Hydrobiologia (2009) 620:163–172
DOI 10.1007/s10750-008-9626-3

PRIMARY RESEARCH PAPER

Spatio-temporal variability of intertidal benthic primary production and respiration in the western part of the Mont Saint-Michel Bay (Western English Channel, France)

D. Davoult · A. Migné · A. Créach · F. Gévaert · C. Hubas · N. Spilmont · G. Boucher

Received: 31 October 2007 / Revised: 22 September 2008 / Accepted: 27 September 2008 / Published online: 21 October 2008

Abstract In situ measurements of both community metabolism (primary production and respiration) and PAM fluorometry were conducted during emersion on intertidal sediments in the Mont Saint-Michel Bay, in areas where oysters and mussels were cultivated. Results highlighted a low benthic metabolism compared to other intertidal areas previously investigated with the same methods. Comparisons between gross community primary production and relative electron transport rates confirmed this statement. More specifically, primary productivity remained very low all over the year, whereas the associated microalgal biomass was estimated to be high. We suggest that the microphytobenthic community studied was characterized by a self-limitation of its primary productivity by its own biomass, as previously shown in Marennes-Oléron Bay for example. The almost permanent high biomass would represent a limiting factor for micromigration processes within the first millimetres of the sediment. This could be explained by very low resuspension processes occurring in the western part of the bay, enhanced by the occurrence of numerous aquaculture structures that could decrease tidal currents in the benthic boundary layer.

Handling editor: N. Desroy

D. Davoult (✉) · A. Migné · C. Hubas
UPMC Univ Paris 6, UMR CNRS 7144 AD2M, Station Biologique de Roscoff, 29682 Roscoff Cedex, France
e-mail: davoult@sb-roscoff.fr

D. Davoult
CNRS, UMR 7144 AD2M, Station Biologique de Roscoff, 29682 Roscoff Cedex, France

A. Migné · G. Boucher
Muséum National d'Histoire Naturelle, UMR CNRS 5178 BOME, CP 53, 57 rue Cuvier, 75231 Paris Cedex 5, France

A. Créach
Université des Sciences et Technologies de Lille 1, UMR CNRS 8016, GEPV, Bat SN2, 59655 Villeneuve d'Ascq Cedex, France

F. Gévaert · N. Spilmont
Université des Sciences et Technologies de Lille I, UMR CNRS 8187 LOG, Station Marine de Wimereux, BP 80, 62930 Wimereux, France

C. Hubas · N. Spilmont
Université du Littoral Côte d'Opale, UMR CNRS 8187 LOG, Maison de la Recherche en Environnement Naturel, 62930 Wimereux, France

Keywords In situ measurements · Microphytobenthos · Intertidal community metabolism · Benthic primary production · Community respiration · PAM fluorometry

Introduction

Microphytobenthos are an important component of estuarine and shallow bay primary production since they may provide up to half of the total primary production in some coastal ecosystems (Perissinoto et al., 2002; Montani et al., 2003). Microphytobenthic primary production is obviously controlled by light availability (Parsons et al., 1984) and temperature (Blanchard et al., 1996; Hancke & Glud, 2004), but some other factors might affect biomass and production, such as sediment dynamics (de Jonge & van Beusekom, 1995; Perkins et al., 2003), nutrient availability (Thornton et al., 2002), grazing (Riera et al., 1996; Pinckney et al., 2003) or bioturbation (Orvain et al., 2006). Because of resuspension processes, microphytobenthos is also considered as a substantial food source for benthic suspension-feeders (Riera & Richard, 1996; Riera, 1998) located in or around mudflats.

In the Mont Saint-Michel Bay, large populations of wild suspension-feeders are encountered, such as bivalves (Veneridae) and Gastropods (*Crepidula fornicata*). The latter has been estimated to be locally the main standing stock of suspension-feeders (≈150,000 tons, Blanchard & Ehrold, 1999) and its population is considered to increase continuously. The Bay is also characterized by an important aquaculture activity, concerning oyster (*Crassostrea gigas* and *Ostrea edulis*) and mussel (*Mytilus edulis*) farming (≈8,900 tons for *C. gigas*, 3,000 tons for *O. edulis* and 11,000 tons for *M. edulis*; Gérard, 2003; Mazurié & Bouget, 2003). Little is known about the trophic capacity of the Bay, and neither phytoplanktonic nor microphytobenthic production have been accurately evaluated. Only Méziane et al. (1997) studied trophic food web in salt marshes of the Bay.

As the Bay is subjected to an important tidal range (up to 14 m in its western part), about half of its area is considered to be intertidal (240 out of 500 km^2). It thus appears important to understand the characteristics of the intertidal community metabolism, mainly primary production, both in terms of temporal (i.e. seasonal) and spatial variability, since a strong sedimentary gradient takes place in the Bay from east to west (Thorin et al., 2001). Cayocca et al. (2008) measured higher resuspension processes in the eastern part of the bay, mainly driven by offshore waves; On the contrary, the western part, protected from waves by the sheltered effect of the western cape (Peak of Grouin, Fig. 1), is mainly driven by tidal dynamics and is characterized by lower resuspension processes, during spring tides and strong mud deposit processes.

The aim of the present study was therefore to estimate both the temporal and the spatial variability of the benthic community primary production and respiration in the western part of the bay where intensive aquaculture takes place. Both in situ carbon dioxide flux measurements at the air-sediment interface and measurements of photosynthesis from PAM (Pulse Amplitude Modulation) fluorometry were carried out in order to understand the benthic photosynthesis efficiency and to compare these

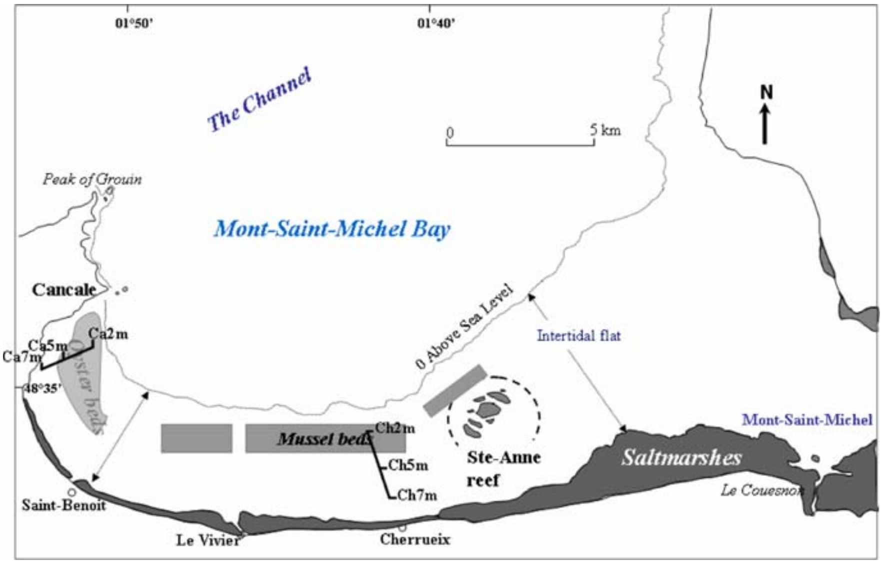

Fig. 1 Location of the two transects (Cancale and Cherrueix) and the studied stations (Ca7m, Ca5m, Ca2m, Ch7m, Ch5m and Ch2m). Mussel beds are French system with wooden pools harbouring cultivated *Mytilus edulis*. Oyster beds are horizontal mesh bags tied to metal trestles arranged in parallel rows

results to those obtained with the same methods in various unexploited areas with different sediment characteristics located along the French coast of the English Channel (Migné et al., 2004, 2007; Spilmont et al., 2005; Spilmont et al., 2006).

Material and methods

Study site

The Mont Saint-Michel Bay covers approximately 500 km^2, of which 240 km^2 constitutes the intertidal area. It is characterized by muddy sediments in its western part and by sandy sediments in its eastern part. Two transects were investigated in the western part of the bay (Fig. 1), the area more sheltered from the swell, where currents are weak and gyrating (Salomon & Breton, 2000), characterized by high sedimentation processes (Thorin et al., 2001; Cayocca et al., 2008). The first transect was located near Cancale, in the muddiest part of the Bay (Ca: about 65–80% mud from offshore to near the shoreline; Bonnot & Olivier, unpubl. data), where most of the oyster farming took place. The second transect was located in the mid part of the Bay, near Cherrueix, in sand (Ch: 4–7% mud; Bonnot & Olivier, unpubl. data), where most of the mussel farming took place. Three stations were defined on each transect, the first one located 7 m above Chart Datum (C.D.), the second one 5 m above C.D. and the third one 2 m above C.D. (Fig. 1). Stations were then, respectively, named Ca7m, Ca5m, Ca2m, Ch7m, Ch5m and Ch2m.

Carbon dioxide flux measurements

Intertidal benthic community primary production and respiration during emersion were assessed through in situ CO_2 exchange measurements in light (community net primary production CNP) and dark (community respiration CR) benthic chambers by infrared gas analysis, 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 CO_2 analysis. Gas exchange was monitored for 10–30 min, depending on the 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 (mgC m^{-2} h^{-1}).

Gross primary production (GPP) was calculated from CNP and CR as:

$$GPP = CNP + CR. \quad (1)$$

Three benthic chambers (0.07 m^2, about 9 l in volume, equipped with Li-Cor Li 800 Infra-red analyser) were used simultaneously, positioned 10 m apart at each station. During light incubations, photosynthetically available radiation (400–700 nm) was measured at the sediment surface using an SA-190 quantum sensor.

The study sites were investigated at the four seasons (April and October 2003; February and August 2004). Measurements were performed at the three stations of each transect when water levels were sufficiently low to allow chamber deployment (April and October 2003). In February and August 2004, measurements were performed only at the 7- and 5-m sites. Additional series of measurements (i.e. three successive light and dark incubations using one benthic chamber) were also performed at Ca5m at five different periods of the year, in 2004, 2005 and 2006, to better determine the seasonal variations of the metabolism.

In order to estimate the primary productivity (or assimilation number, ratio between gross primary production and chlorophyll *a* (Chl.*a*) sediment content, expressed in mgC mgChl.a^{-1} h^{-1}), three sediment samples (1.9 cm^2, 10 mm depth) were randomly taken within each chamber at the end of the experiments for analysis of Chl.*a* according to the method of Lorenzen (1967).

Fluorescence measurements

Fluorescence was measured in situ with a Diving PAM (Heinz Walz, Effeltrich, Germany) under natural ambient light at Ca7m in April and October 2003, August 2004 and June 2005. At the beginning of the experiments, three home-made supports were placed randomly on a quite plane surface of sediment. Each of them carried an axis where it was possible to insert and place the tip of the optic fibre of the fluorometer at a constant distance (2 mm) of the biofilm with a 60° angle to avoid possible shading. This system allowed measuring periodically the effective quantum yield of the photosystem II (Φ_{PSII}), at the three same spots on the sediment. Φ_{PSII} was calculated according to Genty et al. (1989):

$$\Phi_{PSII} = (F'_m - F_t)/F'_m \quad (2)$$

where F_t is the fluorescence steady-state level under ambient light and F'_m, the maximal level of fluorescence measured during a saturating pulse (0.8 s).

Φ_{PSII} can be used to calculate the relative electron transport rate (rETR) as:

$$rETR = \Phi_{PSII} PAR\ 0.5 \quad (3)$$

where PAR (in µmol photons m^{-2} s^{-1}) is the photosynthetically available radiation (400–700 nm) measured at the sediment surface using an SA-190 quantum sensor connected to a data-logger. The term "relative" ETR is used here because the Chl.*a*-specific absorption coefficient, required to calculate the "true" ETR, could not be obtained in the sediment biofilm.

Changes in rETR were followed as a function of the variation in ambient light during the daylight exposure (from dawn to saturating light or from saturating light to dusk) to establish rETR/irradiance curves. The relationship was described by the equation of Webb et al. (1974):

$$rETR = rETR_{max}[1 - \exp(-I/I_k)] \quad (4)$$

where $rETR_{max}$ is the maximal rETR, I the irradiance (µmol photons m^{-2} s^{-1}) and I_k is the saturation onset parameter. The simplex estimation method was used to determine the light-curve parameters $rETR_{max}$ and I_k (Systat 10 software, Systat Software Inc., Richmond, CA, USA).

Data analysis

Comparisons were made between Cancale and Cherrueix using mean values of gross primary production, community respiration, chlorophyll *a* content and primary productivity. Paired data ($n = 10$) obtained at both sites for each given season and each given tidal level were compared using a non-parametric Wilcoxon test (T statistics, Scherrer, 1984).

The rETR was compared to gross primary production with the Pearson correlation coefficient; slopes of linear regressions were then compared using t-statistics.

Results

Gross primary production and community respiration

GPP showed typical seasonal variations at Ca7m, Ca5m and Ch7m, whereas Ch5m exhibited high values in spring and autumn and low values in winter and summer (Fig. 2a). The comparison of values obtained on the two transects at the same level revealed that Cancale was more productive than Cherrueix ($T = 3$, $P < 0.01$).

CR exhibited a marked seasonal trend at Cancale, with maximal values measured in spring and summer. This trend was more pronounced for CR than for GPP at Ca7m and Ca5m, whereas it was not marked at Cherrueix (Fig. 2b). CR was higher at Cancale than at Cherrueix at each tidal level ($T = 6$, $P < 0.05$).

To ease the detection of temporal variations, the sampling dates of the GPP and CR measurements made at Ca5m were converted to Julian days within one Julian year (Fig. 3). GPP did not exhibit any seasonal trend (Fig. 3a), with the lowest values in January 2006 and June 2005 and the highest ones in June and November 2004. On the contrary, seasonal trend of CR was very explicit (Fig. 3b), with the lowest value at the end of November (0.54 mgC m^{-2} h^{-1}) and the highest one (12 mgC m^{-2} h^{-1}) in June.

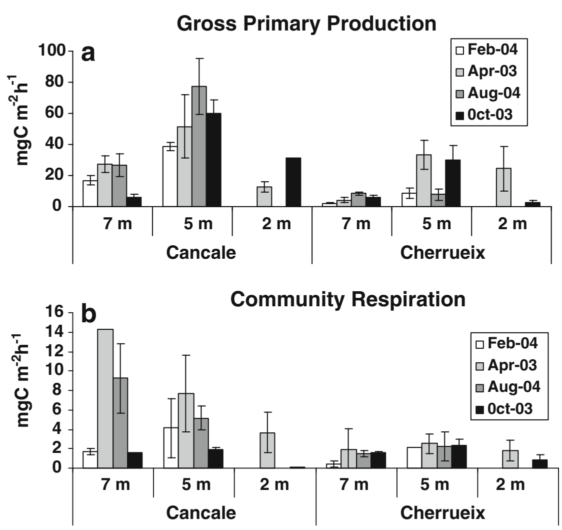

Fig. 2 Seasonal variations (±standard deviation) of **a** gross primary production (mgC m^{-2} h^{-1}) and **b** respiration (mgC m^{-2} h^{-1}) at the three tidal levels of each studied area

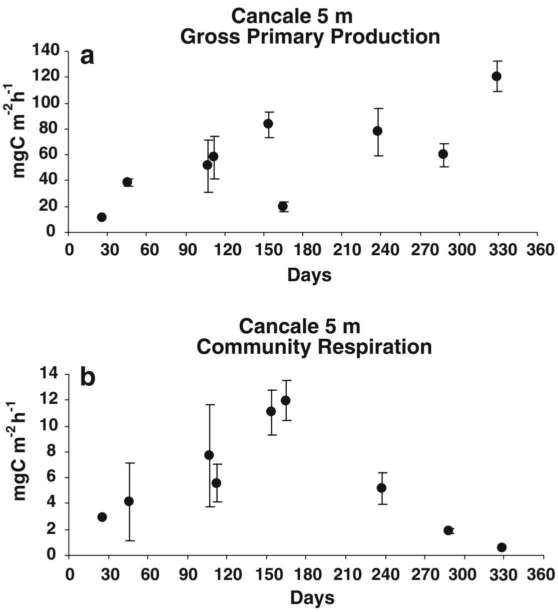

Fig. 3 Temporal variations (±standard deviation) of **a** gross primary production (mgC m^{-2} h^{-1}) and **b** respiration (mgC m^{-2} h^{-1}) measured at Ca5m

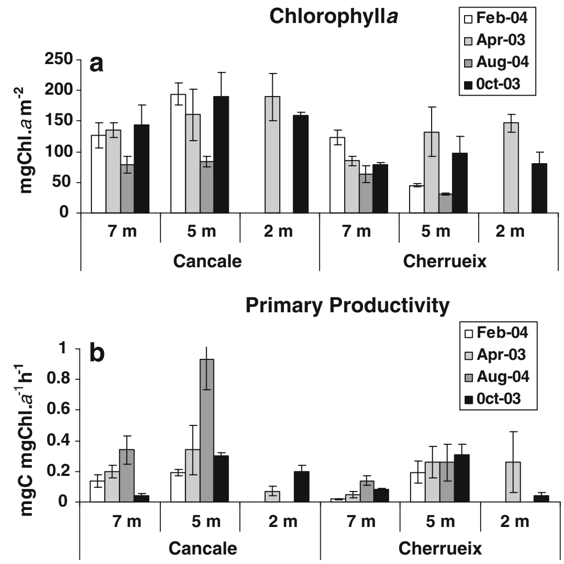

Fig. 4 Seasonal variations (±standard deviation) of **a** Chl.*a* content (mgChl.*a* m^{-2}) and **b** primary productivity (mgC mgChl.a^{-1} h^{-1}) at the three tidal levels of the studied areas

Chlorophyll *a* and primary productivity

Chl.*a* content in the first centimetre of sediment remained high at Cancale all along the year, always between 100 and 200 mgChl.*a* m^{-2}, except in August (Fig. 4a). Regarding the tidal level, Chl.*a* content was always lower at Cherrueix ($T = 0$, $P < 0.01$), between 50 and 150 mgChl.*a* m^{-2}. No consistent patterns could be observed among sampling dates.

The primary productivity (or assimilation number), expressed in mgC mgChl.a^{-1} h^{-1}, was calculated at each station for each date (Fig. 4b). With the exception of Ca5m in August (0.93 mgC mgChl.a^{-1} h^{-1}), primary productivity remained between 0.02 and 0.34 mgC mgChl.a^{-1} h^{-1}. A seasonal trend appeared at Ca7m, Ca5m and Ch7m. There was no significant difference between the two sites ($T = 14$, $P > 0.05$).

In situ fluorescence

The maximum relative electron transport rate ($rETR_{max}$) and the onset saturation parameter (I_k) were calculated from rETR/irradiance curves established during emersion at station Ca7m in April 2003, October 2003, August 2004 and June 2005; they varied according to the season and followed similar patterns (Fig. 5), with a maximal value in August.

GPP calculated from carbon dioxide measurements was regressed against rETR values (mean rETR of the triplicates) obtained simultaneously with the Diving PAM (Fig. 6). The correlation was highly significant ($r = 0.543$, $n = 69$, $P < 0.001$) even if some differences clearly appeared between seasons.

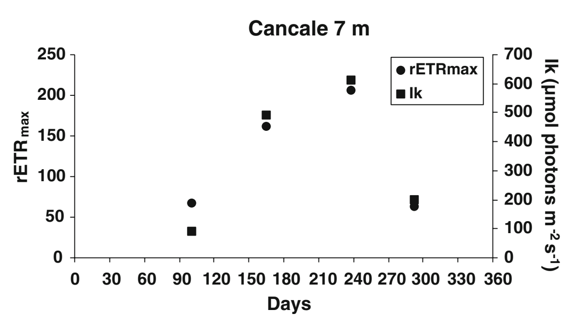

Fig. 5 Temporal variations of maximum relative electron transport rate ($rETR_{max}$) and onset saturation parameter (I_k in µmol photons m^{-2} s^{-1}) measured in situ by PAM fluorometry at Ca7m

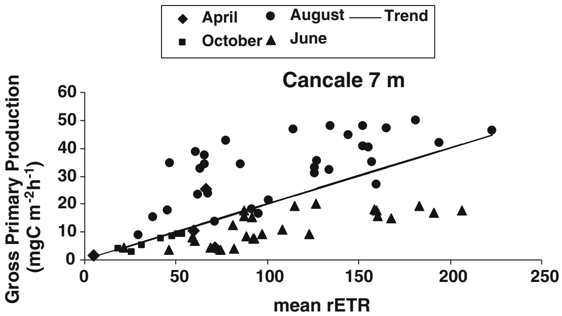

Fig. 6 Relationship between gross primary production (mgC m^{-2} h^{-1}) and relative electron transport rate (mean rETR) measured in situ at Ca7m

Discussion

Seasonal variations of intertidal benthic community metabolism

Community respiration was the only metabolic process to show a clear seasonal trend over the four sampling events at most of the stations; this was confirmed by additional measurements at higher temporal resolution made at Ca5m (Fig. 3b). Benthic respiration is known to follow seasonal variations because it is mainly controlled by temperature (Migné et al., 2004; Hubas et al., 2006).On the contrary, no consistent patterns were observed among sampling dates for gross primary production (Fig. 3a), whereas a very high level of Chl.*a* content was observed all along the year (Fig. 4a). In similar areas such as the Bay of Somme, Chl.*a* content tended to exhibit seasonal variations and primary production was even correlated with it (Migné et al., 2004). In the present study, the lowest values of Chl.*a* content were measured in August; this could be due both to increasing grazing, photoinhibition and thermoinhibition. However, Thorin et al. (2001) highlighted the relative low density of macrozoobenthos in the western part of the bay despite favourable conditions (high sedimentation processes, relatively high organic content in the sediment); thus, grazing and bioturbation might not be major limiting factors in this part of the bay. Furthermore, some endogenous variations such as senescence could also occur and then decrease the Chl.*a* content in microphytobenthos (Méléder et al., 2005). Even if benthic primary production can be mainly controlled both by irradiance and temperature (Blanchard & Guarini, 1998; Migné et al., 2004; Morelissen & Harley, 2007), other factors might overshadow the seasonal variations, such as reduced input of organic waste (Peletier, 1996) or periods of increased rainfall (Montani et al., 2003).

Nevertheless, PAM fluorometry measurements showed seasonal variations (Fig. 5). The depth detected by this technique is limited to the upper layers of the sediment and varies from 100 to 270 µm depending on the granulometry and the organic content of the sediment (Consalvey et al., 2005). Fluorescence parameters ($rETR_{max}$ and I_k) show that the summer communities are the most photosynthetically efficient and that microalgae of the upper layers were acclimated to high irradiance. It could be due to a change of the taxonomic composition of algal communities in summer with dominant photophilic species or to a photoacclimation of microalgae to the increasing light. Benthic diatoms are indeed able to cope with high light by inducing high levels of non-photochemical quenching linked to the development of the xanthophyll cycle (Serôdio et al., 2005; Dimier et al., 2007; van Leewe et al., 2008).

Comparisons with other tidal flats along the French coast of the English Channel

Other studies have previously been carried out with the same methods along the French coast of the English Channel. Figure 7 compares values of productivity obtained with the same benthic chambers (and Chl.*a* also being sampled over 10 mm depth) at different seasons at five sites: respectively, from East to West, at Wimereux on an exposed sandy beach (Spilmont et al., 2005), in the Bay of Somme on a muddy sand (Migné et al., 2004), in the Bay of Seine on sandy mud (Spilmont et al., 2006) and at Cancale and Cherrueix in the Mont Saint-Michel Bay (this study). Ca7m and Ch7m were chosen because these stations were approximately located at the same tidal level as the stations of the other sites.

Primary productivity estimated at Cancale and Cherrueix was among the lowest values, with the exception of several values obtained in the Bay of Seine when Chl.*a* concentrations remained higher than 100 mg m^{-2} (up to 277 mgChl.*a* m^{-2}, Spilmont et al., 2006). Moreover, in the Bay of Seine, values of primary productivity remained between 0.07 and 0.52 mgC mgChl.a^{-1} h^{-1} when Chl.*a* concentration

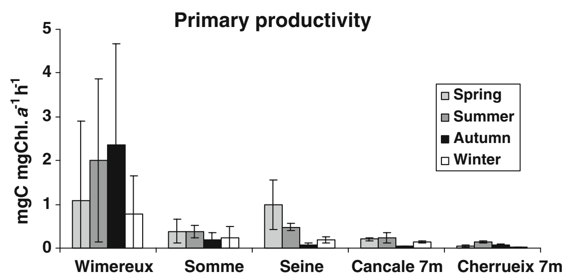

Fig. 7 Seasonal variations of primary productivity (mgC mgChl.a^{-1} h^{-1}) estimated from in situ measurements in five intertidal locations along the English Channel

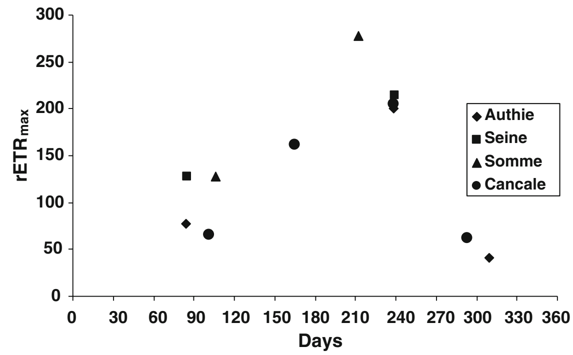

Fig. 8 Comparison of temporal variations of maximum relative electron transport rates ($rETR_{max}$) obtained from in situ measurements in four intertidal locations along the English Channel

remained over 100 mg m^{-2}, whatever the season, whereas they increased up to 0.99 mgC mgChl.a^{-1} h^{-1} for Chl.*a* concentration below 100 mg m^{-2}, for example in spring, during or between high water discharge of the Seine river (Spilmont et al., 2006).

These observations are in accordance with those of Blanchard et al. (2001) who considered that the benthic microalgal biomass increases and follows a logistic-type growth curve, converging towards a maximum value at which primary productivity tends to zero, when grazing and/or resuspension are low. Regarding very high values of microalgal biomass measured both in the Bay of Seine and in the present study, close to the "field maximum" observed in Marennes-Oléron Bay (Blanchard et al., 2001), it can be assumed that the primary production could be limited most of the time in the Mont Saint-Michel Bay by the very high benthic microalgal biomass. Limitation of resuspension in Cancale and Cherrueix could be due to the combination of general conditions of this very sheltered western part of the bay, as already pointed out by Thorin et al. (2001) and Cayocca et al. (2008), and of the occurrence of numerous aquaculture structures that could decrease tidal currents near the bottom and then increase sedimentation processes (mud accumulation between oyster farming structures—that is about one metre high—has been observed to be higher than farming structures height). Moreover, as the western part of the bay is protected from offshore waves, sediment processes are mainly driven by tidal dynamics and resuspension remains much lower than in the eastern part of the bay (Cayocca et al., 2008).

Fluorescence measurements were also compared with results obtained on other mud flats along the French coast of the English Channel. Figure 8 compares values of $rETR_{max}$ obtained with the same diving PAM at different periods of the year at four sites: in the Bays of Somme, Authie and Seine (data from Migné et al., 2007) and at Cancale in the Mont Saint-Michel Bay (this study). The $rETR_{max}$ values showed a very similar trend at these four sites. Migné et al. (2007) showed that a highly significant relationship between CO_2 fluxes and rETR could be calculated by mixing data measured at several sites (Bay of Somme, Bay of Authie and Bay of Seine) and several seasons. A comparison with our present data showed that the range of rETR values was the same as in the other sites, but the GPP was lower. The relationship between CO_2 fluxes and rETR then presented a significantly lower slope ($t = 67.3$, $P < 0.001$) in the Mont Saint-Michel Bay (slope = 0.152) than in other locations (slope = 0.675) (Fig. 9).

However, the rETR is probably overestimated (particularly at high light): first by using PAR measured at the surface of the sediment, second because the apparent Φ_{PSII} as measured at the sediment surface is generally higher than the inherent photosynthetic efficiency of algal cells in the assemblage, due to the influence of fluorescence emitted from deeper sediment layers (Consalvey et al., 2005). The depth of light penetration into the sediment and the overestimation of the calculated Φ_{PSII} with respect to inherent Φ_{PSII} are variable as a function of the sediment characteristics and the density of the biofilm: higher self-shading and organic matter such as EPS contents (Forster & Kromkamp, 2004). A more severe overestimation of rETR measured within

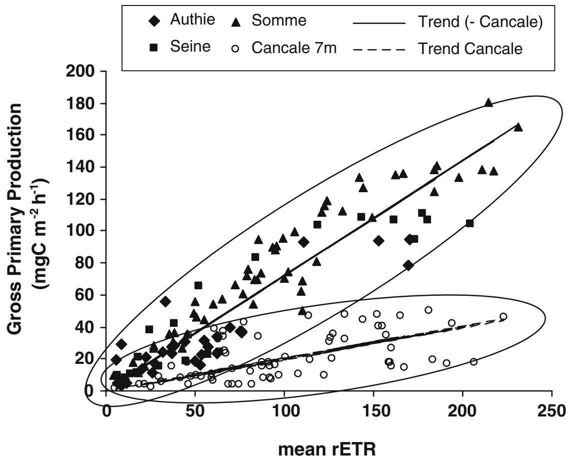

Fig. 9 Comparison of the relationships between gross primary production (mgC m^{-2} h^{-1}) and relative electron transport rates (mean rETR) obtained from in situ measurements at Ca7m and in three other intertidal locations along the English Channel

dense biofilms in Cancale could lead to a lower trend between gross primary production and rETR compared to the other sites.

Values of rETR similar to those obtained in various sites reflected the photosynthesis of cells living at the surface of the sediment but did not take into account the activity of cells located within the first millimetres. Microphytobenthos has been shown to exhibit micromigration within the uppermost layer of the sediment (Kromkamp et al., 1998), allowing a rapid turnover of cells at the sediment surface, and thus optimizing the productivity of the biofilm (Consalvey et al., 2004). It can be hypothesized that high microalgal biomass resulted in the decreasing or even the absence of micromigration processes, which led in the present study to production limitation and to a lower trend between gross primary production and rETR. Thus, our results showed that, if PAM fluorometry gives a good estimation of the photosynthetic capacity of the microphytobenthic community, direct measurements of the primary productivity are needed to understand the actual trophic capacity induced by the microphytobenthic production.

Conclusion

Estimations of benthic photosynthetic activity and metabolism obtained in the present study, as well as the comparison with similar measurements conducted in different bays and estuaries, suggested that local productivity seemed to be limited by microalgal biomass accumulation. This constitutes a confirmation that high Chl.*a* biomass does not necessarily reflect a high primary production. It is also consistent with results obtained by Riera (2007) with stable isotopes and Méziane et al. (1997) with lipid markers who pointed out that microphytobenthos is probably not the main food source for suspension-feeders of the Mont Saint-Michel Bay.

Acknowledgements This work was supported by the French National Programme on Coastal Ecology (PNEC), chantier Baie du Mont Saint Michel. We thank “la Maison de la Baie” (not “de l'abbé”) for warm hospitality, and Hervé Rybarczyk and Renaud Michel for field assistance.

References

Blanchard, M. & A. Ehrold, 1999. Cartographie et évaluation du stock de crépidules (*Crepidula fornicata*) en baie du Mont Saint Michel. Haliotis 28: 11–20.

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

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

Blanchard, G. F., J.-M. Guarini, F. Orvain & P. G. Sauriau, 2001. Dynamic behaviour of benthic microalgal biomass in intertidal mudflats. Journal of Experimental Marine Biology and Ecology 264: 85–100.

Cayocca, F., P. Bassoullet, P. Le Hir, H. Jestin & P. Cann, 2008. Chapter 29. Sediment processes in a shellfish farming environment, Mont Saint Michel Bay, France. In Kusuda, T., H. Yamanishi, J. Spearman & J. Z. Gailani (eds), Sediment and Ecohydraulics: INTERCOH 2005. Elsevier, Amsterdam: 431–446.

Consalvey, M., B. Jesus, R. G. Perkins, V. Brotas, G. J. C. Underwood & D. M. Paterson, 2004. Monitoring migration and measuring biomass in benthic biofilms: the effects of dark/far-red adaptation and vertical migration on fluorescence measurements. Photosynthesis Research 81: 91–101.

Consalvey, M., R. G. Perkins, D. M. Paterson & G. J. C. Underwood, 2005. PAM fluorescence: a beginners guide for benthic diatomists. Diatom Research 20: 1–22.

de Jonge, V. N. & J. J. E. van Beusekom, 1995. Wind- and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. Limnology and Oceanography 40: 766–778.

Dimier, C., F. Corato, F. Tramontano & C. Brunet, 2007. Photoprotection and xanthophyll-cycle activity in three marine diatoms. Journal of Phycology 43: 937–947.

Forster, R. M. & J. C. Kromkamp, 2004. Modelling the effects of chlorophyll fluorescence from subsurface layers on photosynthetic efficiency measurements in microphytobenthic algae. Marine Ecology Progress series 284: 9–22.

Genty, B., J.-M. Briantais & N. R. Baker, 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochimica et Biophysica Acta 990: 87–92.

Gérard, D., 2003. Estimation du stock de moules sur bouchots dans la baie du Mont Saint-Michel. Rapport de Stage IUT informatique et statistiques Vannes. Rapport de laboratoire Ifremer DRV/RA/LCB/2002-001: 36 pp.

Hancke, K. & R. N. Glud, 2004. Temperature effects on respiration and photosynthesis in three diatom-dominated benthic communities. Aquatic Microbial Ecology 37: 265–281.

Hubas, C., D. Davoult, T. Cariou & L. F. Artigas, 2006. Factors controlling benthic metabolism during low tide in an intertidal bay along a granulometric gradient (Roscoff Aber Bay, Western English Channel, France). Marine Ecology Progress Series 316: 53–68.

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

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

Mazurié, J. & J. F. Bouget, 2003. Estimation du stock d'huîtres creuses *Crassostrea gigas*, en élevage en Baie de Cancale en octobre 2002. Rapport de laboratoire Ifremer: 29 pp.

Méléder, V., L. Barillé, Y. Rincé, M. Morançais, P. Rosa & P. Gaudin, 2005. Spatio-temporal changes in microphytobenthos structure analysed by pigment composition in a macrotidal flat (Bourgneuf Bay, France). Marine Ecology Progress Series 297: 83–99.

Méziane, T., L. Bodineau, C. Retière & G. Thoumelin, 1997. The use of lipid markers to define sources of organic matter in sediment and food web of the intertidal salt-marsh-flat ecosystem of Mont-Saint-Michel Bay, France. Journal of Sea Research 38: 47–58.

Migné, A., D. Davoult, N. Spilmont, D. Menu, G. Boucher, J.-P. Gattuso & H. Rybarczyk, 2002. A closed-chamber CO_2 flux method for estimating primary production and respiration in emersed conditions. Marine Biology 140: 865–869.

Migné, A., N. Spilmont & D. Davoult, 2004. In situ measurements of benthic primary production during emersion: seasonal variations and annual production in the Bay of Somme (eastern English Channel, France). Continental Shelf Research 24: 1437–1449.

Migné, A., F. Gevaert, A. Creach, N. Spilmont, E. Chevalier & D. Davoult, 2007. Photosynthetic activity of intertidal microphytobenthic communities during emersion: in situ measurements of chlorophyll fluorescence (PAM) and CO_2-flux (IRGA). Journal of Phycology 43: 864–873.

Montani, S., P. Magni & N. Abe, 2003. Seasonal and interannual patterns of intertidal microphytobenthos in combination with laboratory and areal production estimates. Marine Ecology Progress Series 249: 79–91.

Morelissen, B. & C. D. G. Harley, 2007. The effect of temperature on producers, consumers, and plant-herbivore interactions in an intertidal community. Journal of Experimental Marine Biology and Ecology 348: 162–173.

Orvain, F., P.-G. Sauriau, C. Bacher & M. Prineau, 2006. The influence of sediment cohesiveness on biotirbation effects due to *Hydrobia ulvae* on the initial erosion of intertidal sediments: a study combining flume and model approaches. Journal of Sea Research 55: 54–73.

Parsons, T. R., M. Takahashi & B. Hargrave, 1984. Biological Oceanographic Processes, 3rd edn. Pergamon Press Ltd, Oxford: 330 pp.

Peletier, H., 1996. Long-term changes in intertidal estuarine diatom assemblages related to reduced input of organic waste. Marine Ecology Progress Series 137: 265–271.

Perissinoto, R., C. Nozais & I. Kibirige, 2002. Spatio-temporal dynamics of phytoplankton and microphytobenthos in a South African temporarily-open estuary. Estuarine Coastal and Shelf Science 55: 47–58.

Perkins, R. G., C. Honeywill, M. Consalvey, H. A. Austin, T. J. Tolhurst & D. M. Paterson, 2003. Changes in microphytobenthic chlorophyll *a* and EPS resulting from sediment compaction due to de-watering: opposing patterns in concentration and content. Continental Shelf Research 23: 575–586.

Pinckney, J. L., K. R. Carman, S. E. Lumsden & S. N. Hymel, 2003. Microalgal-meiofaunal trophic relationships in muddy intertidal estuarine sediments. Aquatic Microbial Ecology 31: 99–108.

Riera, P., 1998. $\delta^{15}N$ of organic matter sources and benthic invertebrates along an estuarine gradient in Marennes-Oléron Bay (France): implications for the study of the trophic structure. Marine Ecology Progress Series 166: 143–150.

Riera, P., 2007. Trophic subsidies of *Crassostrea gigas*, *Mytilus edulis* and *Crepidula fornicata* in the Bay of Mont Saint Michel (France): a $\delta^{13}C$ and $\delta^{15}N$ investigation. Estuarine, Coastal and Shelf Science 72: 33–41.

Riera, P. & P. Richard, 1996. Isotopic determination of food sources of *Crassostrea gigas* along a trophic gradient in the estuarine bay of Marennes-Oléron. Estuarine, Coastal and Shelf Science 42: 347–360.

Riera, P., P. Richard, A. Grémare & G. Blanchard, 1996. Food source of intertidal nematodes in the Bay of Marennes-Oléron (France), as determined by dual stable isotopes analysis. Marine Ecology Progress Series 142: 303–309.

Salomon, J.-C. & M. Breton, 2000. Mathematical model of Mont Saint-Michel Bay. In Lefeuvre, J.-C. & E. Feunteun (eds), European Salt Marshes Modelling. European Commission, Work program PL 970655, Final Report, Rennes: 475–530.

Serôdio, J., S. Vieira, S. Cruz & F. Barroso, 2005. Short-term variability in the photosynthetic activity of microphytobenthos as detected by measuring rapid light curves using variable fluorescence. Marine Biology 146: 903–914.

Spilmont, N., A. Migné, A. Lefebvre, L. F. Artigas, M. Rauch & D. Davoult, 2005. Temporal variability of intertidal benthic metabolism under emersed conditions in an exposed sandy beach (Wimereux, eastern English Channel, France). Journal of Sea Research 53: 161–167.

Spilmont, N., D. Davoult & A. Migné, 2006. Benthic primary production during emersion: in situ measurements and potential primary production in the Seine Estuary (English Channel, France). Marine Pollution Bulletin 53: 49–55.

Thorin, S., A. Radureau, E. Feunteun & J.-C. Lefeuvre, 2001. Preliminary results on a high east-west gradient in the macrozoobenthic community structure of the macrotidal Mont Saint-Michel bay. Continental Shelf Research 21: 2167–2183.

Thornton, D. C. O., L. F. Dong, J. C. Underwood & D. B. Nedwell, 2002. Factors affecting microphytobenthic biomass, species composition and production in the Colne Estuary (UK). Aquatic Microbial Ecology 27: 285–300.

Van Leewe, M. A., V. Brotas, M. Consalvey, M. R. Forster, D. Gillespie, B. Jesus, J. Roggeveld & W. W. C. Gieskes, 2008. Photoacclimation in microphytobenthos and the role of the xanthophyll pigments. European Journal of Phycology 43: 123–132.

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