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Annual budget of benthic production in Mont Saint-Michel Bay considering cloudiness, microphytobenthos migration, and variability of respiration rates with tidal conditions

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ABSTRACT

In order to provide an accurate annual rate of net benthic community production, community photosynthetic response to incident irradiance and respiration were measured at different times of the year, at mid-tide level on the muddiest part of the Mont Saint-Michel Bay. As the water turbidity prevented any photosynthesis by the microphytobenthos during immersion periods, primary production was measured only during emersion periods. In contrast respiration was expected to vary according to the tidal cycle and was measured during both emersion and immersion periods. Primary production and respiration rates under emersion were assessed using in situ infra-red gas analysis of CO₂ exchange measured in a benthic chamber. Respiration rates under immersion were assessed through total CO₂ concentration variations in incubated cores.

When respiration rate was considered constant over a day and equal to the rate measured under emerged conditions, the community respiration was 54.56 gC m⁻² yr⁻¹. Taking into account the variations of respiration during the emersion/immersion cycle, community respiration increased to 101.76 gC m⁻² yr⁻¹ (86% increase). Assuming that community primary production varied as a function of irradiance from the time of exposure until flooding, GCP was 53.22 gC m⁻² yr⁻¹ when calculated with theoretical irradiance and 45.86 gC m⁻² yr⁻¹ after correction for cloudiness (14% decrease). Then, by integrating the effect of vertical migration of microphytobenthos, the rate was adjusted to 23.49 gC m⁻² yr⁻¹ (49% decrease). The net community production budget, calculated as the difference between the GCP and the CR budgets taking into account the corrections described above, was -78.27 gC m⁻² yr⁻¹. This example of annual budget calculation highlights the need to integrate several processes occurring over various time scales to accurately reflect the metabolic balance of a system. The results also confirmed the heterotrophic status generally suggested for intertidal muddy sediments.

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1. Introduction

The coastal ocean is considered to play a key role in the global carbon cycle and coastal metabolism has been the subject of a

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number of reviews (e.g., Smith and Hollibaugh, 1993; Gattuso et al., 1998; Gazeau et al., 2004). In order to estimate whether coastal zones are sinks or sources of CO₂, annual rates of community primary production and respiration are necessary to determine the metabolic balance in both pelagic and benthic compartments. Annual rates for metabolic processes must integrate the variability of both production and respiration processes over a number of time scales (day, tide, season, year). This is particularly important for tidal sediment habitats characterized by large fluctuations in environmental parameters in response to the superimposition of diurnal and tidal cycles. In this context, estimates of the annual benthic net production rate, obtained through in situ measurements of carbon dioxide flux at

the community level, have been proposed for diverse tidal sedimentary systems along the French coast of the English Channel (Migné et al., 2004; Spilmont et al., 2005; Hubas and Davoult, 2006; Spilmont et al., 2006, 2007). These estimates integrated the variability of photosynthesis at varying temporal scales (day, spring-/neap-tide cycle, season), and stressed out the importance of considering cloudiness (Migné et al., 2004; Hubas and Davoult, 2006) and the vertical migration of microphyto-benthos (Spilmont et al., 2007) for budget calculation. Nevertheless, potential variability in respiration according to the day/night and low-/high-tide alternations was not assessed.

The Mont Saint-Michel Bay is subjected to one of the world's largest tidal ranges (up to 14 m during spring tides), which leads, together with the gentle slope of the shore, to a tidal flat that is nearly 11 km wide. The western part of the bay, protected and subjected to intensive shellfish farming, is characterised by the accumulation of fine particles (Cayocca et al., 2008). Within the framework of a multidisciplinary project, both temporal and spatial variability of the benthic metabolism under emersion (community primary production under saturating light and community respiration) were estimated in this part of the bay (Davoult et al., 2009). One of the stations surveyed by Davoult et al. (2009) was selected to determine the photosynthetic response of the community to incident irradiance and respiration at different times of the year, in order to establish an annual budget. The selected station was located in the muddiest part of the bay, around mid-tide level. Primary production was only measured during emersion periods, since the water turbidity prevented any photosynthesis by the microphytobenthos during immersion periods (Thorin et al., 2001; Cayocca et al., 2008). Respiration was measured during both periods of emersion and immersion to provide an accurate annual rate of the net community production. The aim of this paper is to integrate the complexity of metabolic processes within intertidal soft sediments into carbon budget calculation and discuss the relative effect of multiple bio-physical parameters, occurring at different time scales.

2. Material and methods

2.1. Study site

The surveyed station was located near Cancale in the western part of the Mont Saint-Michel Bay on the French coast of the English Channel (Fig. 1). This part of the bay is sheltered and characterised by high rates of sedimentation (Cayocca et al., 2008). Mud sediment content was about 80% (Bonnot and Olivier, unpublished data). The station was located around mid-tide level and was subjected to flooding twice a day for 7 h on average per tidal cycle. This was the highest station in the Cancale transect of the Davoult et al. (2009) survey, 7 m above chart datum.

2.2. Carbon dioxide flux measurements

During emersion, benthic community primary production and respiration were assessed through in situ CO_2 exchange measurements under light (net community primary production NCP) and dark conditions (community respiration CR) in a benthic chamber. CO_2 was determined by infra-red gas analysis, as described in Migné et al. (2002). A perspex dome was fitted onto a stainless-steel ring which had been inserted about 10 cm into the sediment and connected in a closed circuit to a CO_2 analyser (LiCor Li-6251 infra-red gas analyser). The surface area of sediment covered was 0.126 m^2 , the volume of trapped air was approximately 25 L. Gas exchange was monitored during 10–30 min, depending on the

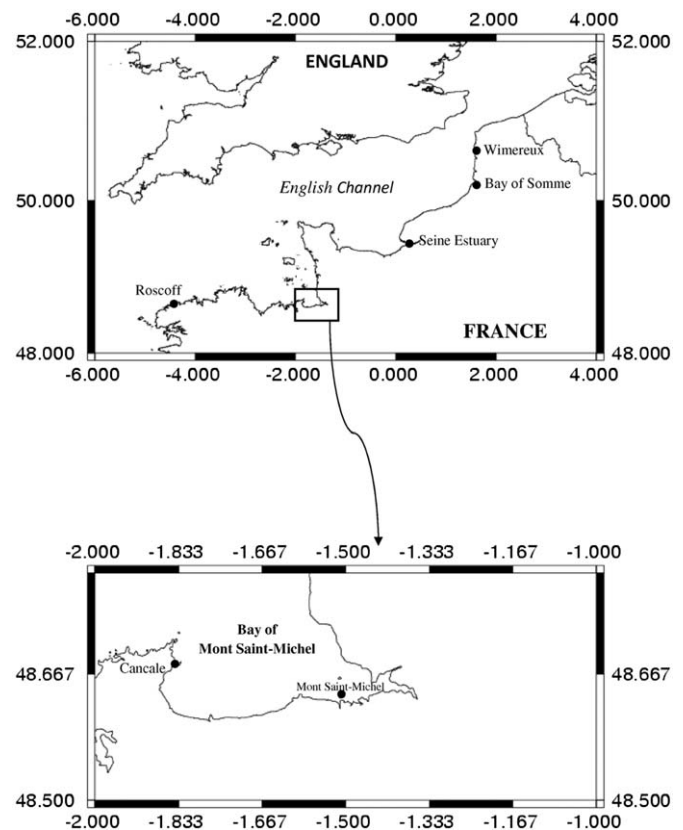


Fig. 1. Location of the study site in the western English Channel

response of the system. Partial pressure of CO_2 was then regressed against time, and the slope was used to express the results at the community level in carbon units ($\text{mgC m}^{-2} \text{ h}^{-1}$).

Gross community primary production (GCP) was calculated as:

$$\text{GCP} = \text{NCP} + \text{CR} \quad (1)$$

During immersion, CO_2 fluxes were calculated using the whole core incubation technique (Denis et al., 2001) performed in the dark at in situ temperature. Four sediment cores were manually collected in perspex tubes (15 cm in diameter; 35 cm in length) at the end of the immersion period, (approximately under 50 cm of water) and rapidly returned to the laboratory. Cores were sealed excluding air bubbles, and bottom water was also sampled from the site and placed in an inflatable reserve tank.

Samples for pH and total alkalinity measurements were taken in the overlying water of the four cores and in the reserve tank at the beginning and at the end of the 8 h incubation periods. Samples were filtered on cellulose acetate membranes ($0.8 \mu\text{m}$) and spiked with HgCl_2 pending potentiometric determination of total alkalinity (Millero et al., 1993) on three sub-samples. The total CO_2 concentrations (TCO_2) were then calculated after Strickland and Parsons (1972) using the formula given in Oviatt et al. (1986).

2.3. Response of photosynthesis to irradiance during emersion

Measurements were carried out from dawn to saturating light in order to estimate GCP as a function of the variation of ambient light. Photosynthetically active radiation (400–700 nm) was measured at the sediment surface using a LiCor SA-190 quantum sensor.

Composite photosynthesis–irradiance (P – I) curves were established using the equation of Webb et al. (1974):

$$P = P_m [1 - \exp(-I/I_k)] \quad (2)$$

where P =GCP (in $\text{mgC m}^{-2} \text{h}^{-1}$), P_m =rate of maximal GCP (GCP_m), I =incident irradiance (in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and I_k =saturation onset parameter. The simplex estimation method (O'Neill, 1971) was used to determine the photosynthetic parameters P_m and I_k (curve-fitting procedure of the "Systat 11" software).

2.4. Annual budgets of potential production

Measurements were repeated at different times over the year and seasonal cycles of photosynthetic parameters and CR were estimated by temporal interpolation (sinusoidal simplex fitting procedure).

Gross community primary production was assumed to be restricted to the diurnal emersion periods because of strong light limitation during flood tide (due to turbidity). GCP was calculated as a function of irradiance during diurnal emersion (using Eq. (2) with a step of one minute) in mgC m^{-2} for each day of the year. Theoretical irradiance (calculated from the sinusoidal curve of daily variation of irradiance) was used as in Migné et al. (2004):

$$I(t) = I_m \sin(\pi t/D) \quad (3)$$

where I_m (in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) is the theoretical maximal irradiance of the day, and D (min) is the day length.

In a first budget, GCP was calculated as a function of this theoretical irradiance from exposure until flooding tide. In a second one, the theoretical irradiance was corrected according to the cloud cover data recording at the nearest meteorological point from "Météo-France".

These budgets were based on the assumption that GCP was exclusively related to light variations from the beginning to the end of emersion, neglecting the effect of microphytobenthos migration demonstrated by Spilmont et al. (2007), i.e. progressive increase or decrease respectively at the beginning of exposure or just before flooding. These authors established a correction formula:

$$TL_{\text{GCP/em}} = 0.52(TL_{\text{em/noon}}) + 37.52 \quad (4)$$

where $TL_{\text{GCP/em}}$ is the time lag (in min) between maximum GCP and emersion time, and $TL_{\text{em/noon}}$ the time lag between emersion time and local noon.

We used this relationship to calculate the progressive increase (or decrease) of GCP as a linear variation at the beginning of exposure (or just before flooding), and included it in the budget.

Net community production was calculated as $\text{NCP} = \text{GCP} - \text{CR}$, either considering the respiration rate to be constant during a 24 h cycle and derived from the rate measured under emersion, or taking into account the variation of the respiration rates according to the tidal cycle.

3. Results

The five composite photosynthesis–irradiance (P – I) curves established between April 2003 and June 2005 (Table 1 and Fig. 2) showed the seasonal variations of the photosynthetic parameters.

The annual variations of the P_m and I_k parameters were estimated by fitting sinusoidal curves:

$$P_m = 31.4 - 5.6 \sin[(2\pi/365)t + 1.8]; (n = 5; R^2 = 0.956) \quad (5)$$

Table 1

Photosynthetic parameters (P_m and I_k) according to the model of Webb et al. (1974) fitted on the data obtained at the survey station in the Mont Saint-Michel Bay between April 2003 and June 2005, number of incubations, determination coefficient and p -value.

Date	P_m ($\text{mgC m}^{-2} \text{h}^{-1}$)	I_k ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	n	R^2	p
11 April 2003	27.5	266	6	0.992	< 0.001
20 October 2003	19.9	283	7	0.990	< 0.001
16 February 2004	36.4	129	9	0.986	< 0.001
25 August 2004	41.9	314	17	0.936	< 0.001
14 June 2005	35.5	754	14	0.983	< 0.001

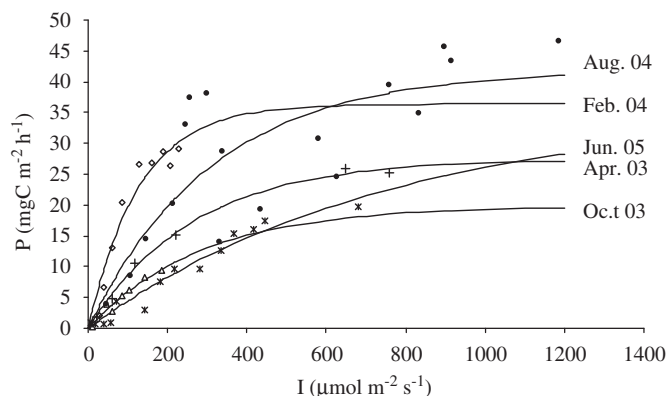


Fig. 2. Composite photosynthesis–irradiance (P – I) curves according to the model of Webb et al. (1974): $P = P_m [1 - \exp(-I/I_k)]$, obtained between April 2003 and June 2005 in the survey station in the Mont Saint-Michel Bay. P is the gross community production expressed in $\text{mgC m}^{-2} \text{h}^{-1}$ and I is the incident irradiance in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$.

where P_m (in $\text{mgC m}^{-2} \text{h}^{-1}$) is calculated as a function of time (t) expressed in days,

$$I_k = 349.2 - 282.0 \sin[(2\pi/365)t + 1.6]; (n = 5; R^2 = 0.908) \quad (6)$$

where I_k (in $\text{mmol m}^{-2} \text{s}^{-1}$) is calculated as a function of time (t) expressed in days.

A seasonal pattern was also observed for the community respiration under emerged and immersed conditions as shown by the sinusoidal fits (even if the limited number of data under immersed conditions prevented the fit from being tested):

$$\text{CR}_e = 6.2 - 6.2 \sin[(2\pi/365)t - 1.0]; (n = 6; R^2 = 0.926) \quad (7)$$

where CR_e is the respiration rate during emersion (in $\text{mgC m}^{-2} \text{h}^{-1}$) at time (t) expressed in days,

$$\text{CR}_i = 15.6 + 9.7 \sin[(2\pi/365)t + 4.8]; (n = 3; R^2 = 1) \quad (8)$$

where CR_i is the respiration rate during immersion (in $\text{mgC m}^{-2} \text{h}^{-1}$) at time (t) expressed in days.

Although the trends were based on a limited set of data, respiration rate appeared to be higher during immersion than during emersion throughout the year (Fig. 3). When the respiration rate was considered to be constant on a 24 h cycle and equal to the one measured under emerged conditions, the annual budget of respiration was 54.56 gC m^{-2} . This was almost doubled when the variation of the respiration according to the tidal cycle was taken into account: 101.76 gC m^{-2} .

Annual budgets of potential GCP, calculated with and without the irradiance correction for cloudiness and with and without including the vertical migration of microphytobenthos are given in Table 2. Assuming that GCP varied as a function of theoretical

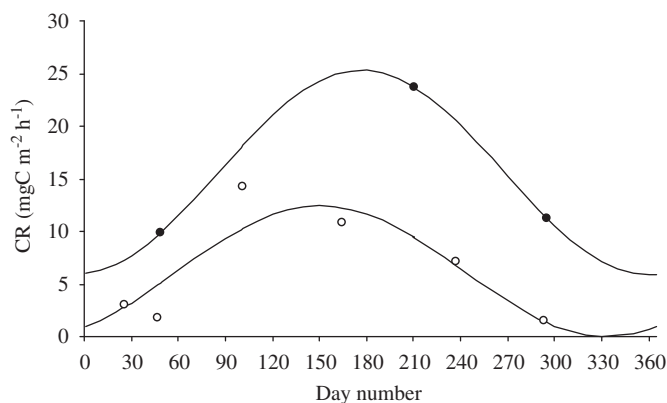


Fig. 3. Sinusoidal curves fitted on respiration rates (CR in $\text{mgC m}^{-2} \text{h}^{-1}$) obtained during the survey (time expressed as day number) under emerged (open circles) and immersed (closed circles) conditions.

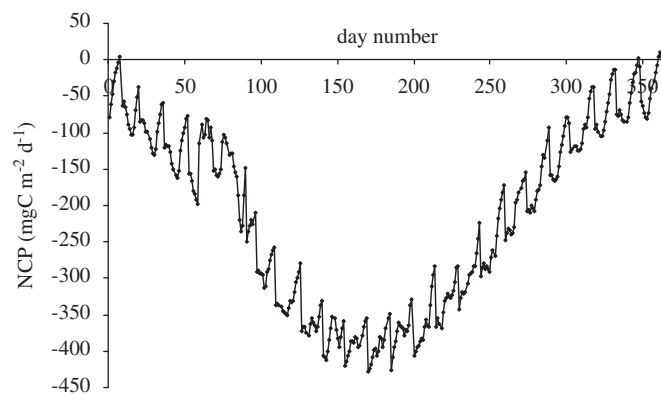


Fig. 4. Annual development of the net daily community production (NCP in $\text{mgC m}^{-2} \text{d}^{-1}$) calculated for the survey station in the Mont Saint-Michel Bay, taking into account the variation in respiration rate with the alternation of emersion and immersion, the irradiance corrected for cloud cover and the migration of microphytobenthos.

Table 2
Various annual budgets of gross and net community production (GCP and NCP in $\text{gC m}^{-2} \text{yr}^{-1}$) at the survey station in the Mont Saint-Michel Bay.

GCP ($\text{gC m}^{-2} \text{yr}^{-1}$)			
Migration	No	Cloudiness	
		No	Yes
		53.22	45.86
	Yes	24.5	23.49
NCP (CR_e) ($\text{gC m}^{-2} \text{yr}^{-1}$)			
Migration	No	Cloudiness	
		No	Yes
		-1.34	-8.7
	Yes	-30.06	-31.07
NCP (CR_e/CR_i) ($\text{gC m}^{-2} \text{yr}^{-1}$)			
Migration	No	Cloudiness	
		No	Yes
		-48.54	-55.9
	Yes	-77.26	-78.27

GCP was estimated with and without irradiance correction for cloudiness and with and without integrating processes of vertical migration of microphytobenthos. NCP was calculated as $\text{GCP} - \text{CR}$, either considering the respiration rate to be constant during a 24 h cycle and derived from the one measured under emersion (CR_e), or taking into account the variation of the respiration rates according to the tidal cycle (CR_e/CR_i).

irradiance from exposure until flooding, the annual budget was 53.22 gC m^{-2} . A decrease of 14% was observed when irradiance was corrected with the cloud cover. Integrating thereafter the effect of the migration of microphytobenthos led to further 49% decrease in the annual carbon budget (23.49 gC m^{-2}).

The most accurate net community production budget was calculated as the difference between the above GCP budget and the CR budget taking into account the alternation of emersion and immersion and corresponded to $-78.27 \text{ gC m}^{-2} \text{yr}^{-1}$ (Table 2). The annual development of daily NCP showed only five days of autotrophy and all occurred during winter (Fig. 4).

4. Discussion

The annual production budgets proposed so far for tidal sedimentary systems along the French coast of the English

Channel were based exclusively on measurements conducted during low tide periods on sediment exposed to air. Indeed, primary production is generally assumed to be restricted to the emersion periods due to the light attenuation in such turbid environments (Colijn, 1982; Brotas and Catarino, 1995; Barranguet et al., 1998; Guarini et al., 2002). Nevertheless, respiration rates are expected to vary according to the alternation of emersion and immersion periods (Dye, 1980; Gribsholt and Kristensen, 2003; Cook et al., 2004). As discussed by Gribsholt and Kristensen (2003), the dependence of gas exchange on water coverage may be due to physical (differences in the diffusive boundary layer and the area of gas exchange) as well as biological effects (differences in metabolic activity of organisms). During daytime emersions, the metabolic activity of organisms could either be enhanced by the increase in sediment temperature, or limited by desiccation, especially at high tidal level and in well drained sand (Dye, 1980). However data required to complete the process are hard to obtain. In the present study of muddy sediment around mid-tide level respiration rates could only be determined on few occasions for both emersion and immersion throughout the year. They were always higher under immersed than under emersed conditions (up to 7 fold higher in October). These measures were in accordance with previous studies performed on temperate intertidal mudflats (Gribsholt and Kristensen, 2003; Cook et al., 2004) and might be explained by the enhanced activity of infauna during inundation. Although the data set is limited, these results clearly showed that dark CO_2 fluxes depend highly on temporal scale imposed by tides. This prevents a simple assessment of daily respiration rate from a measurement performed at a specific tidal state. The accuracy of the respiration budget at the Mont Saint-Michel Bay was therefore improved by taking into account the variation imposed by tidal conditions. However, it can be argued that these determination remain an underestimate. Indeed, respiration measurements were carried out in the dark (to exclude carbon dioxide consumption by photosynthesis) but it is widely recognised that respiration is enhanced by light (Middelburg et al., 2005). Epping and Jorgensen (1996), using the light-dark shift technique with oxygen microelectrode, reported a significant increase of oxygen respiration rate with increasing light, owing to photosynthesis process, in intertidal silty sand. Nevertheless, the significance of this in annual respiration budgets has not been evaluated.

Annual gross community production was calculated as a function of the theoretical irradiance and by ignoring microphytobenthos migratory effect (described in Section 2.4). This value was then compared to production estimates obtained so far,

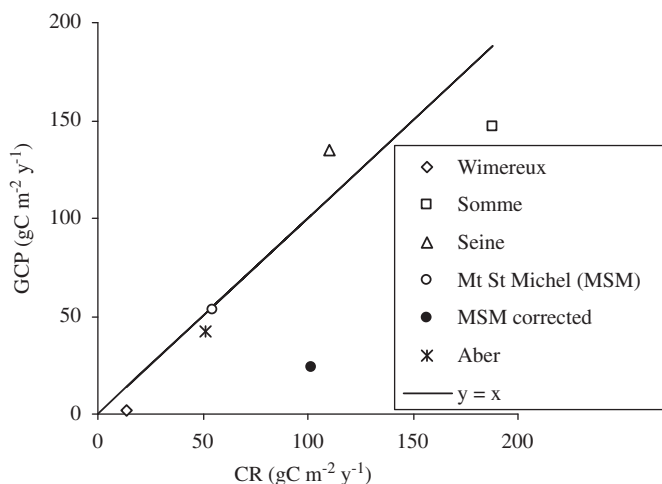


Fig. 5. Annual budget of community respiration (not taking into account the variation in respiration rate with the alternation of emersion and immersion, CR in $\text{gC m}^{-2} \text{yr}^{-1}$) and gross production (not corrected for cloud cover and the migration of microphytobenthos, GCP in $\text{gC m}^{-2} \text{yr}^{-1}$) obtained with the same method and assumptions in the Bay of Mont Saint-Michel and four other sites along the French coast of the English Channel (Somme, Wimereux, Aber, Seine, data respectively from: Migné et al., 2004; Spilmont et al., 2005; Hubas and Davoult, 2006; Spilmont et al., 2006), compared to the corrected budget in the Bay of Mont Saint-Michel.

with the same methodology and extrapolation assumptions. In Fig. 5, GCP is plotted as a function of CR for five tidal sedimentary systems along the French coast of the English Channel (Fig. 1): from East to West, at Wimereux on an exposed sandy beach (Spilmont et al., 2005), in the Bay of Somme on muddy sand (Migné et al., 2004), in the Seine estuary on sandy mud (Spilmont et al., 2006), in the Mont Saint-Michel Bay on mud (this study) and in the Roscoff Aber Bay on muddy sand (Hubas and Davoult, 2006). A strong correlation between GCP and CR was observed ($r=0.937$, $n=5$, $p < 0.01$). Benthic metabolism was the lowest in the exposed sandy beach of Wimereux ($\text{GCP}=1.4 \text{ gC m}^{-2} \text{yr}^{-1}$ and $\text{CR}=14 \text{ gC m}^{-2} \text{yr}^{-1}$) and the highest in the muddy sand of the bay of Somme ($\text{GCP}=147 \text{ gC m}^{-2} \text{yr}^{-1}$ and $\text{CR}=188 \text{ gC m}^{-2} \text{yr}^{-1}$). However, there was no trend between the sediment characteristics and the magnitude of the benthic metabolism. Benthic metabolism appeared to be particularly low at the Mont Saint-Michel Bay compared to other muddy sites. As suggested by Davoult et al. (2009), the microphytobenthic community could be characterized by a self-limitation of productivity by its own biomass. Indeed the microalgae biomass remained important throughout the year, due to a low grazing pressure low occurrence of resuspension events in this sheltered part of the Bay. This biomass would represent a limiting factor for micromigration processes within the first millimetres of the sediment.

The areas represented by data points above the 1:1 line in Fig. 5 (Seine estuary) should be autotrophic with respect to carbon, whereas those below that line should be heterotrophic. However, a net heterotrophic budget can be all the sites considered as the present investigation showed that GCP was overestimated while CR was underestimated. Indeed, the annual respiration budget proposed for the study site in the Bay of Mont Saint-Michel was almost doubled when the variation of the respiration rate with the tidal cycle was taken into account compared to the budget calculated assuming a constant rate. The decrease of annual GCP considering the cloud cover varied between study sites and was about 14% for the present study, 25% for the Bay of Somme (Migné et al., 2004) and 30% for the Aber Bay (Hubas and Davoult, 2006). When the microphytobenthos migration effect was considered for the budget calculation

Table 3

Annual budgets of community respiration (CR) and gross production (GCP) reported for European estuaries (Ems-Dollard and Colne, data respectively from: van Es, 1982; Thorntorn et al., 2002).

Station	CR in $\text{gC m}^{-2} \text{yr}^{-1}$	GCP in $\text{gC m}^{-2} \text{yr}^{-1}$
Ems-Dollard 1	141	232
Ems-Dollard 2	303	162
Ems-Dollard 3	331	202
Ems-Dollard 4	503	439
Ems-Dollard 5	353	212
Colne 2H	226	126
Colne 3H	374	191

tion that decline was even more important for the Bay of Somme (Spilmont et al., 2007) and 54% for the Bay of Mont Saint-Michel. Difference in the relative effect of this correction between sites could be explained by the difference in tidal level and therefore emersion duration per tidal cycle (5.5 h at the study site of Bay of Mont Saint-Michel and 9.5 h at the Bay of Somme).

A comparison with annual rates reported for European estuaries in the review of Gazeau et al. (2004) was also attempted. Only studies assuming that primary production was restricted to the emersion periods were considered and data were given for each station of mid or high tide level, and not influenced by waste water outlets (Table 3). These reported rates appeared globally higher than the ones obtained along the French coast of the English Channel but should be considered as overestimated. Indeed, CR was measured on water-saturated sediments only and annual GCP was obtained by multiplying hourly rates measured around noon. Nevertheless, a strong correlation between GCP and CR was still observed on the pooled data ($r=0.855$, $n=12$, $p < 0.001$). When dealing with annual rates, the magnitude of community respiration is suspected to be controlled by the amount of organic matter supply (Hopkinson and Smith, 2005). The strong correlation observed between benthic primary production and respiration could indicate that autochthonous primary production represents a substantial portion of total organic matter inputs. A net heterotrophic budget is observed at all but one station. This is consistent with the observation that estuaries generally appear to be heterotrophic (Heip et al., 1995; Borges, 2005). The high GCP reported at the sandy station 1 in the Ems-Dollard estuary might be due to an artefact in the method of measurement. GCP was calculated by monitoring oxygen concentration changes in the overlying water. As suggested by the study of Billerbeck et al. (2007), photosynthesis could have been enhanced due to a more efficient transport of solutes to the microalgae with pore water flows in the permeable sands as than on muddy sediments.

5. Conclusion

This example of annual budget calculation highlights the need to incorporate several key processes and time scales to obtain realistic estimate of GCP and determine the metabolic balance of a system, particularly in highly dynamic intertidal sediments. The proposed budget still lacks real integration between the actual respiration values of the alternate periods of submersion and air exposure. This could be improved by using fluxes measured in situ throughout whole tidal cycles. Furthermore, this work is based on assumptions that still need to be assessed: (1) respiration rates measured on incubated core are equivalent to in situ rates; (2) respiration rates measured under dark conditions are equivalent to the ones measured under light and (3) during emersion

periods, benthic primary production is always light limited by the turbidity of the overlying water. However, the heterotrophic status of intertidal sediments was confirmed.

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