In situ measurements of benthic primary production during emersion: seasonal variations and annual production in the Bay of Somme (eastern English Channel, France)

A. Migné[a],*, N. Spilmont[b], D. Davoult[c]

[a]MNHN-DMPA, UMR 5178, Université Paris VI, 61 Rue Buffon, Paris 75231 Cedex 5, France
[b]UMR 8013, Université du Littoral Côte d'Opale, Wimereux, France
[c]UMR 7127, Université Paris VI, Station Biologique, Roscoff, France

Abstract

A survey of benthic primary production during periods of emersion was performed in a muddy-sand station of the Bay of Somme. Primary production and respiration were estimated by in situ measurements of carbon dioxide fluxes using infra-red analysis. Photosynthetic response of the community to incident light and temperature was analysed at different periods of the year. Seasonal variations of the photosynthetic parameters were estimated using the photosynthesis versus irradiance (P–I) curves constructed in February, April, July, August and October. The rate of maximum gross community primary production (P_m), highly correlated to sediment chlorophyll a (Chl a) content, was low in February (6.7 mg C m^{-2} h^{-1}) and high in July (97.7 mg C m^{-2} h^{-1}). Photosynthetic efficiency at low light intensity (α) was positively correlated to P_m. The very high production ($P_m = 126.8$ mg C m^{-2} h^{-1}) and productivity (ratio of P_m and sediment Chl a content) measured in March may be related to the set down of active planktonic microalgae. At five dates, the effects of temperature on primary production seemed to overshadow the role of light. The Q_{10} for primary production varied from 1.2 in August to 3.0 in December. Daily potential primary production was calculated as a function of theoretical and measured irradiance for the period of superimposition of day and emersion. At the annual scale, the potential gross community primary production was 147 g C m^{-2} with theoretical irradiance and 110 g C m^{-2} with measured irradiances. The annual community respiration was 188 g C m^{-2}, leading to a heterotrophic annual budget. The annual pattern of daily production can be largely explained by changes in day length. It is also characterized by a fortnightly variability due to the variation of the total daily irradiance available for photosynthesis caused by the superimposition of the tidal and

*Corresponding author. Fax: +33-1-40-79-31-09.

E-mail address: migne@mnhn.fr (A. Migné).

day/night cycles. Finally, sharp variations occurring with nebulosity can overshadow this fortnightly variability.

1. Introduction

Intertidal mudflat ecosystems have long been established to be highly productive (Pomeroy, 1959; Pamatmat, 1968; Leach, 1970) and production in intertidal areas is generally considered to be higher than in subtidal habitats (Charpy-Roubaud and Sournia, 1990). Indeed, intertidal flats meet the requirements for high primary production: they are exposed to high irradiance due to low water depth and the periodic emersion of the sediment, and they are generally not nutrients limited, particularly in estuaries. Nevertheless, estuaries are also characterized by an elevated global respiration rate and are considered to be net heterotrophic systems whereas the continental shelf is considered to be net autotrophic (Gattuso et al., 1998).

Many investigations of microphytobenthic biomass and production have been conducted in intertidal flats (reviewed by McIntyre et al., 1996; Cahoon, 1999; Underwood and Kromkamp, 1999). Although the methods used are not standardized and have given variable results, it appears that, in contrast to subtidal habitats, benthic microalgae dominate the primary production of intertidal habitats. Taking into account 41 studies in temperate intertidal areas, Cahoon (1999) summarized (mean ± s.d.) the annual benthic microalgal production rates to 111 ± 99 g $C\,m^{-2}$ and noted the great variability of the estimates. This variability is due in part to the lack of a standard method, and also to the inherent variability of intertidal habitat due to patchiness in all scales of time and space. Furthermore, in most of the investigations, the substratum and the microalgae have been manipulated for photosynthetic measurements, which therefore lead to unrepresentative rates (Admiraal and Peletier, 1980). There is still a gap in long-term

in situ surveys, and many questions remain about what factors control microphytobenthic biomass and production and whether predictive models can be generated. Non-destructive methods (oxygen microelectrodes and variable fluorescence techniques) are now widely used to determine high-resolution distribution of microphytobenthos photosynthesis in time and space. However, these techniques have shortcomings. Microelectrodes are extremely fragile and require delicate instrumentation that limits the in situ utilization. Extensive replications are needed to reduce the spatial variability when estimates are scaled up to larger areas. Furthermore, estimating carbon production rates from fluorescence measurements implies the establishment of reliable relationships that remain contentious (Underwood and Kromkamp, 1999). Indeed, experimental data (Perkins et al., 2002) have failed to detect significant correlations between fluorescence parameters and community-level photosynthetic rates (measured by ^{14}C incorporation) in undisturbed microphytobenthic assemblages. Serôdio (2003) found high correlations between fluorescence parameters and gross photosynthetic rate determined with microelectrodes on sediment cores. However, gross oxygen production is not as relevant as carbon fixation as a parameter for quantifying primary production.

This paper aims to estimate benthic primary production in an intertidal flat by in situ measurements of CO_2 fluxes during emersion periods. In the used method (benthic chamber), the sediment is not disturbed and fluxes are measured for the whole community at a relatively large areal scale, integrating the microscale patchiness of microphytobenthos. A seasonal survey was performed on a muddy-sand station of the Bay of Somme, a macrotidal estuary on the northern coast of France. The community photosynthetic response

to incident solar radiation and temperature at different periods of the year was characterized and used to estimate the variation of daily potential primary production and the annual potential primary production.

2. Materials and methods

2.1. Study site

The Bay of Somme (Fig. 1) is a macrotidal estuary of the eastern English Channel (France) with an intertidal area (excluding salt marshes and channels) of $42.5 \, km^2$ occupied by seven distinct biosedimentary facies (McLusky et al., 1996). The survey was performed in the inner sheltered part of the bay (50°13′554N, 1°36′449E), in the muddy-sand facies (median grain diameter of $178 \, \mu m$ with 2% silt). The study site was located in the retention zone, between mean high water of neap tide and mean tide level and was subject twice a day to flooding (on average 3 h per tidal cycle).

2.2. Gas exchange measurement

Net community CO_2 exchange during emersion, including assimilation by microphytobenthos and respiration by phyto- and zoo-benthos, was measured by monitoring the change in CO_2 concentration in a benthic chamber. Details on the design and use of this chamber are given in Migné et al. (2002). It consisted in a dome of Perspex fitted on a stainless-steel ring (pushed into the substratum for 10 cm) and connected to a closed circuit of CO_2 analysis (infra-red gas analyser, LiCor Li-6251). The surface sediment covered was $0.126 \, m^2$, the volume of trapped air was about 25 L, a flow of about $2 \, L \, min^{-1}$ was maintained into the circuit. Incident photosynthetically active radiation (400–700 nm, PAR in μmol quanta $m^{-2} \, s^{-1}$, quantum sensor LiCor Li-192SA) and temperature (thermometer LiCor Li-1400-104) were also measured inside the benthic chamber at the sediment surface. Experiments consisted in a series of measurements carried out at ambient light and in darkness at different periods of the year. At each period, several measurements were carried out at ambient light (from dawn to saturating light or from saturating light to dusk) in order to estimate net community primary production (NCP) as a function of variation of ambient light during the day, and one measurement was carried out in darkness in order to estimate the community respiration rate (CR). Gas exchange was monitored for 10 min, the logging frequency was 1 min for temperature and PAR and 30 s for analyser data (internal temperature and CO_2 concentration). The slope of the partial pressure CO_2 (μmol mol^{-1}) against time (min) measured during light or dark incubations was used to express fluxes at the community level
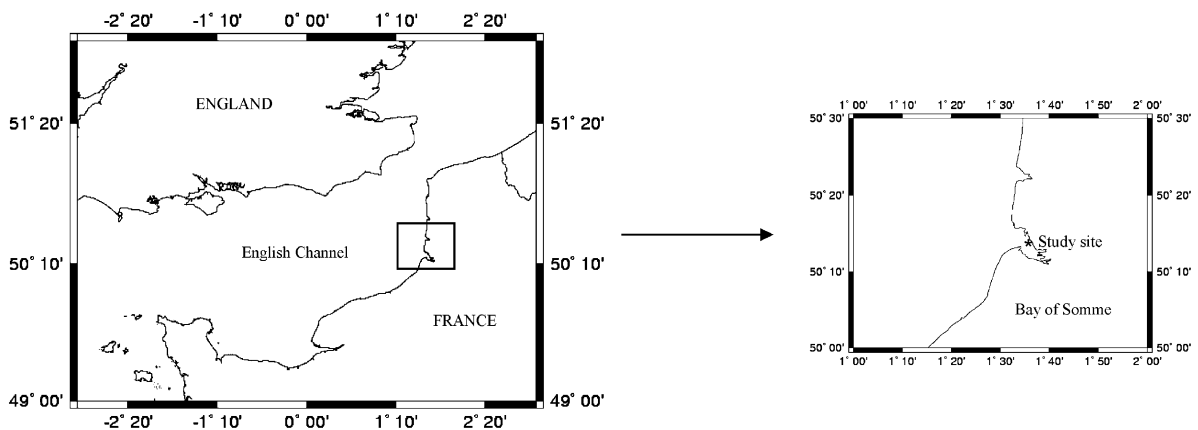

Fig. 1. Location of the study site in the eastern English Channel.

(mmol m^{-2} h^{-1}). The community respiration rate of a given date was added to measurements from individual light incubations to determine gross community primary production (GCP = NCP + CR).

Series of incubations were performed from August 2000 to December 2001 in order to follow seasonal variation of the community metabolism responding to light and temperature variations.

2.3. Sampling and analysis of microphytobenthos biomass

Microphytobenthos was sampled at each date of survey and analysed in terms of chlorophyll *a* (Chl *a*) biomass. At the end of a series of incubations, plastic cores (1.9 cm^2, three replicates) were pushed into the sediment within the chamber down to a depth of 1 cm, where active cells are concentrated (Cadée and Hegeman, 1974; Baillie, 1987; de Jonge and Colijn, 1994), carefully removed and then stored in a cool box, brought back to the laboratory and stored in the dark at $-20\,^\circ$C. For extraction, sections of sediment were placed in 8 mL acetone for 4 h in the dark at $4\,^\circ$C. Samples were then centrifuged at 4000 rpm for 15 min. Chl *a* concentrations in the supernatant were measured by spectrophotometry following Lorenzen (1967) and expressed in terms of Chl *a* per surface unit (mg Chl *a* m^{-2}).

The productivity (P_B in mg C mg Chl a^{-1} h^{-1}, also called assimilation number; Falkowski, 1981) was then calculated as the ratio of GCP and Chl *a* biomass.

2.4. Response of photosynthesis to irradiance

The relationship between photosynthesis and irradiance was described by the equation of Webb et al. (1974):

$$P = P_m[1 - \exp(-I/I_k)], \tag{1}$$

where P is the GCP (in mg C m^{-2} h^{-1}), P_m the rate of maximal GCP, I the incident irradiance (in µmol m^{-2} s^{-1}) and I_k the saturation onset parameter. The simplex estimation method (O'Neill, 1971) was used to determine P_m and I_k parameters (curve-fitting procedure of the "Systat 10" soft-

ware). Each light response curve was analysed for photosynthetic efficiency at low light intensity by calculating initial slope of the light response curve ($\alpha = P_m/I_k$ in g C mol^{-1}).

2.5. Response of photosynthesis to temperature

The relationship between photosynthesis under saturating irradiance and temperature was described by the exponential function:

$$P = a \exp(bT), \tag{2}$$

where P is the GCP under saturating irradiance (in mg C m^{-2} h^{-1}), a and b are constants and T the mean temperature measured in the chamber during the incubation in $^\circ$C. Saturating irradiances corresponded to values of irradiance higher than the value of I_k determined for the period. The simplex estimation method (O'Neill, 1971) was used to determine a and b parameters (curve-fitting procedure of the "Systat 10" software). The Q_{10} for primary production (ratio of primary production rate at $T\,^\circ$C to that at $T-10\,^\circ$C) was then calculated according to this function.

2.6. Potential annual community primary production

The incubations carried out at different periods of the year provided information about temporal variations in parameters of the P–I curve (P_m and I_k). A seasonal cycle of benthic primary production was achieved by temporal interpolation (sinusoidal simplex fitting procedure) of determined parameters. GCP was then calculated, every minute, as a function of irradiance (equation 1). Two kinds of estimation of the potential annual community primary production were then performed, considering on the one hand theoretical variation of irradiance and, on the other hand measured variation of irradiance. The theoretical irradiance implied optimal condition of light and was calculated from the sinusoidal curve of daily variation of irradiance proposed by Lizon et al. (1998):

$$I(t) = I_m \sin(\pi t/D), \tag{3}$$

where I_m (in μmol m^{-2} s^{-1}) is the maximal irradiance of the day, and D (min) is the day length.

The measured irradiance was based on recordings each minute for the year 2002 at a station near the study site (50°45'905N, 1°36'397E).

Microphytobenthos production is assumed to be light limited during flood tide (because of both high turbidity level in estuaries and resuspension during flooding) and therefore to be restricted to the emersion period (Colijn, 1982; Brotas and Catarino, 1995; Barranguet et al., 1998; Guarini et al., 2002). The daily potential community primary production was then calculated here only for the periods of superimposition of day and emersion. Daily estimations were added to estimate the potential community primary production at the annual scale. In order to calculate an annual net community production, a seasonal cycle of community respiration was achieved by temporal interpolation (sinusoidal simplex fitting procedure) of measured respiration rates.

3. Results

Twelve series of CO_2 flux measurements were performed from August 2000 to December 2001 (Fig. 2). Temperature at the sediment surface varied according to the season, and generally exhibited considerable changes on daily basis (Fig. 3). The minimum temperature was 2.8 °C in December 2001 and the maximum was recorded in August 2000 (35.5 °C). Largest changes in
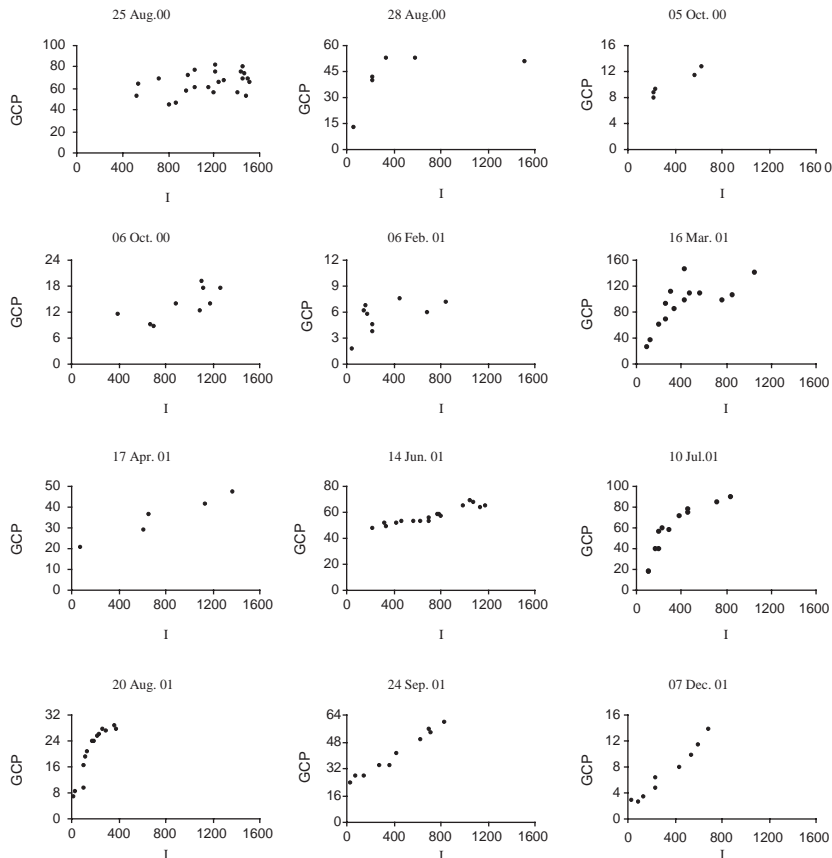

Fig. 2. Gross community primary production (GCP in mg C m^{-2} h^{-1}) measured under varying incident irradiance (I in μmol m^{-2} s^{-1}) between August 2000 and December 2001.

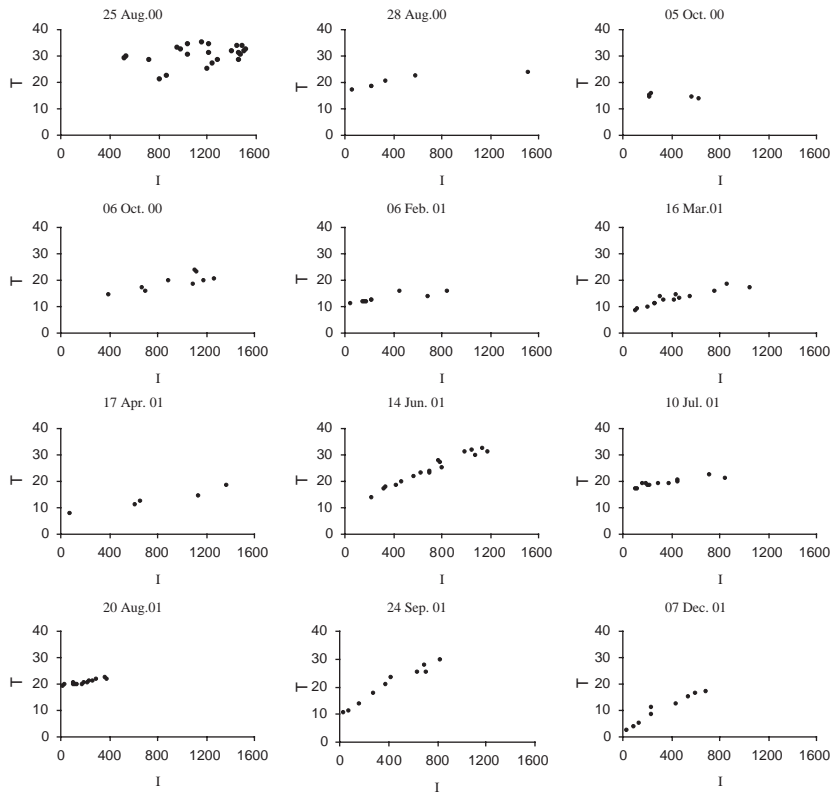Fig. 3. Temperature (T in °C) versus irradiance (I in $\mu mol\, m^{-2}\, s^{-1}$) measured during series of incubations performed between August 2000 and December 2001.

surface sediment temperature during the emersion period (as high as 18.9 °C in September 2001) were generally recorded on clear sky days; in contrary, these variations were limited during cloudy skies. The Chl a content of sediment varied according to the sampling period: with highest contents in July (321 mg m^{-2}) and lowest in February (8 mg m^{-2}, Fig. 4).

3.1. Response of photosynthesis to irradiance

In seven of the 12 series, the number of measurements under and above the saturating light level was enough to describe the relationship between photosynthesis and irradiance (see Fig. 2). Seven photosynthesis irradiance response curves (Table 1 and Fig. 5) were then fitted according to the model of Webb et al. (1974). In the five remaining series, measurements were carried out at
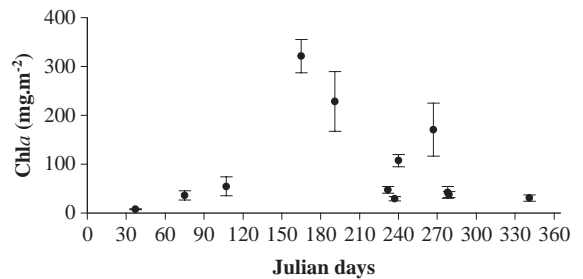

Fig. 4. Sediment microalgal biomass (Chl a in mg m^{-2}: mean ± s.d.) along the year (time expressed as Julian days).

irradiance values above the saturating level, and/or under sharp temperature change (see Fig. 3). These five series are discussed below as a function of temperature.

Data did not show photoinhibition (Fig. 5). Values of the maximum photosynthetic rate (P_m),

Table 1
Photosynthetic parameters (P_m, I_k, α) according to the model of Webb et al. (1974) fitted on data obtained between August 2000 and August 2001, number of incubations and determination coefficient

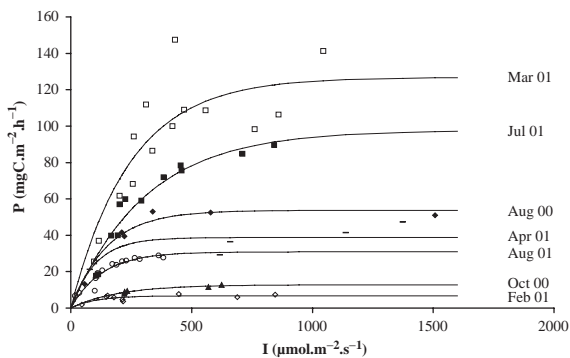| Date (Julian day)	P_m (mg C m^{-2} h^{-1})	I_k (μmol m^{-2} s^{-1})	α (g C mol^{-1})	N	r^2
28 Aug. 2000 (241)	53.72	151	0.099	6	0.996
5 Oct. 2000 (279)	12.75	198	0.018	5	0.997
6 Feb. 2001 (37)	6.69	102	0.018	9	0.959
16 Mar. 2001 (75)	126.79	246	0.143	14	0.969
17 Apr. 2001 (107)	38.75	102	0.106	5	0.974
10 July 2001 (191)	97.71	310	0.088	12	0.989
20 Aug. 2001 (232)	30.88	131	0.065	14	0.990

Fig. 5. Photosynthesis irradiance response curves according to the model of Webb et al. (1974): $P = P_m(1 - \exp(-I/I_k))$, obtained between August 2000 and August 2001. P is expressed in mg C m^{-2} h^{-1} and I in μmol m^{-2} s^{-1}.

Fig. 6. Maximum gross photosynthetic rate (P_m) versus microalgal biomass (Chl a in mg m^{-2}) and regression line forced through origin ($Y = 0.493X$, $n = 6$, $r = 0.975$, $p < 0.001$).

given by the mathematical model, varied according to the period of the year (Table 1). The lowest values of (P_m) were observed in winter (7 mg C m^{-2} h^{-1} in February 2001) and in autumn (13 mg C m^{-2} h^{-1} in October 2000) when microphytobenthos biomass was low (8 and 40 mg Chl a m^{-2}, respectively). A high value of P_m was observed in July (98 mg C m^{-2} h^{-1}) when microphytobenthos biomass was the highest of the year (230 mg Chl a m^{-2}). The highest value of P_m (129 mg C m^{-2} h^{-1}), obtained in March, however was not related to an elevated value of microphytobenthos biomass (36 mg Chl a m^{-2}). With the exclusion of this last data set, a significant linear correlation was evident between P_m and algal biomass (Chl a) ($n = 6$, $r = 0.975$, $p < 0.001$; Fig. 6). As maximum photosynthetic production rate (P_m) was highly correlated to the microphy-
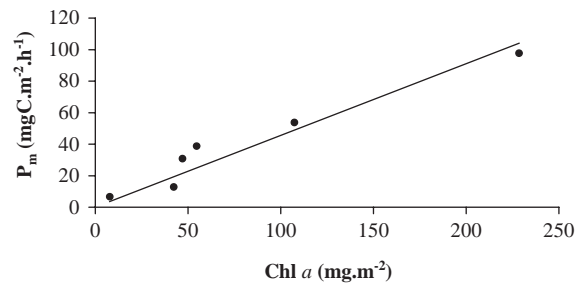
tobenthos biomass, maximum productivity rate (P_{Bm} = ratio of P_m and Chl a sediment content) did not show any seasonal trend. It varied between 0.30 mg C mg Chl a^{-1} h^{-1} in October and 0.85 mg C mg Chl a^{-1} h^{-1} in February, whereas the value observed in March was 3.50 mg C mg Chl a^{-1} h^{-1}. This last value seemed very high as microbenthic algae assimilation number measured in intact sediment cores generally are reported to be less than 1 mg C mg Chl a^{-1} h^{-1} (Colijn and van Buurt, 1975; Rasmussen et al., 1983; Colijn and de Jonge, 1984; Grant, 1986; Cahoon and Cooke, 1992; Brotas and Catarino, 1995; Miles and Sundbäck, 2000).

Photosynthetic efficiency ($\alpha = P_m/I_k$) varied seasonally. Values less than 0.02 g C mol^{-1} were observed in October and February and values between 0.07 and 0.11 were observed in April, July and August (Table 1). The highest value (0.14) was observed in March. There was a significant linear

correlation between α and P_m ($n = 7$, $r = 0.834$, $p < 0.05$).

3.2. Response of photosynthesis to temperature

In the five series of measurements that did not fit to *P–I* curves, primary production under saturating irradiance showed a significant exponential relationship with temperature ($p < 0.001$, Table 2). The Q_{10} calculated according to this model varied seasonally (from 1.2 in June and August to 3.2 in December) and was inversely correlated with the mean incubation temperature ($n = 5$, $r = -0.903$, $p < 0.05$; Fig. 7).

3.3. Potential annual community primary production

In order to estimate the development of P_m throughout the year, a sinusoidal model was fitted

Table 2
Significance of the exponential model adjusted to gross production measurements under saturating irradiances as a function of temperature between August 2000 and December 2001, and Q_{10} according to this model

Model: $P = a\exp(bT)$ Date (Julian day)	r^2	N	Q_{10}
25 Aug. 2000 (238)	0.981	23	1.21
06 Oct. 2000 (280)	0.989	9	2.20
14 Jun. 2001 (165)	0.999	17	1.22
24 Sep. 2001 (267)	0.997	7	1.60
07 Dec. 2001 (341)	0.997	7	3.15

using the six values obtained from August 2000 to August 2001 (the value of March being ignored): $P_m = 40.08 + 39.00\sin[(2\pi/365)x - 1.30]$; $r^2 = 0.874$, where x is the Julian day. The sinusoidal curve fitted on the six values of P_m as well as the mean GCP ($\pm$ s.d.) measured under saturating irradiance along the survey are shown in Fig. 8. A sinusoidal model was also fitted using the six values of I_k ($I_k = 165.67 + 53.91\sin[(2\pi/365)x - 1.84]$; $r^2 = 0.886$).

Assuming that primary production was negligible during immersion and considering optimal conditions of light, the daily GCP varied essentially as a function of the day length, being maximum in summer and minimum in winter (Fig. 9). Within this seasonal pattern, fortnightly fluctuations followed the irradiance availability at the sediment surface caused by the superimposition of tidal and day/night cycles of different periods. For example, daily production was found to decrease 21% between 20 and 29 June and increase 22% between 9 and 11 October. In spring and summer, the day length allows the occurrence of two periods of emersion under saturating light during spring tides and the potential production decreases when only one period occurs during neap tides. In winter and fall, the potential production increases when periods of emersion and maximal irradiances match each other
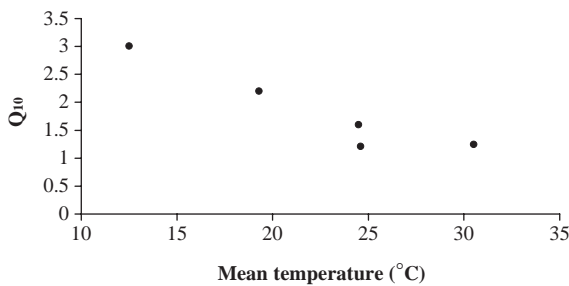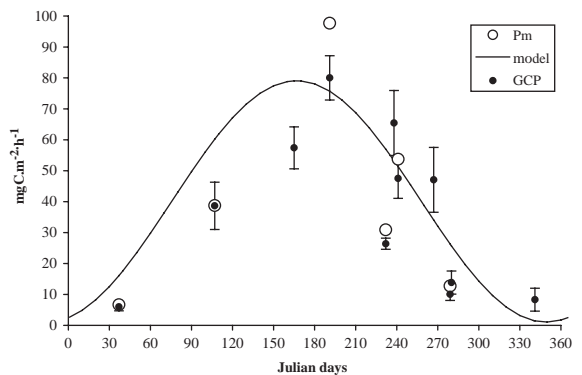

Fig. 7. Q_{10} for primary production versus mean incubation temperature for the series of measurements of August and October 2000 and June, September and December 2001.

Fig. 8. Sinusoidal curve fitted on the six values of P_m obtained according to the model of Webb et al. (1974) and mean GCP ($\pm$ s.d.) measured above the saturating irradiance along the survey (time expressed as Julian days). $P_m = 40.08 + 39.00\sin[(2\pi/365)x - 1.30]$; $r^2 = 0.874$.
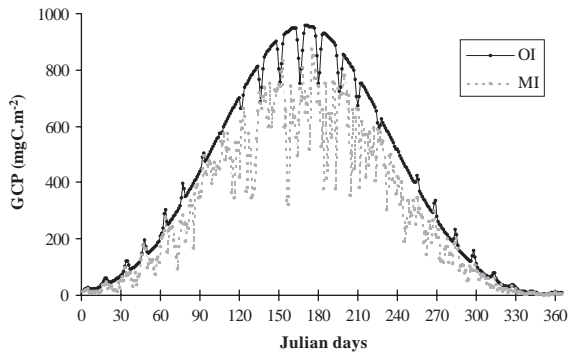
Fig. 9. Potential GCP (in mg $C\,m^{-2}$) as a function of day calculated according to optimal or measured irradiances (OI and MI).

(emersion around noon during neap tides). At the annual scale, GCP was 147 g $C\,m^{-2}$.

Considering measured irradiances, the GCP also varied essentially as a function of the day length (Fig. 9), but fortnightly fluctuations may be hidden by large fluctuations following the irradiance availability caused by the nebulosity. For example, daily production was found to decrease 62% between 2 and 6 June when related to mean measured irradiance during emersion periods of 646 and 91 $\mu mol\,m^{-2}\,s^{-1}$. At the annual scale, GCP was then 110 g $C\,m^{-2}$.

To estimate CR, a sinusoidal model was fitted to the 12 values of respiration measured between August 2000 and August 2001: $CR = 21.45 + 21.00\sin[(2\pi/365)x - 1.56]$; $r^2 = 0.793$, where x is the Julian day. At the annual scale, CR was 188 g $C\,m^{-2}$.

4. Discussion

4.1. Response of photosynthesis to irradiance

The relationships between photosynthetic rate and irradiance, obtained here from exposed sediments during ebb, showed that benthic microalgae maintained maximum production over a wide range of light intensities. There was no indication of a photoinhibitory effect, in accordance with previous in situ measurements in similar tidal flats (Rasmussen et al., 1983). This

suggests that microalgae were not exposed for extended period to a too strong illumination, despite direct exposure of the flat to incident irradiance. This could be partly explained by the microalgae mobility, vertical migration of most of the benthic microalgae ensuring protection from photoinhibition (Barranguet et al., 1998). Furthermore, even non-mobile cells are mixed with sand grains and so submitted to attenuated light. Cells may have been photoinhibited in the very surface sediments, but this was counteracted by the increased production at depth. The shape of the P–I curves did not indicate that microalgae activity was limited by nutrients or inorganic carbon as there was no decrease in photosynthetic activity during the incubations under saturating light. The lack of nutrient limitation has been found in many studies carried on tidal microphytobenthos in estuaries (Serôdio and Catarino, 2000) as nutrients levels in the estuarine sediments are typically far above limiting levels (McIntyre et al., 1996). Conversely, the development of CO_2 limitation during the day at low tide has been argued (Kromkamp et al., 1998; Perkins et al., 2001).

The observed changes of maximum photosynthetic production rate (P_m) were highly correlated to changes in the microphytobenthos biomass with the exclusion of March values. Therefore, maximum productivity rate (P_{Bm} = ratio of P_m and Chl a sediment content) did not show any seasonal trend: it varied between 0.30 mg C mg Chl $a^{-1}\,h^{-1}$ in October and 0.85 mg C mg Chl $a^{-1}\,h^{-1}$ in February whereas the value observed in March was 3.50 mg C mg Chl $a^{-1}\,h^{-1}$. These values of productivity could be underestimated by the inclusion of non-active Chl a in the values used to normalize the rate of production, given that the photic depth in such sediment is usually less than 2 mm (Underwood and Kromkamp, 1999). Except for the value obtained in March, they are in accordance with values reported for sandflats or mudflats when the Chl a content was also measured in the first centimetre: $P_{Bm} < 0.8$ mg C mg Chl $a^{-1}\,h^{-1}$ in the Dutch Wadden Sea (Colijn and van Buurt, 1975) and $P_{Bm} = 0.56$ mg C mg Chl $a^{-1}\,h^{-1}$ in the Tagus Estuary (Brotas and Catarino, 1995). Nevertheless, productivity

rate of microbenthic algae (when measured in situ or in intact sediment cores under saturating light) are usually reported to be less than $1 \, mg \, C \, mg \, Chl$ $a^{-1} \, h^{-1}$, even if the Chl a sediment content was measured in less than $1 \, cm$. Rasmussen et al. (1983) measured productivity rates between 0.16 and $0.57 \, mg \, C \, mg \, Chl \, a^{-1} \, h^{-1}$, in spring and summer in sandflats of the Danish Wadden Sea, taking into account the Chl a sediment content of the two first millimetres. Miles and Sundbäck (2000) measured productivity rates about $0.44 \, mg$ $C \, mg \, Chl \, a^{-1} \, h^{-1}$, in June in the Tagus Estuary, taking into account the chlorophyll sediment content of the three first millimetres. The values observed in March were then particular (a very high production together with a very high productivity). That could indicate a deposit of a great amount of phytoplankton cells on the sediment following a water column spring bloom. Indeed, it has been argued that phytoplankton cells present higher productivity than benthic microalgae (Cahoon and Cooke, 1992). In addition, large blooms due to *Phaeocystis* sp. (Prymnesiophyceae) occurred in the eastern English Channel during spring (Gentilhomme and Lizon, 1998). These settled phytoplankton cells might be capable of photosynthetic activity at low tide. In a sandy bay of the Swedish coast, Sundbäck et al. (1996) observed seasonal sedimentation of live planktonic algae of a shallow site (4 m) and suggested that they contributed significantly to the benthic primary production of the microtidal sandy community.

4.2. Response of photosynthesis to temperature

During our study, temperature ranged between 2.8 and $35.5 \,°C$ which is representative of the temperature changes measured during low tide over an annual period at the mud surface of a temperate bay (Blanchard et al., 1996). The temperature increase in the benthic chamber during incubations (mean $\pm$ s.d. $= 2.2 \pm 1.4 \,°C \, h^{-1}$) was similar to changes measured or modelled for the surface of high level intertidal mud during emersion periods (Blanchard and Guarini, 1998). It varied as a function of tidal phasing and above all as a function of meteorological conditions.

Since intertidal areas are subject to large fluctuations in temperature and seasonal increases in temperature are closely related to increases in PAR, microalgae specific adaptation to temperature has often been suggested in field studies in intertidal environments (Cadée and Hegeman, 1974; Rasmussen et al., 1983; Grant, 1986). Temperature was even assessed to be the main factor regulating microphytobenthic production in silty sediments, with light conditions having only an indirect effect (Blanchard and Guarini, 1996; Barranguet et al., 1998). Conversely, Serôdio and Catarino (2000) considered that, although rapid and large variations in temperature are typical of intertidal environments, the community production may mostly be controlled by temperature independent parameters, such as α, since a large part of the microalgal population is exposed to much lower, and therefore limiting, irradiances. In our survey, the effect of light could be revealed with P–I curves when the range of irradiances included the low values. However, the temperature effect occasionally seemed to overshadow the role of light, particularly in September and December 2001.

For five periods of measurements, an exponential model could be adjusted from the estimations of gross primary production under saturating irradiances as a function of temperature. This is consistent with studies on diatom cultures (Verity, 1981) or sediment cores (Kristensen, 1993) under controlled temperature conditions. In our study, the gross primary production increased with temperature according to the exponential model even when high temperatures were reached ($35.5 \,°C$ in August 2000, $31.7 \,°C$ in June 2001 and $29.9 \,°C$ in September 2001). These results are in opposition to those of the experimental study of Blanchard et al. (1997), who measured, for the four seasons, a progressive increase in production up to an optimum temperature (around $25 \,°C$) beyond which the production declined rapidly. This pattern was obtained from suspensions of isolated motile benthic diatoms which were extracted from intertidal mud. It suggests that the vertical migration of microphytobenthos in intact sediment prevents the exposure to limiting temperatures and thus maximizes photosynthetic

rates. Nevertheless, Rasmussen et al. (1983) measured an optimal temperature for photosynthesis in the field (20 °C in May, 30 °C in September) and Blanchard and Guarini (1998) showed that daily temperature oscillations are still detectable at a depth of 5 cm.

The Q_{10} calculated here according to the exponential model, adjusted on measurements of gross production as a function of temperature, varied seasonally (from 1.2 to 3.2). The effect of temperature on gross production was higher in winter than in summer, and the same trend was obtained when production was normalized to Chl *a*. Studying the sensitivity of benthic primary production to temperature variations on an intertidal sandflat in Nova Scotia, Grant (1986) obtained a linear relationship with a $Q_{10} = 2.0$ whatever the season (spring and fall). When production was normalized to Chl *a*, seasonal production–temperature relationships were significantly different with a Q_{10} of 3.3 in spring and no temperature effect in fall. These seasonal effects might be due to a combination of both physiological acclimation and taxonomical change.

4.3. Potential annual community primary production

Despite differences in *P–I* curves related to variations in temperature, species composition or photo-acclimation by community constituents, photosynthetic parameters obtained by in situ measurements are sufficient to calculate potential daily community production at different periods of the year. Based on *P–I* curves at representative times over the season or the year the model can be extrapolated throughout the whole seasonal or annual cycle to calculate primary production at the seasonal or annual scale (for example, Brotas and Catarino, 1995; Guarini et al., 2002). To our knowledge, no such estimates are available based on measured irradiances for a whole year. The annual GCP calculated here for the Bay of Somme (147 g C m^{-2} with optimal irradiance or 110 g C m^{-2} with measured irradiance) is in the upper range of previously reported rates for benthic microalgae in temperate intertidal habitats: 111 ± 99 g C m^{-2} (Cahoon, 1999). At the annual scale, the benthic system at the study site was net heterotrophic (NCP = -41 g C m^{-2} when optimal condition of light was considered and NCP = -78 g C m^{-2} when measured irradiances were used). It can be assumed that this heterotrophy was stronger since the benthic community respiration was underestimated. Indeed, community respiration measured during emersion has been assumed to be constant for a day while it is expected to increase during immersion (Dye, 1980; Gribsholt and Kristensen, 2003).

Comparisons with other studies remain difficult because of differences in methodology and extrapolation assumptions, but in accordance with studies of Kristensen (1993; GCP = 175 g C m^{-2} yr^{-1} in a Danish Lagoon) or Serôdio and Catarino (2000; GCP = 156 g C m^{-2} yr^{-1} in the Tagus Estuary) the present data suggest that the shape of the annual primary production cycle can largely be explained by seasonal changes in day length. As it was pointed out by Serôdio and Catarino (1999), the annual pattern of daily production can be characterized by a strong fortnightly variability superimposed on the underlying seasonal trend. This fortnightly variability is expected from the variation of the total daily irradiance available for photosynthesis caused by the superimposition of the tidal and day/night cycles. Nevertheless, our estimations based on measured irradiances show that sharp variations in cloudy conditions can overshadow this fortnightly variability.

In an intertidal environment such as the Bay of Somme, changes in environmental parameters within a season are as important as seasonal shifts in determining the shape and magnitude of variations in biological rates. This variation must be considered when extrapolations are made beyond the time scale of the measurement period.

References

Admiraal, W., Peletier, H., 1980. Influence of seasonal variations of temperature and light on the growth rate of cultures and natural populations of intertidal diatoms. Marine Ecology Progress Series 2, 35–43.

Baillie, P.W., 1987. Diatom size distribution and community stratification in estuarine intertidal sediments. Estuarine, Coastal and Shelf Science 25, 193–209.

Barranguet, C., Kromkamp, J., Peene, J., 1998. Factors controlling primary production and photosynthetic characteristics of intertidal microphytobenthos. Marine Ecology Progress Series 173, 117–126.

Blanchard, G., Guarini, J.-M., 1996. Studying the role of mud temperature on the hourly variation of the photosynthetic capacity of microphytobenthos in intertidal areas. Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la vie, Ecologie 319, 1153–1158.

Blanchard, G.F., Guarini, J.-M., 1998. Temperature effects on microphytobenthic productivity in temperate intertidal mudflat. Vie et Milieu 48, 271–284.

Blanchard, G.F., Guarini, J.-M., Richard, P., Gros, P., Mornet, F., 1996. Qualifying the short-term temperature effect on light-saturated photosynthesis of intertidal microphytobenthos. Marine Ecology Progress Series 134, 309–313.

Blanchard, G.F., Guarini, J.-M., Gros, P., Richard, P., 1997. Seasonal effect on the relationship between the photosynthetic capacity of intertidal microphytobenthos and temperature. Journal of Phycology 33, 723–728.

Brotas, V., Catarino, F., 1995. Microphytobenthos primary production of Tagus Estuary intertidal flats (Portugal). Netherlands Journal of Aquatic Ecology 29, 333–339.

Cadée, G.C., Hegeman, J., 1974. Primary production of the benthic microflora living on tidal flats. Netherlands Journal of Sea Research 8, 260–291.

Cahoon, L.B., 1999. The role of benthic microalgae in neritic ecosystems. Oceanography and Marine Biology: an Annual Review 37, 47–86.

Cahoon, L.B., Cooke, J.E., 1992. Benthic microalgal production in Onslow Bay, North Carolina, USA. Marine Ecology Progress Series 84, 185–196.

Charpy-Roubaud, C., Sournia, A., 1990. The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic primary production in the oceans. Marine Microbial Food Webs 4, 31–57.

Colijn, F., 1982. Light absorption in the waters of the Ems-Dollard Estuary and its consequences for the growth of phytoplankton and microphytobenthos. Netherlands Journal of Sea Research 15, 196–216.

Colijn, F., de Jonge, V.N., 1984. Primary production of the microphytobenthos in the Ems-Dollard Estuary. Marine Ecology Progress Series 14, 185–196.

Colijn, F., van Buurt, G., 1975. Influence of light and temperature on the photosynthetic rate of benthic marine diatoms. Marine Biology 31, 209–214.

De Jonge, V.N., Colijn, F., 1994. Dynamics of microphytobenthos biomass in the Ems estuary. Marine Ecology Progress Series 104, 185–196.

Dye, A.H., 1980. Tidal fluctuations in biological oxygen demand in exposed sandy beaches. Estuarine and Coastal Marine Science 2, 1–8.

Falkowski, P.G., 1981. Light-shade adaptation and assimilation numbers. Journal of Plankton Research 3, 203–216.

Gattuso, J.-P., Frankignoulle, M., Wollast, R., 1998. Carbon and carbonate metabolism in coastal aquatic ecosystem. Annual Revue of Ecology and Systematic 29, 405–434.

Gentilhomme, V., Lizon, F., 1998. Seasonal cycle of nitrogen and phytoplankton biomass in a well mixed coastal system (eastern English Channel). Hydrobiologia 361, 191–199.

Grant, J., 1986. Sensitivity of benthic community respiration and primary production to changes in temperature and light. Marine Biology 90, 299–306.

Gribsholt, B., Kristensen, E., 2003. Benthic metabolism and sulfur cycling along an inundation gradient in a tidal *Spartina anglica* salt marsh. Limnology and Oceanography 48, 2151–2162.

Guarini, J.-M., Cloern, J.E., Edmunds, J., Gros, P., 2002. Microphytobenthic potential productivity estimated in three tidal embayments of the San Francisco Bay: a comparative study. Estuaries 25, 409–417.

Kristensen, E., 1993. Seasonal variations in benthic community metabolism and nitrogen dynamics in a shallow, organic-poor Danish lagoon. Estuarine, Coastal and Shelf Science 36, 565–586.

Kromkamp, J., Barranguet, C., Peene, J., 1998. Determination of microphytobenthos PSII quantum efficiency and photosynthetic activity by means of variable chlorophyll fluorescence. Marine Ecology Progress Series 162, 45–55.

Leach, J.H., 1970. Epibenthic algal production in an intertidal mudflat. Limnology and Oceanography 15, 514–521.

Lizon, F., Seuront, L., Lagadeuc, Y., 1998. Photoadaptation and primary production study in tidally mixed coastal waters using a Lagrangian model. Marine Ecology Progress Series 169, 43–54.

Lorenzen, C.J., 1967. Determination of chlorophyll and pheopigments: spectrophotometric equations. Limnology and Oceanography 12, 343–346.

McIntyre, H.L., Geider, R.J., Miller, D.C., 1996. Microphytobenthos: the ecological role of the "secret garden" of unvegeted, shallow-water marine habitats. I. Distribution, abundance and primary production. Estuaries 19, 186–201.

McLusky, D.S., Briche, N., Desprez, M., Duhamel, S., Rybarczyk, H., Elkaïm, B., 1996. The benthic production of the Baie de Somme, France. In: Eleftheriou, A. (Ed.), Biology and Ecology of Shallow Coastal Waters. Olsen & Olsen, pp. 225–231.

Migné, A., Davoult, D., Spilmont, N., Menu, D., Boucher, G., Gattuso, J.-P., Rybarczyk, H., 2002. A closed-chamber CO_2 flux method for estimating intertidal primary production

and respiration under emersed conditions. Marine Biology 140, 865–869.

Miles, A., Sundbäck, K., 2000. Diel variation in microphytobenthic productivity in areas of different tidal amplitude. Marine Ecology Progress Series 205, 11–22.

O'Neill, R., 1971. Function minimization using a simplex procedure. Algorithm AS47. Applied Statistics 21, 338–345.

Pamatmat, M.M., 1968. Ecology and metabolism of a benthic community on an intertidal sandflat. Internationale Revue der gesamten Hydrobiologie 53, 211–298.

Perkins, R.G., Underwood, G.J.C., Brotas, V., Snow, G.C., Jesus, B., Ribeiro, L., 2001. Responses of microphytobenthos to light: primary production and carbohydrate allocation over an emersion period. Marine Ecology Progress Series 223, 101–112.

Perkins, R.G., Oxborough, K., Hanlon, A.R.M., Underwood, G.J.C., Baker, N.R., 2002. Can chlorophyll fluorescence be used to estimate the rate of photosynthetic electron transport within microphytobenthic biolfilms?. Marine Ecology Progress Series 228, 47–56.

Pomeroy, L.R., 1959. Algal productivity in salt marshes of Georgia. Limnology and Oceanography 4, 386–397.

Rasmussen, M.B., Henriksen, K., Jensen, A., 1983. Possible causes of temporal fluctuations in primary production of the microphytobenthos in the Danish Wadden Sea. Marine Biology 73, 109–114.

Serôdio, J., 2003. A chlorophyll fluorescence index to estimate short-term rates of photosynthesis by intertidal microphytobenthos. Journal of Phycology 39, 33–46.

Serôdio, J., Catarino, F., 1999. Fortnightly light and temperature variability in estuarine intertidal sediments and implications for microphytobenthos primary productivity. Aquatic Ecology 33, 235–241.

Serôdio, J., Catarino, F., 2000. Modelling the primary productivity of intertidal microphytobenthos: time scales of variability and effects of migratory rhythms. Marine Ecology Progress Series 192, 13–30.

Sundbäck, K., Nilsson, P., Nilsson, C., Jönsson, B., 1996. Balance between autotrophic and heterotrophic components and processes in microbenthic communities of sandy sediments: a field study. Estuarine, Coastal and Shelf Science 43, 689–706.

Underwood, G.J.C., Kromkamp, J., 1999. Primary production by phytoplankton and microphytobenthos in estuaries. Advances in ecological research 29, 93–153.

Verity, P.G., 1981. Effects of temperature, irradiance, and daylength on the marine diatom *Leptocylindrus danicus* Cleve. I. Photosynthesis and cellular composition. Journal of Experimental Marine Biology and Ecology 55, 79–91.

Webb, W.L., Newton, M., Starr, D., 1974. Carbon dioxide exchange of *Alnus rubra*: a mathematical model. Oecologia 17, 281–291.