

# Community metabolism in temperate maerl beds. I. Carbon and carbonate fluxes

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**ABSTRACT:** Maerl community respiration, photosynthesis and calcification were measured seasonally in the Bay of Brest (France). The dynamics of oxygen, carbon and carbonate fluxes at the water–sediment interface were assessed using benthic chambers. Community respiration (CR) fluctuated in accordance with the seasonal changes in water temperature, from 1.5 mmol C m<sup>-2</sup> h<sup>-1</sup> in winter to 8.7 mmol C m<sup>-2</sup> h<sup>-1</sup> in summer. Mean gross community production (GCP) varied significantly among seasons, according to incident irradiance and temperature, from 3.4 mmol C m<sup>-2</sup> h<sup>-1</sup> in winter to 12.7 mmol C m<sup>-2</sup> h<sup>-1</sup> in summer. Mean annual  $P_{\max}$  for the *P-E* curve was estimated to 13.3 mmol C m<sup>-2</sup> h<sup>-1</sup>. Carbonate precipitation only occurred during light incubations and varied seasonally from 0.7 mmol CaCO<sub>3</sub> m<sup>-2</sup> h<sup>-1</sup> in winter to 4.2 mmol CaCO<sub>3</sub> m<sup>-2</sup> h<sup>-1</sup> in summer. Mean annual  $P_{\max}$  was 3.2 mmol CaCO<sub>3</sub> m<sup>-2</sup> h<sup>-1</sup>. Annual CR was estimated to 407.4 g C m<sup>-2</sup> yr<sup>-1</sup>, and GCP, to 240.9 g C m<sup>-2</sup> yr<sup>-1</sup>. Maerl communities are, therefore, heterotrophic systems (GCP:CR = 0.6), and are a source of CO<sub>2</sub> for surrounding environments. In addition, CO<sub>2</sub> released by calcification averaged 39.2 g C m<sup>-2</sup> yr<sup>-1</sup>. Maerl community annual carbonate production was estimated to 486.7 g CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup>; they are therefore one of the most important carbonate producers in shallow coastal waters.

**KEY WORDS:** Calcareous algae · Community metabolism · *P-E* curves · Primary production · Respiration · Calcification

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## INTRODUCTION

Benthic macroalgal-based communities are expected to create areas of high productivity in shallow coastal waters. They are often known to export carbon to adjacent coastal systems (Duarte & Cebrian 1996). When dominated by calcifying macroalgae, such as corallines, macroalgal-based communities are also significant sites of carbonate production (Canals & Ballesteros 1997). Despite their low growth rate, coralline macroalgae are generally abundant in coastal areas, and they can contribute significantly to benthic primary production and calcification (Littler et al. 1991, Chisholm 2000, 2003, Martin et al. 2005). Widespread in shallow coastal waters throughout the world (Johansen 1981), coralline-dominated communities are therefore of paramount importance in global carbon and carbonate cycles.

Maerl beds refer to communities dominated by free-living coralline algae and their debris (Hall-Spencer et al. 2003). They can occur at high biomasses and over large areas worldwide, and are considered among the more extended benthic communities dominated by macroalgae (Foster 2001). Maerl communities are one of the most diverse marine ecosystems (Hall-Spencer et al. 2003, Wilson et al. 2004). Their complex architecture, resulting from the lattice of branched twig-like thalli, provides a habitat for rich and diverse populations of both autotrophic and heterotrophic organisms (Guillou et al. 2002, Wilson et al. 2004, Grall et al. 2006). In temperate systems, maerl communities are among the most productive benthic systems (Martin et al. 2005). Community primary production and respiration are major processes affecting the carbon cycle. Maerl beds are also considered among the major benthic producers of calcium carbonate in temperate

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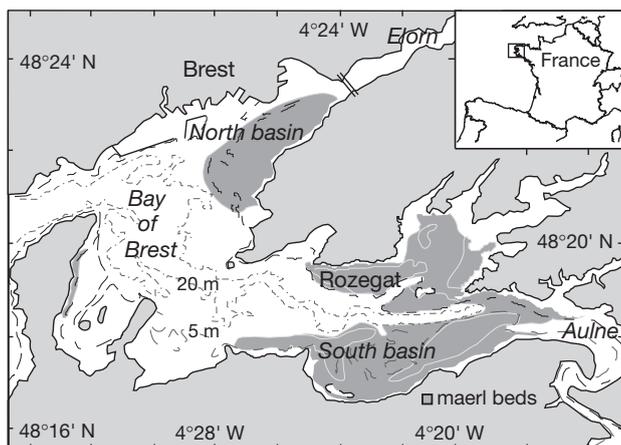


Fig. 1. Map of the Bay of Brest, distribution of maerl beds and locality of the experimental station (Rozegat)

marine environments (Bosence 1980). Their carbonate production and accumulation in temperate systems are close to those reviewed in coral reef environments (Bosence & Wilson 2003). The community carbonate flux, related to calcium carbonate precipitation and dissolution, is an important process, which affects both carbon and carbonate cycles (Gattuso et al. 1998).

Information on temperate maerl community primary production and respiration remains scarce (Martin et al. 2005), and the seasonal variability is unknown. Maerl carbonate precipitation has received little attention in temperate systems (Bosence 1980, Potin et al. 1990, Bosence & Wilson 2003, Martin et al. 2006a), and the calcification of the entire maerl community has never been assessed. Quantifying these processes is, however, fundamental to understanding the carbon and carbonate fluxes in shallow coastal marine systems where they develop. In this context, the aim of this work was to determine the annual primary production, respiration and calcification of a temperate maerl community in the Bay of Brest.

## MATERIALS AND METHODS

**Site description.** The Bay of Brest is a shallow, semi-enclosed system, located at the extreme West of Brittany, France (Fig. 1). The hydrology of the bay is controlled by water exchanges with the Iroise Sea, through a narrow strait (2 km wide), and influenced by the moderate input of 2 rivers (Elorn and Aulne). Maximal tidal range is 7.3 m in the Bay of Brest. More than 50% of the surface of the bay is <5 m in depth below Chart Datum. Maerl beds develop from the limit of spring low tides to a depth of 15 m. They cover about one-third of the bay surface area and comprise princi-

pally the species *Lithothamnion corallioides* (Crouan & Crouan) and to a lesser extent *Phymatholithon calcareum* (Adey & McKibbin). The experiments were performed on the maerl bed of Rozegat, situated between 0.5 and 2.9 m in depth below Chart Datum. This maerl bed is located in the southern basin of the Bay of Brest, far from the disturbances of urban and harbor areas (northern basin; Guillou et al. 2002). Mean temperature measured at the MAREL Iroise Station (Observatoire du Domaine Côtier de l'IUEM) in the west of the Bay of Brest varied from 9.6 to 17.6°C, and mean surface irradiance at solar noon varied from 360 to 1460  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in winter and summer, respectively (Fig. 2). Daylength varied from 8 h in December to 16 h in June. The field experiments took place between March 2002 and October 2004 (Table 1) and were carried out from the RV 'Côtes de la Manche'.

**Field measurements.** Community respiration, production and calcification were investigated by *in situ* incubation experiments. Three replicate enclosures (Boucher & Boucher-Rodoni 1988) were installed by SCUBA divers. PVC rings (25 cm in height) were gently pushed into the substratum, avoiding sediment disturbance. Chambers covered a large area (0.2 m<sup>2</sup>) in order to obtain a realistic representation of irrigating macrofauna (Glud et al. 2003). Acrylic hemispheres were secured to the base to trap a known volume of bottom water, varying from 44.2 to 75.6 l according to the depth of ring insertion into the substratum. Clear chambers were used to assess net community production and calcification in daylight, and opaque chambers were used to estimate community respiration and calcification in dark conditions. A series of incubations

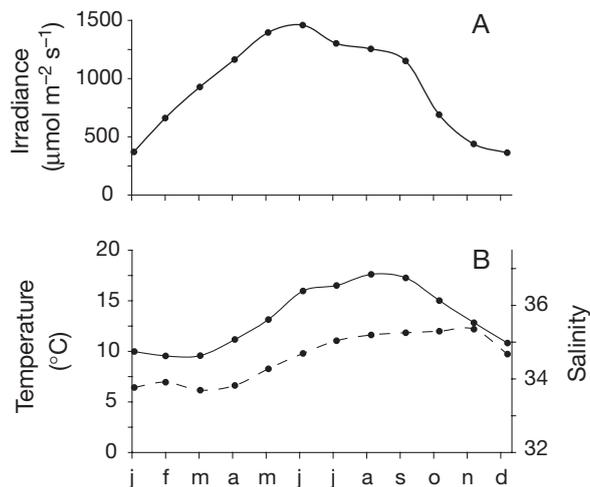


Fig. 2. Evolution (over 1 yr) of mean values of (A) surface irradiance at solar noon; (B) surface water temperature (plain line) and salinity (broken line) recorded at the MAREL Iroise Station for the period from 2002 to 2004

Table 1. Date of experiments and number (n) of incubations under light and dark conditions for each season

Season	Date	Light (n)	Dark (n)
Winter	Feb 2003, Feb 2004	18	9
Spring	Mar–Apr 2002, May 2003, May 2004	42	18
Summer	Sep 2004	6	6
Autumn	Oct 2003, Oct 2004	6	18

were 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. Homogenization of water inside the enclosures was provided by adjustable submersible pumps connected to waterproof batteries. As metabolic response of permeable sediments depends on hydrodynamics (Forja & Gomez-Parra 1998), water flow in each enclosure was adjusted to correspond as far as possible to the hydrodynamics of the surrounding free-flowing water ( $2 \text{ l min}^{-1}$ ). Production and respiration in the bottom water enclosed in the chambers were considered negligible (Martin et al. 2005).

$\text{O}_2$  concentration ( $\text{mg l}^{-1}$ ), salinity (in practical salinity units), temperature ( $^{\circ}\text{C}$ ) and depth (m) were recorded every minute inside each enclosure by a YSI 6920 probe. Water samples were collected inside the chambers for pH and total alkalinity (TA) measurements using 450 ml polyethylene syringes, at the beginning and at the end of the incubations. They were passed through GF/F filters and poisoned by mercuric chloride (DOE 1994). 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 algae. Irradiance ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) was averaged every min. The maerl enclosed in the chambers was sampled at the end of the experiments, by 5 cores of  $36 \text{ cm}^2$  placed randomly in each chamber by the divers.

**Sample processing.** The pH (in total scale) was measured immediately on board using a pH meter (PHM 240, radiometer) standardized with TRIS/HCl and 2-aminopyridine/HCl buffer solutions (DOE 1994). TA was measured on 50 ml sub-samples by the automatic potentiometric method using Gran titration (Titralab TIM 865, radiometer). Total inorganic carbon concentration was calculated from pH, TA, temperature and salinity according to the method of Lewis & Wallace (1998). In the laboratory, the living coralline algae from the cores were isolated and dried at  $60^{\circ}\text{C}$  for 48 h and the ash-free dry weight (AFDW) was calculated after combustion ( $450^{\circ}\text{C}$  for 4 h).

**Data treatment.** The community respiration, net community production and net calcification were cal-

culated by the difference between initial and final concentrations. As the community is dominated by calcifying organisms, the inorganic carbon flux was estimated using the alkalinity anomaly technique (Smith & Key 1975, Chisholm & Gattuso 1991):

$$\begin{aligned} \text{NCP (or CR)}_{\text{O}_2} &= \frac{\Delta\text{O}_2 \times v}{s \times \Delta t} \\ \text{NCP (or CR)}_{\text{DIC}} &= \frac{\Delta\text{DIC} \times v}{s \times \Delta t} - \text{CG} \\ \text{CG} &= \frac{\Delta\text{TA} \times v}{2 \times s \times \Delta t} \end{aligned}$$

where NCP (or CR) is net community production or community respiration ( $\text{mmol O}_2$  or  $\text{DIC m}^{-2} \text{ h}^{-1}$ ); CG is net community calcification ( $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ );  $\Delta\text{O}_2$  is the change in the concentration of dissolved  $\text{O}_2$  during incubation ( $\text{mmol l}^{-1}$ );  $v$  is chamber volume (l);  $s$  is the enclosed surface area ( $\text{m}^2$ );  $\Delta t$  is incubation time (h);  $\Delta\text{DIC}$  is the change in total inorganic carbon ( $\text{mmol l}^{-1}$ );  $\Delta\text{TA}$  is the change in total alkalinity ( $\text{meq. l}^{-1}$ ). Negative fluxes of  $\text{O}_2$ , DIC and  $\text{CaCO}_3$  for NCP, CR and CG correspond to an assimilation of  $\text{O}_2$  and DIC, and a precipitation of  $\text{CaCO}_3$  by the maerl community.

The whole datasets of NCP and CG were plotted as an exponential function  $P$ - $E$  of the *in situ* irradiance  $E$  ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ):

$$\text{NCP (or CG)} = P_{\text{max}}(1 - e^{-E/E_k}) + c \quad (1)$$

where  $P_{\text{max}}$  is the rate of maximum gross community production (or calcification; in  $\text{mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ,  $\text{mmol DIC m}^{-2} \text{ h}^{-1}$ , or  $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ ),  $E_k$  is the minimum saturating irradiance (in  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) and  $c$  is the respiration rate (or night-time calcification; in  $\text{mmol m}^{-2} \text{ h}^{-1}$ ).

Gross community primary production (GCP) corresponds to the difference between NCP and CR. CR, GCP and CG were also related to temperature ( $T$ ) using linear regressions. The relationship between GCP (or CG) and the pooled factors, temperature and irradiance, was then expressed as:

$$\text{GCP (or CG)} = P_{\text{max}}(1 - e^{-E/E_k}) + dT + e \quad (2)$$

where  $d$  is a multiplicative factor and  $e$  is a constant.

Community respiratory (CRQ) and photosynthetic (CPQ) quotients were calculated as  $\text{CRQ} = |\text{CR}_{\text{DIC}}/\text{CR}_{\text{O}_2}|$  and  $\text{CPQ} = |\text{NCP}_{\text{O}_2}/\text{NCP}_{\text{DIC}}|$ , respectively. As  $\text{O}_2$  (or DIC) production and DIC (or  $\text{O}_2$ ) consumption are both affected by natural variability and measurement errors, the community metabolic quotients were calculated by means of functional regressions (Ricker 1973).

Diel GCP and CG were estimated for each month by summing hourly GCP and CG calculated from Eq. (2). Mean monthly surface water temperature and surface-irradiance data were measured at the MAREL Iroise

Station over the period 2002 to 2004. Irradiance data were averaged hourly to obtain the mean daily course of irradiance for each month. Surface irradiance data were transformed into underwater incident irradiance at the mean water depth of the study site (5.6 m) using light extinction coefficients reported for the Bay of Brest ( $0.41 \text{ m}^{-1}$  in winter and  $0.38 \text{ m}^{-1}$  in the other seasons; Martin et al. 2005, 2006a). Dark calcification and respiration measured during the daylight period were considered to be constant throughout the day (Martin et al. 2005, 2006a). Diel CR values were estimated for each month from the linear regression of respiration versus temperature. Annual CR, GCP and CG were calculated by averaging monthly diel values, multiplied by 365. Mean and standard deviation (SD) values for CR, GCP and CG were estimated by Monte Carlo simulations. The parameters of linear regression and Eq. (2) were sampled randomly (500 replicate runs). Diel and annual NCP were evaluated by summing GCP and CR. Seasonal CR, GCP and CG variabilities were assessed by 1-way ANOVAs (normal distribution and equality of variance).

## RESULTS

### Experimental parameters

During the incubations, water depth varied from 2.0 to 9.3 m, according to the tide. Bottom-water temperature varied from  $8.8^\circ\text{C}$  in winter to  $18.9^\circ\text{C}$  in summer, and bottom-water salinity varied from 31.2 to 35.6 (Table 2). Incident irradiance at the bottom ranged between 30 and  $550 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . The average biomass of live maerl thallus was 13055 (SD 4331) g dry wt  $\text{m}^{-2}$ , corresponding to 986 (SD 327) g AFDW  $\text{m}^{-2}$ .

### Community respiratory and photosynthetic quotients

CRQ and CPQ functional regressions explained 87 and 89% of data variability during dark and light con-

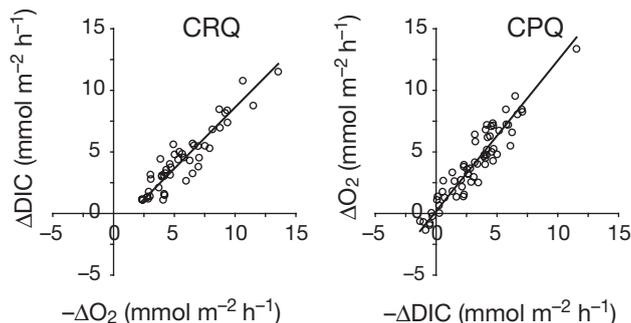


Fig. 3. Relationships between net  $\Delta\text{O}_2$  and  $\Delta\text{DIC}$  (dissolved inorganic carbon) for community respiratory data ( $r^2 = 0.87$ ) and community production data ( $r^2 = 0.89$ ) (CRQ: community respiratory quotient; CPQ: community photosynthetic quotient)

ditions, respectively (Fig. 3). CRQ was 0.99 (SE 0.05) and did not differ significantly from 1 (Z-test,  $Z = 0.10$ ,  $p = 0.23$ ). The intercept was significantly different from zero (Z-test,  $Z = 4.44$ ,  $p < 0.001$ ). Community  $\text{O}_2$  consumption was  $1.33$  (SE 0.07)  $\text{mmol m}^{-2} \text{ h}^{-1}$  when DIC release was nil. CPQ was 1.22 (SE 0.05), and the intercept ( $0.20 \text{ mmol m}^{-2} \text{ h}^{-1}$ , SE 0.01) did not significantly differ from zero (Z-test,  $Z = 1.22$ ,  $p = 0.06$ ).

### Community respiration

Mean CR varied significantly according to the season (1-way ANOVA,  $F = 21.53$ ,  $p < 0.001$  and  $F = 18.24$ ,  $p < 0.001$ , for  $\text{O}_2$  and DIC, respectively; Fig. 4). The highest mean CR was observed in summer ( $-10.1 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ , SD 2.1;  $8.7 \text{ mmol DIC m}^{-2} \text{ h}^{-1}$ , SD 1.5), and the lowest, in winter ( $-2.8 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ , SD 0.5;  $1.5 \text{ mmol DIC m}^{-2} \text{ h}^{-1}$ , SD 0.6). Mean CR did not differ significantly between spring and autumn, with a mean value of  $-5.7$  (SD 1.9)  $\text{mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$  and  $4.2$  (SD 2.1)  $\text{mmol DIC m}^{-2} \text{ h}^{-1}$ . CR increased significantly with water temperature (Table 3), from 0.6 to  $0.7 \text{ mmol m}^{-2} \text{ h}^{-1} \text{ per } ^\circ\text{C}$ . The factor temperature explained  $> 50\%$  of data variability.

### Gross community production

Mean GCP varied significantly among seasons (Kruskal-Wallis,  $H = 19.00$ ,  $p < 0.001$ ), with the highest values in summer ( $14.7 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ , SD 1.8;  $-12.7 \text{ mmol DIC m}^{-2} \text{ h}^{-1}$ , SD 1.2) and the lowest in winter ( $6.1 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ , SD 1.7;  $-3.4 \text{ mmol DIC m}^{-2} \text{ h}^{-1}$ , SD 2.0; Fig. 5). Bottom-water temperature explained 33 and 49% of  $\text{O}_2$

Table 2. Environmental parameters (means) measured during the experiments (SD in parentheses)

Season	Bottom irradiance ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	Bottom-water salinity	Bottom-water temperature ( $^\circ\text{C}$ )	Maerl biomass (g dry wt $\text{m}^{-2}$ )
Winter	65 (57)	31.2 (2.4)	8.8 (0.3)	13604 (383)
Spring	167 (167)	33.4 (1.2)	12.4 (1.5)	12196 (6015)
Summer	110 (83)	35.6 (0.2)	18.9 (0.2)	13529 (6404)
Autumn	37 (40)	34.0 (1.1)	14.0 (0.4)	12887 (4520)

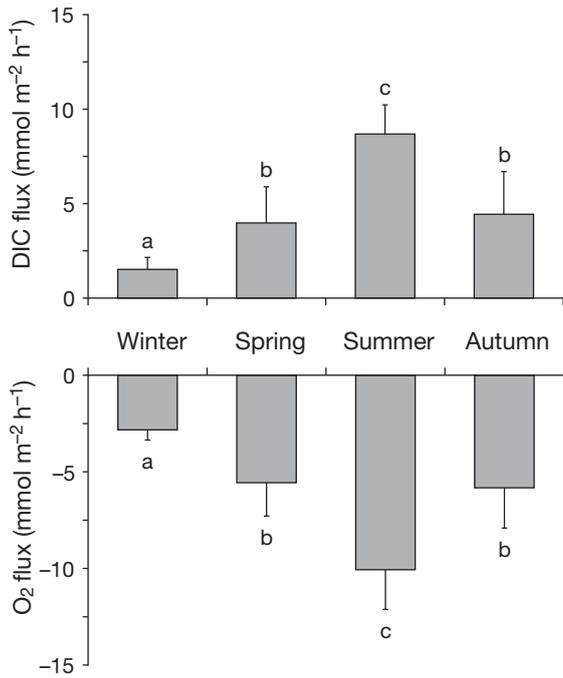


Fig. 4. Seasonal community respiration in DIC release and O<sub>2</sub> consumption. Different letters on bars indicate significant differences ( $p < 0.05$ ) among means (mean + SD;  $n = 6$  to 17)

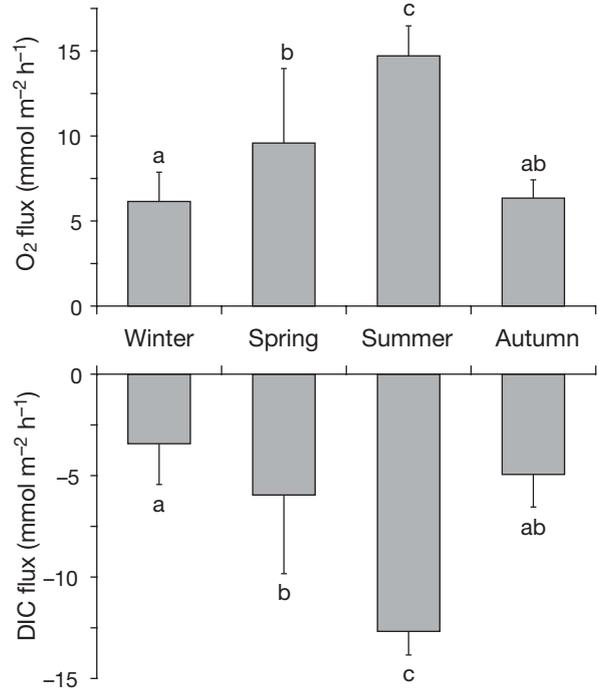


Fig. 5. Seasonal gross community production in O<sub>2</sub> production and DIC uptake. Different letters on bars indicate significant differences ( $p < 0.05$ ) among means (mean + SD;  $n = 6$  to 40)

and DIC variability, respectively (Table 3). A mean annual  $P-E$  curve was fitted to pooled gross production data (Fig. 6, Table 4a). Bottom irradiance explained 68 and 57% of O<sub>2</sub> and DIC variability, respectively. A general model (2) including temperature ( $T$ ) and irradiance ( $E$ ) has been adjusted to O<sub>2</sub> and DIC data (Table 4b). These models explained 75% of GCP variability both in DIC and O<sub>2</sub>. The factor biomass was not considered because maerl biomasses were homogeneous in the study site and this factor has previously been found negligible in the variations of maerl community production (Martin et al. 2005).

Table 3. Values of parameters (SE in parentheses) calculated by linear regressions of community respiration (CR, mmol m<sup>-2</sup> h<sup>-1</sup>), gross community production (GCP, mmol m<sup>-2</sup> h<sup>-1</sup>) and net community calcification (CG, mmol m<sup>-2</sup> h<sup>-1</sup>) versus temperature ( $T$ , °C), expressed as CR (GCP or CG) =  $a \times T + b$  ( $N$ : number of observations;  $r^2$ : proportion of variance explained by the regression;  $p$ : p-value)

	$a$	$b$	$N$	$r^2$	$p$
CR <sub>O<sub>2</sub></sub>	-0.61 (0.09)	2.76 (1.34)	44	0.50	<0.001
CR <sub>DIC</sub>	0.68 (0.09)	-5.12 (1.22)	44	0.59	<0.001
GCP <sub>O<sub>2</sub></sub>	0.86 (0.16)	-1.67 (2.03)	61	0.34	<0.001
GCP <sub>DIC</sub>	-0.93 (0.12)	5.55 (1.48)	67	0.49	<0.001
CG (Light)	-0.33 (0.05)	2.51 (0.63)	64	0.41	<0.001
CG (Dark)	-0.01 (0.04)	0.32 (0.52)	42	0.21	0.764

### Community calcification

Mean CG during dark incubations did not differ significantly from zero for the 4 seasons ( $t$ -test,  $p > 0.05$ ), with  $\Delta TA$  variations ranging from -0.75 (SD 2.11) meq. m<sup>-2</sup> h<sup>-1</sup> in summer to 0.88 (SD 1.77) meq. m<sup>-2</sup> h<sup>-1</sup> in

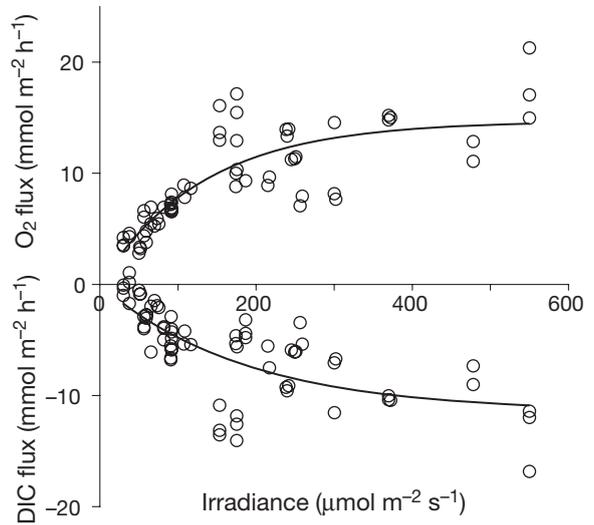


Fig. 6. Relationships between gross community production (DIC consumption and O<sub>2</sub> release) and irradiance (Model 1)

Table 4. Values of parameters (SE in parentheses) calculated by non-linear regressions of gross community production (GCP,  $\text{mmol m}^{-2} \text{h}^{-1}$ ) and net community calcification (CG,  $\text{mmol m}^{-2} \text{h}^{-1}$ ) (a) versus irradiance ( $E$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), expressed as  $\text{GCP}$  (or  $\text{CG}$ ) =  $P_{\text{max}}(1 - e^{-E/E_k}) + c$  (Model 1); and (b) versus both irradiance and temperature ( $T$ ,  $^{\circ}\text{C}$ ), expressed as  $\text{GCP}$  (or  $\text{CG}$ ) =  $P_{\text{max}}(1 - e^{-E/E_k}) + dT + e$  (Model 2) (N: number of observations;  $r^2$ : proportion of variance explained by the regression)

	$P_{\text{max}}$	$E_k$	$c$	$d$	$e$	N	$r^2$
<b>(a) Model 1</b>							
GCP <sub>O<sub>2</sub></sub>	14.50 (1.32)	140 (39)	0.37 (1.54)			61	0.68
GCP <sub>DIC</sub>	-13.29 (1.90)	92 (27)	3.62 (2.20)			67	0.57
CG	-3.20 (0.49)	155 (52)	0.24 (0.16)			64	0.51
<b>(b) Model 2</b>							
GCP <sub>O<sub>2</sub></sub>	12.42 (1.30)	178 (59)		0.43 (0.11)	-2.99 (1.52)	61	0.75
GCP <sub>DIC</sub>	-10.16 (1.69)	84 (26)		-0.62 (0.09)	9.17 (2.01)	67	0.75
CG	-2.91 (0.32)	96 (28)		-0.14 (0.03)	2.22 (0.48)	64	0.58

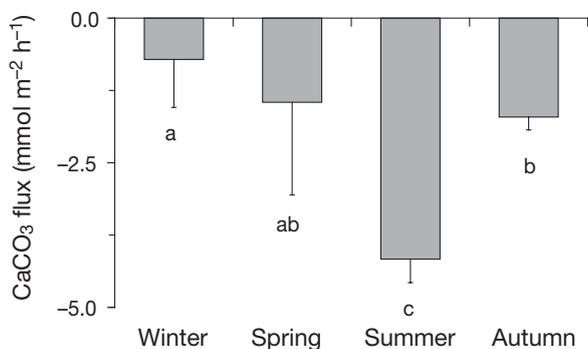


Fig. 7. Seasonal net community calcification during light incubations. Different letters on bars indicate significant differences ( $p < 0.05$ ) among means (mean + SD;  $n = 6$  to 38)

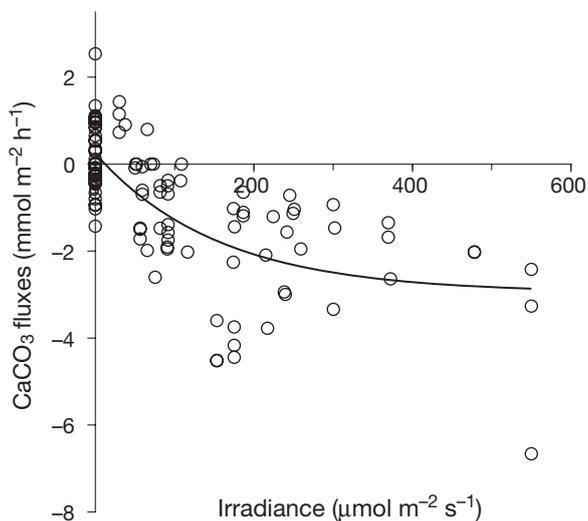


Fig. 8. Relationship between net community calcification and irradiance (Model 1)

autumn. Mean CG during light incubations was negative, indicating  $\text{CaCO}_3$  uptake by the community (Fig. 7), and varied seasonally (Kruskal-Wallis,  $H = 19.00$ ,  $p < 0.001$ ), with the highest values in summer ( $-4.17 \text{ mmol m}^{-2} \text{h}^{-1}$ , SD 0.41) and the lowest in winter ( $-0.71 \text{ mmol m}^{-2} \text{h}^{-1}$ , SD 0.83). Mean CG averaged  $-1.58$  (SD 0.91)  $\text{mmol m}^{-2} \text{h}^{-1}$  in spring and autumn.  $\Delta\text{TA}$  during light incubations varied from  $-8.33$  (SD 0.81)  $\text{meq. m}^{-2} \text{h}^{-1}$  in summer to  $-1.43$  (SD 1.66)  $\text{meq. m}^{-2} \text{h}^{-1}$  in winter. CG values were significantly related to bottom irradiance (Fig. 8, Table 4a) and to bottom-water temperature during light incubations (Table 3). Temperature and irradiance explained 41 and 51 % of data variability, respectively. A general

model (2) including the 2 parameters ( $T$ ,  $E$ ) has been adjusted to the data (Table 4b). This model explains 58 % of CG. The relatively small increase in precision compared with the  $P$ - $E$  relationship (51 %) can be attributed to the significant correlation between irradiance and temperature ( $r = 0.40$ ,  $p < 0.001$ ).

### Diel carbon and carbonate production

Estimated diel CR varied seasonally from 0.39 (SD 0.45)  $\text{g C m}^{-2} \text{d}^{-1}$  in February to 1.96 (SD 0.59)  $\text{g C m}^{-2} \text{d}^{-1}$  in August (Fig. 9). Estimated diel GCP fluctuated from a minimum in January (0.04  $\text{g C m}^{-2} \text{d}^{-1}$ , SD 0.13) to a maximum in August (1.32  $\text{g C m}^{-2} \text{d}^{-1}$ , SD 0.62).

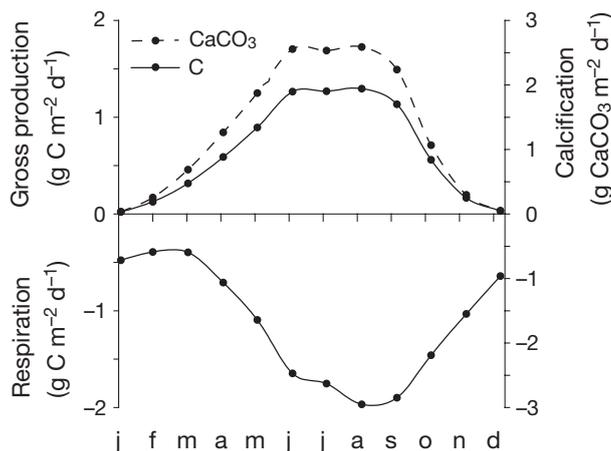


Fig. 9. Evolution of diel estimated community respiration (lower plain line), gross community production (upper plain line) and net community calcification (broken line) for the Rozegat maerl bed

The mean molar ratio between GCP and CR (GCP:CR) was 0.60, and varied seasonally, with a minimum in December and January (0.08) and a maximum in May (0.86). Estimated diel CG also showed seasonal variability, with a minimum in January ( $0.05 \text{ g CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ , SD 0.29) and a maximum in August ( $2.72 \text{ g CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ , SD 1.35). The mean annual molar ratio between CG and GCP (CG:GCP) was 0.24, varying from 0.15 in January to 0.27 in April.

Estimated annual CR and GCP were  $407 \text{ (SD 188) g C m}^{-2} \text{ yr}^{-1}$  and  $241 \text{ (SD 150) g C m}^{-2} \text{ yr}^{-1}$ , respectively. Therefore, estimated annual NCP averaged  $-167 \text{ (SD 337) g C m}^{-2} \text{ yr}^{-1}$ . Estimated annual CG was  $487 \text{ (SD 333) g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ . The ratio ( $\Psi$ ) of  $\text{CO}_2$  released to  $\text{CaCO}_3$  precipitated during calcification, which depends on temperature and salinity (Frankignoulle et al. 1994), varied from 0.65 in August to 0.73 in March in the Bay of Brest.  $\text{CO}_2$  released by calcification was thus  $39 \text{ (SD 27) g C m}^{-2} \text{ yr}^{-1}$ . The total  $\text{CO}_2$  release by the maerl community was  $447 \text{ (SD 215) g C m}^{-2} \text{ yr}^{-1}$ .

## DISCUSSION

### Community respiration

The CR of temperate maerl beds ( $3 \text{ to } 10 \text{ mmol C m}^{-2} \text{ h}^{-1}$ ) is in the range of values published for macroalgal-dominated coastal benthic communities ( $2 \text{ to } 41 \text{ mmol C m}^{-2} \text{ h}^{-1}$ ; review in Middelburg et al. 2005). Data on the respiration of coralline-dominated communities are essentially available for tropical systems (Chisholm 2003). Maerl communities exhibit high respiration rates, most notably when compared to tropical crustose coralline communities ( $2 \text{ to } 5 \text{ mmol C m}^{-2} \text{ h}^{-1}$ ; Chisholm 2003). Indeed, maerl beds shelter a rich population of heterotrophs, resulting from their high biodiversity, and a high faunal biomass that varies from  $10 \text{ g AFDW m}^{-2}$  in winter to  $70\text{--}80 \text{ g AFDW m}^{-2}$  in late-summer at the Rozegat site (Grall 2002, Grall et al. 2006).

CR exhibits strong seasonality, from  $0.4 \text{ g C m}^{-2} \text{ d}^{-1}$  in February and March to  $2 \text{ g C m}^{-2} \text{ d}^{-1}$  in August. Respiration fluctuations appear to be primarily controlled by water temperature ( $>50\%$ ), which is in agreement with most studies on benthic community metabolism (Boucher & Boucher-Rodoni 1988, Cook et al. 2004). CR is controlled by community organism biomass and respiration rates, both correlated with temperature. At the Rozegat maerl bed, faunal biomass exhibits a 7- to 8-fold increase when water temperature rises from  $10^\circ\text{C}$  in winter to  $18^\circ\text{C}$  in summer (Grall 2002, Grall et al. 2006). Annual epiphytic macroalgae also show high seasonal variations from  $0.02 \text{ g dry wt m}^{-2}$  in January to  $2.2 \text{ g dry wt m}^{-2}$  in July, at Rozegat (Guillou et al.

2002). Conversely, maerl biomass shows very little seasonal variation, since maerl is a perennial alga with a very low growth rate, of approximately  $1 \text{ mm yr}^{-1}$  (Blake & Maggs 2003, Bosence & Wilson 2003). The positive relationship between respiration rates and temperature is well known for fauna (Martin et al. 2006b) and macroalgae (Cheshire et al. 1996, Martin et al. 2006a). Microbial and epiphytic microalgal components also show strong seasonality by their adaptation or change in community structure according to temperature fluctuations and the availability of organic and inorganic nutrients (Cammen 1991).

In a previous study (Martin et al. 2006a), we estimated respiration rates of  $0.07$  and  $0.30 \text{ } \mu\text{mol C g}^{-1} \text{ dry wt h}^{-1}$  for isolated *Lithothamnion corallioides* in winter and summer, respectively. Considering these values and the mean biomass of maerl measured in the present study, average respiration rates of the coralline algae may be estimated as  $22.8$  and  $97.2 \text{ mmol C m}^{-2} \text{ d}^{-1}$  in winter and summer, respectively, accounting for 60 to 70 % of total CR. Thus, only about one-third of the CR may be related to faunal, epiphytic algal and microbial respiration. This percentage might be underestimated due to a potential overestimation of the respiration rates of coralline algae in the bottle experiments (Martin et al. 2006a). In our study, we extrapolated the respiration measured during the day over the 24 h periods. However, respiration rates in the light are recognized to be higher than those in the dark, both at individual and at community levels (Middelburg et al. 2005). Thus, diel respiration has probably been overestimated.

The CRQ was equal to 1, but the intercept was different from zero, reflecting oxygen consumption when carbon dioxide fluxes were nil. This oxygen consumption represents 13 to 45 % of the community respiration. This pattern can be related to oxygen consumption through chemical oxidative processes, without DIC production, such as ferrous iron, sulfide, methane, reduced manganese and ammonia oxidations (Boucher et al. 1998, Cook et al. 2004).

### Community primary production

The GCP of maerl beds ( $0.05 \text{ to } 1.3 \text{ g C m}^{-2} \text{ d}^{-1}$ ), including the production of maerl and their epiphytic macro- and microalgae, is lower than the mean value reported for macrophyte-dominated systems ( $\sim 3 \text{ g C m}^{-2} \text{ d}^{-1}$ ; Gattuso et al. 1998). However, maximal GCP ( $15 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) is in the range of values reported for tropical crustose coralline communities ( $6 \text{ to } 15 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ; Chisholm 2003) and for macroalgal-dominated coral reef communities comprised of 20 % calcareous algae ( $10 \text{ to } 20 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ; Gattuso et al. 1997).

GCP displays seasonal variability, with a factor of 3.5 between winter and summer. GCP is principally related to incident irradiance and bottom-water temperature, which explained 75% of the variability. The influence of these 2 parameters on community primary production is well established for macroalgal communities (Cheshire et al. 1996), but also for coralline communities (Roberts et al. 2002, Chisholm 2003). Our results are consistent with the evolution of incident irradiance that varies seasonally in intensity and duration, being 4-fold more intense and 2-fold longer in summer than in winter. Temperature influences positively both macroalgal (Lüning 1990) and microalgal (Light & Beardall 2001) primary production, and has previously been reported for temperate corallines with a maximal production in summer (Blake & Maggs 2003, Martin et al. 2006a). Temperature influences community production by controlling both biomass and production rates of autotrophs. As previously stated, epiphytic algal biomasses vary seasonally, with the highest values in summer and the lowest in winter (Guillou et al. 2002). Despite their comparatively low biomasses, epiphytes can significantly contribute to macroalgal production (Charpy-Roubaud & Sournia 1990). However, the gross production of maerl community epiphytic macroalgae, such as *Soleria chordalis*, was estimated to 0.06 mmol C g<sup>-1</sup> dry wt h<sup>-1</sup> in summer (S. Martin unpubl. data) and, considering a biomass of 2.2 g dry wt m<sup>-2</sup> in summer (Guillou et al. 2002), their contribution to the GCP remains low (0.1 mmol C m<sup>-2</sup> h<sup>-1</sup>). Epiphytic microalgae are abundant in maerl beds, since maerl branch structure is a favorable substrate for their development and facilitates their colonization (Grall 2002, Martin et al. 2005). Their contribution may reach 20 to 50% of the total production of macrophyte-dominated benthic systems (Hemminga & Duarte 2000), and they probably play a major role in the GCP of maerl beds.

Considering the gross production rates of *Lithothamnion corallioides* given by Martin et al. (2006a) for 5 m depth and maerl biomasses, gross production rates of coralline algae may average 0.27 g C m<sup>-2</sup> d<sup>-1</sup> in winter and 1.59 g C m<sup>-2</sup> d<sup>-1</sup> in summer, values 1.5-fold higher than those measured in the present study. The difference between measurements of isolated maerl and the entire community could result from the irradiance reaching the thalli. As reported by Binzer & Sand-Jensen (2002), primary production considerably differs between individual thalli and entire communities. Indeed, when incubated alone, the whole thallus is exposed to light, whereas only the upper layers of maerl receive irradiance in the community. Light attenuation by shading between maerl thalli can be significant, since the layer of living maerl develops up to 3 cm depth into the substratum (Grall 2002, Martin

et al. 2005). In addition, maerl thalli are generally colonized by numerous epiphytic organisms (Guillou et al. 2002, Grall et al. 2006) mixed with mineral and organic particle deposits. This periphyton complex may create a physical barrier to light absorption (Drake et al. 2003), but also to carbon uptake (Sand-Jensen 1977). Epiphytic organisms as well as deposit layers were removed in experiments on isolated coralline algae (Martin et al. 2006a), allowing the thalli to receive more light in the same environmental conditions, with subsequent positive effects on production.

### Community calcification

Measurements of calcification in temperate maerl communities are based on maerl growth rate by the calcimass method (Bosence 1980, Edyvean & Ford 1987, Potin et al. 1990). The present study is a first attempt to measure temperate coralline community calcification rate by the alkalinity anomaly method that is considered the most convenient technique for short-duration experiments (Gattuso et al. 1999). Measurements of CG by this method correspond to the balance between TA decrease (considered as CaCO<sub>3</sub> precipitation) and increase (considered as CaCO<sub>3</sub> dissolution) during incubations, with the assumption that no other processes significantly affect TA. However, changes in TA can also be related to chemical reactions occurring in the sediment, such as sulfate reduction (SO<sub>4</sub><sup>2-</sup> + 2H<sup>+</sup> → H<sub>2</sub>S + 2O<sub>2</sub>; ΔTA = + 2 eq.) and nitrification (NH<sub>4</sub><sup>+</sup> + 2O<sub>2</sub> → NO<sub>3</sub><sup>-</sup> + 2H<sup>+</sup> + H<sub>2</sub>O; ΔTA = -2 eq.; Gattuso et al. 1999, Middelburg et al. 2005). Sulfate reduction can be a significant process modifying TA in sedimentary lagoons (Smith & Hollibaugh 1997), but is negligible in well-oxygenated calcareous sediments (Boucher et al. 1998) such as maerl beds. In the Rozegat maerl community, nitrate fluxes from the sediment to the water column occur only in summer during light incubations and in summer and autumn during dark incubations (Martin et al. 2007, this volume). During light incubations in summer, the mean nitrate production corresponds to a ΔTA of -0.06 meq. m<sup>-2</sup> h<sup>-1</sup> and is likely to cause errors of <1% on CG. However, during dark incubations when ΔTA is close to zero, nitrification can induce >15% variation. Furthermore, the processes of photosynthesis and respiration are coupled with the assimilation and dissimilation of NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup> and HPO<sub>4</sub><sup>2-</sup>, which liberate OH<sup>-</sup> or H<sup>+</sup> (or take up H<sup>+</sup> or OH<sup>-</sup>; Gattuso et al. 1999). These reactions for benthic marine macroalgae are described by Atkinson & Smith (1983) and are based on a C:N:P atomic ratio of 550:30:1. Accordingly, photosynthesis (or respiration) induces ΔTA of -0.05 (or +0.05) eq. mol<sup>-1</sup> of fixed (or released) CO<sub>2</sub> when NH<sub>4</sub><sup>+</sup> is assimilated (or dissimi-

lated) and  $+0.06 \text{ eq. mol}^{-1}$  of fixed  $\text{CO}_2$  when  $\text{NO}_3^-$  is assimilated. During light incubation,  $\text{CO}_2$  uptake by photosynthesis is balanced by  $\text{CO}_2$  release by respiration, with a NCP of 1 to  $4 \text{ mmol m}^{-2} \text{ h}^{-1}$ . Ammonium or nitrate assimilation coupled with these reactions induces  $\Delta\text{TA}$  of  $\pm 0.1$  to  $0.2 \text{ meq. m}^{-2} \text{ h}^{-1}$ , corresponding to 3–8% of total  $\Delta\text{TA}$ . During dark incubations, ammonium or nitrate dissimilation induces  $\Delta\text{TA}$  of  $\pm 0.1$  to  $0.5 \text{ meq. m}^{-2} \text{ h}^{-1}$ , corresponding to 8–70% of total  $\Delta\text{TA}$ . Thus, except during dark incubations when carbonate fluxes were very low, CG was principally influenced by calcification, while other chemical processes had comparatively less impact. Accordingly, the alkalinity anomaly technique appears to be valid for estimating the net community calcification of maerl beds, where calcifying organisms are abundant and where  $\Delta\text{TA}$  from calcification is high and predominant.

$\Delta\text{TA}$  in maerl beds was negative or nil, reflecting that  $\text{CaCO}_3$  precipitation processes (TA decrease) are preponderant compared with  $\text{CaCO}_3$  dissolution or anaerobic respiration processes (TA increase). In addition to the calcareous algae, the contribution of calcifying faunal organisms, such as crustaceans (*Pisidia longicornis* Linnaeus, *Gammarella fucicola* Leach), mollusks (*Venus verrucosa* Linnaeus, *Chlamys varia* Linnaeus, *Tapes* spp.), annelids (*Serpula vermicularis* Linnaeus, *Spirorbis spirorbis* Linnaeus) and bryozoans, to  $\text{CaCO}_3$  precipitation is potentially significant, since they represent a major part of the total biomass of faunal species (Grall 2002). Sea urchins *Psammechinus miliaris* (Gmelin) and *Paracentrotus lividus* (Lamarck) are equally abundant, reaching 3 ind.  $\text{m}^{-2}$  in the Rozegat maerl bed (Guillou et al. 2002).  $\text{CaCO}_3$  dissolution can also occur in maerl beds through carbonate dissolution of accumulated dead maerl or faunal remains. Nevertheless, CG measured during light incubations is high ( $0.7$  to  $4.2 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ ) and falls within the range of values for tropical macroalgal-dominated communities ( $0$  to  $6 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ ; Gattuso et al. 1997). Maximal carbonate production ( $P_{\text{max}}$ ) for maerl beds ( $\sim 3 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ ) is also close to values reported for tropical crustose coralline communities ( $2$  to  $10 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ ; Chisholm 2003), thus emphasizing the role played by maerl beds in temperate ecosystem carbonate budgets.

CG varied seasonally, being 6-fold higher in summer than in winter. Fluctuations in community calcification are primarily influenced by irradiance in intensity and duration, and then by temperature. This study exhibited a strong positive relationship between CG and irradiance. Nil CG during dark incubations reflected the absence of night calcification or a balance between  $\text{CaCO}_3$  precipitation and other phenomena. Low or nil calcification in the dark has previously been observed for coralline algae (El Haikali et al. 2004, Martin et al.

2006a). CG is also positively influenced by temperature, as reported for calcification rates of corallines (Blake & Maggs 2003, Martin et al. 2006a), crustaceans and mollusks (Martin et al. 2006b).

According to Martin et al. (2006a), net calcification rates of the isolated coralline algae can be estimated to  $2.32 \text{ g CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$  in winter and  $9.70 \text{ g CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$  in summer at 5 m depth. These results are between 4- and 8-fold higher than carbonate precipitation directly measured in the community. As previously described for primary production, the maerl incubated in bottles receive more light than maerl in a natural benthic population, explaining the lower calcification for similar biomasses in the community. The CG:GCP ratio for the maerl community is about 3- to 4-fold lower than that for isolated maerl (Martin et al. 2006a). The difference in CG:GCP ratios suggests either a potential carbonate dissolution in the maerl community or a significant contribution of macro- and micro-epiphytes to the community primary production. If we consider a low  $\text{CaCO}_3$  dissolution, epiphytic algae may therefore contribute to 65–75% of the maerl community gross primary production. However, dissolution of  $\text{CaCO}_3$  may be significant, if we consider the results of Potin et al. (1990). The aforementioned authors measured the calcification rates of *Lithothamnion corallioides* in the same area using the buoyant weight technique, given an estimate of community gross calcification of  $880 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ . The carbonate dissolution in the maerl community may thus be estimated to about  $400 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ .

### Carbon and carbonate budgets

The annual GCP ( $240 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) of maerl beds is 4-fold lower than that reported for macrophyte-dominated systems ( $\sim 1000 \text{ g C m}^{-2} \text{ yr}^{-1}$ ; Gattuso et al. 1998). The low carbon production by coralline-dominated communities can be explained by their very low growth rate compared with other macroalgae. However, considering their wide distribution, they may contribute largely to the global carbon production in shallow coastal waters. For instance, annual GCP of maerl beds is 2-fold higher than annual phytoplanktonic production in the Bay of Brest ( $148 \text{ g C m}^{-2} \text{ yr}^{-1}$ ; Del Amo 1996) and, considering that maerl beds represent a third of the bay's surface area, they potentially participate in about a third of the bay's total productivity. Maerl communities can thus be considered as highly productive benthic systems. In spite of their high productivity and in contrast to most macrophyte-dominated communities, which are autotrophic (Duarte & Cebrian 1996, Gattuso et al. 1998), maerl communities remain heterotrophic. The high biomass of het-

erotrophs in maerl beds resulting from their high biodiversity (Grall 2002, Grall et al. 2006) is partly responsible for their heterotrophic status. Maerl communities thus require an external supply of carbon from the surrounding environment in order to function, but the major part of the carbon is provided by the photosynthetic production of the community. If maerl production is not directly available for heterotrophs, epiphytic macro- and microalgal production constitutes the base of numerous detritivorous and herbivorous feeding organisms. For instance, sea urchins feed on epiphytic macroalgae and may control their primary production by ingesting about 90% of this production (Guillou et al. 2002). As they are produced, epiphytes may thus be directly assimilated and decomposed.

Annual maerl community carbonate precipitation ( $490 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) is in the range of values reported for temperate corallines, between 30 and  $1200 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$  (Bosence 1980, Edyvean & Ford 1987, Potin et al. 1990, Bosence & Wilson 2003). This carbonate precipitation on maerl beds is in the lower range of those reported for tropical coralline, from 100 to  $10000 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$  (Chisholm 2000, Payri 2000). Therefore, maerl communities appear to be among the most important carbonate-producing communities in temperate shallow coastal waters. Resulting from the predominance in respiration and the significant calcification of the maerl communities, maerl beds can be considered as source of  $\text{CO}_2$ , as reported for coral reefs (Gattuso et al. 1996).

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