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Primary production and spatial distribution of subtidal microphytobenthos in a temperate coastal system, the Bay of Brest, France

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Abstract

The main objective of this study was to define the primary production and the spatial and temporal distribution of the subtidal microphytobenthic community in a temperate coastal ecosystem, the Bay of Brest. The productivity of the microphytobenthos (MPB) was estimated in winter, spring and late summer, by a series of *in situ* benthic chamber incubations. Oxygen (O_2) and dissolved inorganic carbon (DIC) fluxes were measured at the sediment–water interface in light and dark conditions to determine the net and gross primary production present. Functional regression of the O_2 and DIC data demonstrated that the community photosynthetic quotient (CPQ) for the benthic community was 1. A maximal gross production (P_{max}) of between 0.4 and 0.8 mmol O_2 mg chl a^{-1} h^{-1} was estimated for the MPB in the Bay. E_K values were low, ranging from 57.8 to 83.4 μmol photons m^{-2} s^{-1} and can be considered an adaptation of the MPB to the reduced light levels reaching the sediment–water interface. Two sampling campaigns were undertaken in winter and late summer to measure the biomass of the benthic microalgal community in the Bay. Productivity estimates were combined with this biomass to give the MPB production in all areas of the Bay. Principal components analysis revealed that stations sampled were grouped primarily as a function of their depth, highlighting the importance above all of light availability, and their sediment type, with highest biomass concentrations found in bare muddy sediments. Hierarchical classification allowed the determination of four groups of stations in the Bay defined by their biotic and abiotic differences. The importance of the gastropod *Crepidula fornicata* in conditioning the benthic structural and biochemical environment was also highlighted. Geographical information systems based mapping allowed the representation of the spatial and temporal distribution of biomass and primary production and consequently a determination of the overall MPB production. Average seasonal production estimates for the Bay of Brest ranged from 57 in winter to 111 mg C m^{-2} day^{-1} in late summer and represented from 12–20% of total primary production.

Keywords: microphytobenthos; primary production; spatial distribution; subtidal zone; mapping

1. Introduction

Localised studies of coastal systems, and in particular primary production measurements, are desirable not only in diverse geographical areas but also in areas which are subject to different levels of human pressure. This information would

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allow us to determine the influence of both geographical positioning and anthropogenic affects on the sequestration and emission of anthropogenic CO_2 (Rabouille et al., 2001). Whereas global estimates of phytoplankton productivity are vast (see review in Martin et al., 1987; Longhurst et al., 1995; and estimates for the European coastal zone in Gazeau et al., 2004), estimates of global microphytobenthic productivity are rare. Indeed, recent reviews have underlined the requirement for complementary benthic studies (MacIntyre et al., 1996; Cahoon, 1999). Awareness of the importance of microphytobenthos (MPB) has been considerably heightened in previous decades and in some systems their production can equal or even exceed that of the pelagic phytoplankton (Underwood and Kromkamp, 1999).

The overall aim of the current study was to estimate the subtidal microphytobenthic biomass and production in a temperate coastal ecosystem in order to, on a global scale increase the current knowledge of MPB functioning and their input into carbon cycling by focusing on a previously unstudied site, and on a local scale, compare the relative productivity of the benthic and pelagic communities present.

The Bay of Brest, France, was chosen as a study site for this work for several reasons. First, it is considered an interesting example of an ecosystem whose response to human disturbances differs from the habitual (Cloern, 2001). Nitrate inputs to the system have increased dramatically in the last century (Tréguer and Quéguiner, 1989) and although silica to nitrate ratios have decreased substantially in the last 20 years (Le Pape et al., 1996), the system has shown a surprising resistance to eutrophication. The reason for this is thought to be associated with the proliferation of the exotic gastropod *Crepidula fornicata*. This invasive species traps and recycles silica throughout the productive period thus maintaining pelagic diatom populations in late summer and reducing the seasonality of pelagic primary production (Ragueneau et al., 1994, 2005; Chauvaud et al., 2000).

Second, although the structure and production of the MPB community in the Bay of Brest is currently unknown its possible importance in total carbon production within the system is evident due to the shallow nature of the Bay (Sagan and Thouzeau, 1998). While past studies of this well documented system have focused on phytoplankton dynamics (Del Amo et al., 1997), the influence of invasive species (Grall and Glémarec, 1997; Chauvaud et al., 2000; Martin et al., 2005), and biogeochemical cycling (Ragueneau et al., 1994, 2005; Le Pape et al., 1996) there has been little documentation of the biomass and production of the microphytobenthic compartment (Sagan and Thouzeau, 1998). An understanding of the functioning of these important photoautotrophs, their potential productivity and their influence on the cycling of nutrients will result in a more holistic comprehension of both carbon cycles and food web structure within the Bay and also the responses of the ecosystem to anthropogenic inputs.

The MPB primary production is measured using benthic chambers. This technique has been used extensively in tropical lagoon systems (Boucher et al., 1994; Clavier et al., 1994), intertidal temperate flats (Migné et al., 2004) and most recently in estimating the community metabolism of maerl beds (Martin et al., 2005, 2007a,b). The chambers used in this study have a relatively large cover area (0.2 m^2), thus enabling an integration of the patchiness associated with MPB communities (Jesus et al., 2005). Furthermore this method reduces disturbance of the sediment community and allows observations *in situ*, which maintain the ambient environmental conditions.

The objectives of this work are therefore, to model the relationship between the gross primary production of the MPB and the light through the manipulation of *in situ* benthic chambers at the sediment–water interface in three seasons (winter, spring and late summer), to characterise the spatial distribution of the subtidal MPB biomass in the surface sediments of the Bay of Brest and its relation to biotic and abiotic parameters and finally to combine the collected biomass data with productivity estimates in order to provide an assessment of the importance of MPB productivity in the overall primary production of the Bay of Brest.

2. Materials and methods

2.1. Study site

The Bay of Brest (ca. 180 km^2) is a shallow semi-enclosed ecosystem on the west coast of France. Connection to the adjoining Iroise Sea is by a narrow opening (2 km wide). The Bay is a shallow water system and approximately half of the total area is under 5 m depth (water depth is portrayed as the lowest possible depth in a theoretical low spring tide and so stations at 0 m mark the divide between the subtidal and intertidal zones). The Bay has a maximal tidal amplitude of 8 m during spring tides.

The benthic surface of the Bay of Brest is dominated by two quite particular and extremely different communities. The introduction of the invasive gastropod species *Crepidula fornicata* less then 100 years ago in the Bay, has resulted in the quick proliferation of this filter feeder and its cover extends to approximately half of the benthos (Chauvaud et al., 2000). In the shallower areas of the Bay the coralline red algae, maerl, dominates and the substantial beds it produces cover one-third of the total surface area.

Primary production experiments were undertaken at Sainte Anne du Portzic (48° 21′ 610 N, 4° 33′ 000 W) in the Bay, this site was chosen as it represents the bare sediments in the Bay where neither *C. fornicata* nor maerl beds are found (Fig. 1). The sediment has a median grain size of 100 μm with 29% under 63 μm. Incubations in spring (May), late summer (August/September) 2004 and winter (early March) 2005 using benthic chambers allowed the determination of the MPB productivity for these three seasons. The water depth at the site varied by approximately 5 m during incubations.

Sampling for the determination of the biological and physical elements required to depict the structure of the MPB population in the Bay was carried out over two 4 day periods in March and September 2004 with the assistance of the RV ‘Côtes de la Manche’ and the manipulation of a multi-corer (Bowers and Connelly Mini Corer Special).

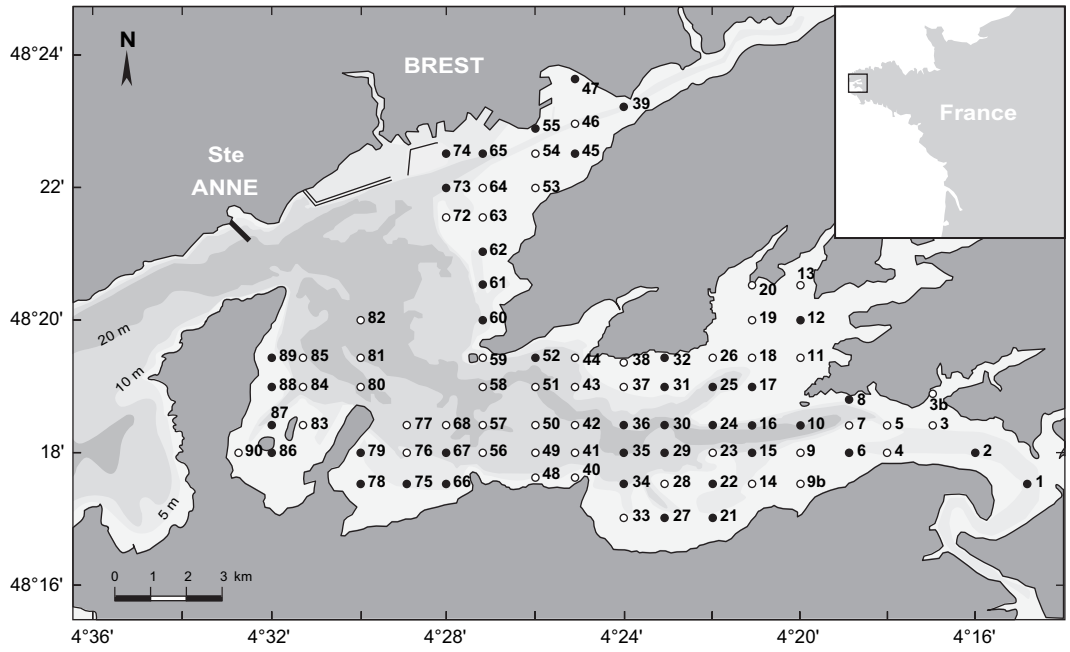

Fig. 1. Representation of the Bay of Brest and determined sampling strategy. Black circles represent the stations from which a complete data set was obtained for both seasons.

2.2. Primary production

Three benthic chambers bases (PVC rings of 25 cm in height) were gently pushed into the substrate by scuba divers the evening before each experiment to ensure a minimal amount of sediment re-suspension. Prior to experimentation acrylic hemispheres were attached to each base thus trapping a volume of 44.2 L to 75.6 L of water, depending on the insertion depth of the base into the sediment. Submersible pumps connected to water-proof batteries were used to homogenise the water within the chambers throughout the incubations, ensuring a constant flow of 2 L min^{-1} which corresponds to the hydrodynamics of the surrounding waters (Martin et al., 2005). Incubations lasted approximately 2 h and were replicated twice daily. In order to ensure proper mixing of the bottom waters the chambers were opened for 30 min between incubations. In each season a total of four benthic chamber incubations (in triplicate) were undertaken to measure oxygen (O_2) and dissolved organic carbon (DIC) fluxes at the sediment–water interface over a 2 day period.

Clear chambers were used for three of the four incubations to measure net community production in light conditions while opaque chambers were used for one of the incubations in order to measure community respiration in darkness. The gross community production in O_2 and DIC was obtained from the difference between light and dark incubations. In order to determine the relationship between these two parameters and furthermore to transform the O_2 production into DIC the relationship between these two parameters was determined using the community photosynthetic quotient (CPQ) which incorporated gross production results from all seasons as $CPQ = |\Delta O_2/\Delta DIC|$.

O_2 concentration (mg L^{-1}), water depth (m), salinity (in practical salinity scale) and temperature (°C) were recorded every minute inside each enclosure using the YSI 6920 multi-parameter logging system. To facilitate the calculation of dissolved inorganic carbon, water samples were collected inside the chambers for pH and total alkalinity (TA) using polyethylene syringes, at the beginning and end of incubations. Water samples for TA were passed through GF/F filters, preserved using mercuric chloride and then stored in darkness at 4 °C until analyses (Dickson and Goyet, 1994).

Photosynthetically active radiation (PAR, 400–700 nm) was recorded at the sediment surface, with a Licor quantameter (LI-192SA, Li-COR Inc., Lincoln, USA), connected to a data logger (Licor 1400, Li-COR Inc., Lincoln, USA). Samples for chlorophyll *a* (chl *a*) and phaeopigments (phaeo) in surface sediments were taken using six cores of 7 cm diameter placed randomly within each chamber at the end of the incubations. Cores were immediately brought to the surface and sub-sampled using a modified version of the cryolander method (Wiltshire et al., 1997). One sub-sample was taken from each core using polycarbonate tubes of 3 cm diameter. The tubes were pushed into the sediment and the surface of each sub-sample was immediately frozen with liquid nitrogen. The frozen sub-samples were stored at −80 °C until treatment and were freeze-dried within the following 48 h.

To ensure a sufficient amount of data points for the construction of seasonal production–irradiance curves the O_2 and PAR data (measured at 1 min intervals within the chambers) were sectioned into 30 min time slots thus allowing for a greater number of points (winter $n = 20$, spring $n = 41$, and late summer $n = 47$) and hence a better interpretation of the processes occurring. Subsequently, the $P–E$ relationship was modelled

allowing the determination of P_{max} (mmol O_2 mg chl a h^{-1}) and E_K (μmol photons m^{-2} s^{-1}) for all three seasons.

2.3. Primary production: sample processing

A pH meter (PHM 240, Radiometer), standardised with Tris–HCl and 2-aminopyridine–HCl buffer solutions (Dickson and Goyet, 1994) was used to measure the pH on board directly after sampling. TA was measured on 50 ml sub-samples by the automatic potentiometric method using Gran titration (Titrilab TIM 865 Radiometer). The total inorganic carbon concentration was calculated from pH, TA, temperature and salinity according to the method of Lewis and Wallace (1998).

The chl a and phaeo contained in the first centimetre of the sediment (homogenised and sub-sampled) was estimated using the method of Lorenzen (1966); 10 ml of 90% acetone was added to each sample that was then kept in the dark and in constant agitation, at 4 °C for approximately 18 h. Subsequently, samples were centrifuged for 5 min at 2000 rpm. Pigment concentrations were measured in the supernatant before and after acidification, respectively, with a Kontron fluorometer (Kontron Instruments AG, Zürich, Switzerland) and subsequently normalised to surface area.

2.4. Primary production: data treatment

The community respiration (CR) and net community production (NCP) were calculated as the difference between the initial and final concentrations (mmol O_2 or DIC m^{-2} h^{-1}) of dissolved oxygen and dissolved inorganic carbon in dark and light incubations respectively as follows:

$$\mathrm{NCP\ (or\ CR)}_{O_2} = \frac{\Delta O_2 \times v}{s \times \Delta t} \quad (1)$$

$$\mathrm{NCP\ (or\ CR)}_{DIC} = \frac{\Delta DIC \times v}{s \times \Delta t} \quad (2)$$

where ΔO_2 and ΔDIC are equal to the change in dissolved oxygen and inorganic carbon respectively during the incubation (mmol l^{-1}), v is the volume of water enclosed by the chamber, s, the surface area (m^2) and Δt, the incubation time (h). The TA at the sediment–water interface can be modified by anaerobic processes such as sulphate reduction, thus only incubations with small TA changes ($\Delta TA < 5$ μeq l^{-1} h^{-1}) were considered for DIC calculations (Forja et al., 2004). Gross community production (GCP) corresponds to the sum of absolute values of net production and respiration.

The normality (Shapiro–Wilk test) and homogeneity of variances (Levene test) of the calculated production and respiration data for each season were verified prior to analysis. As data were shown to be unevenly distributed Kruskal–Wallis tests were performed to test the temporal homogeneity of the data. As oxygen and carbon dioxide fluxes are both affected by natural variability and measurement error, the CPQ was calculated by means of a functional regression (Ricker, 1973).

Gross oxygen production normalised to chl a data (mmol O_2 mg chl a^{-1} h^{-1}) was plotted as an exponential function, P–E, of *in situ* irradiance, E (μmol photons m^{-2} s^{-1}) for all three seasons using the model of Webb et al. (1974).

$$\mathrm{GCP} = P_{max}\left[1 - \exp^{(-E/E_K)}\right] \quad (3)$$

where P_{max} is the maximum rate of gross community production (mmol O_2 mg chl a^{-1} h^{-1}) and E_K is the minimum saturating irradiance (μmol photons m^{-2} s^{-1}).

2.5. Mapping of the Bay

As neither the spatial nor temporal distribution of the MPB biomass in the Bay was known the sampling effort was spatially systematic (Frontier and Pichod-Viale, 1983) with equal distance between each point and encompassing two opposing seasons, winter and late summer (Fig. 1). Sampling of certain zones in the Bay were hampered by the substratum and gaps in the previewed sampling structure were due to dense populations of *C. fornicata* (deeper areas of the south Bay) or maerl beds (shallow zones) and sites containing sandy or rocky substrata (deeper areas of the middle Bay). From a previewed grid containing 90 stations, all the results from 43 stations containing a full spectrum of data for both seasons were used (Fig. 1).

Sampling for the determination of the spatial and temporal distribution of chl a and phaeo concentrations (mg m^{-2}), grain size (μm) and particulate organic carbon (POC) and nitrogen (PON) (mg m^{-2}) were performed using a multi-corer (Bowers and Connelly Mini Corer Special) to ensure minimal disruption of the sediment surface. Cores with visible disruption to the sediment–water interface were discarded and when necessary, sampling was reinitiated. At each station a total of four PVC cores (9 cm diameter) were sampled simultaneously, the first was cut to a depth of 2 cm and stored at 4 °C until analyses for grain size. The final three cores were ordained for POC and PON analysis and chl a and phaeo extraction (six sub-samples). A modified version of the cryolander technique (Wiltshire et al., 1997) was manipulated to sub-sample cores to a depth of 1 cm. The frozen sub-samples were stored at −80 °C until treatment and were freeze-dried prior to analyses.

2.6. Mapping of the Bay: sample processing

The method of Lorenzen (1966) was employed to estimate the chl a and phaeo contained in the first centimetre of the sediment as described in Section 2.3. Sediment grain size was determined from falling velocities in a series of linked settling tubes, after wet sieving (1 mm). The fraction of the sediment less than 1 mm was measured using a Coulter LS200 laser granulometer. The data were then merged and the median grain size and the silt (<63 μm) content were calculated (Flemming and Delafontaine, 2000).

Samples for analyses of POC and PON were passed through a 1 mm sieve and subsequently homogenised. A part of the sample was then pre-combusted at 450 °C for 4.5 h in order

to measure the inorganic particulate carbon and nitrogen. Unaltered and pre-combusted samples were then analysed using a Carlo Erba NA-2500 elemental analyser (Nieuwenhuize et al., 1994). POC and PON were then calculated from difference between the total and inorganic sections.

2.7. Mapping of the Bay: data treatment

In order to obtain an average daily light curve at the sediment–water interface for both sampling seasons, daily irradiance data collected at the water surface over a one month period was averaged to give mean daily irradiance curves. The data were transformed into bottom irradiance data (E) for each station using station depth and previously measured light extinction coefficients for the northern, middle and southern sections of the Bay (Grall, unpublished data). The daily gross community productivity (GCP: mmol O_2 mg chl a^{-1} h^{-1}) was calculated for each station using the exponential Webb et al. (1974) model and the photosynthetic parameters (P_{max}, E_K) defined for both seasons. The production per unit (mg) of chl a was then multiplied by the actual concentration of chl a at each station and transformed into carbon using the pre-determined community production quotient (CPQ) to give gross daily production estimates (mg C m^{-2} day^{-1}) for each station.

The normality (Shapiro–Wilk test) and equality of variance (Levene test) of physical and biological data sets for all stations was verified prior to statistical analysis. Relationships between sets of biological data (chl a, phaeo, POC, PON, primary production) were determined using one-way ANOVAs for normal data and Kruskal–Wallis tests for data sets which were not normal. Post hoc comparisons between data were subsequently tested using Fisher LSD and Mann–Whitney tests respectively.

The variability of the biomass within seasons, within stations and for the entire ensemble of data measured was calculated as:

$$\text{Variability}: \left(\frac{\text{SD}}{\text{mean}}\right) \times 100 \quad (4)$$

where SD is equal to the standard deviation. The relationship between the reduced centred chl a and the physical variables measured (water depth, median grain size and silt fraction) was analysed using a Pearson's correlation and a principle components analysis (PCA) was subsequently applied (XLSTAT statistical software). First, the physical and biological variables were reduced to two principal components axes (PCA1 and PCA2). Relationships between variables and PCA1 and PCA2 were then identified leading to the construction of a correlation biplot. An ascendant hierarchical classification (AHC) procedure was manipulated (Lebart et al., 1982) to produce a dendogram from clustering of a Bray–Curtis dissimilarity matrix. The significance of differences between defined groups was determined by one-way analysis of similarity (ANOSIM) randomisation tests (Clarke, 1993).

2.8. Mapping of the Bay: map formulation

In order to portray the spatial distribution of the microphytobenthic production in winter and late summer an interpolation was performed using Surfer 8.0. This software provides several tools for linear krigging and allows the use of breaklines for constraining the interpolation in user-defined limits. It also provides a facility for importing or exporting data from and to a geographical information system (i.e. ArcGIS 8.3).

The breakline datafile is based on the zero (lower spring tide level) and the 20 m isobaths processes from the bathymetric database managed by the French Naval Hydrographical Agency (SHOM). Both the production data and the breakline were then processed into Surfer 8.0 to interpolate the sampled data set with a 100 m linear krigging. Finally the resulting grid was exported to ArcGIS 8.3 and spatial analysis functions were used to compute the total production for the Bay.

3. Results

3.1. Environmental parameters during primary production measurements

Bottom water temperatures varied between months with average values ranging from 8.8 (SD 0.1) °C in winter to 13.3 (SD 0.3) °C in spring and 17.2 (SD 0.2) °C in late summer. The daily average bottom irradiance ranged from 105.3 (SD 67.1) μmol photons m^{-2} s^{-1} in winter to 174.6 (SD 65.8) μmol photons m^{-2} s^{-1} in spring and 112.1 (SD 60.8) μmol photons m^{-2} s^{-1} in summer. The length of the day period was 9 h in March, 14 h in May and 12 h in early September. Salinity values did not differ largely between months and remained within the range of 35.25–35.5. The biomass of MPB, depicted by the concentration of chl a in the first centimetre of the sediment, showed significant differences between spring and the other two seasons (Kruskal–Wallis, $H = 16.92$, $p = 0.00$). Lowest values (±SD) were encountered in winter (7.5 ± 2.7 mg m^{-2}), followed by summer (8.5 ± 1.7 mg m^{-2}) and spring (13.2 ± 4.4 mg m^{-2}). Phaeo concentrations (±SD) differed significantly (Kruskal–Wallis, $H = 10.19$, $p = 0.00$) between late summer, when highest levels were observed (20.7 ± 4.1 mg m^{-2}) and spring (17.0 ± 5.3 mg m^{-2}), and late summer and winter (16.9 ± 2.5 mg m^{-2}).

3.2. Seasonal community respiration and production

Lowest dark O_2 fluxes (±SD) were measured in winter (-0.8 ± 0.1 mmol O_2 m^{-2} h^{-1}) with considerably higher values in spring (-2.9 ± 0.0 mmol O_2 m^{-2} h^{-1}) and late summer (-2.7 to -1.9 mmol O_2 m^{-2} h^{-1}). Community dark DIC fluxes (±SD) showed little variability between seasons, although the lowest respiration was recorded in winter and the highest in late summer (winter: 1.6 ± 0.8 mmol DIC m^{-2} h^{-1}, spring: 1.4–2.0 mmol DIC m^{-2} h^{-1} and late summer: 1.4–3.9 mmol DIC m^{-2} h^{-1}).

Regression of DIC and O_2 data showed a lack of any linear correlation ($p = 0.984$). This is probably due to the low

number of data points (7) available. The functional regression of gross O_2 and DIC fluxes did however explained 89% of data variability during light conditions (Fig. 2) and the CPQ calculated did not differ significantly from 1 (Z-test = 1.11, $p = 0.27$) showing that any disparities in measurements using either method did not surpass the dark respiration observations. Similarly, the intercept at the origin (-0.04 ± 0.03 mmol m^{-2} h^{-1}) did not differ significantly from zero (Z-test = 0.74, $p = 0.46$).

Regression analysis showed a weak correlation between temperature and GCP hence this parameter was not considered in the construction of P–E curves (GCP_{O2}, $r^2 = 0.16$, $p = 0.07$ and GCP_{DIC}, $r^2 = 0.07$, $p = 0.26$). Gross community production (mmol m^{-2} h^{-1}) was significantly correlated to the surface sediment chl a concentration ($p = 0.00$) which explained 55% and 54% of O_2 and DIC variability; production data were therefore normalised to this variable.

Mean gross carbon production (mmol mg chl a^{-1} h^{-1}) measured as DIC did not differ significantly (Kruskal–Wallis, $H = 1.43$, $p = 0.49$) between seasons (spring: 0.38 (SD 0.25), late summer: 0.25 (SD 0.22), winter: 0.26 (SD 0.25) mmol DIC mg chl a^{-1} h^{-1}), however significant differences (Fisher test) were found between winter and spring when production was calculated using O_2 fluxes; spring: 0.29 (SD 0.22), late summer: 0.31 (SD 0.13) and winter: 0.20 (SD 0.19) mmol O_2 mg chl a^{-1} h^{-1}.

P–E curves were fitted to the sectioned O_2 data giving information on the seasonal variations of production parameters (Table 1 and Fig. 3). The models explained 72% of the variability in winter and spring and 63% of the variability in late summer. Modelled curves did not differ largely between winter and late summer and P_{max} was quite similar for the two seasons (Table 1). There was however a two-fold increase in P_{max} between spring and the other two seasons (Table 1).

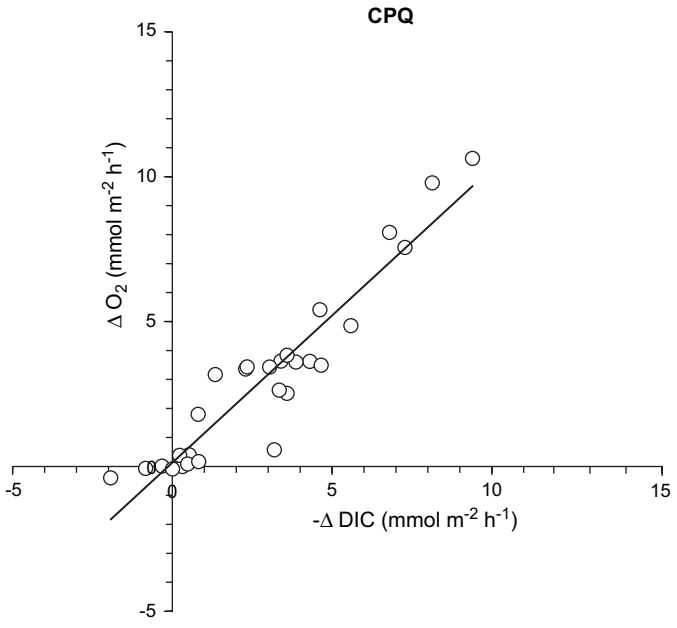

Fig. 2. Relationship between calculated absolute net calculated ΔDIC and measured ΔO_2 during benthic chamber incubations ($r^2 = 0.89$).

Table 1
Photosynthetic parameter estimates derived from model predictions of O_2 data cut into 30 min blocks for the three seasons measured. P_{max} values are in mmol O_2 mg chl a h^{-1}, E_K values are in μmol photons m^{-2} s^{-1}. SE is equal to the standard error of the estimation; n is the number of points used in model calculation

Season	n	r^2	E_K	SE	P_{max}	SE
Winter	20	0.72	57.77	28.72	0.44	0.07
Spring	41	0.72	83.35	48.99	0.77	0.15
Late summer	47	0.63	74.58	28.71	0.42	0.07

The maximum E_K was estimated for spring followed by late summer and winter. The variation indicated that the MPB community response followed closely the trend in light availability at the sediment–water interface.

3.3. Mapping of the Bay: principal components analysis and hierarchical classification

The two principle components axes (PCA) generated for the physical and biological variables accounted for 68% of the total variation between stations (Fig. 4A) and can be attributed to two main variables: sediment type (median grain size and silt fraction) and water depth; PCA1 and PCA2 accounted for 42% and 26% of the variability respectively. PCA1 was dominated by negative loadings for depth (30%) and positive loadings for chl a in winter (35%) and late summer (34%). PCA2 had positive loadings for silt content (49%) and median grain size (48%).

Hierarchical classification, using a Bray–Curtis dissimilarity matrix and the Ward method of aggregation, was performed to determine groups of similar stations in the ecosystem (Figs. 4B and 5). ANOSIM tests confirmed the significant difference between identified groups (global $R = 0.972$, $p < 0.05$). Stations were grouped into four distinct classes and are henceforth named Crepidula (13 stations), Maerl (13 stations), Mud (12 stations) and Fine Sand (5 stations). Group names were chosen due to their relevance to the physical and biological description of the substrata (Tables 2 and 3).

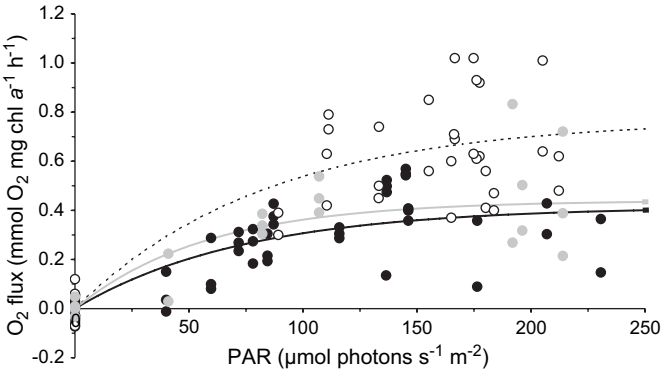

Fig. 3. Relationship between O_2 fluxes measured using benthic chambers and irradiance values measured *in situ*. Circles represent *in situ* measured values in winter (grey), spring (white) and late summer (black). Lines represented exponential curves fitted to experimental data in winter (grey line), spring (dotted line) and late summer (black line).

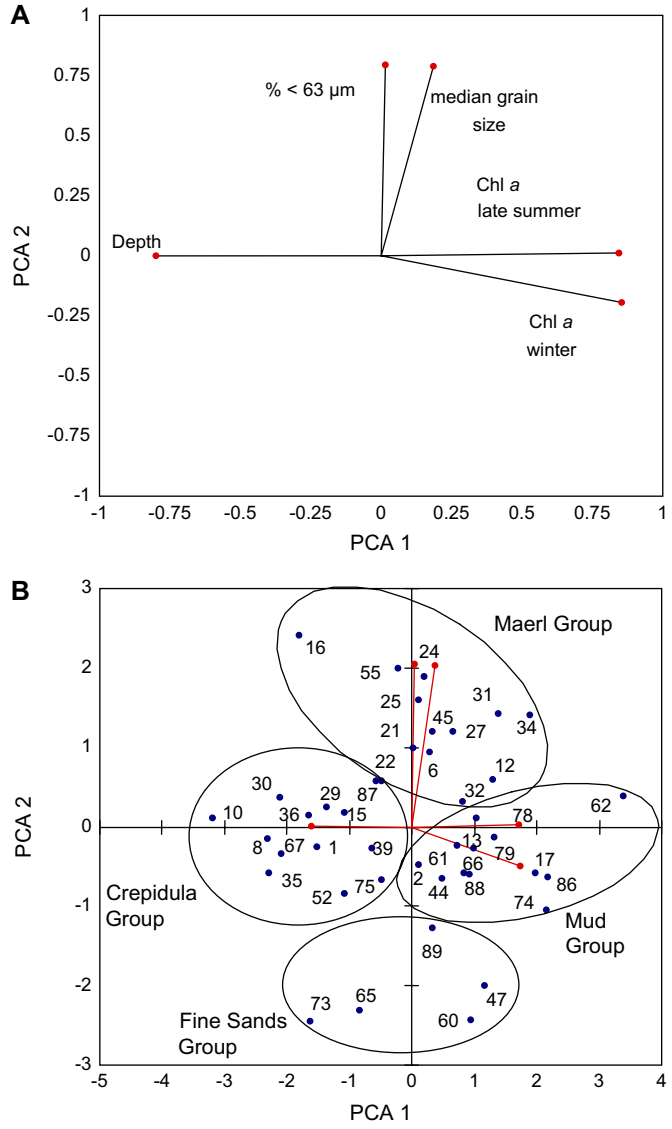

Fig. 4. Vector diagram (A) indicating the loadings on PCA1 and PCA2 and biplot of stations (B). Coding of stations refers to the station number.

3.4. Inter- and intra-group variations

The significant importance of seasonal differences in biological parameters (chl *a*, production, phaeo, POC and PON) within the four groups was determined using Mann–Whitney tests after negative results for normality and variance. Significant differences in production were found between seasons for the Crepidula ($p = 0.009$), Maerl ($p = 0.001$), and Mud groups ($p = 0.002$) (Fig. 6). These differences were replicated in the chl *a* concentrations of the Maerl ($p = 0.000$) and Crepidula groups ($p = 0.005$), however there was no significant seasonal difference between chl *a* for the Mud group ($p = 0.560$). The Fine Sands group demonstrated no seasonal differences for production or chl *a*. Phaeo, POC and PON did not differ significantly between seasons for any of the groups. Ratios of POC:PON (data not shown) showed no significant differences between groups except for the Crepidula and Fine Sands groups in late summer with the latter being significantly higher ($p = 0.029$), the average ratio for all seasons and all groups was 12.5 (±1.3).

The lowest production estimates were calculated for the Crepidula group in both seasons (44 ± 34 mg C m^{-2} day^{-1} in winter and 103 ± 56 mg C m^{-2} day^{-1} in late summer). The production (113 ± 50 mg C m^{-2} day^{-1} in winter and 218 ± 85 mg C m^{-2} day^{-1} in late summer) for the maerl group was not significantly different from the Fine Sands group in winter or the Mud and Fine Sands group in late summer (Fig. 6). Muddy stations showed the highest chl *a* concentrations (Table 2) and productivity (183 ± 77 mg C m^{-2} day^{-1} in winter and 268 ± 67 mg C m^{-2} day^{-1} in late summer) and the lowest amounts of fauna in both seasons (Table 3). This group is positioned positively along PCA1 (Fig. 4B) due to their high amount of sediment under 63 µm and the low median grain size (Table 2). Stations in the last group identified, the Fine Sands group, are distinguished by their low silt levels percentages of sediment grains <63 µm (Table 2). The MPB primary production in this group ranged between 128 ± 100 mg C m^{-2} day^{-1} in winter and 196 ± 115 mg C m^{-2} day^{-1} in late summer.

3.5. Microphytobenthic primary production estimates

The geostatistical analysis reveals that the distribution and amplitude of microphytobenthic primary production was larger in late summer than in winter (Fig. 7). The krigged maps for both seasons display common characteristics indicating a similar spatial structure with highest production found in the shallowest areas of the Bay. Overall average seasonal production estimates for the entire Bay considering all depths were 57 mg C $m^{-2}day^{-1}$ in winter and 111 mg C $m^{-2}day^{-1}$ in late summer.

4. Discussion

4.1. Productivity estimates

The data provided in this study is a first glance at the potential primary productivity of the subtidal MPB community in the Bay of Brest, France. The CPQ of 1.07 was in the range of values previously observed for pelagic phytoplankton (Ryther, 1956; Williams and Robertson, 1991) and other benthic systems (Clavier et al., 1994; Martin et al., 2007a) allowing for the transformation of O_2 fluxes into carbon production.

It should be noted that the production estimates shown in this study do not take into consideration the diurnal vertical migration of subtidal MPB at the sediment–water interface. The duration of the incubations (2 h) allows for the substantial MPB migration occurring during this period to alter considerably the productive biomass at the sediment surface (Ní Longphuirt et al., 2006). Although a significant correlation was found between the production and the chl *a* in the first centimetre of the sediment and the *P–E* curves were calculated as a function of this potentially productive biomass, solely cells at the sediment surface where light is available can in reality photosynthesise. A closer relationship may have been obtained

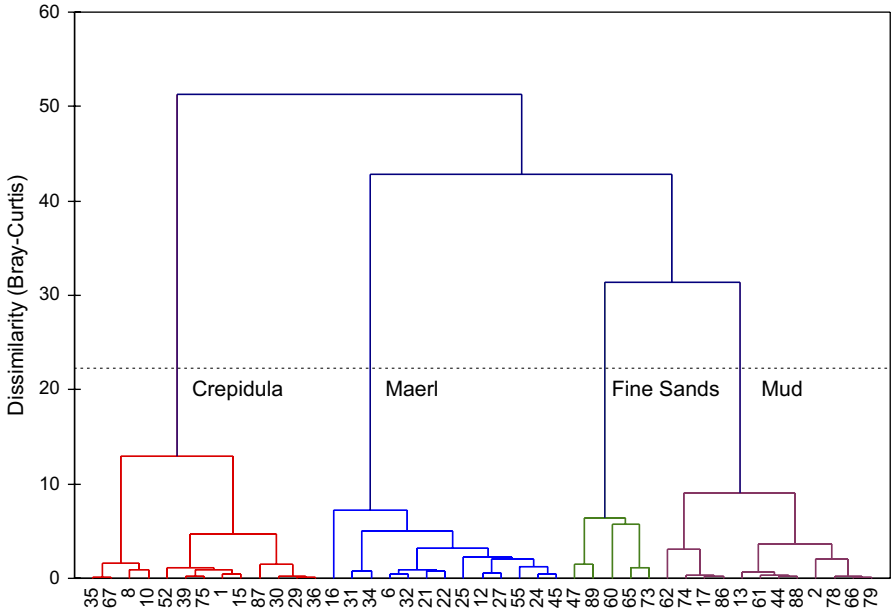

Fig. 5. Dendogram produced from the clustering of a Bray–Curtis dissimilarity matrix of stations for the two sampling periods (winter and late summer). The numbers on the *x*-axis represent stations sampled.

between production and chl *a* if the actual biomass present at the sediment surface was compared to production (Migné et al., 2004). Moreover, it is possible that the production per unit of chl *a* is slightly underestimated. This could result in possible errors in the overall daily production estimations.

Temperature was not shown to have an influence on the production, although values doubled between winter and late summer the highest production was observed in spring when temperatures were at median levels. Between seasons the response of the MPB to temperature may have been masked by the community reaction to average light availability, particularly between winter and late summer when measured PAR values were quite similar while temperatures rose by 10 °C. Furthermore, possible changes in the community structure make comparisons between seasons difficult due to species specific adaptations to ambient temperatures (Suzuki and Takahashi, 1995).

Estimated photosynthetic parameters showed seasonal variation (Table 1). The maximum gross photosynthetic rate, P_{max}, is in accordance with measurements from other subtidal sites (P_{max}: 0.01–1.51 mmol O_2 mg^{-1} chl *a* h^{-1}) for a range of measuring techniques (Sundbäck and Jönsson, 1988; Light and Beardall, 2001). The marked seasonality in this parameter follows the trend of available light at the sediment surface; this is concurrent with the results of Light and Beardall (2001) and Blanchard and Montagna (1992) in which the regulating influence of light on P_{max} estimates was demonstrated.

The photosynthetic parameter E_K or the minimum saturating irradiance of the community is independent of biomass and so provides us with a good index of the photoacclimation of the MPB. Estimates were in the lower range of values reported for other temperate subtidal MPB communities; E_K: 30–265 µmol photons m^{-2} s^{-1} (Sundbäck and Jönsson, 1988; Blanchard and Montagna, 1992; Light and Beardall, 2001). E_K varied temporally, and similar to P_{max} reflects the seasonality of light availability. Indeed, judging from average *in situ* light conditions for each season which were above E_K at all times, the photosynthesis of the MPB community was not light-limited. This suggests a physiological flexibility of the *in situ* community which allows for the optimisation of the

Table 2
Physical parameters and pigment concentrations for groups defined by hierarchical classification. Depth (m) refers to the average water depth for the group; average PAR (µmol photons m^{-2} s^{-1}) to the average light availability at the sediment surface calculated from surface concentrations and predetermined extinction coefficients for the Bay of Brest, median refers to median grain size (µm) and <63 µm to the percentage of sediment under 63 µm. Average chl *a* concentrations in winter and late summer are represented by Chl *a* W and Chl *a* LS (mg m^{-2}), respectively. Similarly, average phaeopigment concentrations in winter and late summer are represented by Phaeo W and Phaeo LS (mg m^{-2}) respectively and average particulate organic carbon by POC W and POC LS (mg m^{-2}). Standard deviations are in parentheses

Group	Depth	Average PAR winter	Average PAR late summer	<63 µm	Median	Chl *a* W	Chl *a* LS	Phaeo W	Phaeo LS	POC W	POC LS
Crepidula	11.3 (6.5)	68.0 (98.3)	136.5 (170.6)	59.1 (8.5)	93.1 (184.8)	1.7 (0.5)	2.7 (0.5)	10.7 (3.1)	12.1 (3.9)	16.2 (8.3)	16.1 (10.2)
Maerl	4.2 (3.7)	146.5 (158.9)	401.4 (352.1)	61.8 (5.9)	3302.9 (1041.6)	2.7 (0.7)	4.1 (1.3)	14.9 (4.9)	16.5 (5.0)	20.0 (4.5)	18.3 (8.5)
Mud	4.2 (2.5)	177.2 (167.2)	342.5 (290.3)	58.7 (4.9)	264.6 (752.4)	4.6 (1.3)	5.4 (1.0)	12.3 (4.5)	14.1 (6.2)	19.9 (9.8)	15.5 (7.2)
Fine Sands	3.8 (4.8)	217.6 (254.6)	382.2 (398.0)	24.3 (9.7)	111.8 (18.6)	3.1 (1.7)	3.7 (1.7)	9.5 (2.7)	11.5 (3.0)	17.4 (12.0)	12.6 (6.6)

Table 3
Mean faunal biomass for the groups of stations determined by hierarchical classification are represented in the table. Data is compiled from previous studies in the Bay of Brest (Grall unpublished; Grall et al., 2006) for winter and late summer (g dry weight m^{-2}). Standard deviations are in parentheses

	Crepidula	Maerl	Mud	Fine Sands
Winter				
Deposit feeders	14.3 (2.4)	16.1 (1.4)	6.7 (0.8)	11.9 (1.3)
Filter Feeders	9.5 (1.3)	4 (0.8)	0.6 (0.1)	1.2 (0.4)
Others	7.4 (1.0)	9.3 (0.8)	3.6 (0.7)	3.1 (1.4)
Total	31.2	29.4	10.9	16.2
Late summer				
Deposit feeders	36.5 (3.7)	43.3 (4.2)	12.8 (1.3)	27.6 (3.3)
Filter Feeders	29.9 (6.3)	14 (3.1)	0.9 (0.1)	2.5 (0.9)
Others	23.1 (2.7)	23.6 (1.8)	4.7 (1.0)	6.0 (2.8)
Total	89.5	80.9	18.4	36.1

ambient environmental situation. Also, the data infer that the maximal production rather than the minimum saturation irradiance has the most essential control on the seasonal productivity of the MPB.

The calculation of the primary production for each station in the Bay of Brest was estimated from biomass–irradiance relationships obtained in one specific site in the Bay. Differences in photo-adaptation and community composition could lead to a significant modification of responses to irradiance at different sites within the Bay. In their study on the temperate shallow water ecosystem, Light and Beardall (2001) demonstrated a large influence of light availability on P_{max} in different sites increasing two-fold between deep (10 m) and shallow sites (1 m) for winter periods, but inversely with deeper sites revealing a 40% higher value in summer. In their study E_K values were only marginally different between sites at different depths although values did exhibit a unimodal seasonal distribution. In the present study the seasonal dynamic in photosynthetic parameters is portrayed, nevertheless site specific differences, relating to water depth, are undefined. This could lead to a slight over-estimation of production in deeper sites and an underestimation in shallow areas.

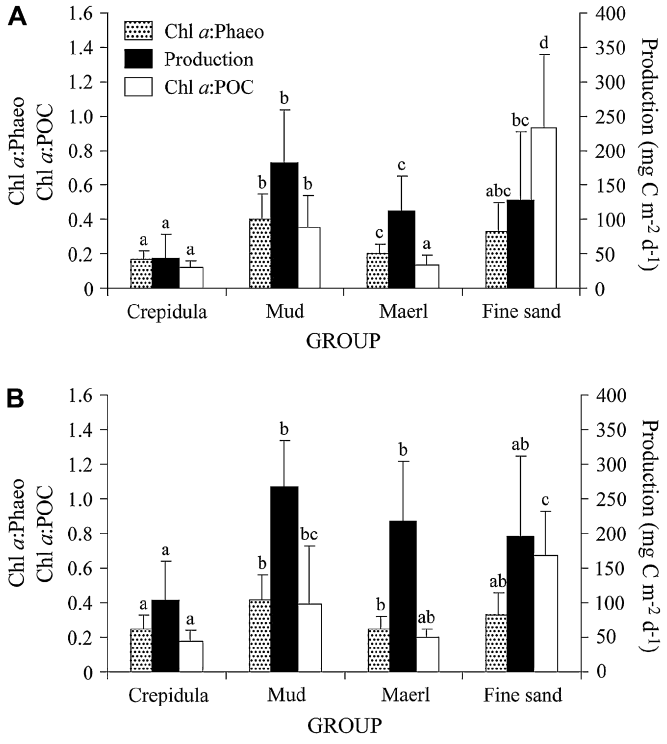

Fig. 6. Mean daily production and the ratio of mean chl *a* to phaeo and POC for the four groups identified in winter (A) and late summer (B). Different letters on bars indicate significant differences (Mann–Whitney tests, $P < 0.05$) between groups.

4.2. Mapping of the Bay: spatial scales of biomass distribution

The spatial distribution of MPB is known to be highly heterogeneous. This patchiness can occur on several scales, of micrometers to meters (MacIntyre et al., 1996; Moreno and Niell, 2004; Jesus et al., 2005) and is one of the main difficulties associated with scaling up measurements of MPB activity to larger areas, and when comparing the results of different studies. In the current study, the variability in MPB biomass followed a hierarchical pattern from the local to the ecosystem level with lowest variations of the chl *a* concentrations occurring within stations (28% in winter and 24% in late summer), followed by variations within groups (44% in winter and 39% in late summer) and finally variations within all samples (60% in winter and 43% in late summer). These results are in agreement with observations in previous studies (Sundbäck, 1984; Garrigue, 1998) moreover; the same variability structure between large and small scales has also been noted (Light and Beardall, 1998; Moreno and Niell, 2004).

Abiotic (water depth, sediment type, nutrient availability) and biotic (faunal and floral communities) variables present in the environment can operate on different scales to determine the spatial distribution and structure of the MPB communities (Asmus, 1982; Davis and McIntire, 1983). While nutrient availability and floral and faunal incidence can delineate intra-station variability and patchiness, larger scale distinctions, as shown by the PCA are the result of water depth and sediment type control. This is concurrent with past studies of MPB communities (Brotas et al., 1995; Cahoon, 1999; Moreno and Niell, 2004). Water depth represents the amount of light reaching the sediment surface, which in deeper sites will impede on the primary production of the MPB. In this study the correlation of chl *a* concentrations with the silt fraction are in agreement with the studies reviewed in Underwood and Kromkamp (1999) which suggested that muddy sediments contain higher concentrations of chl *a* than sandy sediment, the reverse relationship is however often observed (Cahoon, 1999; Cahoon and Safi, 2002). Sediment type is an expression not only of the sediment grains size but also indicates the presence of certain associated physical and biochemical variables which influence the benthic communities. Both muddy and sandy sediments contain environmental elements which could be advantageous to MPB communities; this is discussed in more detail in Section 4.5.

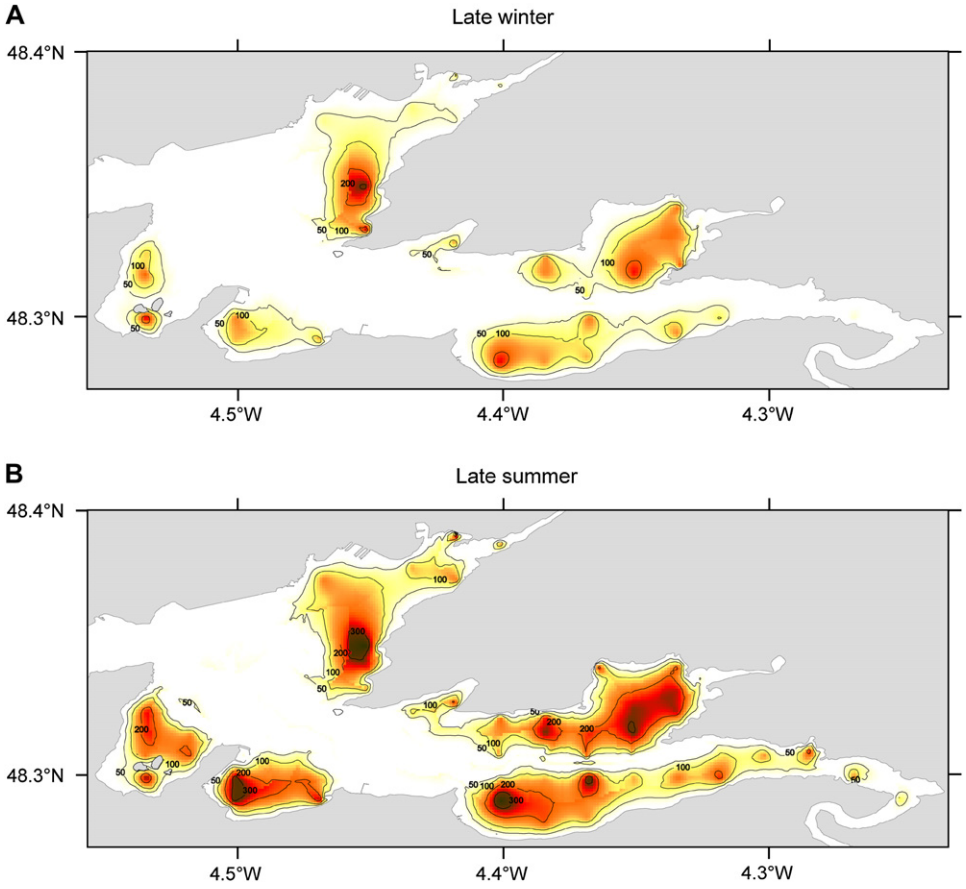

Fig. 7. 100 m linear krigging of the spatial production (mg C m^{-2} day^{-1}) of MPB in the Bay of Brest in winter (A) and late summer (B) periods.

4.3. Crepidula group

The Crepidula group was placed negatively along PCA1 and is characterised by its profound average depth and lowest median grain size. This area demonstrates the highest faunal biomass, indeed this group is situated in areas containing the suspension feeding gastropod *C. fornicata*, which has proliferated in the deeper areas of the Bay (average density: 260 individuals m^{-2}), colonising approximately 50% of the benthic surface (Chauvaud et al., 2000). The low median grain size found at these stations has been shown to reflect the silting and consequent homogenisation of the sediment by the *C. fornicata* present (Thouzeau et al., 2000).

The low chl *a* and primary production estimates of the Crepidula group could be explained by the placement of this group in the deeper areas of the Bay where irradiation for MPB photosynthesis is reduced. A similar trend of decreasing chl *a* with water depth was described by Garrigue (1998) in a tropical lagoon and Sundbäck (1984) in a temperate area.

The presence of the filter feeding *C. fornicata* at the sediment–water interface results in the trapping and subsequent condensing of large amounts of suspended organic material at the sediment–water interface. Lowest ratios of chl *a* to phaeo were recorded for this group which reflect the highest concentrations of detrital material (Niell, 1980; Brotas et al., 1995; Herlory et al., 2004). Moreover, ratios of chl *a* to organic material, in this case POC, are also considerably low suggesting the presence of low quality sediments where the organic matter is in general of low-autotrophic capacity relative to the organic matter present and thus more inclined to be allochthonous (Niell, 1980; Moreno and Niell, 2004).

Previous studies have outlined the importance of *C. fornicata* metabolism and calcification for the cycling of carbon within the Bay of Brest; however awareness of a benthic phototrophic community in these zones has been minimal (Martin et al., 2006). While low light levels reaching the benthos lead to a limitation of benthic gross community photosynthesis, the presence of high fluxes of silicates, phosphates and dissolved nitrogen due to the remineralisation of large amounts of organic material create optimal nutrient conditions for microalgal growth. The works of Asmus and Asmus (1991) on mussel beds in the Wadden Sea and indeed Martin et al. (2006) on the *C. fornicata* beds at the site have highlighted the possible importance of nutrient release by filter feeding communities for the microalagal community, benthic or pelagic.

Furthermore, the MPB need to be considered as a possible food source for this filter feeder and other fauna as they are found not only at the sediment–water interface, but also attached to the calcareous shells of the gastropod (Fig. 8). The *C. fornicata* live in stacks with younger individuals attached to the shells of older generations, the MPB also attached to the shells could therefore act as a food source for the

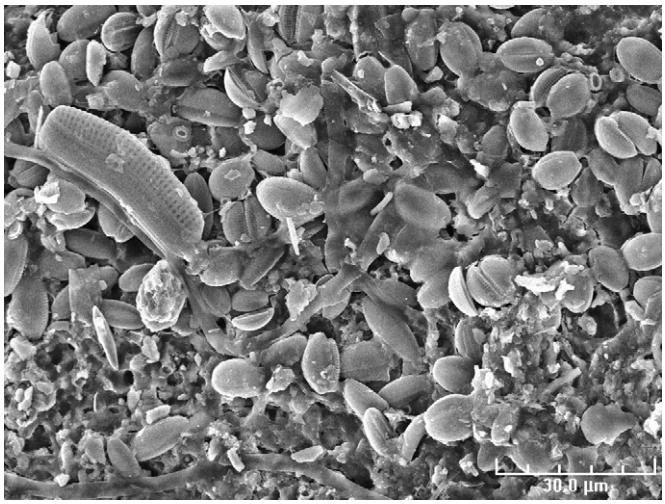

Fig. 8. Epiphytic diatoms attached to the shell of a *C. fornicata* sampled at 5 m water depth in the Bay of Brest, France.

individual positioned above. The attached MPB communities have not as yet been quantified, but could be speculated to increase substantially primary production estimates in these areas.

4.4. Maerl group

Stations classed into the Maerl group, while showing a large silt fraction have a distinctly high grain size median relating to the presence of the red coralline algae maerl in samples. Maerl beds are predominant in the shallow areas of the Bay and cover approximately 30% of the surface area. High faunal diversity and a high macroalgal biomass are present at these sites (Grall et al., 2006). The Maerl group demonstrates the highest concentrations of phaeo and subsequently low ratios of chl *a* to phaeo and POC, which could be an expression of the presence of high amounts of organic material not specifically associated with the MPB assemblage.

The benthic heterotrophic community is fuelled by the primary production (pelagic and benthic) and as for the Crepidula group the biomass and production present would certainly be an important food supply for the benthic fauna (Nozais et al., 2005). Grall et al. (2006), combining species distribution within the maerl community with stable isotope data for invertebrates and their food sources, have shown that 23% of the macrozoobenthic biomass could be sustained by MPB production within this area. Moreover, the oxidisation of the sediments by the photosynthesis of the MPB could be considered a source of oxygen for the respiration of the benthic heterotrophs (Glud et al., 2002).

4.5. Mud and Fine Sands groups

Our study showed a larger chl *a* concentration and production in muddy sediments as opposed to sandy sediments, although the production was not significantly different according to the statistical tests. A number of recent studies have discussed and justified the quantification of higher biomass and production in either muddy or sandy sites of the same ecosystem (Cahoon and Safi, 2002; Billerbeck et al., 2007), underlining the presence of two separate schools of thought.

Sites with high silt contents can be considered an ideal niche for MPB as they exhibit larger amounts of available nutrients (Garrigue, 1998; Underwood and Kromkamp, 1999). This has been related to their lower hydrodynamic forcings and thus larger quantities of organic material. Although nutrient concentrations in interstitial waters were not determined in our study, the muddy sediments showed lower chl *a*:POC ratios in both seasons suggesting higher quantities of organic matter for remineralisation. The Fine Sands group on the other hand showed a relatively high ratio of chl *a*:POC in both seasons and the lowest concentrations of phaeo suggesting that a large portion of the organic material present is in fact viable phototrophic biomass. However, sandy sites have higher solute transport due to high re-suspension and mixing which can result in the flushing of the sediments and promote a fast recycling of organic matter (Ehrenhauss et al., 2004) which has been thought to increase production even in times when overall organic mater concentrations are lower (Billerbeck et al., 2007).

Further considerations include the light penetration depth and MPB communities of the different sediment types. Light infiltration into sandy sediments is higher than muddy sediments resulting in a higher potential production in deeper layers (Billerbeck et al., 2007). MPB species in sandy sediments are however mainly attached to the sand grains (epipsammic) and therefore at the will of the hydrodynamic forces present which may carry them into deeper sediment layers due to the high mixing in these areas. The largely epipelic MPB communities in muddy areas can migrate up to the sediment–water interface and avail of the higher light present therefore actively increasing the amounts of light to which they are exposed regardless of the influence of physical forcings (Ní Longphuirt et al., 2006).

Grazing pressure can also have a substantial impact in these two system types. In the current study the lower faunal abundance present in muddy sites compared to sandy sediments may have resulted in a reduction of this pressure and therefore influenced the biomass concentrations.

The balance between the amount of biomass and production in areas with differing sediment grain almost certainly fluctuates depending on the varying force of each of the factors mentioned above. This can be reflected in the higher production quantified at times in either muddy or sandy sites in previous studies (Underwood and Kromkamp, 1999; Cahoon and Safi, 2002; Billerbeck et al., 2007). One common rule cannot therefore be identified for all studies but rather the influence of the ensemble of environmental factors needs to be considered on a system to system basis.

4.6. Importance of the MPB for overall ecosystem production

The production estimates calculated for the Bay of Brest (57 mg C m^{-2} day^{-1} in winter and 111 mg C m^{-2} day^{-1} in

late summer) fall within the range of average yearly production estimates in Cahoon et al. (1999) for subtidal temperate zones with similar depths (0–211 mg C m^{-2} day^{-1}). In the context of the European coastal system (0–200 m) the Bay of Brest presents a considerably higher level of microphytobenthic production than the overall average production of 18 mg C m^{-2} day^{-1} presented in the review of Gazeau et al. (2004).

Preceding surveys undertaken over an entire year and using ^{14}C incubations integrated over the whole water column have allowed for the estimation of phytoplanktonic production within the Bay system (Del Amo et al., 1997; Leynaert, unpublished data). Considering an average of both studies production is estimated at 180 mg C m^{-2} day^{-1} in winter and 403 mg C m^{-2} day^{-1} in summer. Comparison between pelagic and benthic phytoplankton production reveals that the pelagic production is dominant per unit area with the MPB representing between 22% and 36% of the overall combined microalgal (MPB and phytoplankton) production.

Primary production estimates of maerl bed communities from a recent study in the Bay by means of benthic chamber incubations are 160 mg C m^{-2} day^{-1} in winter and 1240 mg C m^{-2} day^{-1} in summer (Martin et al., 2007a). The inclusion of maerl systems into overall production estimations in the Bay revealed that MPB represent 12–20% of the known production when pelagic and benthic systems are also considered Table 4. It should be noted however that the production of maerl beds in the Bay is largely influenced by the epiphytic MPB which colonise their thalli (Martin et al., 2005). These attached communities have been estimated to contribute as much as 50% to the total production in macrophyte systems (Heip et al., 1995; Hemminga and Duarte, 2000).

Macrophyte communities (seagrass and macroalgae) are also considered to be extremely productive and net production estimates of between 1.7 and 20 g C m^{-2} day^{-1} have been observed in temperate sites (review in Charpy-Roubaud and Sournia, 1990). Indeed, in the Bay, seagrass beds, even though they cover a much smaller surface area, can represent up to three times the production of maerl communities (Martin et al., 2005). At present, estimates for the Bay are unavailable but should be considered in the future if a realistic quantification of the overall primary production is to be obtained.

MPB are a source of O_2 for heterotrophs through their photosynthetic processes (Glud et al., 2002) and in turn faunal respiration releases dissolved inorganic carbon for photosynthesis (Glud et al., 1992; Kühl et al., 1996). Thus, there is a tight spatial and temporal coupling between production and consumption of organic carbon and oxygen in the system and the fate of the abundant heterotrophic communities in the Bay could be largely reliant on the benthic production observed which ensures a substantial oxygenation of the benthic system.

Table 4
Primary production estimates in winter and late summer for the Bay of Brest and division of the total primary production. Primary production is presented in kg C day^{-1} in considering the total area of the Bay (180 km^{-2}). Maerl beds represent 30% of the overall area

	September	% total	March	% total	Reference
Maerl beds	74400	45	9600	18	Martin, 2005
MPB	19980	12	10260	20	Present study
Phytoplankton	72600	43	32400	62	Del Amo et al., 1997; Leynaert, unpublished 2001

5. Conclusion

This study allows for a first estimation of the biomass and primary production of MPB within the Bay of Brest. In this ecosystem, which is considered to be largely heterotrophic, MPB could act as an important source of organic carbon for faunal consumption and may be the base of numerous food webs. This work not only emphasises the influence of physical variables (grain size and water depth) on the spatial structure of MPB communities but also demonstrates that a consideration of the entire benthic structure (faunal and macroalgal composition, availability of organic material) is important if a complete understanding of the functioning of benthic coastal environments is to be achieved. The presence of invasive species such as *Crepidula fornicata* can not only increase the nutrient availability for the MPB in subtidal areas but can also act as a substrate for attached MPB species. The significance of the primary production of attached microalgal, rarely if ever considered in ecosystem carbon budgets, has been highlighted in this study. If we consider the large amount of surfaces, be they biotic (macroalgae, fauna) or abiotic (rock surfaces, manmade structures), present in coastal intertidal and subtidal zones it is evident that these often forgotten primary producers could input a substantial amount of organic carbon into coastal systems. Furthermore the tight coupling between benthic heterotrophic and autotrophic community processes through respiration, photosynthesis, remineralisation and nutrient uptake processes needs to be acknowledged.

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