BMC Ecology

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# *Posidonia oceanica* meadow: a low nutrient high chlorophyll (LNHC) system?

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Published: 21 August 2002

*BMC Ecology* 2002, **2**:9

Received: 16 May 2002
Accepted: 21 August 2002

This article is available from: http://www.biomedcentral.com/1472-6785/2/9



## Abstract

**Background:** In spite of very low nutrient concentrations in its vicinity – both column and pore waters-, the *Posidonia oceanica* of the Revellata Bay displays high biomass and productivity. We measured the nutrient fluxes from the sediment into the water enclosed among the leaf shoots ("canopy water") to determine if it is possible source of nutrients for *P. oceanica* leaves.

**Results:** During the summer, the canopy water appears to act as a nutrient reservoir for the plant. During that period, the canopy water layer displays both a temperature 0.5°C cooler than the upper water column, and a much higher nutrient content, as shown in this work using a very simple original technique permitting to sample water with a minimal disturbance of the water column's vertical structure.

Despite low nutrient concentrations in pore water, mean net fluxes were measured from the sediment to the canopy water. These fluxes are sufficient to provide 20% of the mean daily nitrogen and phosphorus requirement of the *P. oceanica* shoots.

**Conclusion:** An internal cycling of nutrients from *P. oceanica* senescent leaves was previously noted as an efficient strategy to help face low nutrient availability. The present study points out a second strategy which consists in holding back, in the canopy, the nutrients released at the water-sediment interface. This process occurs when long leaves, during poor nutrient periods in the water column, providing, to *P. oceanica*, the possibility to develop, high biomass, high chlorophyll quantities in low nutrient environment (a Low Nutrients High Chlorophyll system).

## Background

The Revellata Bay (Corsica, Northwestern Mediterranean) is considered as a typical oligotrophic area characterised by quasi permanent low level of nutrient related to unimportant agricultural and industrial activities, small local population, low rainfall regime and low runoff from river. Only occasionally, when winds are blowing for several days from NE, a significant input of nutrient rich deep water occurs [1,2]. Recently, a nitrogen and silica limitation of the surface waters, occurring in the last decade, has been pointed out with a drastic reduction of phytoplankton biomass in relation with an increase of the sea surface water temperature. The nutrients and the chlorophyll *a* concentrations in the water column were low, even during the winter-spring phytoplankton bloom (*i.e.* 0.2–0.3 µmol $L^{-1}$ for nitrate and <0.4 µg $L^{-1}$ chlorophyll *a* concentrations in February-March) [3]. Compared to other meadows [4], the nutrient pore water concentrations are very low in the Revellata Bay (table 1) while its canopy displays a biomass as large as many other meadows in the

**Table 1: Porewater nutrient concentrations Pore water nutrients in the sediment beneath meadows of different species (μmol $L^{-1}$) ([1]ammonium data, [2]nitrate data).**

| | Site | Total Nitrogen | Phosphorus | Reference |
|---|---|---|---|---|
| | | **Seagrass** | | |
| Meadows world-wide | | 86[1]; 3.4[2] | 12 | [35] |
| | | **Posidonia oceanica** | | |
| Spain | | | | |
| | Blanes | 645[1+2] ± 776 | 6.0 ± 8.4 | [4] |
| | Giverola | 297[1+2] ± 376 | 10.8 ± 12.3 | |
| Corsica | | | | |
| | Revellata Bay | 6[1]; 0.3[2] | 15 | [36] |
| | | 6.9[1+2] ± 2.9 | 1.3 ± 0.6 | [37] |

Mediterranean Sea [5,6]. The meadow is highly productive – leaf annual primary production estimated to 730 g of dry weight $m^{-2}$[7] -, even more than in some regions like Banyuls and Sardinia.

Recently, seagrasses have been shown to profit from mechanisms which diminish their dependence on the nutrient availability. One of these mechanisms appears to be related to the leaf longevity. An extended leaf longevity lowers the frequency of leaf formation and extends the time available to reclaim nutrients from mature leaves, thus reducing nutrient demands [8]. In this regard, the high *P. oceanica* leaf longevity (345 days) appears to be an advantage compared to other seagrass species (mean leaf longevity: 88 days; range: 4–345 days). [9] report a nitrogen and phosphorus resorption efficiency of 20.4% and 21.9% in seagrasses. In *P. oceanica*, these resorption efficiencies have been estimated to 37% and 44% for nitrogen and phosphorus respectively by [10]. In the Revellata Bay, the annual nitrogen requirements of *P. oceanica* are encountered by the leaves uptake for 25 to 45%, by the roots for 15 to 35% and by an internal recycling for 40% [11,12]. This, while important, is however not sufficient to explain the high primary production regarding the low nutrient availability.

At variance with the HNLC regions (High-Nitrate, Low-Chlorophyll) encountered in the North and South Equatorial Pacific Ocean and in the Arctic [13] where standing stocks of phytoplankton remain low in spite of high nitrate and phosphate concentrations, the *P. oceanica* meadow of the Revellata Bay apparently behaves as a LNHC system (Low-Nutrient, High-Chlorophyll). The question then arises how *P. oceanica* meadows manage apparent very low nutrient availability to produce high quantities of living matter; for example the *P. oceanica* seagrass bed of the Revellata Bay displays a net primary production of about 230 gC $m^{-2}$ $year^{-1}$[5,7].

These high biomass and production in spite of very low levels of nutrients (LNHC) in the vicinity of the seagrasses observed in Revelatta Bay correspond to the characteristics encountered in tropical zones [14,15]. Nutrient fluxes have been estimated in a tropical zone meadow [16] and represent 0.53–1.56 gN $m^{-2}$ $year^{-1}$ and 0.14–0.42 gP $m^{-2}$ $year^{-1}$.

In this work, we have examined the nutrient conditions in the vicinity of the *P. oceanica* meadow of the Revellata Bay (pore water, canopy water and column water) and we have estimated the nutrient fluxes (nitrite+nitrate, ammonium and phosphate) from the sediment into the canopy using a benthic chamber. The results were used to evaluate the potential contribution of this source to meadow production.

## Results

### *The P. oceanica leaves and water canopy*

The mean length of the leaves was 64.1 ± 18.8 cm (n = 43) and 18.0 ± 11.1 cm (n = 78) in June and October 1999 respectively. In June, the sediment was not visible through the canopy and the canopy water was 0.5°C cooler (n = 10) than in the upper water column. A typical visible water transition layer of a high temperature gradient was vis-

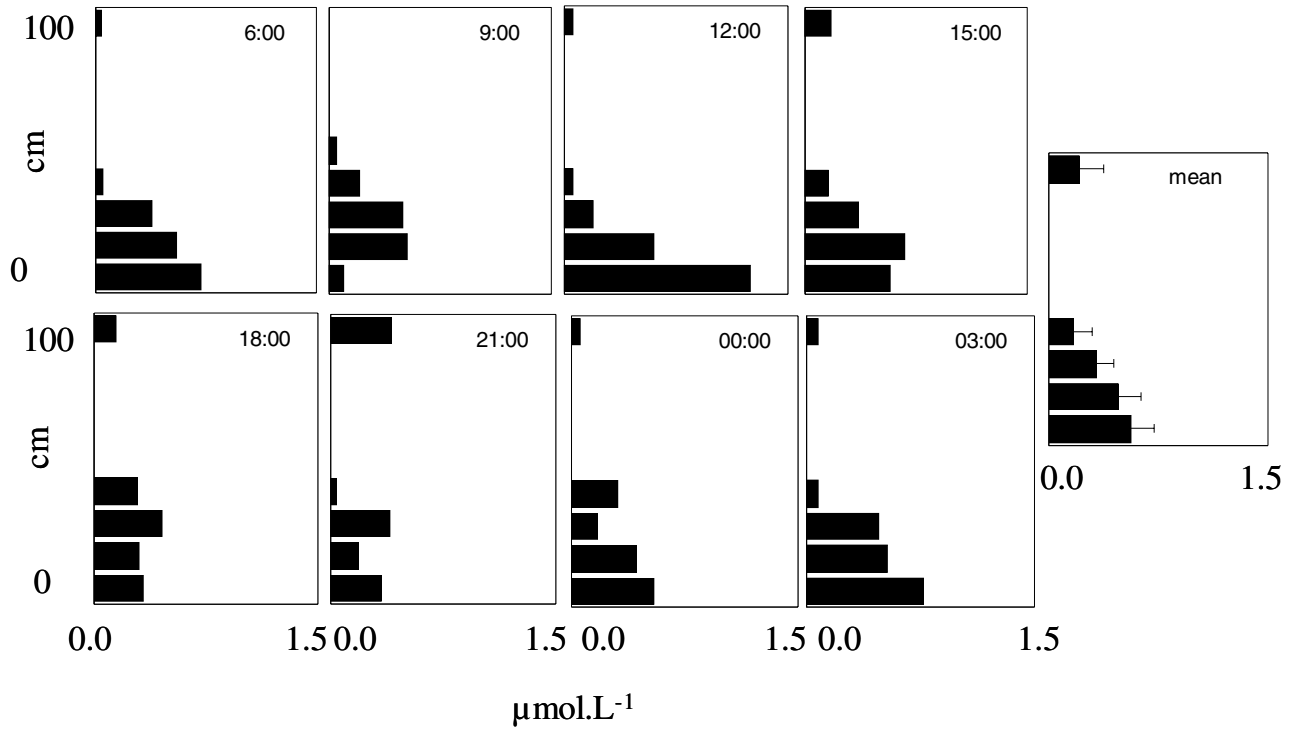


**Figure 1**
**Nitrite+nitrate profile in the canopy water in June 1999** Nitrite+nitrate concentrations (µmol $L^{-1}$) of the canopy water at 10, 15, 30, 50 and 100 cm above the sediment in the *P. oceanica* meadow of the Revellata Bay in June 1999.

ually observable at this interface. In October, no temperature difference was observed between the canopy and column waters (n = 10) and the sediment was visible among the shoots. At the neighbouring of the study site, the shoot density was 415 ± 156 shoot $m^{-2}$ (n = 20), measured in October 1999.

With the sample collection tube system, in June 1999, the water sample obtained at 5, 15, 30 cm was the canopy water. The mean nutrient concentration in this water layer was 0.50 ± 0.46 µM; 0.19 ± 0.09 µM and 0.08 ± 0.08 µM for $NH_4^+$, $NO_2^-$+$NO_3^-$ and $PO_4^{3-}$ respectively. All the nutrients generally displayed higher concentrations in the first 15 cm above the sediment (figures 1,2,3). However, during this period, nutrients in the water column, 5 metres above the seagrass bed, were generally under the detection limit and in all cases, these concentrations were lower than in the canopy, 15 cm above the sediment.

In October 1999 (figures 4,5), the $PO_4^{3-}$ concentrations above and in the canopy were generally lower than the detection limit (data not shown). The temporal variations of N concentration gradients were significant. The first 12 hour (9:00, 11:00, 15:00, 22:00, 7:00 samples), data were obtained during a storm (winds of 17 m/s: data from Météo France – Calvi), during which water column nutrient concentrations were homogeneous in and above the canopy (mean 1). After 12 hours, when a calm sea was reestablished (10:00 and 15:00), the gradient reappeared (mean 2). The nutrient concentrations of the water column above and in the canopy were similar, in opposition to the data obtained in June.

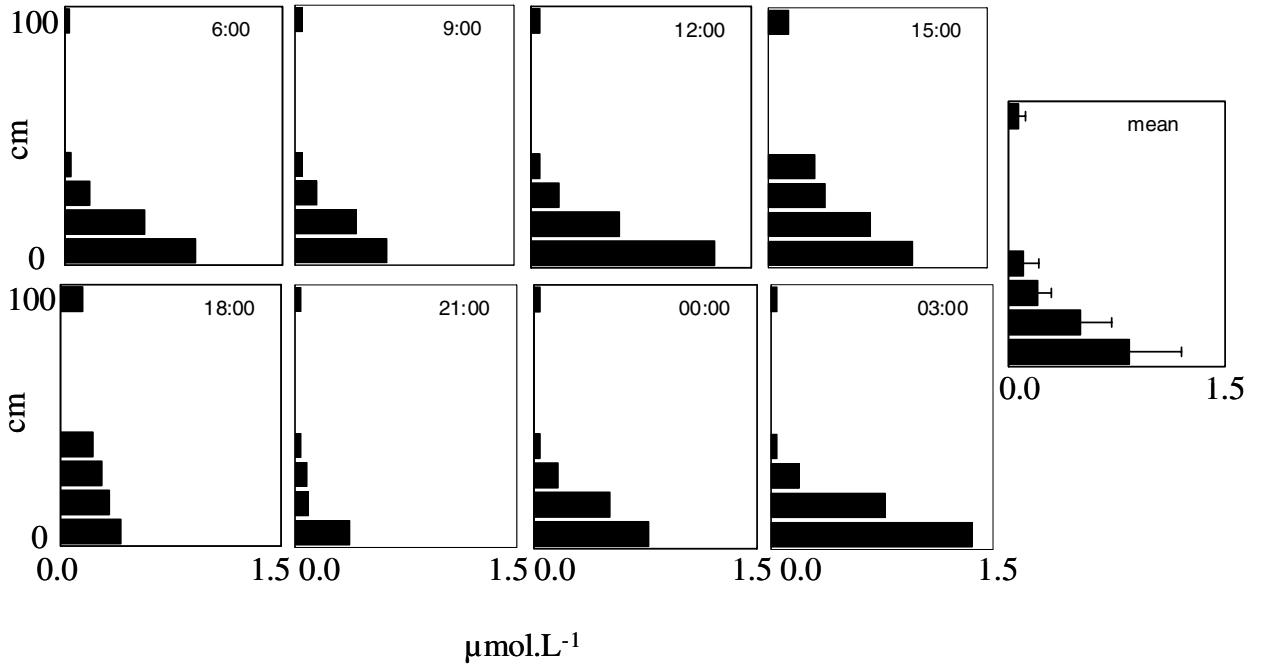


**Figure 2**
**Ammonium profile in the canopy water in June 1999** Ammonium concentrations (µmol $L^{-1}$) of the canopy water at 10, 15, 30, 50 and 100 cm above the sediment in the *P. oceanica* meadow of the Revellata Bay in June 1999.

### *Fluxes*

Table 2 shows the mean fluxes of nitrite+nitrate, ammonium and orthophosphate estimated with the benthic chamber and with the benthic cylinder in February, June, October 1997 and in June 1999 respectively. The nutrient fluxes were maximum in February and were minimum for the ($NO_2^-$+$NO_3^-$) and $PO_4^{3-}$ in June.

## Discussion

### *The P. oceanica leaves and water canopy*

The *P. oceanica* meadow of the Revellata Bay at 10 m depth is to be considered a dense meadow according to [13]. The mean length of the leaves of *P. oceanica* shoots is in good agreement with data obtained since 1975 at same periods of the year at 10 m depth [5,6]. The seasonal variation between June and October 1999 corresponds to the annual leaf growth cycle: maximum lengths reached in June or July, decrease from August or September (related to a great appearance of necrosis on the tips) to December or January during heavy storms with a high proportion of leaf fall. From February on, the leaves length regularly increases (*i.e.*[5,6]).

The sample collection tube system has permitted to point out the effect of the *P. oceanica* canopy on the nutrient distribution from the sediment to the column water. During the summer, when the leaves are long, the meadow forms a barrier enclosing the water and its nutrients in the canopy. The canopy water is a specific layer with measurable different chemical (nutrients) and physical (temperature) properties than the column water. During the winter, the leaves are shorter and the "barrier" effect of the canopy is

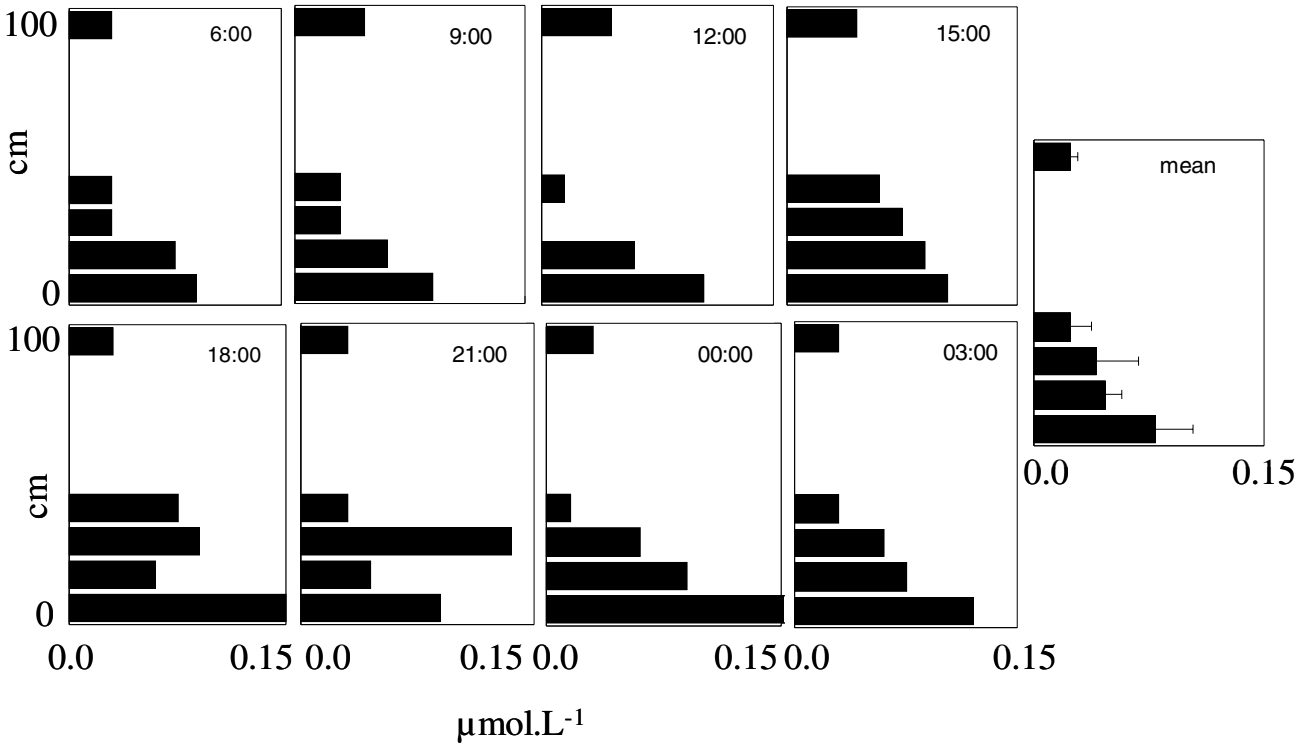


**Figure 3**
**Orthophosphate profile in the canopy water in June 1999** Orthophosphate concentrations (µmol $L^{-1}$) of the canopy water at 10, 15, 30, 50 and 100 cm above the sediment in the *P. oceanica* meadow of the Revellata Bay in June 1999.

diminished, furthermore higher currents associated with seasonal storms homogenised all the water column to the sediment. It is known that the seagrass canopies have the capacity to modify current velocity and waves [18,19] causing a decrease in water movement on the sediment water interface and affecting nutrient fluxes from sediment to column water.

### *Fluxes*

Our results about the nutrient fluxes, obtained with the benthic chamber, on the sandy small patches of the *P. oceanica* meadow in the Revellata Bay are consistent with previous data obtained on flux measurements in seagrass meadow (*i.e.* 228 to -363 µmol N – ammonium – $m^{-2}$ $d^{-1}$ in [20]), much lower than fluxes estimated till now in estuaries and intertidal zones (*i.e.* -2191 to -19704 µmol N – ammonium – $m^{-2}$ $d^{-1}$ in [21]).

The ranges of our data were large, such a high variability, already mentioned by other authors, is due to both small scale heterogeneous physical, chemical and biological processes of the sedimentary environments and actual temporal variability of nutrient fluxes [19]. For example, [23] noted that the benthic fluxes showed a good relationship with bioturbation.

Concerning the seasonal variation, our results are not similar to some literature data which have pointed out a direct relation between the magnitude of the fluxes and the water temperature. Generally, minimum fluxes have been obtained during low temperature periods [24,25]. In fact,

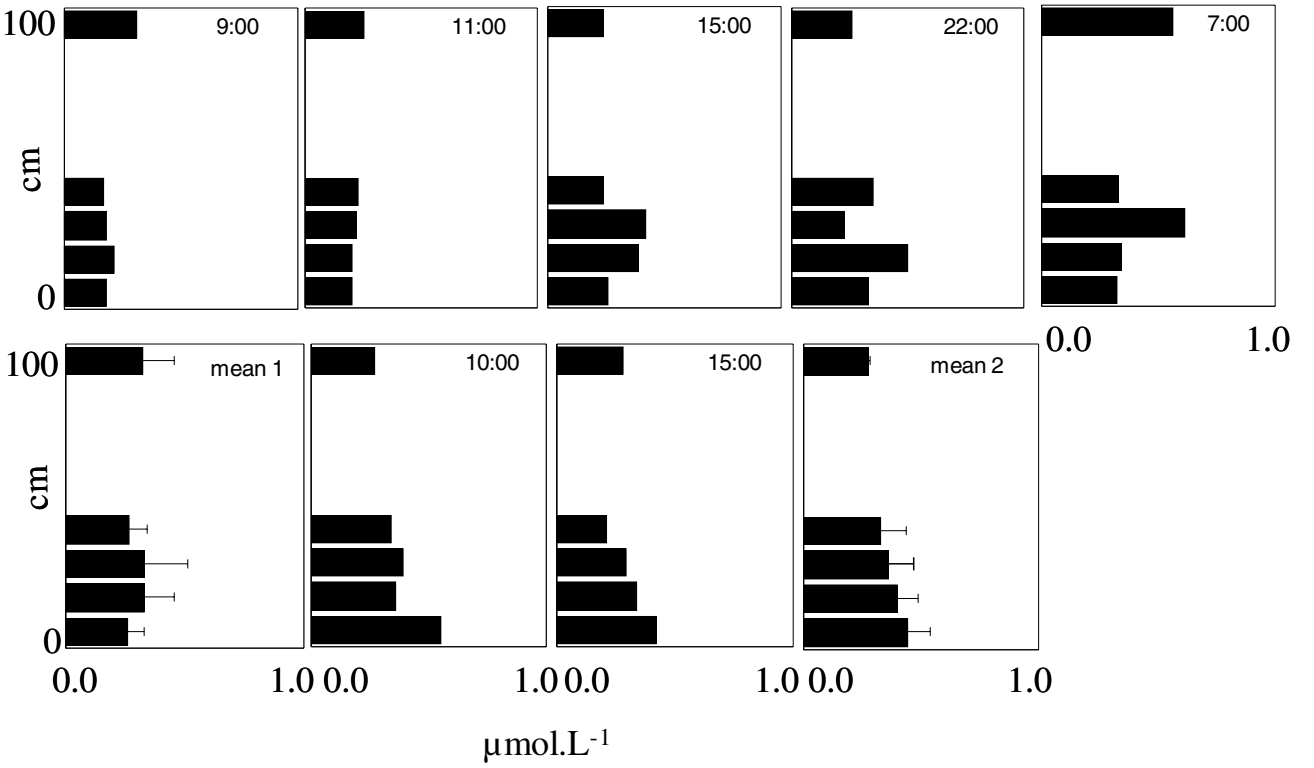


**Figure 4**
**Nitrite+nitrate profile in the canopy water in October 1999** Nitrite+nitrate concentrations (µmol $L^{-1}$) of the canopy water at 10, 15, 30, 50 and 100 cm above the sediment in the *P. oceanica* meadow of the Revellata Bay in October 1999.

like in other Mediterranean meadows (see [26]), in the Revellata Bay, registered water temperature were higher in October than in June and than in February.

Taking into account mean values, the fluxes calculated in June 1997 with the benthic chamber are higher as compared to the fluxes calculated in June 1999 using the cylinder (table 2). This probably is not an artefact due to the different methods used (benthic chamber and cylinder) as previously discussed in [24] and [27] but reflects the interannual variation of environmental conditions like the pore water nutrient content. In June 1997, the nutrient gradients between the pore water and the column water was higher than in June 1999 related to higher nutrients concentrations in the pore water. The releasing of nutrients from the sediment is obviously promoted by the higher vertical gradient. In fact, for the $NH_4^+$ and (nitrite+nitrate), in spite of the great variation of our data, a direct correlation appeared between the mean concentration gradient between the pore water and the canopy water and the mean fluxes (table 3). That means that our calculated nitrogen fluxes from the nutrient concentration evolution with time (benthic chamber) and from the concentration gradient in the column water (benthic cylinder) directly correspond with the measured gradient concentration between pore water and canopy water.

Our results obtained both with the benthic chamber and the cylinder show that N and P from sediment diffuse into the water column. In spite of the low concentrations encountered in the Revellata Bay, both in pore and column

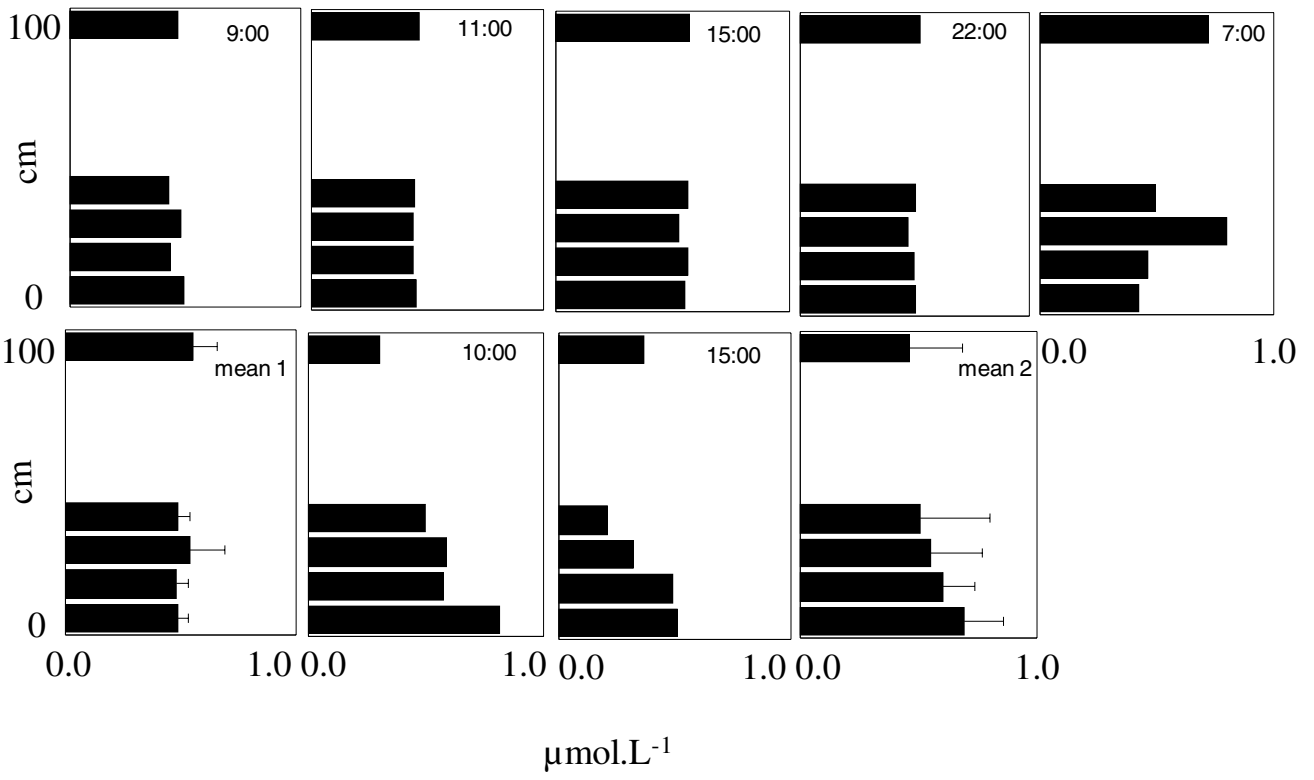


**Figure 5**
**Ammonium profile in the canopy water in October 1999** Ammonium concentrations (µmol $L^{-1}$) of the canopy water at 10, 15, 30, 50 and 100 cm above the sediment in the *P. oceanica* meadow of the Revellata Bay in October 1999.

**Table 2: Nutrient fluxes Nitrite+nitrate, ammonium and orthophosphate fluxes (µmol $m^{-2}$ $day^{-1}$) calculated from results obtained in February, June and October 1997 with a benthic chamber and in June 1999 with a benthic cylinder settled in the *P. oceanica* meadow of the Revellata Bay at 10 m depth (mean ± standard deviation; number of observation into brackets).**

| | Method | $NO_2^-+NO_3^-$ | $NH_4^+$ | $PO_4^{3-}$ |
|---|---|---|---|---|
| February 1997 | chamber | -495 ± 573 (2) | -5700 ± 763 (2) | -1395 ± 1018 (2) |
| June 1997 | chamber | 98 ± 81 (8) | -528 ± 547 (8) | -59 ± 243 (10) |
| October 1997 | chamber | -452 ± 423 (2) | 133 ± 242 (8) | -862 ± 995 (8) |
| June 1999 | cylinder | -77 ± 98 (8) | -60 ± 98 (8) | -2 ± 6 (8) |

water, the fluxes of nutrients across sediment to the canopy water are a potential important source of nitrogen and phosphate for the *P. oceanica* canopy.

It is now well known that seagrasses use ammonium, nitrate and phosphate found in both the column and sediment waters (see [8,28]). Nutrients levels available for seagrass meadows are generally low and the biomass formation is often limited by nutrient availability. Among the seagrasses, *P. oceanica* have been shown to diminish its dependence on nutrients by an important leaf longevity which allows a better efficiency of nutrients recycling from senescent leaves.

## Conclusions

In the Revellata Bay, at 10 metres depth, the nitrogen resorption of *P. oceanica* leaves has been shown to represent 40% of the annual nutrient budget of the plant [11,12]. The mean daily nitrogen requirement of the plant covering 1 $m^2$ has been estimated to 1500 µmol [11,12]. Considering a weight N/P Redfield ratio of 10 for *P. oceanica*, the similar phosphorus requirement could be estimated to 150 µmol P $m^{-2}$ $d^{-1}$. From the present work, the mean annual nutrient fluxes (*i.e.* -31, -269 and -37 µmol $m^{-2}$ $d^{-1}$ for $NO_2^-$+$NO_3^-$, $NH_4^+$ and $PO_4^-$ respectively) across the sediment could provide 20% of the nitrogen and phosphorus requirement of the plant.

However, it must be taken into account that primary producers (epiphytes, phytoplankton...) occur in the canopy and in its vicinity competes with P. oceanica leaves for these nutrients released by sediments. In this regard, during calm weather events, often occurring during the summer, the appearance of a nutrient rich layer in the canopy is an additional factor which favour *P. oceanica* vs phytoplankton during a period when the nutrients in the column water are often below the detection limits in the Revellata Bay (as measured by [3]).

Such a "barrier" effect played by the leaves during the period of high biomass which corresponds with low nutrient concentrations in the column water in the Revellata Bay is therefore to be added to the known meadow strategies which permit a high development of biomass in oligotrophic zone. To conclude, the apparent paradox of *P. oceanica* meadows growing in very oligotrophic environments can be explained by the addition of two strategies:

- the high leaf longevity which allows a significant internal cycling of nutrients from senescent leaves,

- the formation by the canopy of a nutrient rich water layer which largely increases the nutrient availability for the meadow during periods when nutrients are virtually absent of the column water.

## Materials and Methods

The *P. oceanica* meadow of the Revellata Bay (Calvi, Corsica) covers about 60% of the total surface of the bay [29] between 5 m and 38 m depth. All samplings and experiments were carried out at ten metres depth in front of the Oceanographic station STARESO (figure 6).

Ten shoots were collected by Scuba diving in June and October 1999, at 10 metres depth to record biometrical data. The shoots were weighed after lyophilisation. The juvenile, intermediate and adult leaves were separated and measured according to [30]. The shoot density (number of shoots per square metre) was estimated by counting the number of shoots within a 30 cm diameter circle according to [31].

**Table 3: Relation between fluxes and nutrient concentrations Ammonium and nitrite+nitrate concentrations (µmol L-1) in the column, canopy and pore waters in the P. oceanica meadow of the Revellata Bay at 10 m depth (mean ± standard deviation; number of sample into brackets); correlation coefficient (r2) between the concentration gradient at the water-sediment interface (canopy and pore-water) and the fluxes (from table 2) at this interface.**

| | Column water | Canopy water | Pore water | $r^2$ |
|---|---|---|---|---|
| **$NH_4^+$** | | | | |
| February 1997 | 0.10 ± 0.10 (3) | ≤ 0.05 (21) | 3.5 ± 5.0 (22) | 0.62 |
| June 1997 | 0.05 ± 0.03 (5) | 0.07 ± 0.04 (16) | 3.7 ± 3.5 (51) | |
| October 1997 | 0.14 ± 0.09 (7) | 0.15 ± 0.12 (14) | 2.8 ± 2.1 (10) | |
| June 1999 | 0.10 ± 0.06 (15) | 0.50 ± 0.50 (16) | 1.3 ± 2.6 (10) | |
| **$NO_2$+$NO_3$** | | | | |
| February 1997 | 0.07 ± 0.03 (3) | 0.07 ± 0.04 (21) | 0.8 ± 2.1 (22) | 0.90 |
| June 1997 | 0.15 ± 0.04 (3) | 0.18 ± 0.04 (16) | 0.2 ± 0.4 (51) | |
| October 1997 | 0.18 ± 0.09 (7) | 0.09 ± 0.04 (14) | 0.7 ± 0.7 (10) | |
| June 1999 | 0.05 ± 0.03 (15) | 0.19 ± 0.09 (16) | 0.2 ± 0.2 (10) | |


**Figure 6**
**Experimental site** Location of the Revellata Bay and Research Station STARESO near Calvi along the Corsican coast.

The canopy and column water temperatures were measured with a mercury thermometer (0,1°C) in June and in October 1999.

The nutrient concentration gradients in the canopy water were measured with an original sample collection tube system. The fluxes across the sediment were estimated by the use of a classical benthic chamber. The nutrient concentration gradients in the water column were measured with a benthic cylinder. The three systems are hereafter described.

***The sample collection tube system (figure 7a)***
The vertical profiles of the column water in the canopy were obtained with a set of tubes fixed at known depths in the water column such as they allow a vertical sampling of undisturbed water. A diver carefully attached a syringe to the lowest tube (5 cm height) and sucked water in, ejecting the first 65 ml of sample (volume of the tube) and sampling the next 45 ml of water. The same procedure was then repeated with 4 other syringes for the 15, 30, 50 and 100 cm heights. Additional water column samplings were made above the seagrass bed at 5 m depth. The water samples were frozen.

Measurements have been performed every 3 hours a day, in June and October, when the height of the canopy is high and low respectively.

***The classical benthic chamber (figure 7b)***
An opaque cylindrical shape plexiglas chamber was used (diameter 12 cm, height 6 cm). Twenty four hours before starting the experiment, the base of the benthic chamber

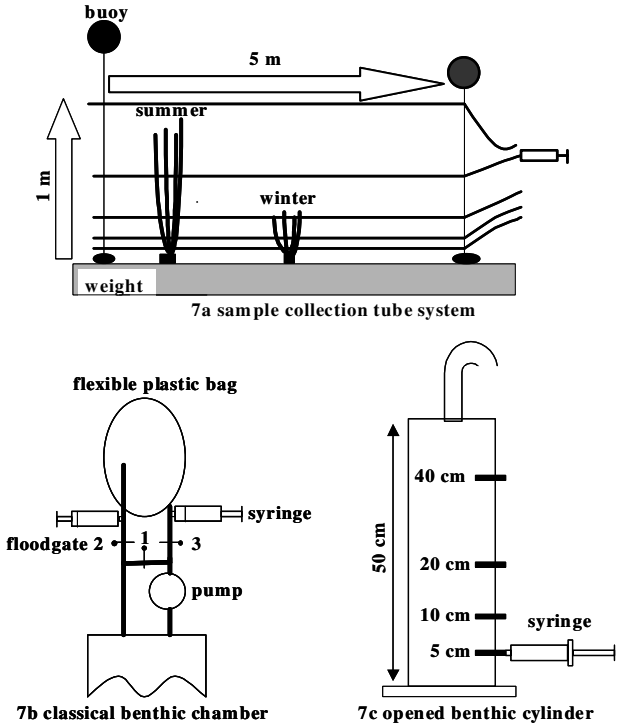


**Figure 7**
**Diagrams of apparatus** Diagrams of the apparatus used to assess the concentration gradient in the canopy: sample collection tube system (7a) and to assess the nutrient fluxes: benthic chamber (7b) and benthic cylinder (7c).

was carefully pushed in the sand of a small patch (20 $cm^2$) in the sediment of the meadow.

At the beginning of the experiment, the top of the chamber was screwed on, the pump, tubing and flexible plastic bag were settled by a diver. The pump (discharge of 0.5 L $min^{-1}$) prevents water inside the chamber from stratifying, so that samples obtained are representative of the whole volume of the chamber.

During incubation, sampling was performed periodically ($T_0$, $T_4$, $T_8$, $T_{16}$, $T_{20}$ and $T_{32}$ minutes) to determine the nutrient concentrations. The samples were collected following a simple procedure: seven syringes were filled with column water (syringe 1 to 7). At $T_0$: the pump was switched on, floodgate n°1 closed, floodgate n°2 and n°3 opened; syringe 1 and syringe $T_0$ were plugged in. After 3 minutes (time required for a complete homogenisation of the water inside the system), the floodgate 1 was opened, the 2 and 3 were closed, 40 ml of water was collected with syringe $T_0$ after what the 40 ml of the syringe 1 were injected into the system. The floodgates 2 and 3 were opened again while the floodgate 1 was closed. The samples were frozen directly after collection.

The measurements have been performed in February, June and October in 1997.

### *The opened benthic cylinder (figure 7c)*

The benthic cylinder is a plexiglas chamber (50 cm height, diameter: 12 cm), with a small opening on the top (diameter: 1.5 cm). Once the cylinder carefully settled on the sandy patch sediment of the meadow by a diver, the column water was collected inside owing to a fixed tube system at 5, 10, 20 and 40 cm above the sediment with 4 syringes. This procedure was regularly repeated every 3 hours during a day.

### *Pore water sampling*

Pore water was sampled by Scuba diving with PVC syringes connected a 10 cm long needle entirely pushed in the sediment at 10 cm depth; the water collected was directly filtered through a Whatman GF/C (1.2 µm).

### *Nutrient analysis*

Nitrogen ($NH_4^+$ and nitrite+nitrate) and orthophosphate concentrations in the water (pore, canopy and column) were analysed with an autoanalyser (SKALAR) by the classical method [32] for an automated system [33] adapted for oligothophic seawater (detection limits: 0.1, 0.02 and 0.05 µM for ammonium, nitrite+nitrate and orthophosphate respectively).

According to the first law of Fick, the flux of matter across a surface ($J_D$, µmol $cm^2$ $d^{-1}$) can be estimated as follow:

$$J_D = D_s (\partial C/\partial z)$$

where

$D_s$: the diffusion coefficient ($cm^2$ $s^{-1}$),

$(\partial C/\partial z)$: the concentration gradient across the sediment water-interface.

Positive values indicate a nutrient movement from the water column into the sediment.

A diffusion coefficient $D_s$ of 16 $10^{-6}$ $cm^2$ $s^{-1}$ was used for $NH_4^+$ and ($NO_2^-$+$NO_3^-$) and of 7 $10^{-6}$ $cm^2$ $s^{-1}$ for orthophosphate according to [34] for marine sediment.

### *Flux calculations*

In the benthic chamber, the volume of water remained constant during the incubation and the fluxes were calculated from the slope of the concentration values versus

time multiplied by the ratio of chamber volume to the covered surface area. Internal concentrations were previously corrected to take into account the dilution due to subsequent sampling.

The fluxes obtained by benthic chambers incorporate diffusion and bioturbation effects on porewater solute exchange.

In the cylinder, the fluxes were calculated considering that the water movement during the sampling was negligible.

Data are presented as mean ± standard deviation, minimum and maximum.

## Authors' contributions

SG: design of the study, in situ work, measurement, calculation and redaction of the manuscript.

NL: *in situ* work and measurement

JMB: coordinator of ARC and FRFC, critical review of the draft

## Acknowledgements

This work was supported by grants from the Belgian National Fund for Scientific Research (FRFC 2.4570.97) and from the French Community of Belgium (ARC-97/02-212). We acknowledge G. Lacroix for providing critical comments on methodology.

The authors acknowledge *R. Biondo* for providing technical and diving assistance and also thank *C. Beans* for correcting grammatical and spelling mistakes.

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