_{d0} + A_t \times C_t \qquad (2)$$

C_d is the concentration of ammonium or nitrate in the dissolved phase after the N tracer addition. A_{d0} and C_{d0} are respectively the natural N abundance and the initial concentration of nitrate or ammonium in the dissolved phase. A_t and C_t are respectively the ^{15}N abundance (99.0% ^{15}N) and the concentration of the added tracer. A_{d0} was fixed at 0.37% ^{15}N, as the importance of the natural variation of this term is small compared to the variations of the tracer terms.

For A_d calculation when initial nutrient concentrations were undetectable, we consider C_{d0} to be equal to the analytical detection limit. Detection limit was estimated to be 0.02 and 0.05 μM for nitrate and ammonium, respectively. This probably introduces an overestimation of uptake in such conditions, but we consider our measurements to be within an order of magnitude.

Fig. 3. *Nitrate and ammonium concentrations measured in the water column of Revellata Bay. Measurements correspond to initial samplings made in the experimental chambers used for ^{15}N uptake measurements.*

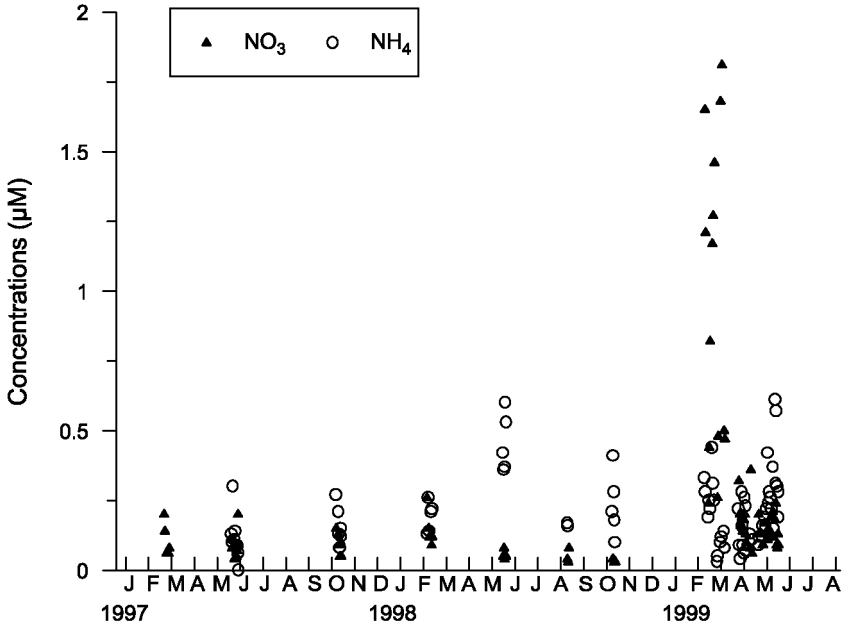


Fig. 4. *Concentrations of particulate organic nitrogen in the water column during ^{15}N uptake experiment done at 10 m depth in Revellata Bay. Each value corresponds to one experiment.*

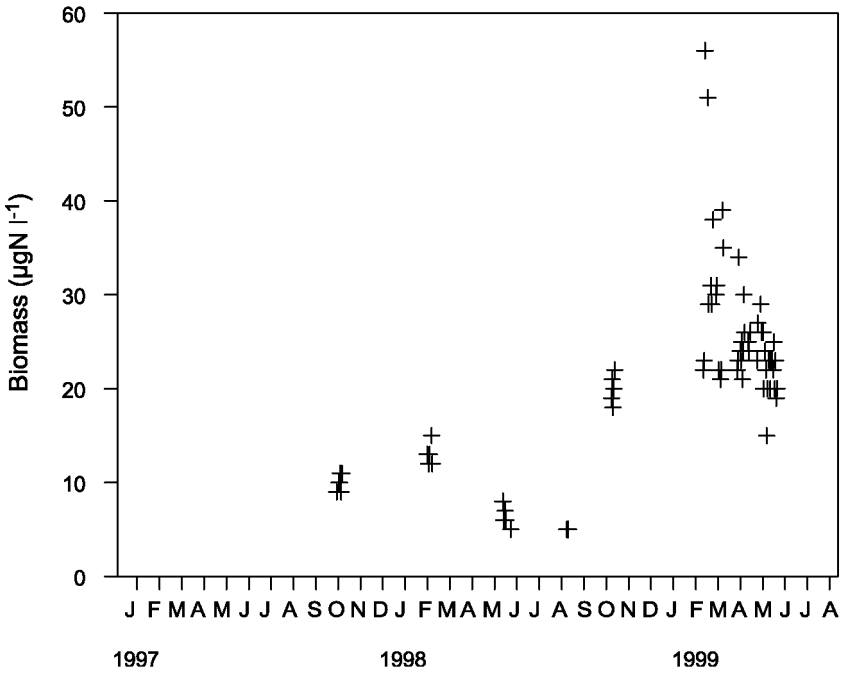


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***Fig. 5**. Weight evolution of P. oceanica leaves (a), their epiphytes (b) and of the macroalgae H. scoparia (c) in Revellata Bay at 10 m depth from October 1997 to June 1999.*

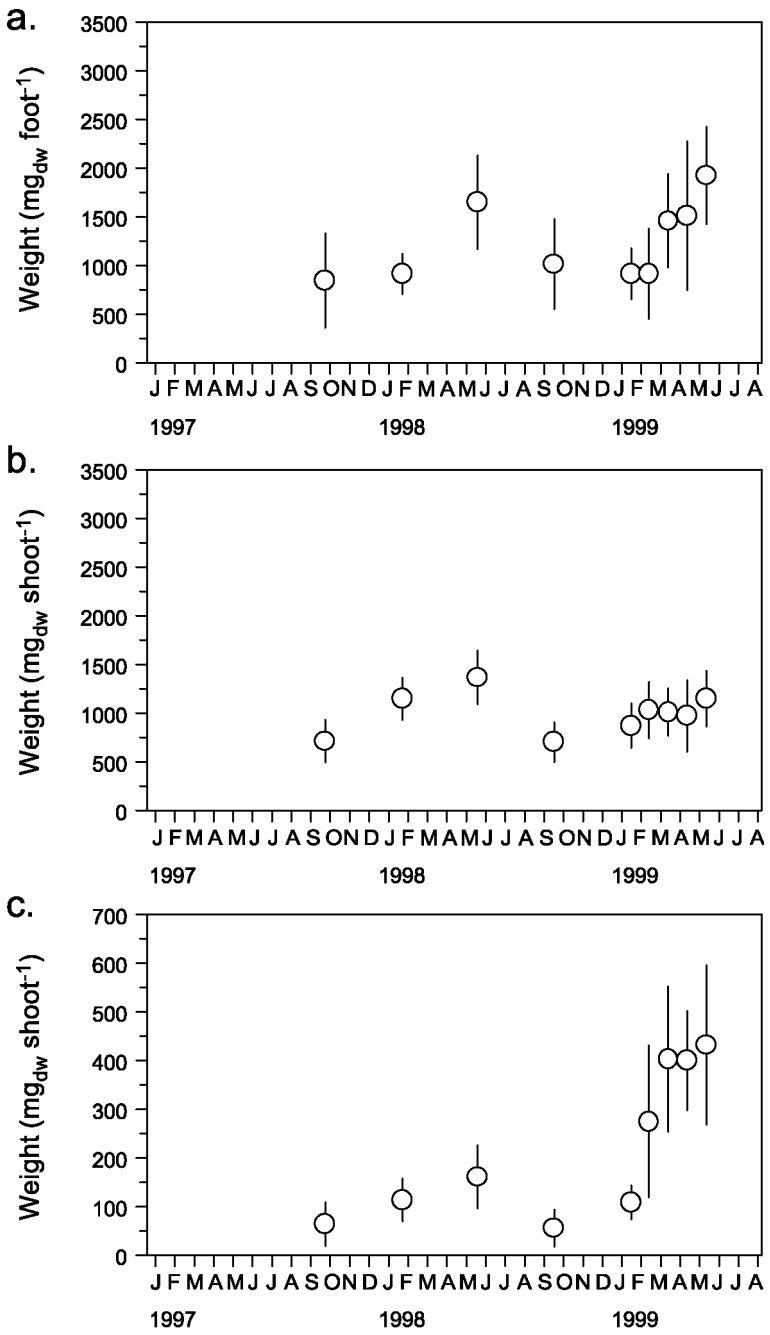
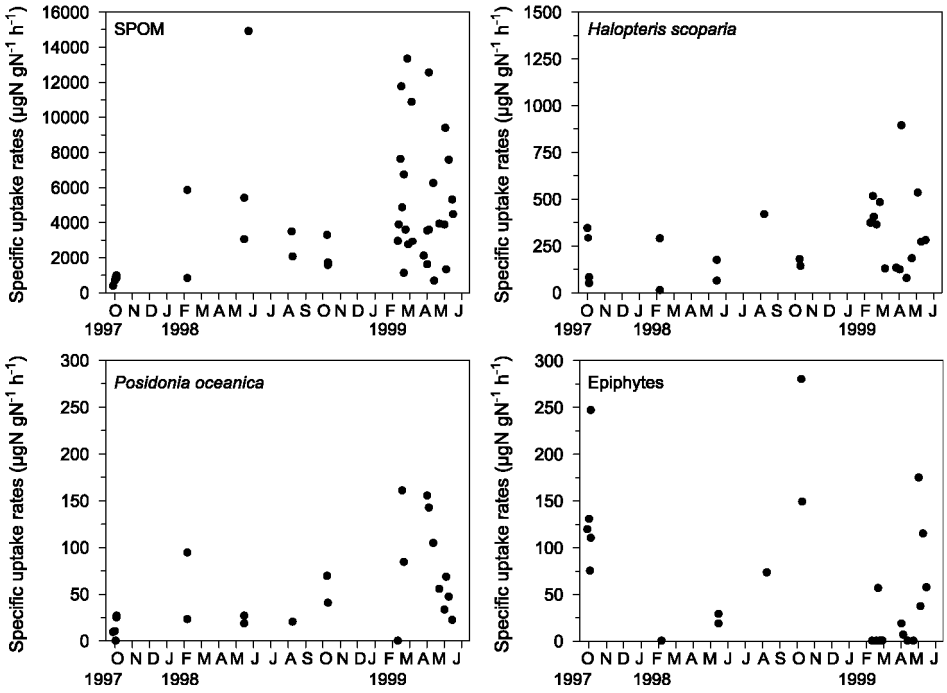


Fig. 6. *Temporal variations of the specific uptake rates of nitrate by benthic and planktonic primary producers in Revellata Bay, measured between October 1997 and June 1999 at 10 m depth. Each point corresponds to one experiment. Data for Posidonia leaves are already presented in Lepoint et al. (2002b).*



3. Results

Water column concentrations of NO_3 and NH_4 were very low and were comparable to the concentrations of other coastal zones in the NW Mediterranean (e.g. Delgado et al.,1994) (Fig. 3). In 1999, a peak of nitrate is registered at the beginning of spring. NH_4 in the water column did not show a clear seasonal pattern during this study.

SPOM concentrations in terms of nitrogen were maximum in April 1999 and minimal in August 1998 (Fig. 4). Concentrations measured in February-March 1998 were very different than in February-March 1999.

The C:N ratios of SPOM ranged from 4 to 18 (w/w), indicating a high variability of the SPOM composition. In our data, C:N ratios were maximum in June and August 1998 and minimum during spring 1999. During this time, the C:N ratios were relatively constant and close to 5, which corresponds to living plankton. The *Posidonia* leaf weights were minimum in October and maximum in June 1999 (Fig. 5), which follows the classical leaf biomass pattern described for this species (e.g., Buia et al., 1992; Alcoverro et al., 1995). The leaf epiphyte and *H. scoparia* weight showed a quite similar seasonal pattern. The leaf epiphyte community represented between 15% and 40% of the leaf weight (mean: 20 ± 13).

The C:N ratios of the different primary producers are well documented in the literature (e.g., Atkinson and Smith, 1983; Duarte, 1992). Our results fit the general tendency reported in these studies (Table 1).

The average nitrate and ammonium specific uptake rates, respectively, V_{NO3} and V_{NH4}, measured for SPOM were significantly higher than those of the other producers (Mann-Whitney test, $p < 0.005$) (Table 1). The average V_{NO3} and V_{NH4} for *H. scoparia* were significantly higher than those of leaf epiphytes and *Posidonia* leaves. The V_{NO3} and V_{NH4} of epiphytes and *Posidonia* leaves did not differ significantly.

The V_{NH4} of SPOM were significantly higher than the V_{NO3} (Mann-Whitney test, $p < 0.005$) (Table 1). The V_{NO3} and V_{NH4} of other primary producers did not differ significantly.

Both V_{NO3} and V_{NH4} showed relatively large temporal variations (Figs. 6 and 7, respectively). The V_{NO3} of macroalgae and SPOM were maximal in February-March 1999, contrary to the V_{NO3} of epiphytes, which were

minimal at this time (Fig. 6). The V_{NO3} *of P. oceanica* leaves were also maximal during this period (Lepoint et al., 2002b). Except in spring 1999, the V_{NO3} of the macrobenthic producers were less variable than those of the SPOM and leaf epiphytes.

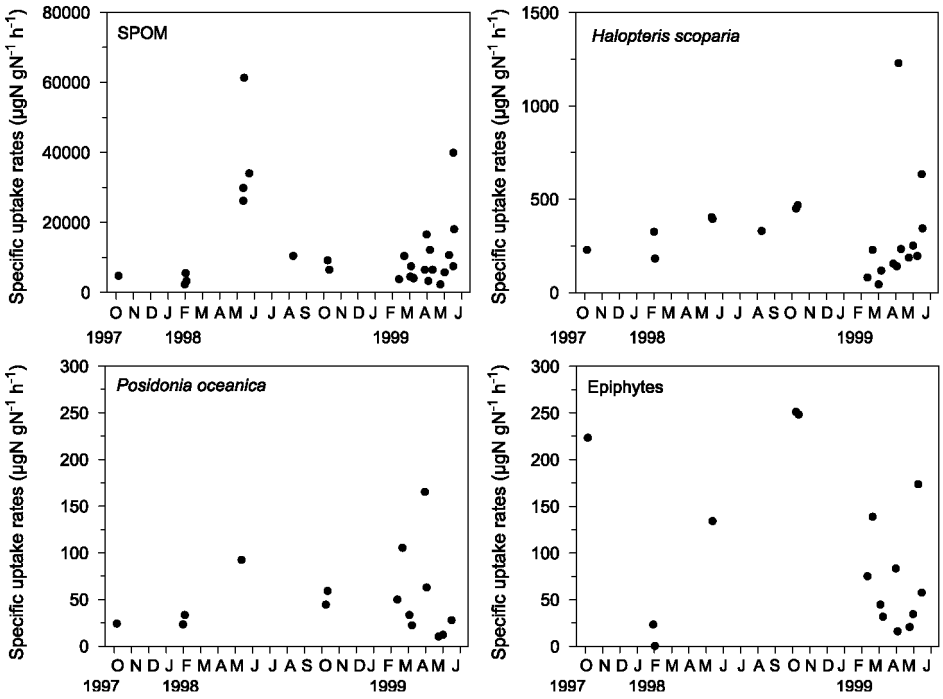
The V_{NH4} of all producers were maximum in June or in October and minimum in February (Fig. 7).

***Table 1** : Mean (± S.D.) of C:N ratios, ammonium and nitrate specific uptake rates measured for SPOM and benthic primary producers at 10 m depth in Revellata Bay during ^{15}N tracer experiments performed from February 1997 to June 1999*

Types	C:N (w/w)	n_s	$V_{NH4,}$ µg N g N^{-1} h^{-1}	n_e	$V_{NO3,}$ µg N g N^{-1} h^{-1}	n_e
SPOM	6 ± 3	75	10184 ± 11572	54	3776 ± 4388	92
Posidonia leaves	31 ± 9	60	47 ±45	26	43 ±64	58
Posidonia leaf epiphytes	9 ± 2	98	104 ± 107	28	74 ±91	64
H. sconaria	27 ±10	320	270 ± 222	36	260 ± 275	66

n_s = number of samples; n_e = number of experiments.

***Fig.** 7. Temporal variations of the specific uptake rates of ammonium by benthic and planktonic primary producers in Revellata Bay, measured between October 1997 and June 1999 at 10 m depth. Each point corresponds to an experiment. Data for Posidonia leaves are already presented in Lepoint et al. (2002b).*



4. Discussion

The ^{15}N methods allows to simultaneously measure N uptakes of several primary producers, as the N abundance is measured in all the primary producers present in the experimental bell (except the bacterial component). These uptakes are measured at ambient concentrations of nutrient, but are affected by some experimental and biological biases, reviewed, for example, by Dugdale and Wilkerson (1986), Collos (1987) or Legendre and Gosselin (1997) for phytoplankton. It is difficult to estimate the impact of these different biases on our measurements. Isotopic dilution (i.e. the dilution of the dissolved ^{15}N pool by the $^{14}NH_4$ produced by the remineralisation process, Glibert et al., 1982) and DON production (Bronk et al., 1994) induce an underestimation of V (as they provoke an overestimation of A_d, the denominator in Eq. (1)). In oligotrophic water, uptake fluxes for phytoplankon could be underestimated by about 50% because of isotopic dilution (Glibert et al., 1982) and 15% because DON production (Slawyk et al., 2000). We employed a relatively short incubation time to minimise (but not to suppress) these effects and to avoid the complete exhaustion of substrate. We consider our values as

representative of the real order of magnitude of in situ uptake rates.

The V_{NO3} and V_{NH4} of SPOM were 10-1000 times higher than those of benthic producers. The *V* for macroalgae were intermediary between SPOM values and other benthic producers. Seagrass leaves and epiphytes showed the lowest values. This observation corresponds to the functional scheme described by different authors in eutrophic or mesotrophic ecosystems (e.g., Duarte, 1995; Pedersen and Borum, 1996; Valiela et al., 1997). The Fare highly variable and the causes of this variability are unclear, although they are biologically significant. We are unable to establish a clear relation between one environmental factor and specific uptake rate variations. The most evident relation appears in February-April 1999 when the V_{NO3} of SPOM, seagrass and macroalgae are the highest and correspond to the highest NO_3 concentrations in the water column.

With N uptake and N biomass measurements, we calculated the N uptake fluxes by the different producers (µg N m^{-2} h^{-1}). SPOM results were integrated on a water column 10 m in depth, assuming that its distribution is homogeneous for this height (e.g., Brohée et al., 1989). The total N uptake flux was minimum in October 1997 and maximum in February 1999 (Fig. 8). Maximal fluxes were recorded when phytoplankton biomass and V_{NO3} were maximum. This contrasts with the situation observed in 1998 when phytoplankton biomass and NO_3 concentrations were low. The occurrence of phytoplanktonic bloom in Revellata Bay relies on the seasonal entrance of deep and nutrient enriched waters. This entrance is closely related to the occurrence of N-NE winds (Brohée et al., 1989; Skliris et al., 2001). It appears that this occurrence was significantly lower in 1998 than in 1999 (Meteo France, unpublished data, Calvi airport). The difference of N uptake fluxes between February 1998 and 1999 are mainly due to the increase in SPOM uptake, and not to variation of benthic plant uptake.

When the uptake fluxes are integrated on a water column 10 m in depth, the contribution of benthic producers to N uptake ranged from 20% to 70% of the total uptake flux (mean: 40%) (Fig. 8). The epiphytic community seems to play a minor role in these fluxes, which contrasts with the results of Dudley et al. (2001) in a mesotrophic estuary of the Australian coast. The contribution of benthic producers could appear higher than expected from specific uptake measurements. Indeed, specific uptakes *(V)* for SPOM are one to three orders of magnitude higher than those of other producers. However as the benthic producers constitute the majority of the N particulate biomass of the ecosystem at 10 m depth, the difference in specific uptake rates appears partly compensated by the difference in N biomass. Temporal variation of N uptake flux in the ecosystem is therefore not only related to *V* variation, but also to N biomass variation.

Of course, if we consider the N uptake fluxes in the whole Revellata Bay, and not only for 10 m depth water column, the N uptake flux by the phytoplankton clearly becomes dominant, as phytoplankton is present in the whole volume of the bay, while the extension of benthic primary producers is limited to the bottom surface area from 0 to about 40 m depth. We performed a rough estimation of N stocks and uptake fluxes in February-March 1999 and May-June for the whole Revellata Bay (Fig. 9). For this purpose, we used biomass and uptake measured at 10 m depth, an approximation of the bay volume and the known area covered by the different benthic communities (Janssens, 2000).

During the phytoplanktonic bloom, nitrate and ammonium uptakes have the same importance. After the bloom, and probably most of the year, the uptake of ammonium is largely dominant, showing that pelagic primary production in Revellata Bay is mainly based on nitrogen regenerated in the water column. Sediment could also be a significant source of ammonium. Indeed, Gobert et al. (2002) show the existence of positive out-fluxes of nutrients from seagrass sediment to the above water column.

In the N uptake budget at the scale of the bay (Fig. 9), benthic contribution to N uptake flux is reduced to 5-10% of the total N uptake flux. However, the contribution of microphytobenthos to the N uptake flux, which was not assessed in this study, should increase the contribution of benthic primary producers in the nitrogen budget of the Revellata Bay.

The contribution of benthic macrophytes to the total N flux is relatively low, but it constitutes a significant transfer of pelagic N into the benthic compartment. The benthic plants act as a biological pump incorporating the pelagic N into the benthic compartment for a time longer than the characteristic time of phytoplankton dynamics (month-years vs. day-week). Most of this N incorporated in the macroalgae and in *P. oceanica* seasonally returns in the pelagic compartment by the trophic or the detritic pathways. For example, the N turnover time in *Posidonia* leaves of Revellata Bay was estimated by a long-term N experiment to be about 15 months (Lepoint et al., 2002a). However, if N is integrated in the belowground material of the seagrass bed, sequestration time can be several years (up to a thousand years). Indeed, the belowground compartment of *P. oceanica* meadows are known to be a sink for diverse elements such as N or P (Mateo and Romero, 1997; Mateo et al., 1997).

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***Fig. 8**. Mean values (a) of N uptake fluxes measured between October 1997 and June 1999 in Revellata Bay at 10 m depth and relative contributions (b) of benthic and planktonic primary producers to these fluxes. Sums of nitrate and ammonium uptake fluxes.*

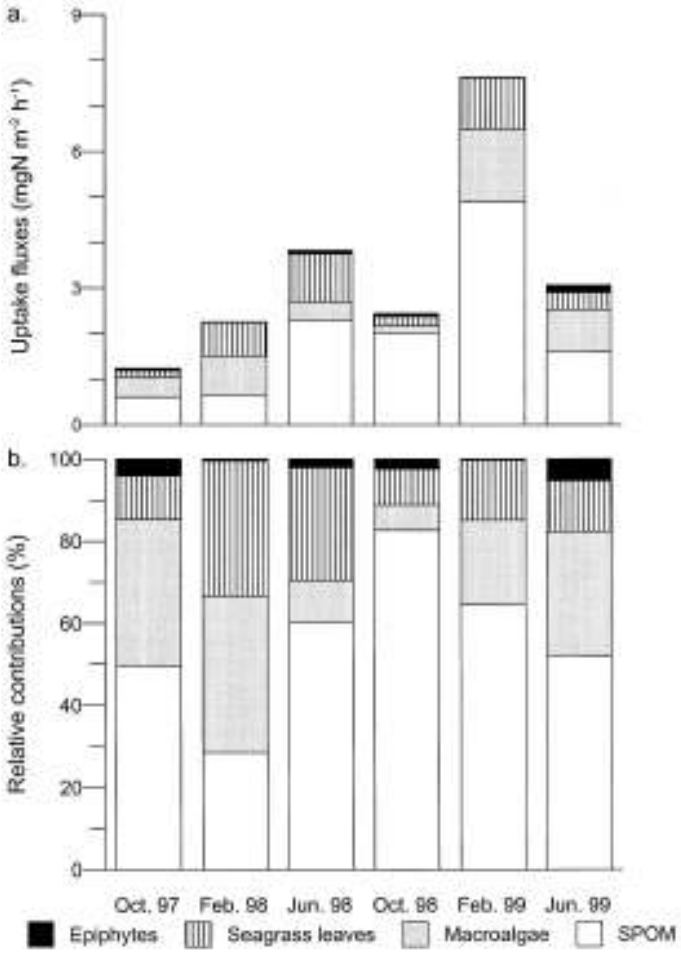
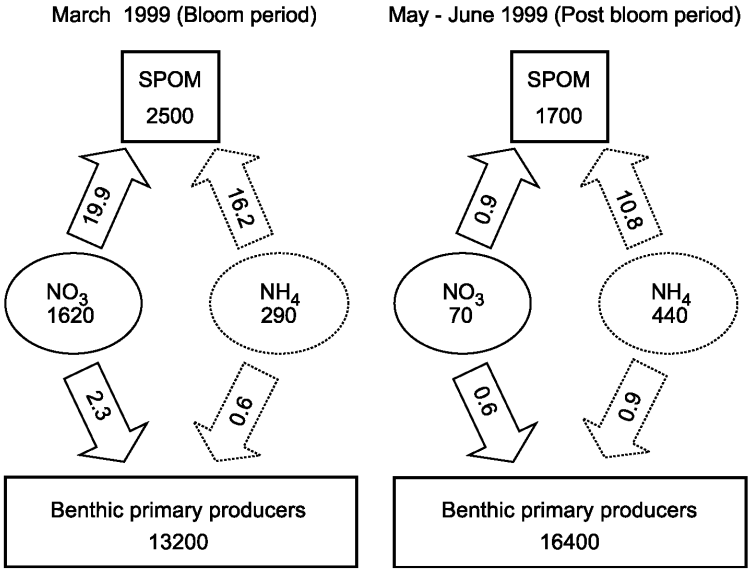


***Fig. 9.** Nitrogen stocks and uptake fluxes in Revellata Bay during and after the phytoplanktonic bloom in spring 1999. N stocks are expressed in kg N Bay^{-1} and N uptake fluxes in kg N h^{-1} Bay^{-1}. Benthic primary producers stocks correspond to the sum of the N stock of macroalgae, Posidonia leaves and their epiphytes. Belowground biomass of Posidonia is not taken into account.*



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