

Benthic primary production during emersion: In situ measurements and potential primary production in the Seine Estuary (English Channel, France)

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Abstract

A two year survey of benthic primary production during periods of emersion was performed on two stations of an intertidal mudflat (a muddy-sand station and a muddy station) in the Seine Estuary (English Channel, France). The goals of this study were to investigate the seasonal variations of metabolism, to estimate daily potential primary production variation at the annual scale and to estimate the annual potential primary production of the mudflat. Primary production and respiration were estimated by in situ measurements of carbon dioxide fluxes. Chlorophyll *a* concentration exhibited a great variability on both locations. Gross community production ranged from ca. 0 to 77 mg C m⁻² h⁻¹ at the muddy-sand location and from ca. 0 to 122 mg C m⁻² h⁻¹ at the muddy location. Community respiration showed a seasonal trend following temperature variations (up to 28.51 mg C m⁻² h⁻¹ in the muddy-sand and up to 23.40 mg C m⁻² h⁻¹ in the mud). Daily potential primary production was calculated, according to seasonal variations of photosynthetic parameters calculated using three photosynthesis versus irradiance curves obtained for the muddy location. The annual gross community primary production was 135 g C m⁻² yr⁻¹, leading to a low autotrophic annual budget, considering an annual community respiration of 110 g C m⁻² yr⁻¹. © 2005 Elsevier Ltd. All rights reserved.

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1. Introduction

Estuaries are the main transition zones between continental freshwater and oceans. In order to estimate whether estuaries are sinks or sources of CO₂ one needs to understand the processes that determine the balance between primary produced organic matter and its consumption by respiration. The average primary production in estuaries (including both benthic and pelagic production) as estimated by various authors has been calculated by Smith

and Hollibaugh (1993) as 300 ± 100 g C m⁻² yr⁻¹. Although many investigations of benthic primary production have been conducted in estuaries, in most of them the substrate and the microalgae have been manipulated for photosynthetic measurements, which therefore lead to unrepresentative rates (Admiraal and Peletier, 1980).

Non-destructive methods (oxygen microelectrodes and variable fluorescence techniques) are now used in microphytobenthos photosynthesis studies but scaling measurements up to larger area rates is contentious (Underwood and Kromkamp, 1999). We used a method (benthic chamber) where the sediment is not disturbed and the patchiness of microphytobenthos is integrated (Migné et al., 2002).

The present study aims to estimate benthic primary production in an intertidal mudflat in the Seine Estuary by in situ measurements of CO₂ fluxes during emersion period.

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2. Materials and methods

2.1. Study site

The Seine River is the biggest outflow into the English Channel (Fig. 1). Its catchment area is 78 000 km² in which 40% of the French population and economic activity is situated. The study site is located on the biggest mudflat of the Seine Estuary (3.2 km²). Measurements were performed seasonally on two stations: a muddy-sand sediment (about 15% mud; 49°26.882 N/00°14.592 E) and a muddy sediment (about 50% mud; 49°26.841 N/00°14.622 E) which is the dominating facies on the mudflat. Both stations are located between mean high water of neap tides and mean tide level and are subject twice a day to flooding

(semi-diurnal tidal regime). The survey was performed from March 2001 to January 2003 (ten series of measurements at approximately two months interval) to estimate seasonal variation of benthic community metabolism.

2.2. Community metabolism measurements

Air-sediment CO₂ exchange, including uptake by micro-phytobenthos and respiration by phyto- and zoo-benthos, was measured by monitoring the change in CO₂ concentration in a stream of air passing over a section of the community enclosed in a benthic chamber. Details on the design and use of this chamber are described in Migné et al. (2002). Experiments were carried out at ambient light and in darkness in order to estimate net community primary production (NCP) and community respiration (CR) respectively. Fluxes are expressed at the community level (mg C m⁻² h⁻¹). The dark incubation rate on a given date was added to measurements from individual light incubations to determine gross community primary production (GCP = NCP + CR).

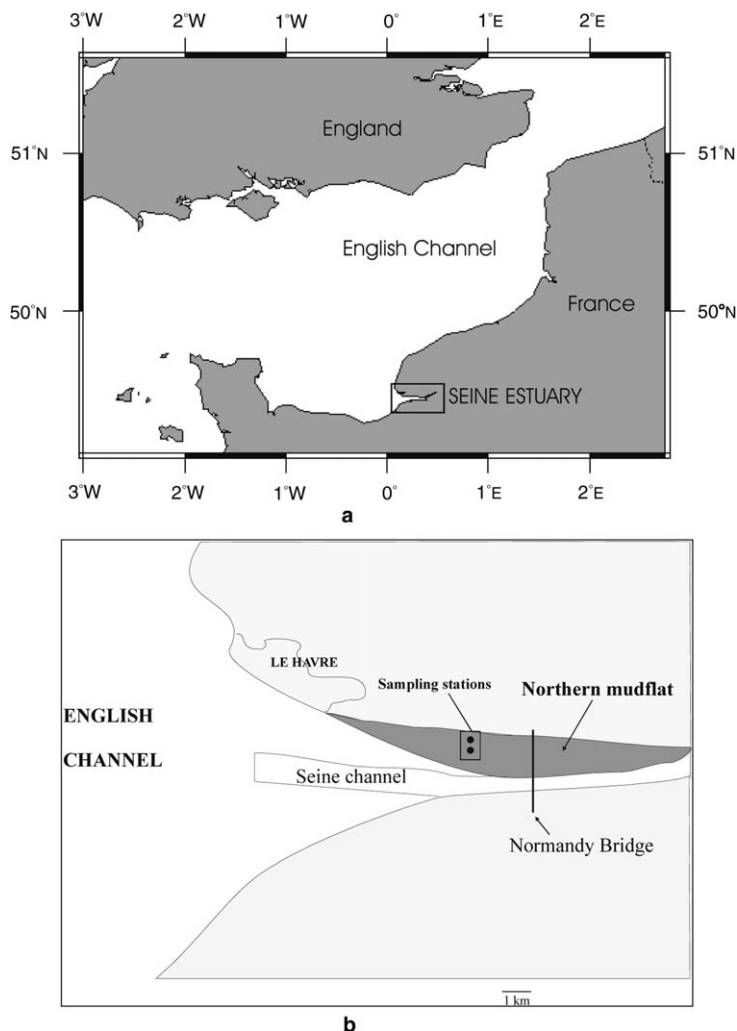


Fig. 1. (a) Location of the Seine Estuary (English Channel, France), (b) location of the sampling area.

2.3. Chlorophyll *a* biomass determination

Chlorophyll *a* is usually used as an index for primary producers biomass (MacIntyre et al., 1996). Plastic cores (1.9 cm², 3 replicates) were pushed into the sediment down to a depth of 1 cm, carefully removed and then stored in a cool box, brought back to the laboratory and stored in the dark at –20 °C. For extraction, sections of sediment were placed in 8 mL acetone for 4 h in the dark at 4 °C. Samples were then centrifuged at 4000 rpm for 15 min. Chlorophyll *a* concentration in the supernatant was determined by spectrophotometry following Lorenzen (1967) and expressed in terms of chlorophyll *a* per surface unit (mg Chl *a* m⁻²).

2.4. Functional response to irradiance

Some experiments were performed from dawn to saturating light or from saturating light to dusk in order to estimate microphytobenthic response to light variations. Photosynthesis–irradiance response curves (*P*–*I*) were fitted to the data for one day, according to the model proposed by Webb et al. (1974):

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

where *P* = GCP (in mg C m⁻² h⁻¹), *P_m* = rate of maximal GCP, *I* = incident irradiance (in μmol m⁻² s⁻¹) and *I_k* = saturation onset parameter.

2.5. Potential annual community primary production

Because of strong light limitation during flood tide, microphytobenthos production is assumed to be restricted to the emersion period in turbid estuaries (Barranguet et al., 1998). The daily potential community primary production was then calculated considering the period of superimposition of day and emersion. Optimal condition of light was calculated from the sinusoidal curve of daily variation of irradiance:

$$I(t) = I_m \sin(\pi t/D), \quad (2)$$

where *I_m* (in μmol m⁻² s⁻¹) is the maximal irradiance of the day, and *D* (min) is the day length.

Gross community primary production was calculated as a function of irradiance (Eq. (1)), the rate of maximum GCP (*P_m*) and the saturation onset parameter (*I_k*) have been estimated from the fitting of sinusoidal models using values obtained at different periods of the year. GCP was estimated every minute and added for the period of superimposition of day and emersion for each day of the year to obtain an estimation at the annual scale. In order to calculate an annual net community primary production, community respiration was estimated for each day of the year from the fitting of a sinusoidal model using values measured in the study site at different periods of the year.

3. Results

3.1. Chlorophyll *a*

A great variability was observed in chlorophyll *a* concentrations and no seasonal trend was detected at any location (Fig. 2). Chl *a* concentration was higher on the muddy-sand location for each sampling date (Wilcoxon *T* test), ranging from 69.2 to 276.9 mg m⁻² (174.2 ± 62.2 mg m⁻², mean ± S.D.) in the muddy sand and from 55.0 to 179.3 mg m⁻² (103.5 ± 50.5 mg m⁻²) in the mud.

3.2. Gross community primary production

Values of GCP measured under saturating irradiance were plotted for each location (Fig. 3). On both of them, the maximum of GCP was measured in spring. Nevertheless, a seasonal trend allowing to fit a sinusoidal curve was observed only on the muddy location:

$$\text{GCP} = 44.28 + 38.71 \sin[(2\pi/365)x - 20.00] \quad (3)$$

$$n = 8, r^2 = 0.837,$$

where *x* is the julian day (Fig. 3b).

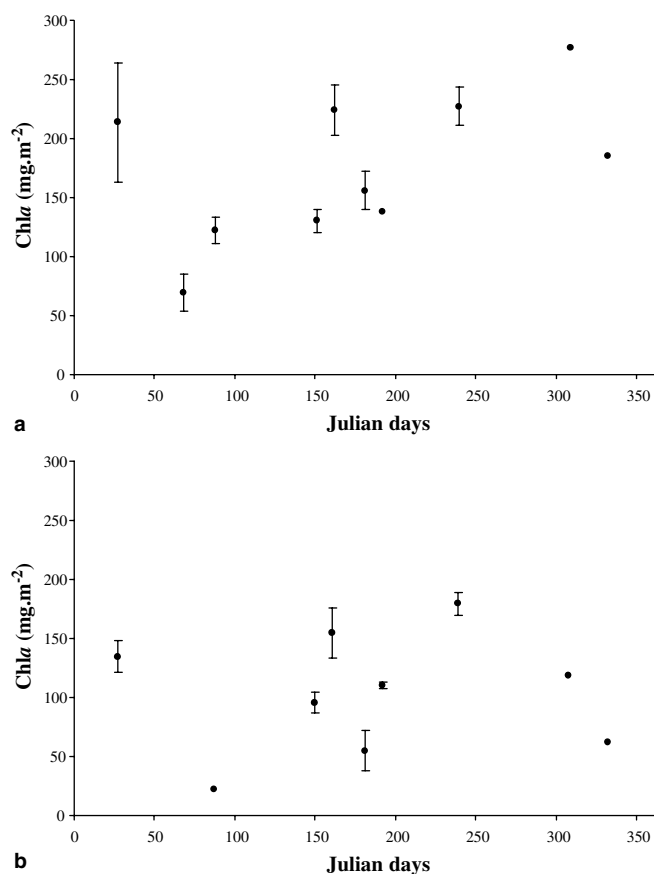


Fig. 2. Annual development of Chlorophyll *a* concentration (mean ± S.D. in mg m⁻²) (a) on the muddy-sand station and (b) on the muddy station.

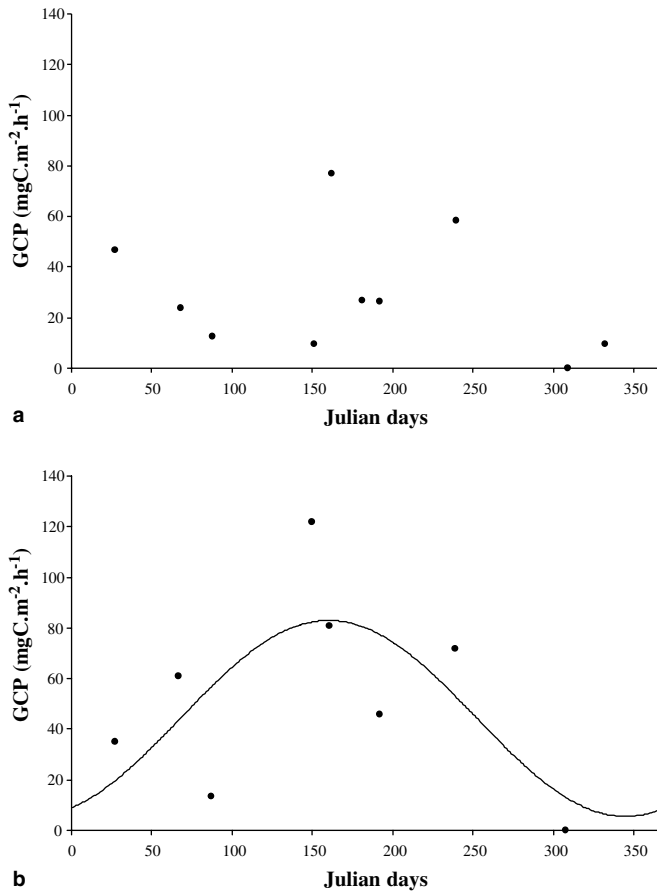


Fig. 3. Values of gross community production (GCP in $\text{mg C m}^{-2} \text{h}^{-1}$) measured under saturating irradiance (a) on the muddy-sand station and (b) on the muddy station (and adjusted sinusoidal model).

The model gives the highest GCP at the end of spring ($82.99 \text{ mg C m}^{-2}$ the 9th of June).

3.3. Community respiration

For both the locations, community respiration showed a seasonal trend following the seasonal variations of temperature. Significant correlations between CR and temperature (when available) were calculated for the two locations (muddy-sand: $n = 8$, $r = 0.881$, $p < 0.01$; mud: $n = 9$, $r = 0.903$, $p < 0.001$). A sinusoidal curve was fitted for each series of data (Fig. 4):

$$\text{CR}_{\text{muddy-sand}} = 14.71 + 13.80 \sin\left[\left(\frac{2\pi}{365}\right)x + 10.53\right] \quad (4)$$

$$n = 10, r^2 = 0.915,$$

$$\text{CR}_{\text{mud}} = 12.55 + 10.85 \sin\left[\left(\frac{2\pi}{365}\right)x + 10.55\right] \quad (5)$$

$$n = 10, r^2 = 0.931,$$

where x is the Julian day.

CR seemed to be higher on the muddy-sand location than on the muddy one; using the models, the highest CR values are expected to be in summer and at the same time on both locations (muddy-sand: $28.51 \text{ mg C m}^{-2} \text{h}^{-1}$ on July 29th; mud: $23.40 \text{ mg C m}^{-2} \text{h}^{-1}$ on July 27th).

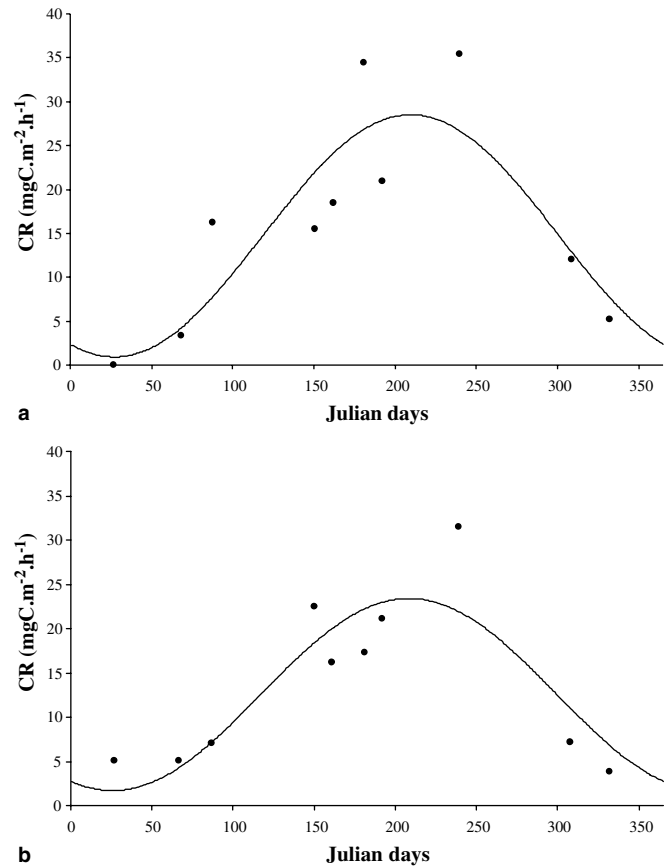


Fig. 4. Community respiration (CR in $\text{mg C m}^{-2} \text{h}^{-1}$) measured on the two locations ((a) muddy-sand; (b) mud) and adjusted sinusoidal models.

3.4. Functional response to irradiance and potential annual community primary production on the muddy location

Only three photosynthesis–irradiance response curves could be fitted on the 10 series of measurements for the muddy location (Fig. 5). In the remaining seven series measurements were carried out at irradiance values above or

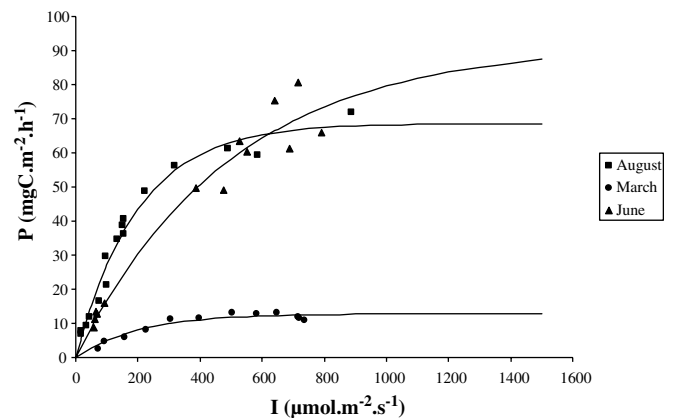


Fig. 5. Photosynthesis–irradiance curves (GCP in $\text{mg C m}^{-2} \text{h}^{-1}$ and I in $\mu\text{mol m}^{-2} \text{s}^{-1}$) obtained on the muddy location in March ($P = 12.8[1 - \exp(-I/204)]$, $r^2 = 0.991$, $n = 12$), June ($P = 91.9[1 - \exp(-I/498)]$, $r^2 = 0.989$, $n = 13$) and August ($P = 68.6[1 - \exp(-I/199)]$, $r^2 = 0.994$, $n = 16$).

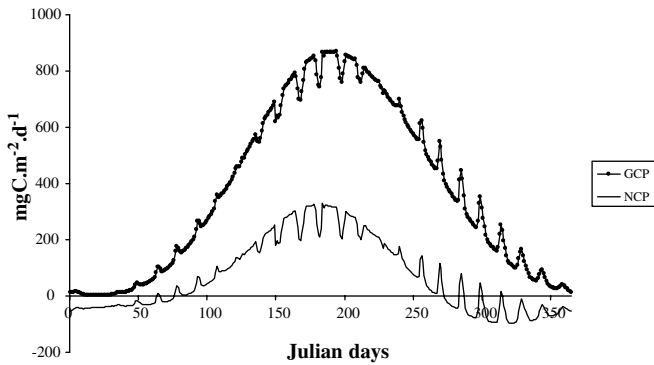


Fig. 6. Annual development of potential gross community production (GCP in $\text{mg C m}^{-2} \text{ h}^{-1}$) and net community production (NCP in $\text{mg C m}^{-2} \text{ h}^{-1}$) at the muddy location.

below the saturating level, and/or under sharp temperature change.

In order to estimate the development of P_m and I_k all along the year, a sinusoidal model was fitted using the 3 values obtained for August 2001, March 2002 and June 2002:

$$P_m = 46.00 + 45.50 \sin[(2\pi/365)x + 10.63] \quad (6)$$

$$n = 3; r^2 = 0.965,$$

$$I_k = 284.00 + 200.00 \sin[(2\pi/365)x - 1.32] \quad (7)$$

$$n = 3; r^2 = 0.859,$$

where x is the Julian day.

Assuming no primary production during immersion because of high turbidity levels in estuaries (Barranguet et al., 1998; Seródio and Catarino, 2000) and considering optimal conditions of light, the potential annual GCP was $135 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Fig. 6). Using the sinusoidal curve obtained with community respiration data (Eq. (5)) and assuming that benthic respiration was constant during 24 h, the annual community respiration was $110 \text{ g C m}^{-2} \text{ yr}^{-1}$. The location seemed to be characterized by an alternation between heterotrophic (winter) and autotrophic (summer) periods (Fig. 6).

4. Discussion

Chlorophyll a concentrations were within the range of values given by MacIntyre et al. (1996) for intertidal mudflats: $33\text{--}184 \text{ mg m}^{-2}$ in the Ems-Dollard Estuary (Colijn and de Jonge, 1984), $10\text{--}500 \text{ mg m}^{-2}$ in the Bay of Fundy (Hargrave et al., 1983). Microphytobenthic biomass usually shows great seasonal variations with a peak in spring or summer. For example, in the Ems-Dollard Estuary (The Netherlands), Colijn and Dijkema (1981) found concentrations varying from 5 to 245 mg m^{-2} and De Jonge and Colijn (1994) from 10 to 420 mg m^{-2} . The amplitude of variations measured in the present study were lower than those found in most estuarine habitats and, as previously described by some authors (Riznyk et al., 1978; Lukatelic and McComb, 1986; Plante-Cuny and Boday, 1987), no

summer biomass peak was detected. In most studies, seasonal variations were estimated using a great number of measurements (276 and 221 for Colijn and Dijkema, 1981 and De Jonge and Colijn, 1994, respectively) on relatively short periods (10 and 35 months, respectively). In our study, the lack of biomass estimations in some periods may have led to weak information of these variations. Sagan and Thouzeau (1998) pointed out that, in the Bay of Brest (France), subtidal microphytobenthos blooms were strongly correlated with environmental factors, such as river floods, water temperature and the spring/neap tidal cycle. In particular, maximum chlorophyll biomass occurred at neap tides. In the present study, no direct correlation was found with either river floods or with the tidal cycle. Because these factors will interact with each other but have different characteristic frequencies, it is effectively difficult to assess the magnitude of their perturbation for microphytobenthic populations, particularly in terms of deposit or erosion of the surface sediment.

Community respiration showed a seasonal trend following temperature variations, as has been observed in various studies (Asmus, 1982 and Grant, 1986 on intertidal sandflats; Van Es, 1982 on estuarine mudflats). In most marine habitats, benthic respiration is mainly the result of microfaunal activity (Schwinghamer et al., 1986; Piepenburg et al., 1995). In assessing the factors controlling bacterial production in marine sediments, Cole et al. (1988) and Sander and Kalff (1993) found significant relationships between bacterial production rates and temperature and substrate supply (i.e. sedimentary organic carbon concentrations). Thus, the highest values of community respiration are not only explained by seasonal fluctuations in temperature, but also by seasonal cycles of bacterial production. These cycles are often characterized by one or more peaks in spring and autumn; these peaks mostly coincide with peaks in organic carbon inputs (Chardy and Dauvin, 1992), mainly from microphytobenthos (Middelburg et al., 2000). The highest values of community respiration measured here could be attributed to bacterial heterotrophic activity following the high primary production period, but an important shift between the highest GCP (June) and the highest CR (August) was observed. This might be due to high allochthonous organic carbon inputs all along the year, the limiting factor for microbial production then being temperature. Annual community respiration rates estimated in our study ($129 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the muddy-sand location and $110 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the muddy location, using Eqs. (4) and (5), respectively) are an order magnitude lower than the data compiled by Heip et al. (1995). For example, Boynton and Kemp (1985) estimated a benthic respiration of $288 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the Chesapeake Bay. However, the method we used for these estimations (respiration values integrated over 24 h) must slightly underestimate the community respiration rate during immersion: it has been shown that benthic respiration could be higher during this period (Toulmond, 1976; Dye, 1980; Gribsholt and Kristensen, 2003).

The daily GCP varied essentially as a function of irradiance, being maximum on July 13th ($869.7 \text{ mg C m}^{-2} \text{ d}^{-1}$), when day length and irradiance are maximal, and minimum on January 23th ($2.4 \text{ mg C m}^{-2} \text{ d}^{-1}$; Fig. 6). Within the seasonal pattern, fortnightly fluctuations followed the irradiance availability at the sediment surface caused by the superimposition of tidal and day/night cycles with different periods. This annual pattern, characterized by a strong fortnightly variability superimposed on the underlying seasonal trend, is similar to that shown by Serôdio and Catarino (1999) for the Tagus Estuary. In the Eastern English Channel, low water levels of neap tides occur around midday; microalgae are then exposed to saturating irradiance, irrespective of season. On the contrary, low water levels of spring tides occur at the beginning and the end of the day. In winter, daytime being shorter, microalgae are never exposed to saturating irradiance during spring tides; highest winter GCP are then expected during neap tides. In summer, days are longer and the sediment is then exposed longer to saturating daylight during the two periods of emersion of spring tides; highest summer GCP are then expected during spring tides. These fluctuations in daily production were comparable in amplitude with those occurring at the seasonal scale and underlined the day-length influence on GCP. For example, daily gross production was found decreasing of 13% between 27 June and 30 June and increasing of 60% between 7 and 10 November. Despite differences in methodology, the order of magnitude of the GCP is the same than those given by Heip et al. (1995: $116 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the Ythan Estuary; $106 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the Falsmouth Bay; $136 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the Westerschelde) and Serôdio and Catarino (2000: $156 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the Tagus Estuary). Using the same calculation method, the same order of magnitude was obtained in the Bay of Somme (GCP = $147 \text{ g C m}^{-2} \text{ yr}^{-1}$, Migné et al., 2004). In the Seine Estuary, the annual net budget calculated for the muddy location was $25 \text{ g C m}^{-2} \text{ yr}^{-1}$, that is slightly autotrophic. This value is in contradiction with those given by Gattuso et al. (1998) who pointed out that all coastal ecosystems, except estuaries, are net autotrophic. Nevertheless, the real budget might be less autotrophic or balanced because, as seen before, the annual CR could be underestimated, and the annual GCP was overestimated because of the use of theoretical irradiance in the calculation.

Few attempts, based on in situ measurements, have previously been made to estimate annual benthic community production on estuarine unvegetated sediments. This work is a significant contribution to this topic, but much remains to be done to understand the variability induced by environmental parameters and to consider these variations when extrapolations are made.

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