# Community metabolism in temperate maerl beds. II. Nutrient fluxes

## Sophie Martin[1,2,*], Jacques Clavier[1], Laurent Chauvaud[1], Gérard Thouzeau[1]

[1]**LEMAR, Laboratoire des Sciences de l'Environnement Marin, UMR CNRS 6539, Institut Universitaire Européen de la Mer, Technopôle Brest-Iroise, Place Nicolas Copernic, 29280 Plouzané, France**

[2]***Present address:*  Laboratoire d'Océanographie de Villefranche-sur-Mer, CNRS, and Université Pierre et Marie Curie–Paris VI, BP 28, 06234 Villefranche-sur-Mer Cedex, France**

ABSTRACT: Maerl community ammonium ($NH_4^+$), nitrate + nitrite ($NO_3^- + NO_2^-$), dissolved silicic acid (DSi) and phosphate ($PO_4^{3-}$) fluxes were measured seasonally in the Bay of Brest (France). Nutrient exchanges at the sediment–water interface were assessed using benthic chambers. Nutrient fluxes differed between light and dark conditions, and fluctuated seasonally, with minimum values in winter and spring and maximum values in summer and autumn. In the dark, net community fluxes of $NH_4^+$, $NO_3^- + NO_2^-$, DSi and $PO_4^{3-}$ varied from 53 to 226 µmol N m$^{-2}$ h$^{-1}$, –107 to 70 µmol N m$^{-2}$ h$^{-1}$, 18 to 180 µmol Si m$^{-2}$ h$^{-1}$ and 5 to 19 µmol P m$^{-2}$ h$^{-1}$, respectively. In the light, $NH_4^+$, $NO_3^- + NO_2^-$, DSi and $PO_4^{3-}$ fluxes ranged from 17 to 110 µmol N m$^{-2}$ h$^{-1}$, –223 to –10 µmol N m$^{-2}$ h$^{-1}$, –34 to 112 µmol Si m$^{-2}$ h$^{-1}$ and 1 to 12 µmol P m$^{-2}$ h$^{-1}$, respectively. Temperature, community respiration, gross community production and bottom water dissolved oxygen and nutrient concentrations mainly controlled seasonal fluctuations of benthic nutrient fluxes. Annual net community fluxes of dissolved inorganic nitrogen (DIN), DSi and $PO_4^{3-}$ were 6 g N m$^{-2}$ yr$^{-1}$, 10 g Si m$^{-2}$ yr$^{-1}$ and 2 g P m$^{-2}$ yr$^{-1}$, respectively. Annual gross community uptakes of DIN, DSi and $PO_4^{3-}$ were 12 g N m$^{-2}$ yr$^{-1}$, 9 g Si m$^{-2}$ yr$^{-1}$ and 1 g P m$^{-2}$ yr$^{-1}$, respectively. Nutrient supply from the maerl community to the water column contributed potentially to between 18 and 55 % of the annual phytoplanktonic production in the Bay of Brest.

KEY WORDS:  Calcareous algae · Community metabolism · Nutrient fluxes · Nitrogen · Phosphorus · Silicon

## INTRODUCTION

Benthic communities play an important role in the nutrient cycling of shallow coastal waters (Dalsgaard 2003, Soto-Jimenez et al. 2003, Cook et al. 2004, Eyre & Ferguson 2005, Gibbs et al. 2005). In shallow environments, much of the organic matter decomposition occurs near the sediment–water interface, with associated release of nutrients to the water column (Cowan & Boynton 1996). If microbial degradation of organic materials constitutes one of the main processes in nutrient regeneration, benthic fauna enhances these sediment processes via organic matter consumption, nutrient excretion and stimulation of microbial communities by bioturbation (Gilbert et al. 1998, Newell et al. 2002). In macrophyte-dominated communities, nutrient release to the water column is balanced by autotrophic processes that act as a sink for nutrients

(Valiela et al. 1997, Dudley et al. 2001, Lepoint et al. 2004). Numerous studies have, therefore, highlighted the contribution of phytobenthos in improving water quality by absorption and reduction of nutrients (Soto-Jimenez et al. 2003). Nutrient fluxes at the water–sediment interface have been investigated for seagrass meadows (Eyre & Ferguson 2002, Qu et al. 2003, Lepoint et al. 2004), microalgal-dominated communities (Sundbäck et al. 2000, An & Joye 2001, Cook et al. 2004) and floating macroalgal-dominated communities in eutrophic environments (Viaroli et al. 1996, Eyre & Ferguson 2002). However, despite their large distribution, the influence of slow-growing macroalgal-dominated communities on nutrient cycling is still poorly known.

Maerl beds are distributed worldwide and considered to be among the most diversified benthic ecosystems in temperate environments (Hall-Spencer et al.

2003). They constitute free-living coralline algae, with a complex, branched, twig-like thalli structure that hosts numerous macro- and microalgal epiphytes (Guillou et al. 2002, Grall et al. 2006). Maerl beds are also a habitat for a diversified and abundant community of heterotrophs involved in the recycling of nutrients. Slow-growing macroalgae, such as corallines, have relatively low nutrient requirements (Ferdie & Fourqurean 2004). However, the rich associated micro- and macro-epiphytic algal populations may have a high capacity for primary production and nutrient uptake (Viaroli et al. 1996). Located in the upper layers of sediment, maerl and its associated epiphytic algae may control the exchange of nutrients between the sediment and the water column, as previously reported for benthic microalgae (Krause-Jensen et al. 1999, Dalsgaard 2003).

Despite their wide distribution and their major influence on carbon and carbonate cycling in shallow coastal waters (Martin et al. 2005, 2007, this volume), the role of temperate maerl communities on nutrient fluxes has never been assessed. The aim of the present study was to evaluate their influence on dissolved inorganic nutrient (ammonium, nitrites and nitrates, silicates and phosphates) exchanges across the sediment–water interface, and to assess their contribution to nitrogen, silicon and phosphorus cycling in the shallow coastal waters where they develop.

## MATERIALS AND METHODS

**Study site.** A detailed description of the study site is given in Martin et al. (2007). The field experiments took place at the Rozegat maerl bed (see Fig. 1 in Martin et al. 2007), situated between 0.5 and 2.9 m in depth below Chart Datum, and were carried out seasonally between March 2002 and October 2004 from the RV 'Côtes de la Manche'. Dates of experiments and number of incubations under light and dark conditions for each season are detailed in Martin et al. (2007). Mean daylengths measured at the MAREL Iroise Station (Observatoire du Domaine Côtier de l'IUEM) in the west of the Bay of Brest were 10.3 h in winter, 15 h in spring, 13.7 h in summer and 9.3 h in autumn.

**Incubation protocol.** Benthic chambers were used in triplicate to assess *in situ* community nutrient fluxes at the water–sediment interface. The characteristics of the enclosures are described in Martin et al. (2007). Clear and opaque chambers were used to estimate nutrient fluxes under light and dark conditions, respectively. A series of incubations was carried out for 120 min and replicated up to 2 times daily. The enclosures were opened for 30 min between successive incubations to restore ambient conditions. A LI-COR

quantum sensor (LI-192SA) was deployed inside 1 of the clear hemispheres to record the photosynthetically active radiation (PAR, 400 to 700 nm) available for the enclosed photosynthetic organisms. Irradiance (µmol $m^{-2} s^{-1}$) was averaged every minute. Dissolved oxygen (DO) concentration (mg $l^{-1}$), salinity (in practical salinity units), temperature (°C) and depth (m) were recorded every minute inside each enclosure by a YSI 6920 probe.

**Sampling and analysis.** Water samples were collected for ammonium ($NH_4^+$), nitrate + nitrite ($NO_3^- + NO_2^-$), dissolved silicic acid (DSi) and phosphate ($PO_4^{3-}$) measurements using 450 ml polyethylene syringes, at the beginning and at the end of the incubations. Samples for $NH_4^+$ were directly transferred into 100 ml glass flasks, and reagents were added immediately. Flasks were stored in the dark pending analysis. Samples for $NO_3^- + NO_2^-$ and $PO_4^{3-}$ were passed through GF/F filters and then immediately frozen in polyethylene vials (–20°C). Samples for DSi were filtered on 0.2 µm cellulose acetate filters and stored in a cool dark place pending analysis. $NH_4^+$ concentrations were determined using the phenol-hypochlorite method (Solorzano 1969). $PO_4^{3-}$ concentrations were determined manually by the method described by Murphy & Riley (1962). $NO_3^- + NO_2^-$ and DSi concentrations were measured using a Technicon Auto Analyzer III (Bran & Luebbe), according to Tréguer & Le Corre (1975). Concentrations of $NO_3^- + NO_2^-$ were analyzed according to Bendschneider & Robison (1952), and DSi, according to Strickland & Parsons (1968). Temperature, DO, chlorophyll *a* (chl *a*) and dissolved inorganic nutrient concentrations in surface waters were provided by the SOMLIT (Service d'Observation en Milieu LITtoral, INSU-CNRS) Station situated in the Bay of Brest for the sampling period from 2002 to 2004.

**Data treatment.** Net community fluxes of dissolved inorganic nutrient under light and dark conditions were calculated by the difference between initial and final concentrations during the incubations:

$$NCF_L \ (or \ NCF_D) = \frac{\Delta c \times v}{s \times \Delta t} \qquad (1)$$

where $NCF_L$ (or $NCF_D$) stands for net community fluxes of nutrient species under light (or dark) conditions (µmol $m^{-2} h^{-1}$), $\Delta c$ is the change in nutrient concentration during the incubation (µmol $l^{-1}$), $v$ is the chamber volume (l), $s$ is the enclosed surface area ($m^2$) and $\Delta t$ is the experiment duration (h). Gross community fluxes (GCF; µmol $m^{-2} h^{-1}$) correspond to the difference between $NCF_L$ and $NCF_D$.

Diel net community fluxes (DNCF; mmol $m^{-2} d^{-1}$) and daily gross community fluxes (DGCF; mmol $m^{-2} d^{-1}$) of a nutrient species were calculated as follows:

$$DNCF = (NCF_L \times 10^{-3} \times L) + (NCF_D \times 10^{-3} \times D) \quad (2)$$

$$DGCF = GCF \times 10^{-3} \times L \quad (3)$$

where $L$ and $D$ are the light and dark periods (h), respectively. For calculations, nutrient fluxes measured in the dark were considered constant throughout the day. The annual estimates of net community fluxes of the nutrient species were calculated by summing the seasonal fluxes.

ANOVAs were performed to test seasonal and light/dark differences in nutrient fluxes and followed by Tukey tests to separate sets of homogeneous data. Normal distribution (Shapiro-Wilks test) and equality of variance (Levene test) were verified prior to analysis, otherwise Kruskal-Wallis tests, followed by Mann-Whitney $U$-tests, were performed. Spearman test was used to explore correlations between variables. Molar ratios of community nutrient fluxes ($Y$:$X$) were calculated by means of functional regressions (Ricker 1973), since $Y$ and $X$ are both affected by natural variability and measurement errors.

## RESULTS

### Surface water parameters

In the Bay of Brest, mean surface water temperature varied from 9°C at the end of winter to 18°C at the end of summer (Fig. 1). During the sampling period, surface water DO concentrations reached maxima in March and April (310 to 323 µmol l$^{-1}$) and then
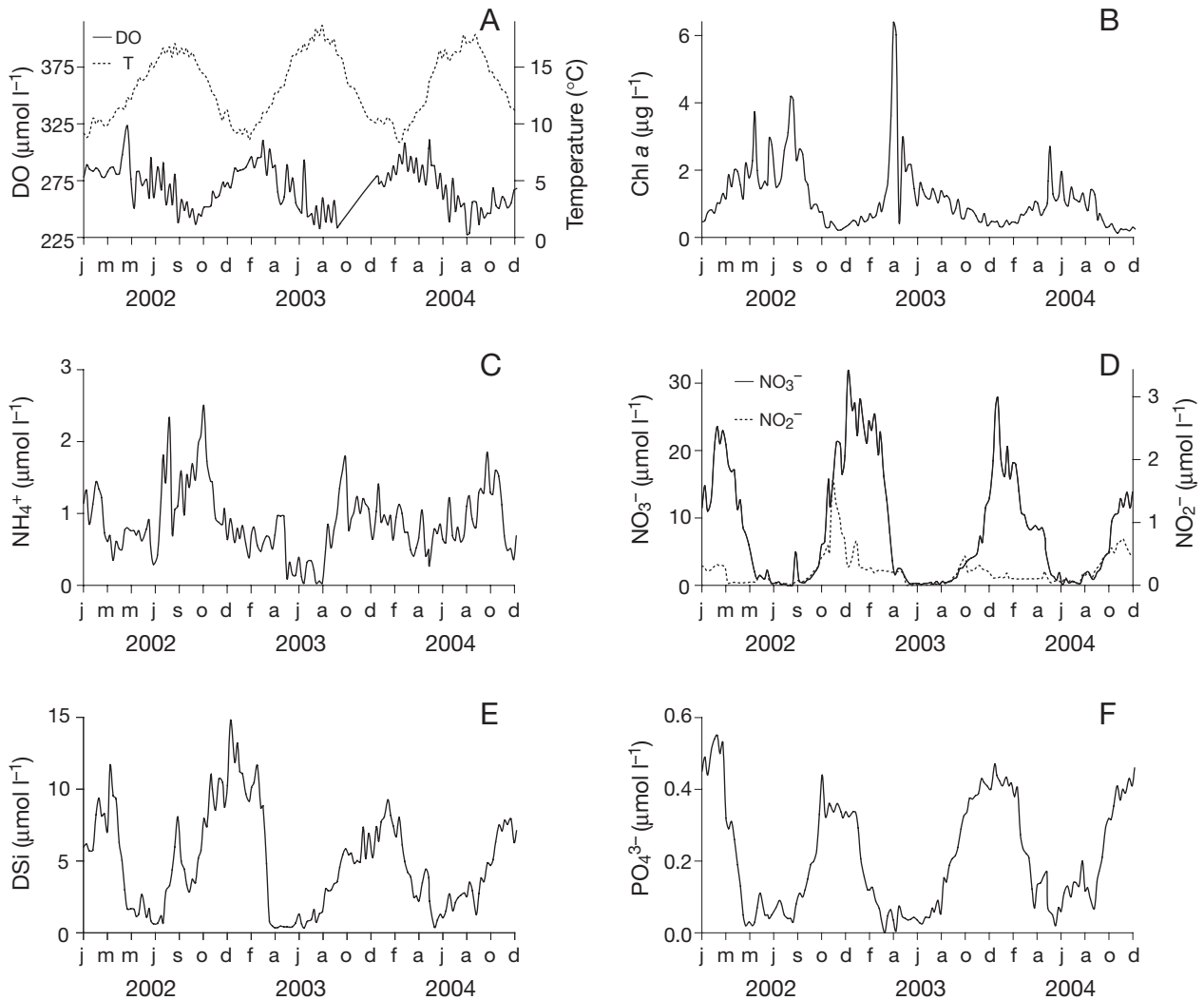
Fig. 1. Temporal variability in (A) temperature (T), dissolved oxygen (DO), (B) chlorophyll *a* (chl *a*), (C) NH$_4^+$, (D) NO$_3^-$, NO$_2^-$, (E) dissolved silicic acid (DSi) and (F) PO$_4^{3-}$ concentrations in surface water at MAREL Iroise Station (Bay of Brest) during the period 2002 to 2004

decreased between August and October (229 to 237 µmol l$^{-1}$). Chl *a* concentrations were low from October to February (<0.5 µg l$^{-1}$) and were marked by an increase in April and May that varied among years, with 3.7 µg l$^{-1}$ in May 2002, 6.4 µg l$^{-1}$ in April 2003 and 2.7 µg l$^{-1}$ in May 2004. $NH_4^+$ concentrations remained low (<2.5 µmol l$^{-1}$) and were highly variable throughout the year. $NO_3^-$, $NO_2^-$, DSi and $PO_4^{3-}$ concentrations exhibited seasonal variations from maxima in autumn and winter to minima during the period of maximum phytoplankton production in spring and summer. $NO_3^-$ concentration varied from zero between June and September to 23.6–31.8 µmol l$^{-1}$ in January and February. $NO_2^-$ concentrations accounted for 6% (from 0 to 20%) of $NO_3^-$ concentrations on average. DSi concentrations decreased from 9.2 to 14.8 µmol l$^{-1}$ in January and February to 0.4–0.7 µmol l$^{-1}$ from May to July. $PO_4^{3-}$ concentrations remained low, varying from zero in May to 0.4–0.6 µmol l$^{-1}$ between November and February.

### Bottom water parameters

During the incubations, bottom irradiance ranged from 30 to 550 µmol m$^{-2}$ s$^{-1}$; bottom water temperature, from 8.8 to 18.9°C; and salinity, from 31.2 to 35.6. Bottom water DO concentrations were highest in winter and spring and lowest in summer and autumn, varying from 338 µmol l$^{-1}$ (126% saturation) in spring to 259 µmol l$^{-1}$ (101% saturation) in autumn (Fig. 2). DO concentration was significantly correlated with the water temperature (Spearman test, $R_s = 0.43$, $p < 0.001$) and followed the same time course as that observed in the surface water. $NH_4^+$ varied from 0.7 µmol l$^{-1}$ in spring to 1.9 µmol l$^{-1}$ in autumn (see Fig. 3). $NO_3^-$ + $NO_2^-$ concentration reached 46.5 µmol l$^{-1}$ in winter, and was the dominant form of dissolved organic nitrogen (DIN), except in summer (0.6 µmol l$^{-1}$). $PO_4^{3-}$ (0.1 to 0.5 µmol l$^{-1}$) and DSi (5.3 to 17.0 µmol l$^{-1}$) were highest in autumn and winter and lowest in spring and summer. Seasonal variations in dissloved inorganic nutrients in bottom water were similar to those observed in surface water.

### Community dissolved inorganic nitrogen fluxes

$NH_4^+$ fluxes differed significantly between dark and light conditions, and according to seasons (Table 1, Fig. 3A). $NH_4^+$ fluxes were taken up at a greater rate or released at a lower rate under light conditions compared to under dark conditions. $NCF_L$ of $NH_4^+$ increased from 16.7 (SD 34.0) µmol m$^{-2}$ h$^{-1}$ in winter to 110.0 (SD 48.7) µmol m$^{-2}$ h$^{-1}$ in summer and autumn, and $NCF_D$ increased from 53.4 (SD 26.0) µmol m$^{-2}$ h$^{-1}$ to 213.7 (SD 116.3) µmol m$^{-2}$ h$^{-1}$, respectively. GCF of $NH_4^+$ varied from –29.0 (SD 66.4) µmol m$^{-2}$ h$^{-1}$ in winter to –150.0 (SD 166.6) µmol m$^{-2}$ h$^{-1}$ in summer. $NCF_L$ values were correlated with temperature, community respiration (CR) and gross community production (GCP; Martin et al. 2007), while $NCF_D$ values were correlated with temperature, bottom water DO concentration and CR (Table 2). Bottom water $NO_3^-$ + $NO_2^-$ concentration was also correlated with $NH_4^+$ fluxes.

Dark and light conditions had a significant influence on $NO_3^-$ + $NO_2^-$ fluxes (Table 1, Fig. 3B), with a lower

Table 1. Results of statistical tests performed to test the influence of (A) light and dark conditions and (B) seasons on nutrient fluxes. The statistical tests are *F* for ANOVA and *H* for Kruskal-Wallis. Superscripted letters (a, b, c) indicate significant differences between seasons (Tukey test or Mann-Whitney test, p > 0.05) (nd: no difference; DSi: dissolved silicic acid; $NCF_L$, $NCF_D$: net community fluxes of nutrient under light and dark, respectively; W: winter; Sp: spring; Su: summer; A: autumn)

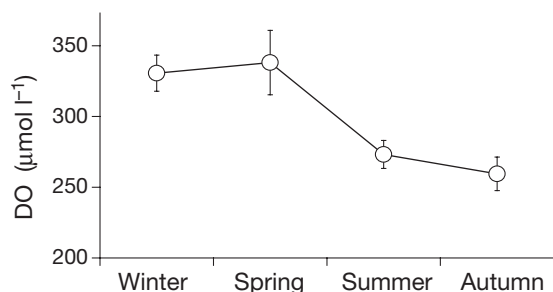| Nutrient | Test | p | N | |
|---|---|---|---|---|
| **(A) Light and dark condition effect** | | | | |
| $NH_4^+$ | $H = 20.10$ | <0.001 | 109 | |
| $NO_3^-$ + $NO_2^-$ | $H = 4.71$ | 0.030 | 85 | |
| DSi | $F = 21.03$ | <0.001 | 104 | |
| $PO_4^{3-}$ | $H = 11.83$ | <0.001 | 94 | |
| | | | | |
| **(B) Season effect** | | | | |
| **$NCF_L$** | | | | |
| $NH_4^+$ | $F = 11.64$ | <0.001 | 65 | W[a] – Sp[a] – Su[b] – A[b] |
| $NO_3^-$ + $NO_2^-$ | $H = 7.27$ | 0.064 | 42 | nd |
| DSi | $F = 5.12$ | 0.003 | 59 | W[a] – Sp[a] – Su[b] – A[ab] |
| $PO_4^{3-}$ | $F = 10.49$ | <0.001 | 53 | W[a] – Sp[a] – Su[b] – A[a] |
| | | | | |
| **$NCF_D$** | | | | |
| $NH_4^+$ | $F = 8.24$ | <0.001 | 44 | W[a] – Sp[b] – Su[c] – A[bc] |
| $NO_3^-$ + $NO_2^-$ | $F = 12.24$ | <0.001 | 43 | W[a] – Sp[b] – Su[c] – A[c] |
| DSi | $F = 1.48$ | 0.234 | 45 | nd |
| $PO_4^{3-}$ | $F = 7.56$ | <0.001 | 41 | W[a] – Sp[ac] – Su[b] – A[bc] |



Fig. 2. Seasonal evolution of DO concentration (µmol l$^{-1}$) in the bottom water at Rozegat. Error bars: SD of mean values (n = 12 to 53)

release in light than in darkness. $NO_3^- + NO_2^-$ fluxes under dark conditions differed significantly between seasons (Table 1). $NCF_D$ of $NO_3^- + NO_2^-$ varied from –174.9 (SD 147.2) µmol m$^{-2}$ h$^{-1}$ in winter to 72.8 (SD 80.0) µmol m$^{-2}$ h$^{-1}$ in summer and autumn. GCF of $NO_3^- + NO_2^-$ varied from –32.9 (SD 47.5) µmol m$^{-2}$ h$^{-1}$ in summer to –151.7 (SD 293.7) µmol m$^{-2}$ h$^{-1}$ in spring. $NCF_L$ values of $NO_3^- + NO_2^-$ were slightly correlated with bottom water DO concentration, $GCP_{O_2}$ and bot-

tom water $NH_4^+$ concentration (Table 2). $NCF_D$ was highly correlated with temperature, bottom water DO concentration, CR and bottom water $NO_3^- + NO_2^-$ concentration, and slightly correlated with bottom water $NH_4^+$ concentration.

$NCF_L$ of DIN ($NH_4^+ + NO_3^- + NO_2^-$) was negative in winter and spring and positive in summer and autumn, increasing from –237.2 (SD 541.6) µmol m$^{-2}$ h$^{-1}$ in winter to 143.1 (SD 82.9) µmol m$^{-2}$ h$^{-1}$ in summer.
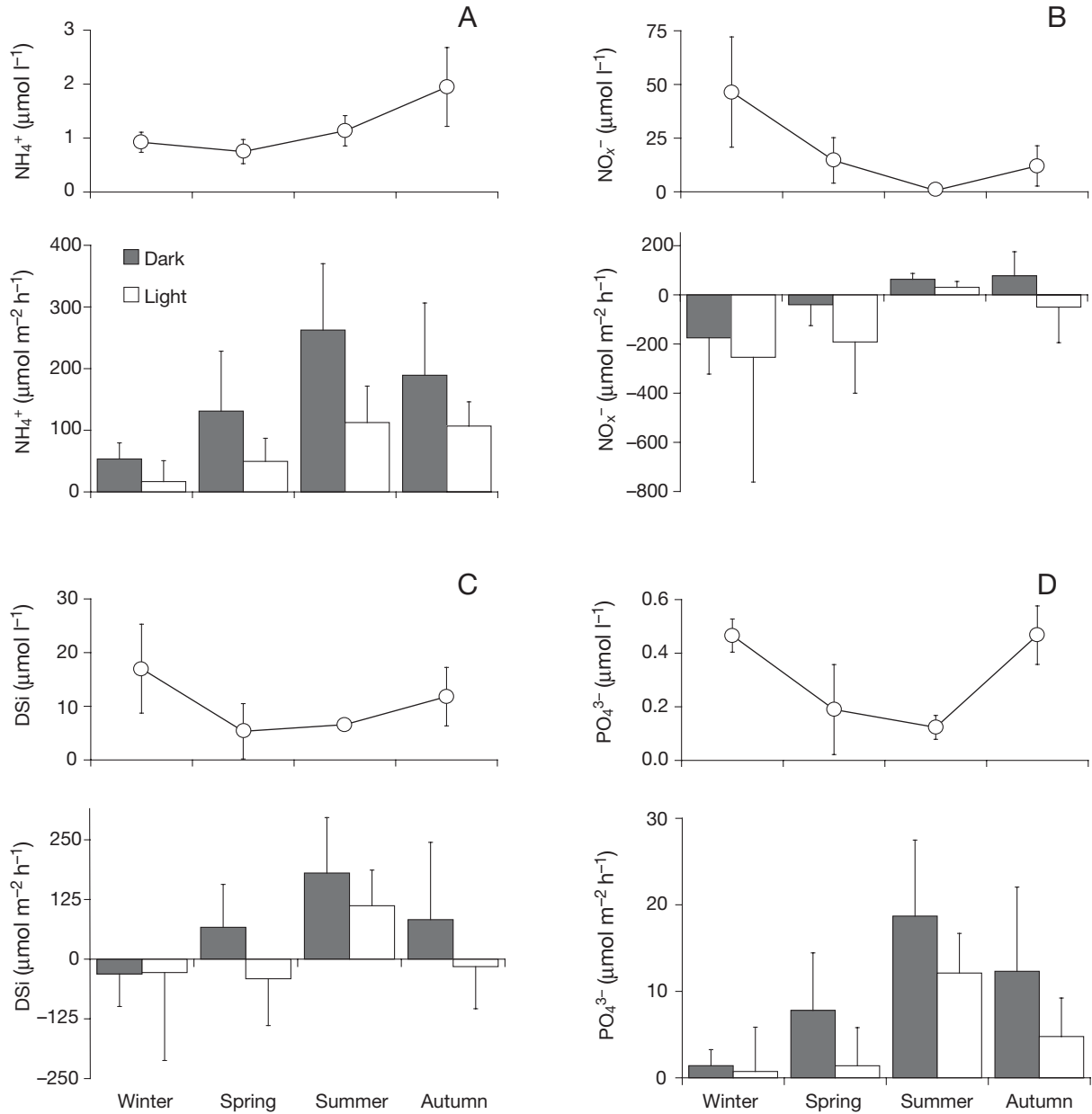


Fig. 3. (A) $NH_4^+$, (B) $NO_x^-$ ($NO_3^- + NO_2^-$), (C) DSi and (D) $PO_4^{3-}$ seasonal concentrations in bottom water at the start of the incubation (upper panels) and fluxes under dark and light conditions (lower panels). Mean irradiances were 65.4 (SD 57.1), 167.1 (SD 167.4), 109.6 (SD 82.7) and 36.9 (SD 40.5) µmol m$^{-2}$ s$^{-1}$ in winter, spring, summer and autumn, respectively. Error bars: SD of mean values (n = 6 to 38)

Table 2. Spearman ($R_s$) correlations calculated between bottom water temperature (T), bottom water dissolved oxygen concentration (DO), bottom irradiance ($E$), surface water chl $a$ concentration, gross community production in $O_2$ ($GCP_{O_2}$) and dissolved inorganic carbon ($GCP_{DIC}$), community respiration in $O_2$ ($CR_{O_2}$) and in DIC ($CR_{DIC}$), bottom-water concentration of $NH_4^+$, $NO_3^-$ + $NO_2^-$ ($NO_x^-$), DSi and $PO_4^{3-}$ and fluxes during light ($NCF_L$) and dark incubations ($NCF_D$) of the nutrient species $NH_4^+$, $NO_x^-$, DSi and $PO_4^{3-}$. Values of GCP and CR are from Martin et al. (2007). Significant correlations are given in bold print, ***p < 0.001, **p < 0.01, *p < 0.05

|  | $NCF_L$ |  |  |  | $NCF_D$ |  |  |  |
|  | $NH_4^+$ | $NO_x^-$ | DSi | $PO_4^{3-}$ | $NH_4^+$ | $NO_x^-$ | DSi | $PO_4^{3-}$ |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| T | **0.62***** | 0.10 | **0.59***** | **0.47***** | **0.63***** | **0.56***** | **0.65***** | **0.54***** |
| DO | −0.18 | **−0.41*** | −0.18 | −0.20 | **−0.43**** | **−0.62***** | **−0.35*** | −0.29 |
| $E$ | 0.19 | −0.05 | 0.25 | 0.28 | −0.09 | −0.15 | 0.22 | 0.03 |
| Chl $a$ | 0.06 | −0.18 | 0.09 | −0.01 | −0.09 | −0.15 | 0.22 | 0.03 |
| $GCP_{O_2}$ | **0.37**** | **0.31*** | **0.55***** | **0.55***** | 0.04 | 0.20 | 0.33 | 0.27 |
| $GCP_{DIC}$ | **−0.46***** | −0.20 | **−0.65***** | **−0.58***** | −0.21 | −0.32 | −0.39 | −0.31 |
| $CR_{O_2}$ | **−0.69***** | −0.21 | **−0.51***** | **−0.54***** | **−0.59***** | **−0.42**** | −0.20 | **−0.63***** |
| $CR_{DIC}$ | **0.59***** | 0.23 | **0.67***** | **0.56***** | **0.71***** | **0.46**** | **0.43**** | **0.66***** |
| $[NH_4^+]$ | −0.11 | **0.36*** | −0.16 | 0.13 | 0.29 | **0.35*** | 0.02 | 0.26 |
| $[NO_x^-]$ | **−0.52***** | −0.12 | **−0.67***** | **−0.46***** | **−0.48**** | **−0.53***** | **−0.61***** | **−0.42**** |
| $[DSi]$ | **−0.34**** | 0.16 | **−0.65***** | −0.18 | −0.13 | −0.05 | **−0.43**** | −0.09 |
| $[PO_4^{3-}]$ | **−0.25*** | 0.13 | **−0.52*** | **−0.29*** | −0.11 | −0.00 | **−0.33*** | −0.05 |

$NCF_D$ of DIN ranged from negative values in winter (−121.5 µmol m$^{-2}$ h$^{-1}$, SD 173.3) to positive values in the other seasons, with a maximum in summer of 326.0 (SD 131.2) µmol m$^{-2}$ h$^{-1}$.

### Community dissolved silicic acid fluxes

DSi fluxes differed significantly between dark and light incubations (Table 1, Fig. 3C), being taken up more and released less in light than in the dark. $NCF_L$ of DSi varied seasonally (Table 1), with significant differences between winter (−28.0 µmol m$^{-2}$ h$^{-1}$, SD 184.2) and summer (111.9 µmol m$^{-2}$ h$^{-1}$, SD 74.6). GCF of DSi varied from 3.1 (SD 252.2) µmol m$^{-2}$ h$^{-1}$ in winter to −107.7 (SD 188.0) µmol m$^{-2}$ h$^{-1}$ in spring. DSi fluxes were highly influenced by temperature, $CR_{DIC}$ and bottom water DSi concentration, and to a lesser extent by bottom water $PO_4^{3-}$ concentration (Table 2). $NCF_L$ values of DSi were also correlated with GCP and $CR_{O_2}$, and $NCF_D$, with bottom water DO concentration.

### Community dissolved inorganic phosphate fluxes

Following a similar pattern to $NH_4^+$ fluxes, $PO_4^{3-}$ fluxes were significantly different under dark and light conditions (Table 1, Fig. 3D), with a greater release under dark than under light conditions. $NCF_L$ of $PO_4^{3-}$ varied seasonally (Table 1) from a mean value of 1.5 (SD 4.8) µmol m$^{-2}$ h$^{-1}$ between autumn and spring to 12.1 (SD 4.6) µmol m$^{-2}$ h$^{-1}$ in summer. $NCF_D$ ranged

from 5.0 (SD 6.0) µmol m$^{-2}$ h$^{-1}$ in winter and spring to 14.2 (SD 9.7) µmol m$^{-2}$ h$^{-1}$ in summer and autumn. GCF of $PO_4^{3-}$ varied from −0.7 (SD 7.0) µmol m$^{-2}$ h$^{-1}$ in winter to −7.5 (SD 14.2) µmol m$^{-2}$ h$^{-1}$ in autumn. $PO_4^{3-}$ fluxes were highly correlated with temperature, CR and bottom water $NO_3^-$ + $NO_2^-$ concentration, but less with bottom water $PO_4^{3-}$ concentration (Table 2). $NCF_L$ values of $PO_4^{3-}$ were also highly influenced by GCP.

### Molar ratios of community nutrient fluxes

Functional regressions for C:N, C:Si and C:P during dark conditions (NCFD) explained 48, 27 and 57% of data variability, respectively (Fig. 4). C:N was 13.5 (SE 1.6), C:Si was 19.3 (SE 2.5) and C:P was 279.3 (SE 28.6); these ratios were significantly superior to the typical stoichiometric ratios (C:N:Si:P = 106:16:16:1; Redfield et al. 1963, Brzezinski 1985; $Z$-test, p < 0.001). The intercepts were significantly different from zero ($Z$-test, p < 0.001). DIC releases were 2.4 (SE 0.3) mmol m$^{-2}$ h$^{-1}$, 2.8 (SE 0.4) mmol m$^{-2}$ h$^{-1}$ and 1.9 (SE 0.2) mmol m$^{-2}$ h$^{-1}$ when DIN, DSi and $PO_4^{3-}$ fluxes were nil, respectively. For a nil DIC flux, $NCF_D$ values were −180 (SE 21) µmol DIN m$^{-2}$ h$^{-1}$, −144 (SE 19) µmol DSi m$^{-2}$ h$^{-1}$ and −6.8 (SE 0.7) µmol $PO_4^{3-}$ m$^{-2}$ h$^{-1}$. Ratios were not calculated for $NCF_L$, because fluxes were often opposite (making ratio calculations meaningless).

### Nitrogen, silica and phosphorus budgets

DNCF of $NH_4^+$ were always positive, varying from a minimum in winter to a maximum in summer (Table 3A). DNCF of $NO_3^-$ + $NO_2^-$ were negative in winter and spring and positive in summer and autumn, with a minimum in winter and a maximum in summer. DNCF of DIN were negative in winter and spring and positive in summer and autumn, varying from −4.21 (SD 8.04) mmol m$^{-2}$ d$^{-1}$ in winter to 5.32 (SD 2.49) mmol m$^{-2}$ d$^{-1}$ in summer. The same pattern was observed for DNCF of DSi. DNCF of $PO_4^{3-}$ were low (<0.5 mmol m$^{-2}$ d$^{-1}$); they were positive and increased from winter to summer. DGCF were negative (gross uptake), except for DSi in winter (Table 3B). Maximum DGCF were observed in summer for $NH_4^+$ and in spring for $NO_3^-$ + $NO_2^-$, DSi and $PO_4^{3-}$. Minimum DGCF was observed in winter, except for $NO_3^-$ + $NO_2^-$, which occurred in summer.
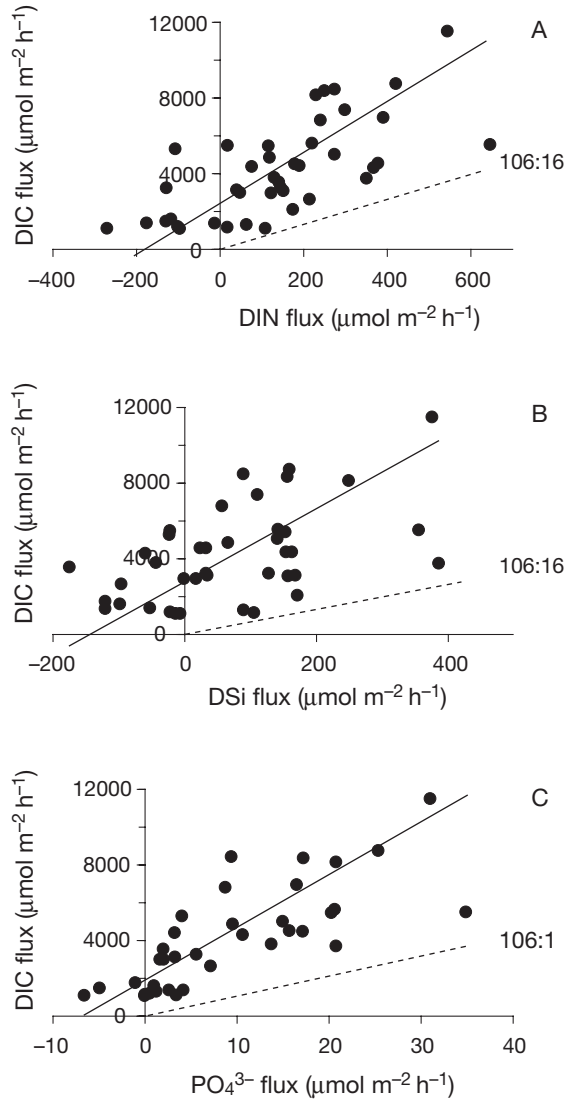
Fig. 4. Relationships between net community dissolved inorganic carbon (DIC) flux and net community (A) dissolved inorganic nitrogen (DIN), (B) dissolved silicic acid (DSi) and (C) $PO_4^{3-}$ fluxes during dark incubations. Net community flux of DIC corresponds to the community respiration ($CR_{DIC}$) reported in Martin et al. (2007). Dotted line represents the typical Redfield and Brzezinski stoichiometric ratios (C:N:Si:P = 106:16:16:1; Redfield et al. 1963, Brzezinski 1985)

Annual net community N flux was positive (13.9 g N $m^{-2}$ $yr^{-1}$, SD 7.9) for $NH_4^+$, but negative for $NO_3^-$ + $NO_2^-$ (−8.3 g N $m^{-2}$ $yr^{-1}$, SD 18.5). Thus, annual net flux of DIN in the maerl community corresponded to a N release of 5.6 (SD 26.4) g N $m^{-2}$ $yr^{-1}$. Annual net community release of DSi was 9.5 (SD 26.9) g Si $m^{-2}$ $yr^{-1}$ and that of $PO_4^{3-}$ was 2.0 (SD 1.5) g P $m^{-2}$ $yr^{-1}$. The mean molar N:Si:P ratio of annual net community fluxes was estimated to 6:5:1. Annual gross community DIN uptake was 11.7 (SD 26.1) g N $m^{-2}$ $yr^{-1}$, with 48%

Table 3. Mean seasonal variations (SD in parentheses) of (A) diel net community fluxes (DNCF) and (B) daily gross community fluxes (DGCF) of $NH_4^+$, $NO_3^-$ + $NO_2^-$, DSi and $PO_4^{3-}$ (mmol $m^{-2}$ $d^{-1}$)

| | $NH_4^+$ | $NO_3^-$ + $NO_2^-$ | DSi | $PO_4^{3-}$ |
|---|---|---|---|---|
| **(A) DNCF** | | | | |
| Winter | 0.90 (0.71) | −5.01 (7.25) | −0.72 (2.83) | 0.03 (0.08) |
| Spring | 1.92 (1.44) | −3.23 (3.89) | −0.01 (2.28) | 0.09 (0.13) |
| Summer | 4.25 (1.92) | 1.07 (0.57) | 3.39 (2.22) | 0.36 (0.15) |
| Autumn | 3.78 (2.09) | 0.68 (2.78) | 1.07 (3.20) | 0.23 (0.18) |
| **(B) DGCF** | | | | |
| Winter | −0.38 (0.62) | −0.81 (6.75) | 0.03 (2.60) | −0.01 (0.07) |
| Spring | −1.22 (2.02) | −2.28 (4.41) | −1.62 (2.82) | −0.10 (0.17) |
| Summer | −2.06 (2.28) | −0.45 (0.65) | −0.94 (2.61) | −0.09 (0.18) |
| Autumn | −0.77 (1.45) | −1.18 (2.26) | −0.91 (2.33) | −0.07 (0.13) |

in the form of $NH_4^+$ and 52% in the form of $NO_3^-$ + $NO_2^-$. DSi and $PO_4^{3-}$ uptake were 8.8 (SD 13.2) g Si $m^{-2}$ $yr^{-1}$ and 0.7 (SD 0.7) g P $m^{-2}$ $yr^{-1}$, respectively. The mean molar N:Si:P ratio of annual gross community uptake was estimated at 35:13:1.

## DISCUSSION

### Significance of dissolved inorganic fluxes

The seasonal variations in dissolved inorganic nutrient fluxes in the maerl community were manifest for both light and dark incubations. All nutrient species exhibited a similar seasonal pattern, with minimum fluxes in winter and maximum in summer. The maerl community is, on an annual basis, a net source of N, P and Si, despite the potentially high nutrient-assimilation capability of community autotrophs, including coralline algae and epiphytic macro- and microalgae. With regard to nitrogen, the maerl community represents an annual source of $NH_4^+$ and a sink for $NO_3^-$ + $NO_2^-$. Sediments are generally described as an important source of $NH_4^+$ (Cabrita & Brotas 2000, Rowe et al. 2002). Indeed, $NH_4^+$ is the first inorganic product in the regeneration of organic material via bacterial mineralization and heterotroph excretion. The high faunal abundance in maerl beds (Hall-Spencer et al. 2003, Grall et al. 2006) enhances organic matter consumption and $NH_4^+$ excretion, and stimulates microbial communities by sediment mixing (Cowan & Boynton 1996). The maerl community $NH_4^+$ release in light and dark incubations (20 to 260 μmol $m^{-2}$ $h^{-1}$) corresponds to 70–100% of the community DIN release. $NH_4^+$ release is close to that measured for communities of dense assemblage of the invasive mollusk, *Crepidula fornicata* L., in the Bay of Brest (90 to

330 µmol m$^{-2}$ h$^{-1}$; S. Martin unpubl. data) and falls within the top range of values reported for macrophyte-dominated communities and productive estuaries (–100 to 200 µmol m$^{-2}$ h$^{-1}$; Cabrita & Brotas 2000, Cook et al. 2004, Eyre & Ferguson 2005). Conversely, sediments are generally considered to be a sink for $NO_3^- + NO_2^-$ (Seitzinger et al. 1984, Nedwell & Trimmer 1996), which agrees with the net annual uptake of $NO_3^- + NO_2^-$ in the maerl community. $NO_3^- + NO_2^-$ are formed in oxic sediments through the nitrification process (from $NH_4^+$ to $NO_3^-$) and consumed through denitrification in anoxic sediments (from $NO_3^-$ to $N_2$) and diffusion into sediment or absorption onto particulate matter (Pritchard & Schubel 1981). Net community fluxes of $NO_3^- + NO_2^-$ in this study (–250 to 80 µmol m$^{-2}$ h$^{-1}$) are within the lower range of values reported for coastal sediment communities (–150 to 200 µmol m$^{-2}$ h$^{-1}$; Cowan & Boynton 1996, Rowe et al. 2002, Cook et al. 2004, Eyre & Ferguson 2005). DSi fluxes in the maerl community reflect the balance between assimilation by benthic siliceous organisms, especially benthic diatoms and some sponges, and regeneration mainly from the dissolution of diatom frustules (Ragueneau et al. 2002). In the maerl community, DSi was taken up in winter and spring and released in summer and autumn, which is consistent with the seasonal pattern observed for estuarine sediments (Cowan & Boynton 1996, Caffrey et al. 2002). DSi fluxes in the maerl community (–40 to 180 µmol m$^{-2}$ h$^{-1}$) were quite comparable to those given for other sediment communities in the Bay of Brest (90 to 120 µmol m$^{-2}$ h$^{-1}$; S. Martin unpubl. data) and for estuarine sediments (–50 to 400 µmol m$^{-2}$ h$^{-1}$; Cowan & Boynton 1996). Maerl community $PO_4^{3-}$ fluxes were always positive, indicating the predominance of mineralization processes. $PO_4^{3-}$ release changed with time similarly to $NH_4^+$, indicating a relatively constant N:P ratio in the organic matter. $PO_4^{3-}$ fluxes in the maerl community (1 to 20 µmol m$^{-2}$ h$^{-1}$) remained low compared to the other nutrient fluxes. $PO_4^{3-}$ may be adsorbed to iron hydroxides and calcite (Caffrey et al. 2002), the latter process probably being predominant in rich carbonate sediments such as maerl beds. $PO_4^{3-}$ fluxes were lower than those measured in other benthic communities in the Bay of Brest (5 to 40 µmol m$^{-2}$ h$^{-1}$; S. Martin unpubl. data), but within the range of those in other temperate sediments (–15 to 40 µmol m$^{-2}$ h$^{-1}$; Koop et al. 1990, Cowan & Boynton 1996).

Under dark conditions, in the absence of autotrophic processes, determination of stoichiometric flux ratios gives information on the origin of the biogenic matter mineralized. The C:N and C:P flux ratios of NCF$_D$, corresponding to the ratio of DIC to DIN and DIP released from organic matter decomposition, were between the ratios for phytoplankton detritus (C:N:P = 106:16:1;

Redfield et al. 1963) and for macroalgal detritus (C:N:P = 550:30:1; Atkinson & Smith 1983). The mineralization of organic matter in the maerl community thus corresponds to a mixture of particulate matter from both origins. The C:Si flux ratio of NCF$_D$ was about 3-fold higher than expected values, assuming a standard stoichiometric C:N:Si:P ratio of 106:16:16:1 (Redfield et al. 1963, Brzezinski 1985). Accordingly, the C regeneration from diatom decomposition corresponds to about one-third of the total C released by the community. Diatoms may originate from the water column or directly from the microphytobenthos.

A significant difference was found between nutrient fluxes under dark and light conditions. The measurements of GCF suggest nutrient assimilation by maerl community autotrophs in light conditions, thus providing an estimation of their control on the release of mineralized inorganic nutrients from sediment to the water column. The algae of the maerl community seem to act as an efficient filter for N, Si and P, since we observed a significant decrease from 35 to 80 % in the release of nutrients between dark and light conditions. This filter effect has already been documented in microphytobenthos and macroalgal-dominated communities (Dalsgaard 2003). However, some processes other than autotrophic assimilation differ between light and dark and affect GCF, such as nitrification and the subsequent coupled nitrification–denitrification that is stimulated by the supply of DO from primary production in light (An & Joye 2001). Furthermore, even when incubations are performed in the dark, nutrient uptake by autotrophs may persist. Dark nutrient assimilation has been reported for microphytobenthos (Dalsgaard 2003) and possibly other macrophytes (Eyre & Ferguson 2002). Finally, nutrient assimilation may occur from the sediment pore water without any shift in the bottom water nutrient concentrations. As nutrient assimilation is not simultaneously related to irradiance, we did not find obvious relationships between bottom irradiance intensity and nutrient fluxes in light conditions. Coralline algae and epiphytes are exposed to inorganic nitrogen in the form of $NH_4^+$ as well as $NO_3^-$. Both forms were assimilated by the maerl community, except in summer, as there was a 5-fold higher $NH_4^+$ gross uptake when the $NO_3^-$ concentration was close to zero. The gross community DIN assimilation is thus controlled by the availability of $NH_4^+$ or $NO_3^-$ in the water column.

### Factors influencing seasonal sediment–water fluxes

CR is an indicator of organic matter mineralization through decomposition by microorganisms or excretion by fauna, while GCP is an indicator of the organic

matter available for mineralization. Accordingly, CR, GCP and nutrient fluxes were highly correlated and evolved together in the maerl community, with maximum nutrient releases in summer, during the period of high productivity and respiration (Martin et al. 2007), and minimum values in winter. The major part of the organic matter provided by the community photosynthetic production can be used by community heterotrophs. If maerl production is not directly available for heterotrophs, epiphytic macro- and microalgal production constitute the base of the photosynthetic product mineralization.

Maerl community nutrient fluxes were positively and highly correlated with temperature, increasing from a minimum (9°C) in winter to a maximum (19°C) in summer. Indeed, processes, such as mineralization, autotroph and heterotroph metabolic rates and biomass, molecular diffusion or DO concentration, are temperature dependent. Such a relationship between nutrient sediment–water exchange rates and temperature has previously been reported (Cowan & Boynton 1996, Qu et al. 2003).

Community DIN fluxes were correlated with bottom-water DO concentration, which is inversely correlated with temperature. DO concentration may influence nitrification and denitrification, since oxygen penetration into the sediment stimulates the aerobic process of nitrification (Al-Rousan et al. 2004). Community respiration during dark incubations may cause depletion in DO at the end of the incubation, especially in summer and autumn, when the DO concentrations are the lowest and the respiration rates the highest. When DO concentrations are low, $NH_4^+$ is the major DIN species (Al-Rousan et al. 2004), which agrees with $NH_4^+$ representing >70% of the DIN release in summer and autumn. However, the maximum release of $NO_3^- + NO_2^-$ was also observed in summer and autumn, suggesting that an increase of $NH_4^+$ production, possibly due to increasing organic matter supply and decomposition rate in the sediments, implies subsequent $NH_4^+$ oxidation to $NO_3^-$ via nitrification. The latter involves the presence of sufficient DO in bottom water.

The nutrient concentrations in bottom water were closely related to $NO_3^- + NO_2^-$ and DSi fluxes. These fluxes were directed from the water column to the sediment in winter, due to the relatively high bottom-water $NO_3^- + NO_2^-$ and DSi concentrations. This result involves the absorption of $NO_3^- + NO_2^-$ and DSi onto particulate matter or diffusion into the sediment (Pritchard & Schubel 1981). Strong correlation between $NO_3^-$ uptake by the benthic community and water column $NO_3^-$ concentration has previously been observed (Cabrita & Brotas 2000). $NO_3^- + NO_2^-$ flux was also correlated with bottom-water $NH_4^+$ concentration.

The maximum bottom water concentrations of $NH_4^+$ measured in summer and autumn may thus influence $NO_3^- + NO_2^-$ release from the sediment via nitrification processes. Conversely, $NH_4^+$ and $PO_4^{3-}$ fluxes were not or were poorly correlated with $NH_4^+$ and $PO_4^{3-}$ concentrations in bottom water, since they are the first chemical products of organic material mineralization.

The sedimentation of phytoplankton, indicated by increasing chl $a$ concentration in the water column, may influence benthic nutrient fluxes (Cowan & Boynton 1996, Al-Rousan et al. 2004). However, we did not observe any correlation between chl $a$ concentration in the water column and benthic nutrient fluxes. Relatively low phytoplanktonic production and sedimentation would have little influence on the latter, compared to other processes in the study area.

## Nitrogen, silicon and phosphorus cycles

The maerl community in the Bay of Brest is a source of nutrients and, on an annual basis, contributes to 20–55% of the bay's phytoplanktonic production (Table 4). Considering that the maerl community covers about one-third of the surface of the Bay of Brest, it contributes from 5 to 20% of its total pelagic production. Nutrient regeneration in benthic communities may supply a significant proportion of the phytoplanktonic nutrient demand (Koop et al. 1990, Cowan & Boynton 1996, Ragueneau et al. 2002, Al-Rousan et al. 2004). Nutrient supply is particularly important in

Table 4. Calculated annual N, Si and P phytoplanktonic demand in the Bay of Brest and the fraction of the N, Si and P potentially supplied to the water column or taken up for autotrophic production by the maerl community. Nutrient release that could sustain phytoplanktonic production, as well as gross community nutrient uptake, was estimated per square meter and considering the total surface of the bay. Phytoplanktonic demand was estimated by converting phytoplanktonic C production measured in the Bay of Brest (148 g C m$^{-2}$ yr$^{-1}$; Del Amo 1996) to phytoplanktonic N, P and Si production, assuming a stoichiometric C:Si:N:P ratio of 106: 16:16:1 (Redfield et al. 1963, Brzezinski 1985)

| | N | Si | P |
|---|---|---|---|
| Phytoplanktonic nutrient demand (mol m$^{-2}$ yr$^{-1}$) | 1.86 | 1.86 | 0.12 |
| Net community nutrient supply per square meter (%) | 21 | 18 | 55 |
| Net community nutrient supply in the bay (%) | 7 | 6 | 18 |
| Gross community nutrient uptake per square meter (%) | 45 | 17 | 21 |
| Gross community nutrient uptake in the bay (%) | 15 | 6 | 7 |

summer, when nutrient release from the benthos is maximal and nutrient concentration in the water column is minimal. The potential limitation of pelagic primary production by nutrient availability in the Bay of Brest has previously been reported (Del Amo et al. 1997, Chauvaud et al. 2000, Ragueneau et al. 2002). Del Amo et al. (1997) also reported that primary production in the Bay of Brest was limited primarily by P and Si, even if some N limitation occurs in summer. As reported in our study for the period 2002 to 2004, the low N concentration in summer coincides with the depletion of $NO_3^- + NO_2^-$ in the water column, resulting from low river nutrient loading and high phytoplanktonic production. The Si limitation observed in the bay is a common feature in shallow coastal ecosystems with elevated N loading (Cloern 2001). Si limitation influences phytoplankton composition, with a related shift from siliceous (diatoms) to non-siliceous (flagellates) species, especially toxic dinoflagellates (Conley et al. 1993, Cloern 2001, Ragueneau et al. 2002). The contribution of nutrient release from the sediment can hinder nutrient limitation of overlying waters, especially in relatively shallow systems where sediments are an important nutrient source (Nixon 1981). In the Bay of Brest, Si release from the *Crepidula fornicata* invasive species community has been suggested to mask the potentially negative effects of elevated N inputs, *C. fornicata* acting as a biologically active silicate pump (Chauvaud et al. 2000, Ragueneau et al. 2002). In the maerl community, the annual N:Si flux ratio measured was slightly >1, suggesting that, on an annual basis, this community does not affect the nutrient limitations in the water column. However, the potential N supply to the water column, especially in summer when $NO_3^- + NO_2^-$ concentrations are very low, may reduce N limitation and favor phytoplanktonic production. The maerl community may also reduce P limitation in the water column, with a mean annual N:P flux ratio 2 times lower than the Redfield ratio. The potential N uptake by gross autotrophic production of the maerl community in the Bay of Brest is estimated to be 45% of the phytoplanktonic production, while the Si and P uptakes averaged 15 and 20%, respectively (Table 4). Thus, the maerl community may reduce or even reverse N effluxes from the benthic zone in the bay. Such results supply arguments for the preservation of these fragile communities in shallow coastal waters.

## LITERATURE CITED

Al-Rousan S, Rasheed M, Badran M (2004) Nutrient diffusive fluxes from sediments in the northern Gulf of Aqaba, Red Sea. Sci Mar 68:483–490

An S, Joye SB (2001) Enhancement of coupled nitrification–denitrification by benthic photosynthesis in shallow estuarine sediments. Limnol Oceanogr 46:62–74

Atkinson MJ, Smith SV (1983) C:N:P ratios of benthic marine plants. Limnol Oceanogr 28:568–574

Bendschneider K, Robison NJ (1952) A new spectrophotometric determination of nitrite in seawater. J Mar Res 11:87–96

Brzezinski MA (1985) The Si:C:N ratio of marine diatoms: interspecific variability and the effect of some environmental variables. J Phycol 21:347–357

Cabrita MT, Brotas V (2000) Seasonal variation in denitrification and dissolved nitrogen fluxes in intertidal sediments of the Tagus estuary, Portugal. Mar Ecol Prog Ser 202: 51–65

Caffrey JM, Harrington N, Ward B (2002) Biogeochemical processes in a small California estuary. 1. Benthic fluxes and pore water constituents reflect high nutrient freshwater inputs. Mar Ecol Prog Ser 233:39–53

Chauvaud L, Jean F, Ragueneau O, Thouzeau G (2000) Long-term variation of the Bay of Brest ecosystem: benthic–pelagic coupling revisited. Mar Ecol Prog Ser 200:35–48

Cloern JE (2001) Our evolving conceptual model of the coastal eutrophication problem. Mar Ecol Prog Ser 210: 223–253

Conley DJ, Schelske CL, Stoermer EF (1993) Modification of the biogeochemical cycle of silica with eutrophication. Mar Ecol Prog Ser 101:179–192

Cook PLM, Revill AT, Butler ECV, Eyre BD (2004) Carbon and nitrogen cycling on intertidal mudflats of a temperate Australian estuary. II. Nitrogen cycling. Mar Ecol Prog Ser 280:39–54

Cowan JLW, Boynton WR (1996) Sediment–water oxygen and nutrient exchanges along the longitudinal axis of Chesapeake Bay: seasonal patterns, controlling factors and ecological significance. Estuaries 19:562–580

Dalsgaard T (2003) Benthic primary production and nutrient cycling in sediments with benthic microalgae and transient accumulation of macroalgae. Limnol Oceanogr 48: 2138–2150

Del Amo Y (1996) Dynamique et structure des communautés phytoplanctoniques en écosystème côtier perturbé: cinétiques de l'incorporation du silicium par les diatomées. PhD thesis, Université de Bretagne Occidentale, Brest

Del Amo Y, Le Pape O, Tréguer P, Quéguiner B, Ménesguen A, Aminot A (1997) Impacts of high-nitrate freshwater inputs on macrotidal ecosystems. I. Seasonal evolution of nutrient limitation for the diatom-dominated phytoplankton of the Bay of Brest (France). Mar Ecol Prog Ser 161: 213–224

Dudley BJ, Gahnström AME, Walker DI (2001) The role of benthic vegetation as a sink for elevated inputs of ammonium and nitrate in a mesotrophic estuary. Mar Ecol Prog Ser 219:99–107

Eyre BD, Ferguson AJP (2002) Comparison of carbon production and decomposition, benthic nutrient fluxes and denitrification in seagrass, phytoplankton, benthic microalgae- and macroalgae-dominated warm-temperate Australian lagoons. Mar Ecol Prog Ser 229:43–59

Eyre BD, Ferguson AJP (2005) Benthic metabolism and nitrogen cycling in a subtropical east Australian estuary (Brunswick): temporal variability and controlling factors. Limnol Oceanogr 50:81–96

Ferdie M, Fourqurean JW (2004) Responses of seagrass communities to fertilization along a gradient of relative availability of nitrogen and phosphorus in a carbonate environment. Limnol Oceanogr 49:2082–2094

Gibbs M, Funnell GA, Pickmere S, Norkko A, Hewitt J (2005) Benthic nutrient fluxes along an estuarine gradient of the pinnid bivalve *Atrina zelandica* in summer. Mar Ecol Prog Ser 288:151–164

Gilbert F, Stora G, Bonin P (1998) Influence of bioturbation on denitrification activity in Mediterranean coastal sediments: an *in situ* experimental approach. Mar Ecol Prog Ser 163:99–107

Grall J, Le Loc'h F, Guyonnet B, Riera P (2006) Community structure and food web based on stable isotopes ($\delta^{15}$N and $\delta^{13}$C) analysis of a North Eastern Atlantic maerl bed. J Exp Mar Biol Ecol 338:1–15

Guillou M, Grall J, Connan S (2002) Can low sea urchin densities control macro-epiphytic biomass in a north-east Atlantic maerl bed ecosystem (Bay of Brest, Brittany, France)? J Mar Biol Assoc UK 82:867–876

Hall-Spencer JM, Grall J, Moore PG, Atkinson RJA (2003) Bivalve fishing and maerl-bed conservation in France and the UK—retrospect and prospect. Aquat Conserv Mar Freshw Ecosyst 13:33–41

Koop K, Boynton WR, Wulff F, Carman R (1990) Sediment–water oxygen and nutrient exchanges along a depth gradient in the Baltic Sea. Mar Ecol Prog Ser 63: 65–77

Krause-Jensen D, Christensen PB, Rysgaard S (1999) Oxygen and nutrient dynamics within mats of the filamentous macroalga *Chaetomorpha linum*. Estuaries 22: 31–38

Lepoint G, Gobert S, Dauby P, Bouquegneau JM (2004) Contributions of benthic and planktonic primary producers to nitrate and ammonium uptake fluxes in a nutrient-poor shallow coastal area (Corsica, NW Mediterranean). J Exp Mar Biol Ecol 302: 107–122

Martin S, Clavier J, Guarini JM, Chauvaud L and 5 others (2005) Comparison of *Zostera marina* and maerl community metabolism. Aquat Bot 83:161–174

Martin S, Clavier J, Chauvaud L, Thouzeau G (2007) Community metabolism in temperate maerl beds. I. Carbon and carbonate fluxes. Mar Ecol Prog Ser 335:19–29

Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. Anal Chim Acta 27:301–318

Nedwell DB, Trimmer M (1996) Nitrogen fluxes through the upper estuary of the Great Ouse, England: the role of the bottom sediments. Mar Ecol Prog Ser 142:273–286

Newell RIE, Cornwell JC, Owens MS (2002) Influence of biodeposition and microphytobenthos on sediment nitrogen dynamics: a laboratory study. Limnol Oceanogr 47: 1367–1379

Nixon SW (1981) Remineralization and nutrient cycling in coastal marine ecosystems. In: Neilson BJ, Cronin LE (eds) Estuaries and nutrients. Humana Press, Clifton, NJ, p 111–138

Pritchard DW, Schubel JR (1981) Physical and geological processes controlling nutrient levels in estuaries. In: Neilson BJ, Cronin LE (eds) Estuaries and nutrients. Humana Press, Clifon, NJ, p 47–82

Qu W, Morrison RJ, West RJ (2003) Inorganic nutrient and oxygen fluxes across the sediment–water interface in the inshore macrophyte areas of a shallow estuary (Lake Illawarra, Australia). Hydrobiologia 492:119–127

Ragueneau O, Chauvaud L, Leynaert A, Thouzeau G and 8 others (2002) Direct evidence of a biologically active coastal silicate pump: ecological implications. Limnol Oceanogr 47:1849–4854

Redfield AC, Ketchum BH, Richards FA (1963) The influence of organisms on composition of seawater. In: Hill MN (ed) The sea, Vol II. Wiley, New York, p 26–77

Ricker WE (1973) Linear regression in fishery research. J Fish Res Board Can 30:409–434

Rowe GT, Cruz-Kaegia ME, Morse JW, Boland GS, Escobar Briones EG (2002) Sediment community metabolism associated with continental shelf hypoxia, northern Gulf of Mexico. Estuaries 25:1097–1106

Seitzinger SP, Nixon SW, Plison MEQ (1984) Denitrification and nitrous oxyde production in a coastal marine ecosystem. Limnol Oceanogr 29:73–83

Solorzano L (1969) Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol Oceanogr 14:799–801

Soto-Jimenez MF, Paez-Osuna F, Bojorquez-Leyva H (2003) Nutrient cycling at the sediment–water interface and in sediments at Chiricahueto marsh: a subtropical ecosystem associated with agricultural land uses. Water Res 37: 719–728

Strickland JDH, Parsons TR (1968) A practical handbook of seawater analysis. Bull Fish Res Board Can 167:49–80

Sundbäck K, Miles A, Goransson E (2000) Nitrogen fluxes, denitrification and the role of microphytobenthos in microtidal shallow-water sediments: an annual study. Mar Ecol Prog Ser 200:59–76

Tréguer P, Le Corre P (1975) Manuel d'analyses des sels nutritifs dans l'eau de mer. LOC-UBO, Brest

Valiela I, McClelland J, Hauxwell J, Behr PJ, Hersh D, Foreman K (1997) Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnol Oceanogr 42:1105–1118

Viaroli P, Bartoli M, Bondavalli C, Christian RR (1996) Macrophyte communities and their impact on benthic fluxes of oxygen, sulphide and nutrients in shallow eutrophic environments. Hydrobiologia 329:105–119