

Short-term variability of intertidal benthic community production during emersion and the implication in annual budget calculation

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ABSTRACT: Short-term variability in benthic community primary production was studied during the course of emersion on a study site located in the Bay of Somme (eastern English Channel, France). Primary production was estimated at the community level through *in situ* measurements of carbon dioxide fluxes (infra-red analysis) in benthic chambers. Throughout the emersion period, gross community production (GCP) exhibited strong variations that were strongly correlated with natural variations in light. Light response curves explained the variations in GCP during the greater part of the emersion period, and vertical migrations of the microphytobenthos were suggested to explain the remaining variations (i.e. just before or just after immersion of the study site). A time lag was observed between the start of emersion and the maximum GCP, which was positively correlated with the time lag between emersion and local noon. The introduction of this time lag within the annual budget calculation enhanced production variability at a 2 wk time scale (i.e. tidal cycle), but light variability at the small time scale (i.e. cloudiness) remained the major factor inducing production variability. Results highlighted that omitting the time lag between emersion time and the maximum GCP within annual budget calculations led to large overestimations of annual GCP, since the annual budget for the study site was recalculated as being 67 g C m⁻² yr⁻¹ compared to 110 g C m⁻² yr⁻¹ when the short-term variability was not taken into account.

KEY WORDS: Microphytobenthos · Vertical migration · Primary production · Intertidal environment · Temporal variability

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INTRODUCTION

The microphytobenthos are an important component of estuarine primary production since they may provide as much as one-third of the total benthic primary production in some estuarine systems (Sullivan & Moncrieff 1988). They are mainly composed of pennate diatoms, with vertical migration of cells over the course of the emersion period being widely studied (see Con-

salvey et al. 2004, Underwood et al. 2005 and references therein). Other microphytobenthic taxa are also able to migrate (e.g. Euglenophyta: Kingston 2002) and surface cell microcycling has also been hypothesised, with cells of different taxa moving up and down within the biofilm (Kromkamp et al. 1998, Perkins et al. 2002, Underwood et al. 2005) to avoid exposure to inhibiting light levels, high temperature, or nutrient limitation. The rapid movements of diatoms are facili-

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tated through the production of extracellular polymeric substances (EPS; Underwood et al. 1995, Smith & Underwood 1998). Although the pattern of migration may appear to be simple (upwards migration prior to the daytime exposure and downwards migration prior to high tide/darkness), many factors are involved in the migration process, and the ultimate driving force remains unknown (Consalvey et al. 2004). Migration rhythms are indeed partly endogenous, since they can be maintained in the laboratory in the absence of external stimuli, but are mainly controlled by tidal and light cycles (e.g. Serôdio et al. 1997, Mithavkar & Anil 2004). As reviewed by Consalvey et al. (2004), changes in the taxonomic composition, CO₂, and/or nutrient limitation, as well as disturbance by waves, rain, or predators, are also suspected to impact migration.

Microphytobenthos migration results in large fluctuations in chlorophyll *a* concentration in the photic zone of the sediment (e.g. Serôdio et al. 1997, Perkins et al. 2001, Brotas et al. 2003, Tolhurst et al. 2003). This causes significant and rapid variations in the rates of primary production (Brotas et al. 2003) and has been highlighted as an important factor in the modelling of the primary production in intertidal areas (Pinckney & Zingmark 1993, Serôdio & Catarino 2000). Short-term variability in the primary production of microphytobenthos is related to changes in biomass, light quality and availability (Barranguet et al. 1998). These factors may interact with each other, but have different variability frequencies; it is therefore difficult to partition their impact on microphytobenthic populations.

Traditional methods used for monitoring microphytobenthic primary production are destructive as, for example core sampling. More recently, non-destructive *in situ* methods, such as oxygen microelectrodes (Brotas et al. 2003) and variable fluorescence measurements (Serôdio et al. 1997, Kromkamp et al. 1998, Serôdio & Catarino 2000, Perkins et al. 2001, Brotas et al. 2003), have been used. However, scaling up these measurements to larger areas is contentious, and the validity of estimation of carbon production rates from fluorescence measurements is still being fiercely debated (e.g. Perkins et al. 2002, Brotas et al. 2003).

In the present study, we used a closed-chamber CO₂ flux method for estimating short-term variations of primary production in relation to diurnal and tidal cycles over the course of emersion in the Bay of Somme (eastern English Channel). Community primary production was measured *in situ* in undisturbed sediment at a relatively large areal scale. The effects of short-term variability on the temporal patterns of variability of microphytobenthic primary production at larger time scales were assessed by recalculation of a previous annual primary production budget for the study site (Migné et al. 2004).

MATERIALS AND METHODS

The study was carried out in the Bay of Somme, a macrotidal estuary of the eastern English Channel (France). The experimental site, located in a muddy-sand facies (median grain diameter of 178 µm with 2% mud; 50° 13.554' N, 01° 36.449' E) between mean high water of neap tide and mean tide level, and subjected twice a day to flooding (semi-diurnal tidal regime), was described in Migné et al. (2004).

Community primary production during emersion was measured by monitoring the change in CO₂ concentration in a benthic chamber, as described in Migné et al. (2002). A Perspex dome was fitted on a stainless-steel ring pushed into the sediment down to about 10 cm and connected to a closed circuit of CO₂ analysis (infra-red gas analyser LiCor Li-6251). The surface covered and the volume of trapped air were 0.126 m² and 25 l, respectively. Each individual incubation lasted for about 15 min (with a logging frequency of 30 s for CO₂ concentration). Incident photosynthetically active radiation (400 to 700 nm, PAR in µmol m⁻² s⁻¹) and air temperature were measured inside the chamber at the sediment surface.

Four experiments were conducted to estimate short-term variations in primary production under natural irradiance during the emersion period: 20 August 2001, 29 April 2003, 25 September 2003 and 1 August 2004. Experiments consisted in a series of incubations under ambient light in order to estimate net community production (NCP) and an incubation in darkness to estimate community respiration (CR). CR was added to measurements from individual light incubations to determine gross community production (GCP).

The relationships between GCP and light (*P/E* curves) were described using the equation given by Webb et al. (1974):

$$P = P_m [1 - \exp(-E/E_k)] \quad (1)$$

where *P* is the GCP (mg C m⁻² h⁻¹), *P_m* the rate of maximal GCP, *E* the light intensity (µmol m⁻² s⁻¹) and *E_k* the saturation onset parameter.

The effect of short-term variability on microphytobenthic primary production at the annual scale was assessed by recalculating the annual budget published by Migné et al. (2004). In the former, GCP was calculated as a function of PAR from exposure until flooding. In many cases (when emersion periods matched with midday), microphytobenthos was then considered to be light saturated as soon as the sediment was exposed. In the present study, short-term variability was integrated in the calculation to permit progressive decrease and increase of primary production during emersion, with respect to tides and light environment. Annual community production was estimated using

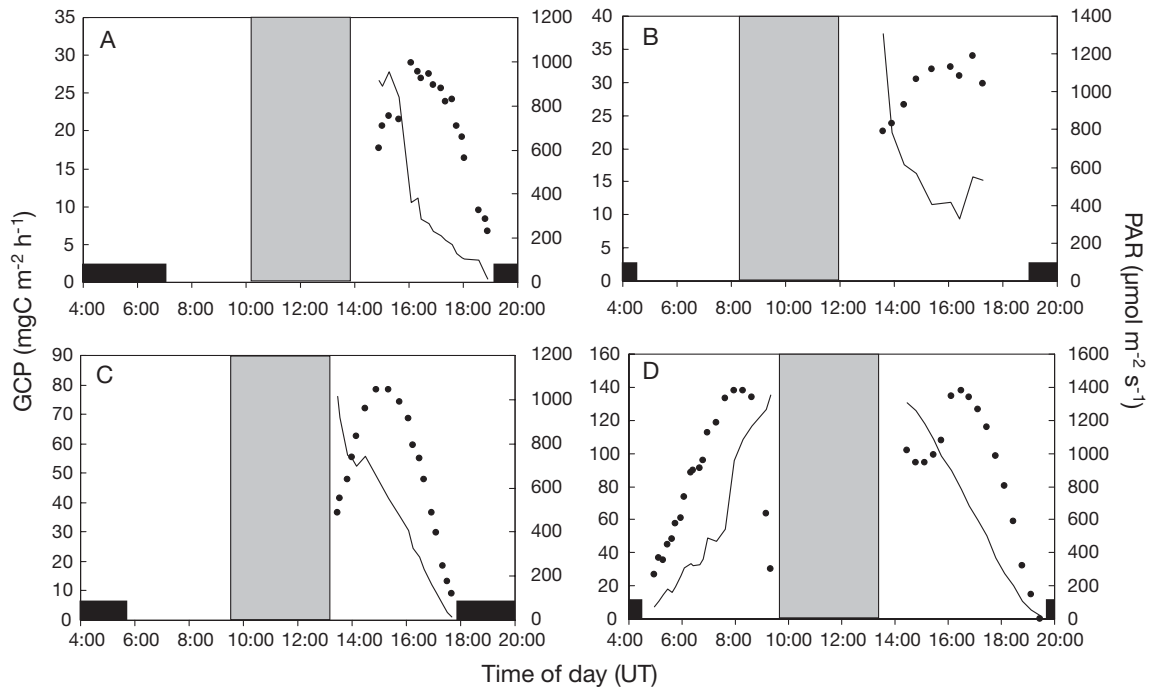


Fig. 1. Time course of gross community production (GCP, $\text{mg C m}^{-2} \text{h}^{-1}$, dots, left axis) and irradiance (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$, line, right axis) recorded during experiments conducted in the Bay of Somme on (A) 20 August 2001, (B) 29 April 2003, (C) 25 September 2003 and (D) 1 August 2004. Black horizontal bars represent the night periods; shaded bars represent immersion periods

both optimal irradiance (OI: calculated after a theoretical equation and assuming no perturbation by clouds) and measured irradiance (MI: using PAR measured near the study site in intervals of 1 min), assuming that microphytobenthic production was light limited during immersion. The impact of the integration of this variability at different time scales was assessed through spectral analysis.

RESULTS

For each experiment conducted at the beginning of the emersion period (Fig. 1), the first measurements were performed when PAR was far above the saturating level (E_k) previously estimated as $112 < E_k < 220 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the Bay of Somme (Migné et al. 2004). GCP nevertheless increased, reached a maximum value and then decreased together with decreasing irradiance, except on 29 April (Fig. 1B). Conversely, for the experiment conducted at the end of the emersion period (1 August 2004 a.m.), primary production rates first increased with increasing irradiance and then started to decrease when irradiance was high (Fig. 1D). Good correlations between GCP and PAR (>99% of the variance explained by the P/E relationships obtained by fitting the model from Webb et al. 1974) were found after maximum GCP

was reached, except for 29 April (Fig. 2). The rapid decrease of PAR observed in April 2003 ($519 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 20 min, see Fig. 1B) suggested an intense and durable cloudy spell during measurements. Since microphytobenthic populations are usually not able to instantly react to sharp variations in light intensity, it was then impossible to establish the light response curve.

The time required for microphytobenthos to reach its maximum primary production rate after emersion differed between experiments; it was ca. 165 min on 20 August 2001 (Fig. 1A), 200 min on 29 April 2003 (Fig. 1B), 110 min on 25 September 2003 (Fig. 1C) and 190 min on 1 August 2004 (Fig. 1D). When measurements were conducted at the end of the emersion period (1 August 2004 a.m.), primary production started to decrease ca. 100 min before flooding (Fig. 1D). The time lag (TL, in min) between maximum GCP and emersion time ($\text{TL}_{\text{GCP/em}}$) was significantly correlated with the time lag between emersion time and local noon ($\text{TL}_{\text{em/noon}}$):

$$\text{TL}_{\text{GCP/em}} = 0.52 (\text{TL}_{\text{em/noon}}) + 37.52 \quad (2)$$

where $n = 5$, $r = 0.943$ and $p < 0.01$.

This last relation was used to correct the annual budget published by Migné et al. (2004). For each day of the year $\text{TL}_{\text{GCP/em}}$ values were calculated as a function of $\text{TL}_{\text{em/noon}}$; GCP was then calculated using optimal

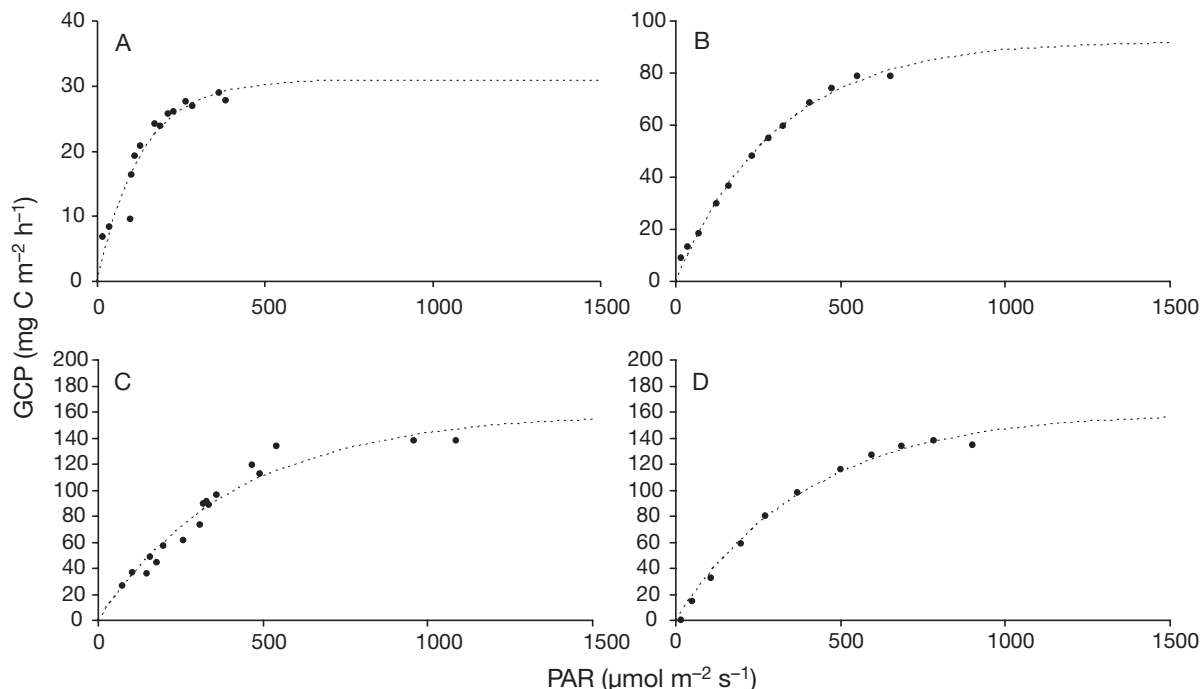


Fig. 2. Photosynthesis versus irradiance (P/E) curves constructed for periods before and after maximum GCP was reached: (A) 20 August 2001 [$P = 30.9 (1 - e^{-E/131})$, $n = 14$, $r^2 = 0.990$], (B) 25 September 2003 [$P = 92.4 (1 - e^{-E/309})$, $n = 12$, $r^2 = 0.999$], (C) 1 August a.m. [$P = 158.0 (1 - e^{-E/414})$, $n = 17$, $r^2 = 0.992$] and (D) 1 August p.m. [$P = 159.8 (1 - e^{-E/402})$, $n = 11$, $r^2 = 0.992$]

and measured irradiance (OI and MI). Budget calculation was extrapolated to a whole year to enable comparisons with previously published budgets. This led to an annual GCP budget of $90 \text{ g C m}^{-2} \text{ yr}^{-1}$ considering

OI and of $67 \text{ g C m}^{-2} \text{ yr}^{-1}$ considering MI (Fig. 3). In contrast, these budgets were, respectively, 147 and $110 \text{ g C m}^{-2} \text{ yr}^{-1}$ when short-term variability was not taken into account (Migné et al. 2004). This variability per se thus accounted for a decrease of 39% in the annual budget. Migné et al. (2004) concluded a net heterotrophic budget for the study site (considering an annual community respiration of $188 \text{ g C m}^{-2} \text{ yr}^{-1}$). This result is not questioned, but reinforced, since the budget would be -98 and $-121 \text{ g C m}^{-2} \text{ yr}^{-1}$ using optimal and measured PAR, respectively.

The highest relative differences induced by this correction in budget calculation were observed in winter and fall (Fig. 4). On each day of the year, GCP was overestimated for at least 37.5 min (when emersion matched with local noon; see Eq. 2) in the previous budget. This duration represents a greater proportion of the total day length in fall and winter (e.g. 490 min day length on 21 December) than in spring and summer (e.g. 970 min day length on 21 June). The correction impact was low during winter and fall

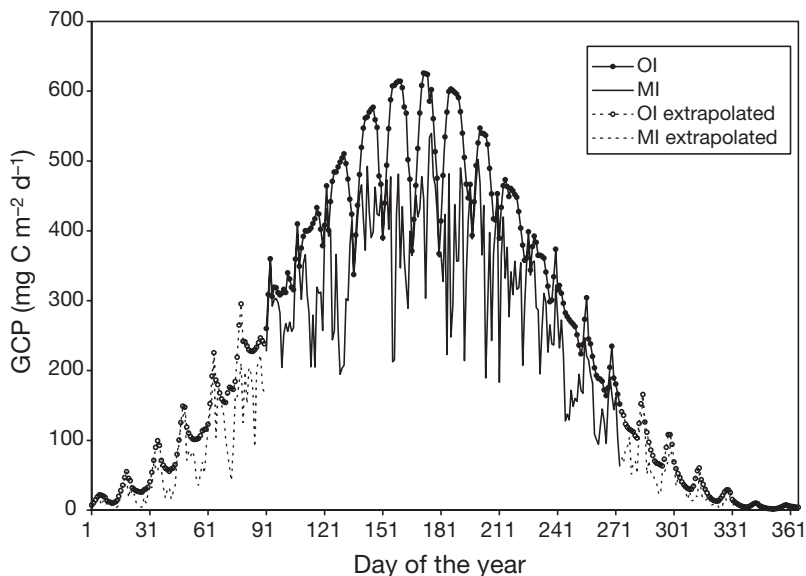


Fig. 3. Gross community production (GCP, $\text{mg C m}^{-2} \text{ h}^{-1}$) calculated for each day of the year, according to optimal or measured irradiances (OI, MI, respectively), after introducing in the calculation a variable time lag between maximum GCP and emersion time (dashed lines correspond to the period when data were extrapolated)

neap tides, when emersion matched with a non-saturating PAR period at the study site. Conversely, neap tide periods correspond to the highest discrepancies at the end of spring/beginning of summer, when only 1 of the 2 emersion periods matching with local noon occurred during daytime. The strongest fluctuations once every 2 wk, estimated as a decrease in daily production of 21% in summer (June) and an increase of 22% in autumn (October) by Migné et al. (2004), were refined here as being 27 and 37%, respectively (Fig. 3).

The induced variability every 14 d can be better illustrated through Fourier power spectral analysis (Fig. 5), in which the variability (i.e. the variance) of a given pattern was decomposed as a function of the time scale. The Fourier power spectra calculated with and without consideration of the time lag between maximum GCP and emersion time for optimal and measured light conditions indicated that when optimal irradiance was considered (Fig. 5A) the spectral density $E(f)$ (i.e. the variance) was lower when this variable time lag was considered, except for frequencies f bounded between 0.0618 and 0.0743 d^{-1} . This corresponded to a mean period ($1/f$) of 14.8 d (2 wk variability). The spectra obtained when measured irradiance was considered (Fig. 5B) showed the higher variability induced by cloudiness; the 2 curves have similar patterns, but that calculated in the previous budget remains clearly higher. Light availability thus remained the major factor inducing variability, but, when the budget was corrected, the relative importance of the 2 wk variability on the annual variability increased by about 3-fold when optimal irradiance was

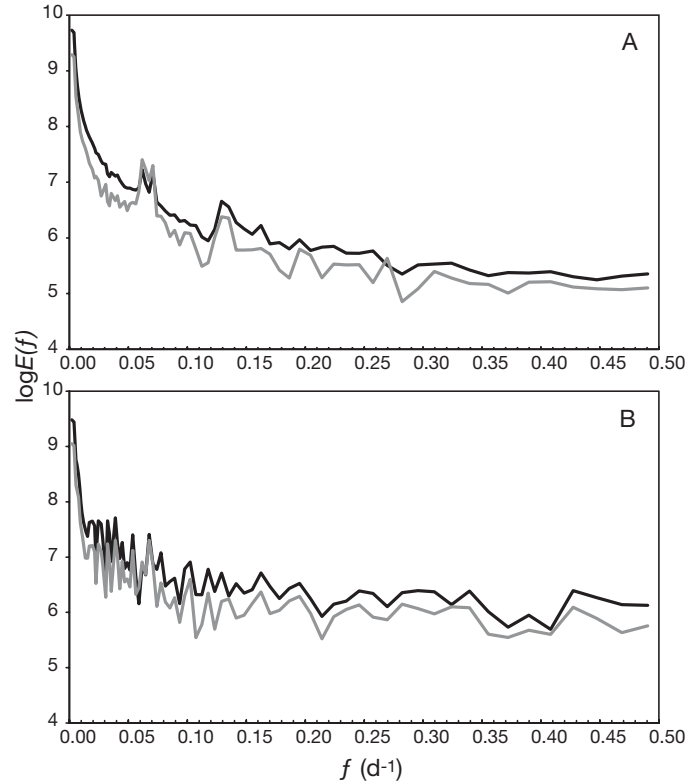


Fig. 5. Fourier power spectra $E(f)$ of the GCP calculated for time series considering optimal irradiance (A) and measured irradiance (B), with the variable time lag between maximum GCP and emersion time included (grey line) or not (black line)

considered (from 0.18 to 0.62%) and by about 2-fold when measured irradiance was considered (from 0.28 to 0.58%).

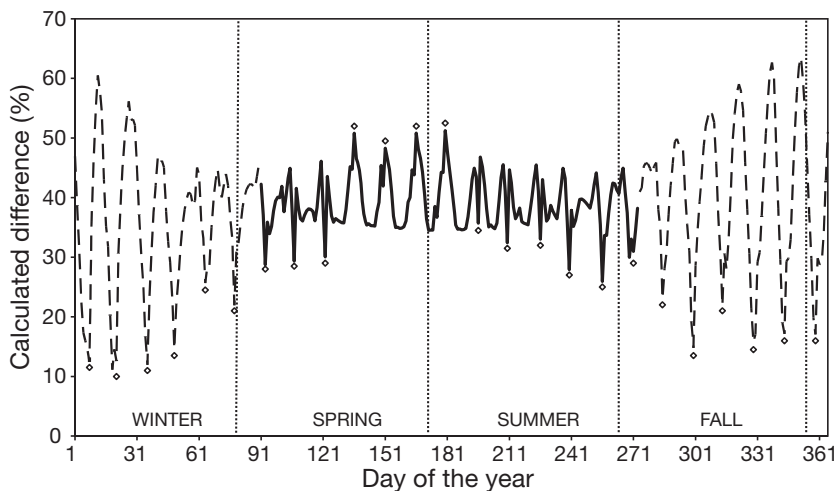


Fig. 4. Difference between daily GCPs estimated with and without consideration of a variable time lag between maximum GCP and emersion time (present study and Migné et al. 2004, respectively), expressed as the percentage of the previously published budget for each day of the year. Rhomb indicates neap tide, and the dashed lines correspond to the period when data were extrapolated

DISCUSSION

In the present study we used a non-destructive technique to monitor short-term variations in benthic primary production *in situ*. Previously, Brotas et al. (2003) and Underwood et al. (2005) studied the variability in microphytobenthic primary productivity over a diurnal cycle using non-destructive *in situ* methods (micro-electrodes and PAM fluorescence). As pointed out by these authors, *in situ* measurements are needed, since it is very difficult to simulate variability in the factors controlling primary production in the laboratory, especially their short-term variability. Furthermore, the method we used allowed us to carry out relatively short incuba-

tions (about 15 min), compared to other incubation techniques such as ^{14}C uptake and oxygen exchange rates, and was adequate to calculate carbon budgets, since measurements were performed at the community level.

Despite these different methods and units, the variations in GCP in the course of emersion measured in the present study seemed to be consistent with those reported in laboratories and *in situ* studies (we used a photosynthetic quotient of 1.2 to convert O_2 fluxes into CO_2 fluxes for comparisons). A strong hour-to-hour GCP variability was indeed previously observed: from about 0 to $150 \text{ mg C m}^{-2} \text{ h}^{-1}$ by Serôdio & Catarino (2000) and from 87 to $243 \text{ mg C m}^{-2} \text{ h}^{-1}$ by Brotas et al. (2003). The observed pattern in the short-term variability of primary production may be ascribed to many factors, i.e. light availability, temperature, desiccation, CO_2 , or nutrient limitation. Temperature has been shown to have an important effect on photosynthetic rates under saturating irradiance at the study site (Migné et al. 2004), but the weak variations in temperature under saturating irradiance measured in the present study ($<1^\circ\text{C}$) were not able to change drastically the primary production. Light availability inducing migration of the motile fraction of the microphytobenthos can thus mainly be considered to be involved in the observed short-term variability. Indeed, it has been shown that GCP was closely correlated to irradiance during sunrise and sunset (Fig. 2), and, above all, a positive correlation between the time lag between maximum GCP and emersion time and the time lag between emersion time and local noon was highlighted (Eq. 2). Previous studies already showed that maximum biomass and production seemed to occur when low tide matched with local noon (Pinckney & Zingmark 1991, Mitbavkar & Anil 2004). This may be explained by an increase in the depth of the photic zone; microalgae in the upper sediment are then in a favourable light environment without the need to migrate and additional light is provided to buried microalgae. The increase in production as a response to a decrease in irradiance on each experimental date after the immersion period (Fig. 1) could be interpreted as negative phototaxis (downward vertical migration of microphytobenthos under supersaturating irradiances). We can argue that this pattern was most likely due to a tidal effect (downward migration of the cells to protect from resuspension) since Eq. (2) does not validate a phototaxis hypothesis (GCP reached its maximum more quickly when emersion matches with local noon, i.e. with high irradiance).

Nevertheless, Eq. (2) was calculated using a dataset in which the timing of immersion was always approximately at the same time, i.e. when immersion matched with local noon (Fig. 1), and we then implicitly made

the assumption that the correlation was as significant when immersion and noon did not occur together. Furthermore, morning and afternoon data were gathered to calculate the relationship, even if emersion was prior to the light period for the morning data set, whereas emersion was during the light period and hence just prior to the maximum GCP and around the time of maximum PAR for the afternoon cases. Even making these assumptions, our results agreed with previous studies, but it appeared that a more accurate relationship could be obtained by treating morning and afternoon cases separately, more data for the morning then being needed.

Short-term variability in chl *a* biomass and primary production seems to be time, taxon and location specific. Observed maximal chl *a* biomass in the surface sediment after the beginning of exposure is highly variable (ca. 90 min, Tolhurst et al. 2003; ca. 300 min, Perkins et al. 2001) and appeared to decrease ca. 70 min before flooding (Perkins et al. 2001). Furthermore, Perkins et al. (2002) and Underwood et al. (2005) have shown that significant changes may take place in the species composition of the upper microphytobenthos at a short time scale (minutes). Even when chl *a* biomass was not monitored during the experiments, variation in biomass in the photic zone on 1 August 2004 (Fig. 1D) was evidenced by large shifts between GCP just before emersion ($30 \text{ mg C m}^{-2} \text{ h}^{-1}$) and GCP just after emersion ($102 \text{ mg C m}^{-2} \text{ h}^{-1}$). Furthermore, seasonal and inter-annual variations in specific composition of the microphytobenthos (not measured) may also be involved in the measured GCP variations. This was, however, not confirmed by Migné et al. (2004), who did not observe variations in biomass or primary production between years in their pluri-annual set of data.

The introduction of the variable time lag between maximum GCP and local noon into the budget calculation enhanced variability at a temporal scale of once every 2 wk. Serôdio & Catarino (2000) also showed that the production variability every 14 d increased when migratory rhythms were considered, and it was much higher than the variability obtained in the present study. This can be related to the strong seasonal pattern obtained in our study through the introduction of sinusoidal curves in our model (see Fig. 3), whereas the data of Serôdio & Catarino did not exhibit such a seasonal pattern (see their Fig. 10). In our study, the variability for a period of 177 d, which corresponds to about half the year, was about 20%.

Despite the great decrease in the primary production budget calculation due to the introduction of the variable time lag, the annual GCP calculated ($90 \text{ g C m}^{-2} \text{ yr}^{-1}$ with optimal irradiance and $67 \text{ g C m}^{-2} \text{ h}^{-1}$ with measured irradiance) was still in the range of values

given by Cahoon (1999) for temperate intertidal areas ($111 \pm 99 \text{ g C m}^{-2} \text{ yr}^{-1}$). The new annual NCP calculated (-98 and $-121 \text{ g C m}^{-2} \text{ yr}^{-1}$ using optimal and measured PAR, respectively) reinforced the conclusion that the study site was a net heterotrophic environment, as generally expected for estuarine areas. While temporal variations in primary production in connection with the physical and the biological environment are now better understood, respiration estimations still remain a critical issue. In the present study, annual respiration was underestimated for at least 2 main reasons: we considered that respiration was not light nor tide dependant (i.e. constant throughout the day and night and throughout emersion and immersion), while some studies have shown that this is generally not the case. Respiration rates in the light may be higher than those in the dark (Epping & Jørgensen 1996), and respiration is expected to increase during immersion (Gribsholt & Kristensen 2003).

It still appears to be critical to develop production models that consider the variability of both production and respiration rates at several time scales, ranging from hourly to seasonal, particularly when results are extrapolated to larger spatial scales. The improvement of these calculations will ultimately result in more accurate estimates of the primary production of the coastal benthic ecosystem. This first step is needed before assessing how increasing human perturbations will affect the overall metabolic potential of coastal ecosystems, e.g. through changes in ecosystem functioning and sea level rise.

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