

Freshwater seepages and ephemeral macroalgae proliferation in an intertidal bay: II. Effect on benthic biomass and metabolism

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ABSTRACT

Intertidal soft-sediments biomass and metabolism are naturally heterogeneous in time and space at different scales. Particular perturbations such as freshwater seepages and seasonal proliferation of ephemeral macroalgae can intermittently and/or locally create additional variability in these systems. Since the impacts of such environmental stresses on natural processes are not well understood, the hypothesis that they would affect the functioning of the benthic system was tested. An intertidal bay whose structure and functioning has been previously described and where a carbon budget has been calculated, was chosen. The results showed that the metabolism of the intertidal sediments was greatly impacted by the above perturbations. Freshwater seepage increased meiofauna and microalgae biomasses and enhanced the total benthic metabolism (increasing community respiration and gross primary production until 4 and 2 fold respectively) without altering its seasonal trend. Ephemeral macroalgae proliferation had a more important effect on the total benthic metabolism, increasing community respiration and gross primary production 8 and 12 fold respectively and leading to a change in the seasonal trend.

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1. Introduction

Intertidal sediments, which are naturally characterised by strong environmental gradients, play an important role in the production and remineralisation of organic matter (Raffaelli and Hawkins, 1999). Benthic community metabolism measurements have mostly been used to quantify these processes and to investigate their spatial and temporal heterogeneity (see for example van Es, 1982 and references therein). Large spatial variability linked to physico-chemical gradients and seasonal cycles have been described and have been taken into account for budget calculations (Migné et al., 2009 and references therein). However, less attention has been given to patterns at smaller spatial scale that may create some heterogeneity in benthic community metabolism. For instance, freshwater seepages have the potential to create estuarine conditions near the point of discharge, thereby largely altering local benthic features in terms of habitat, community structure and productivity (Miller and Ullman, 2004). Another widespread phenomenon that alters the benthic community structure and functioning of intertidal sediments is the seasonal

proliferation and accumulation of ephemeral macroalgae to the shore (Havens et al., 2001).

The small tidal Roscoff Aber bay (Western English Channel, France), in which structure and functioning has been described along the tidal gradient (Hubas et al., 2006), offered the opportunity to study both these local perturbations simultaneously. Ouisse et al. (2011) showed a clear effect of freshwater seepage and a more diffusive effect of ephemeral macroalgae proliferation both on benthic community composition (meio- and macrofauna) and on the food web. The hypothesis, that these perturbations could also alter benthic biomass and community metabolism, remained to be tested. The present paper therefore aimed to assess and compare the effects of freshwater seepages and proliferation of ephemeral macroalgae on the microalgae, meio- and macrofauna biomasses and on the total benthic metabolism measured during low tide using benthic chambers.

2. Materials and methods

2.1. Study sites

The Roscoff Aber bay (about 1 km long and 2 km wide) is entirely located above mid-tide level. The bay is subjected to a low but constant river water input in its southern part and includes various

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types of sediment from muddy to sandy. Freshwater seepages occur near the river entrance in a zone characterised by very-fine sands. The bay is regularly affected by an ephemeral proliferation of *Enteromorpha* spp. (genus morphologically defined) forming large macroalgal mats on sand in its eastern part. Two sites were surveyed inside that bay: the first one located in the larger freshwater seepage (the Freshwater site), the second one located in the area submitted to the ephemeral proliferation of *Enteromorpha* spp. (the *Enteromorpha* site). For each site, an impacted and a control point were sampled. The impacted points (FW and E here after) were into the freshwater seepage (discriminated by the absence of *Arenicola marina* defaecation casts) and the macroalgal mat respectively. The control points (C_{FW} and C_E here after) were selected less than 10 m away, in areas owing the same sediment features than the impacted points. At each period of sampling (7 periods from February to December 2007), salinity was measured in interstitial water (3 replicates, 3 cm depth) on the two points of freshwater site and macroalgal mat was sampled (3 replicates, 0.1 m²) from the *Enteromorpha* site to estimate its biomass as dry weight.

2.2. Macro- and meiofauna biomass

Macro- and meiofauna were sampled at low tide on the two points of each site from February to December 2007 (7 sampling periods). Three sediment quadrats (0.1 m², 10 cm depth) were sampled for macrofauna (>2 mm) analysis. Organisms were identified at the species level and their biomass expressed in ash free dry weight (assessed by the combustion of the dried organisms in muffle furnace at 520 °C for 6 h). Three sediment cores (2.9 cm², 2 cm depth) were sampled for meiofauna analyses. Meiofauna was extracted from the sediment using colloidal silica soil Ludox™ HS-40 (Colijn and de Jonge, 1984) as described in Burgess (2001). Major meiofauna taxa were identified and carbon biomass was inferred using 1 µg C ind⁻¹ (Manini et al., 2003).

2.3. Benthic community metabolism and algae biomass

Benthic community primary production and respiration were assessed during emersion through *in situ* CO₂ exchange measurements in light (community net 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 CO₂ analysis. Gas exchange was monitored for 10–60 min, depending on the response of the system. Partial pressure of CO₂ was then regressed against time, and the slope

was used to express the results at the community level in carbon units (mg C m⁻² h⁻¹).

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

$$\text{GPP} = \text{CNP} + \text{CR} \quad (1)$$

For each site, two benthic chambers (0.07 m², about 10 L in volume, equipped with Li-Cor Li 800 Infra-red analyser) were used simultaneously, at impacted and control points. At least one light plus dark incubation was performed at each point and period. When possible, 3 light plus dark incubations were performed. During light incubations, photosynthetically available radiation (400–700 nm) was measured at the sediment surface using an SA-190 quantum sensor. Care was taken to perform the measurements with PAR above 350 µmol photons m⁻² s⁻¹, the minimum value of the saturation onset light defined in that area by Hubas and Davoult (2006). Three sediment samples (1.9 cm², 10 mm depth) were randomly taken within each chamber at the end of the experiments for analysis of total chlorophyll a (Chla, according to the method of Jeffrey and Humphrey (1975)) as a proxy for algae biomass. The mean of the three values was used to estimate the primary productivity (or assimilation number, ratio between gross primary production and Chla sediment content, expressed in g C g_{Chla}⁻¹ h⁻¹).

The study sites were investigated at 7 sampling periods (in mean spring tide condition) from February to December 2007. Measurements began 3 h after high tide.

2.4. Statistical analysis

Mann–Whitney tests were used to compare small independent groups at each measurement date. Sinusoidal curves were used to identify seasonal patterns of biomass and metabolism (curve-fitting procedure of the “Systat 11” software, n = 7) and the fits were tested by ANOVA. Significant sinusoidal trends allowed estimating and comparing the theoretical dates of maximum values.

3. Results

The mean interstitial salinity varied from 5.7 ± 1.6 to 20.4 ± 5.0 at the freshwater seepage point (see Table 1 in Ouisse et al., 2011) and was always significantly lower than at the control (Mann–Whitney test, p < 0.05) where it varied from 28.9 ± 3.1 to 33.5 ± 1.5.

The *Enteromorpha* spp. biomass showed a seasonal pattern (Fig. 1) that could be fitted by a sinusoidal model (R² = 0.894, p < 0.01) with a mean value of 313.06 g_{DW} m⁻².

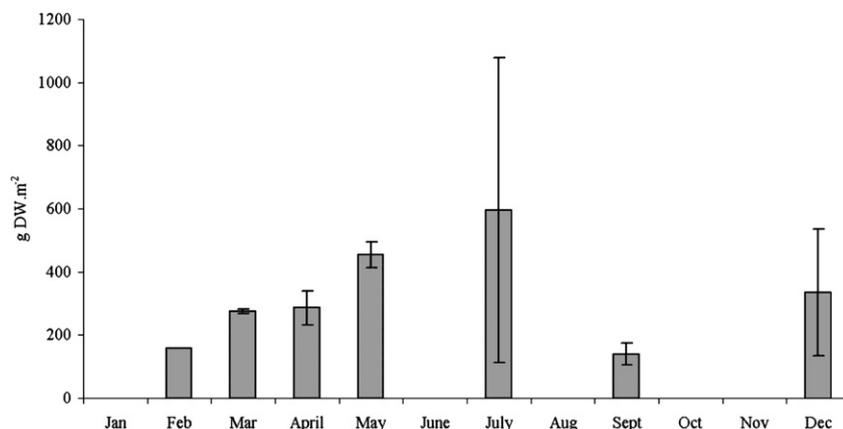


Fig. 1. Temporal variation of *Enteromorpha* spp. mean biomass (g_{DW} m⁻²). Error bars are SD (n = 3).

3.1. Meiofauna and macrofauna biomass

At the freshwater site, the meiofaunal biomass showed a seasonal pattern that could be fitted by a sinusoidal model both at control and impacted points ($R^2 = 0.991$ and 0.952 respectively, $p < 0.001$). The meiofaunal biomass was significantly lower (Mann Whitney test, $p < 0.05$) at the FW than at the C_{FW} point in February, March, April and May (Fig. 2a). The macrofaunal biomass did not show any seasonal trend at the freshwater site. The mean over the seven periods of sampling was 19.03 ± 2.36 $g_{AFDW} m^{-2}$ at the C_{FW} and 13.80 ± 2.34 $g_{AFDW} m^{-2}$ at the FW point. The macrofaunal biomass was significantly lower (Mann Whitney test, $p < 0.05$) at the FW than at the C_{FW} point in February (Fig. 2b).

At the *Enteromorpha* site, the meiofaunal biomass showed a seasonal pattern that could be fitted by sinusoidal models ($R^2 = 0.972$, $p < 0.001$ at C_E point and $R^2 = 0.916$, $p < 0.01$ at E point). The meiofaunal biomass was significantly higher (Mann Whitney test, $p < 0.05$) at the E than at the C_E point in May and September (Fig. 3a). The macrofauna biomass showed a seasonal pattern that could be fitted by a sinusoidal model at both control and impacted point of the *Enteromorpha* site ($R^2 = 0.794$, $p < 0.05$ and $R^2 = 0.961$, $p < 0.001$ respectively). The macrofaunal biomass was significantly lower (Mann Whitney test, $p < 0.05$) at the E than at the C_E point in December (Fig. 3b).

3.2. Respiration and primary production

At the freshwater site, community respiration showed a seasonal pattern that could be fitted by a sinusoidal model both in control and

impacted points ($R^2 = 0.843$, $p < 0.01$ and $R^2 = 0.985$, $p < 0.001$ respectively). Community respiration was significantly higher (Mann Whitney test, $p < 0.05$) at the FW than at the C_{FW} point in April (Fig. 4a). Gross primary production showed a seasonal pattern that could be fitted by a sinusoidal model at both control and impacted points of the freshwater site ($R^2 = 0.933$ and $R^2 = 0.930$ respectively, $p < 0.001$). GPP was significantly higher (Mann Whitney test, $p < 0.05$) at FW than at C_{FW} point in April (Fig. 4b). Microphytobenthos biomass was higher at FW than at the C_{FW} point throughout the year (Mann Whitney test, $p < 0.05$). The mean over the seven periods of sampling was 368.85 ± 51.78 $mg_{Chla} m^{-2}$ at the FW point and 178.62 ± 29.90 $mg_{Chla} m^{-2}$ at the C_{FW} point. Productivity (ratio between gross primary production and Chla sediment content) did not differ between C_{FW} and FW points. It varied from 0.040 $g C g_{Chla}^{-1} h^{-1}$ in March to 0.153 ± 0.110 $g C g_{Chla}^{-1} h^{-1}$ in May at the C_{FW} point and from 0.034 $g C g_{Chla}^{-1} h^{-1}$ in February to 0.124 ± 0.068 $g C g_{Chla}^{-1} h^{-1}$ in May at the FW point (Fig. 4c).

At the *Enteromorpha* site, community respiration showed a seasonal pattern that could be fitted by a sinusoidal model both in control and impacted points ($R^2 = 0.962$, $p < 0.001$ and $R^2 = 0.928$, $p < 0.01$ respectively). CR was increased from 3 to 8 times at E compared to C_E point. The difference was significant (Mann Whitney test, $p < 0.05$) at each time it could be tested (March, April, May and September, Fig. 5a). Gross primary production showed a seasonal pattern that could be fitted by a sinusoidal model only at the C_E point ($R^2 = 0.923$, $p < 0.01$). GPP was significantly higher (Mann Whitney test, $p < 0.05$) at the E than at the C_E point each time it could be tested (March, April, May and September, Fig. 5b), a probable result of the significantly higher chlorophyll a biomass at the E point throughout

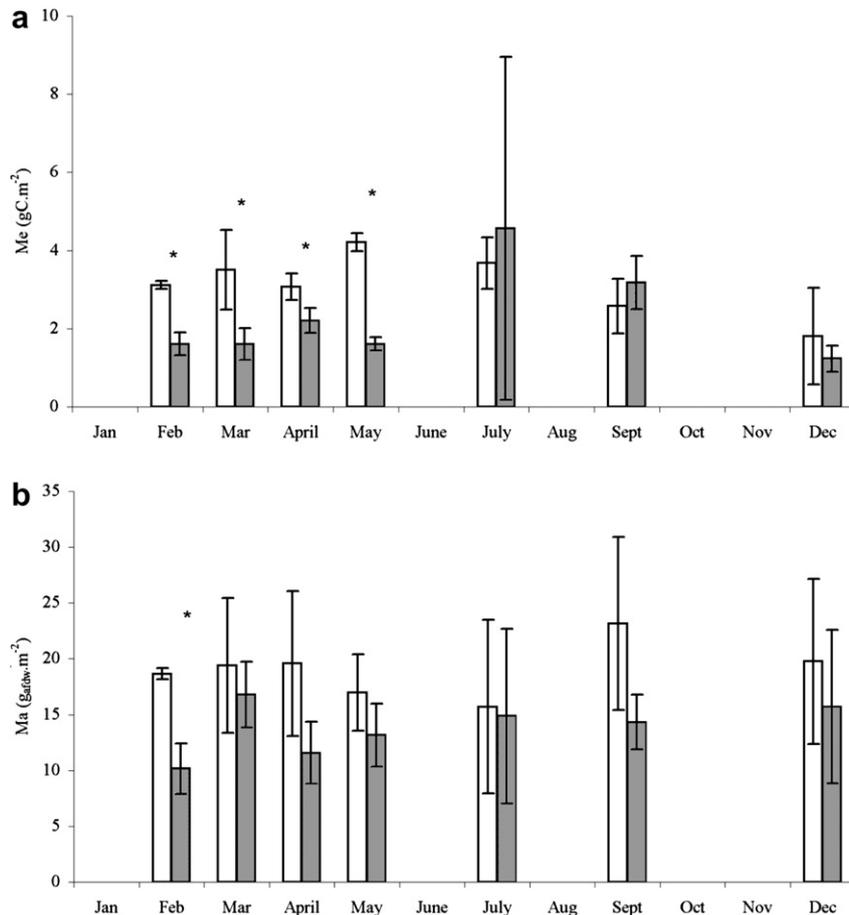


Fig. 2. Temporal variation of mean biomass of (a) meiofauna (Me in $g C m^{-2}$) and (b) macrofauna (Ma in $g_{afdw} m^{-2}$) in control (white bars) and impacted by freshwater seepage (grey bars) points. Error bars are SD ($n = 3$). * indicates a significant difference between control and impacted points (Mann–Whitney test, $p < 0.05$).

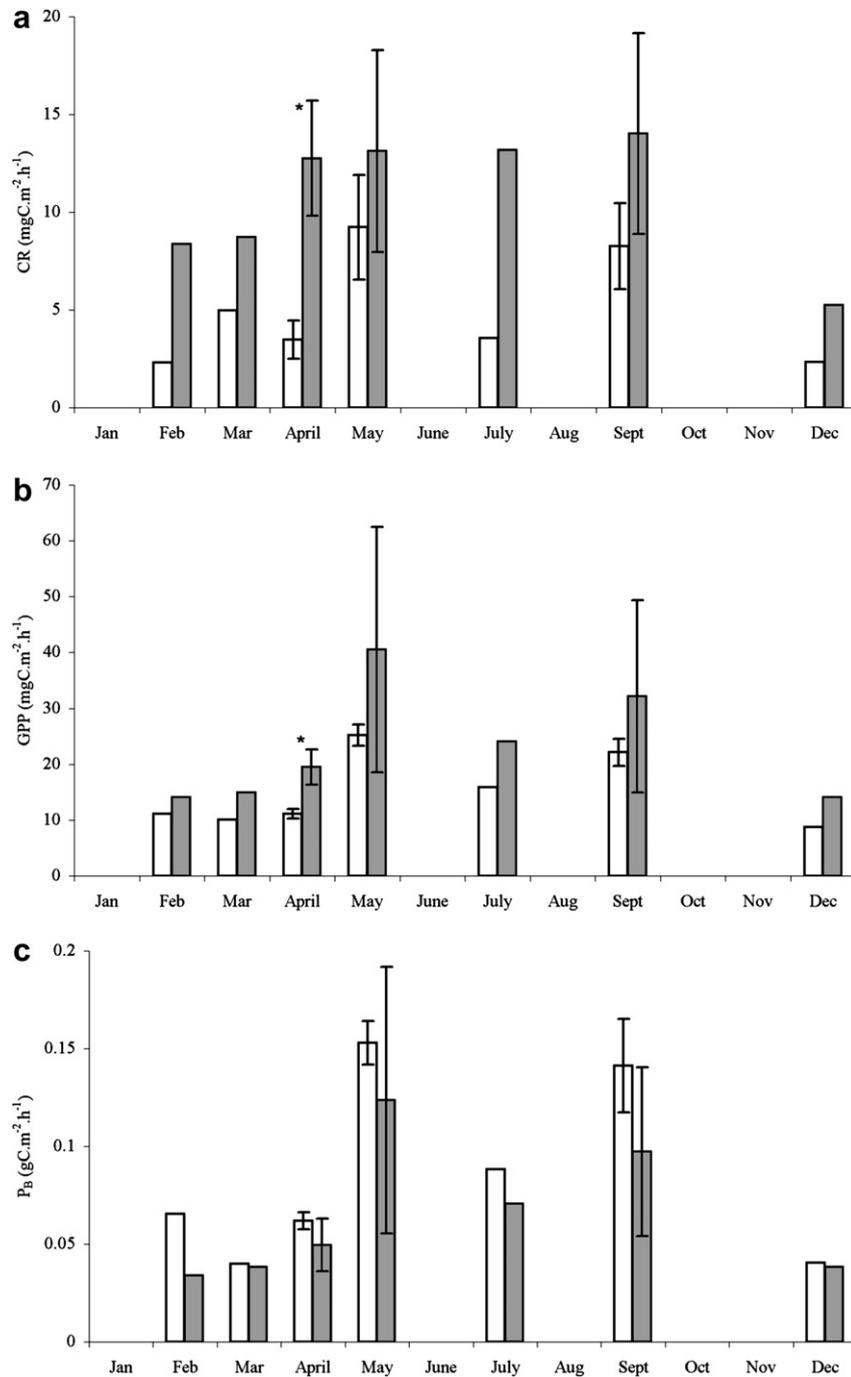


Fig. 4. Temporal variation of mean (a) benthic community respiration (CR in $\text{mg C m}^{-2} \text{ h}^{-1}$), (b) gross primary production (GPP in $\text{mg C m}^{-2} \text{ h}^{-1}$) and (c) productivity (P_B in $\text{g C g}_{\text{Chla}}^{-1} \text{ h}^{-1}$) in control (white bars) and impacted by freshwater seepage (grey bars) points. Error bars are SD ($n = 3$). * indicates a significant difference between control and impacted points (Mann–Whitney test, $p < 0.05$).

freshwater seepage site (respectively on the 29th of June and the 8th of July) and at the control point of the *Enteromorpha* site (on the 29th of June). This did not coincide with the maximum meiofaunal biomass and confirms the major role of temperature in controlling the total benthic respiration. Despite this, effects on benthic metabolism were likely to occur through the complex interactions between sediment dwellers (meio- and macrofauna) that could differ in impacted and control points.

The total benthic metabolism was enhanced by the two disturbances. The freshwater seepage increased community respiration

and gross primary production (almost 4 and 2 fold respectively compared to the control point in April). The higher primary production was linked to higher sediment chlorophyll a content at the freshwater seepage than at control point throughout the year. This high microphytobenthic biomass (average $369 \text{ mg}_{\text{Chla}} \text{ m}^{-2}$) is in the upper range of values reported for European estuaries (Underwood and Kromkamp, 1999). Primary production is regulated by bottom-up (light and nutrients loading) as well as top-down (grazing) processes. It has been suggested that groundwater discharge could constitute an important pathway for nutrient

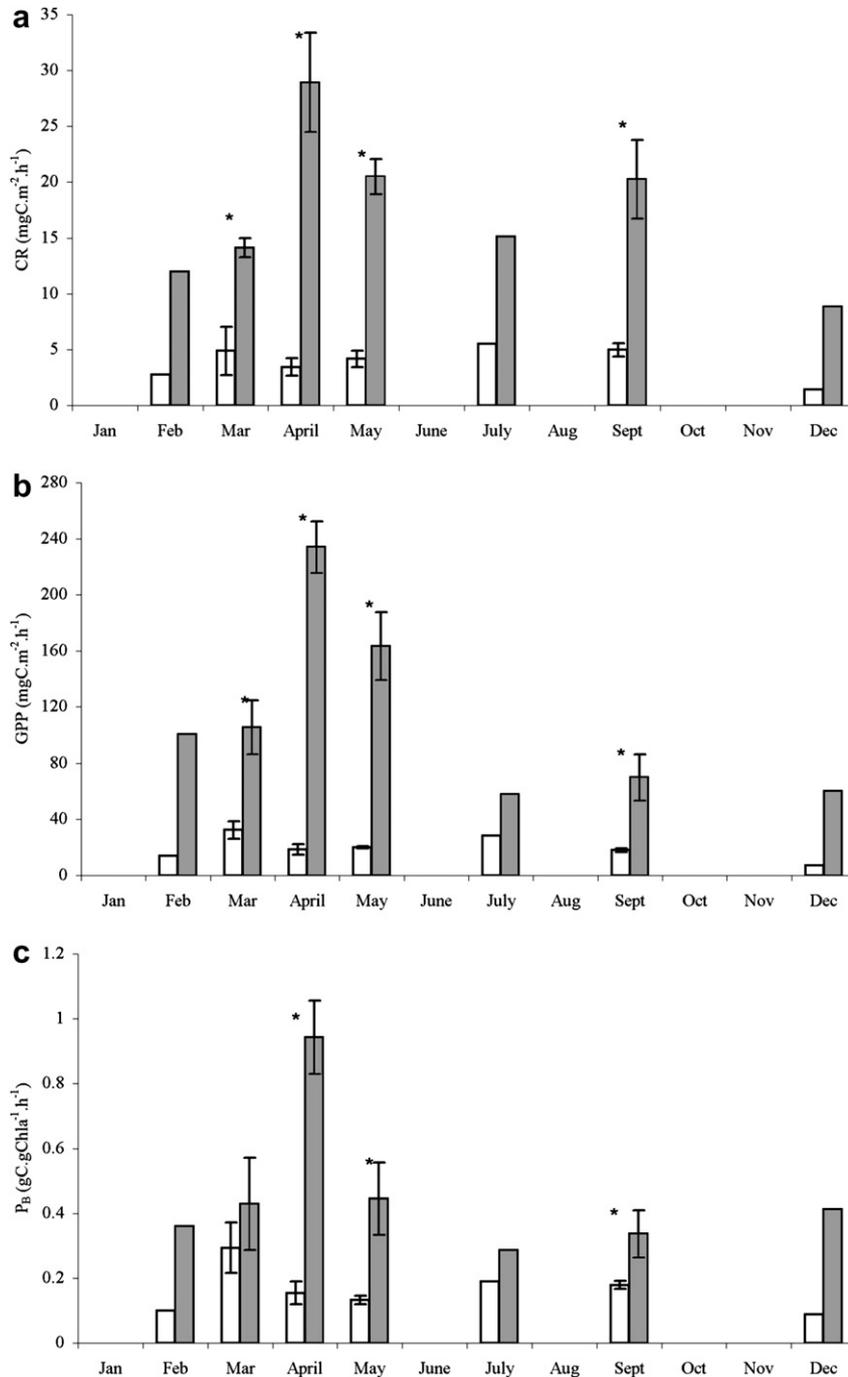


Fig. 5. Temporal variation of mean (a) benthic community respiration (CR in $\text{mg C m}^{-2} \text{h}^{-1}$), (b) gross primary production (GPP in $\text{mg C m}^{-2} \text{h}^{-1}$) and (c) productivity (P_B in $\text{g C g}_{\text{Chla}}^{-1} \text{h}^{-1}$) in control (white bars) and *Enteromorpha* spp. proliferation (grey bars) points. Error bars are SD ($n = 3$). * indicates a significant difference between control and impacted points (Mann–Whitney test, $p < 0.05$).

delivery. Johannes (1980), for example, found nitrate and silicate concentrations in groundwater to be up to two times higher than in receiving waters. That could enhance primary production when it might otherwise be nutrient limited. However, Hubas et al. (2006) measured abundant nutrient standing stocks in sediment pore water in the bay. Furthermore, using multivariate analysis they demonstrated that benthic primary production was not likely to be limited by nutrient concentrations. Freshwater seepage could also enhance advective pore water flows and thus stimulate primary production as it has been suggested in permeable sands (Billerbeck

et al., 2007). Microphytobenthos is a significant source of food for grazers among sediment or surface dwellers. The macrofauna community of both freshwater seepage and control points was dominated by the surface grazer *Hydrobia ulvae*. However, its biomass was much lower at the freshwater seepage than at control throughout the year (average 6.81 ± 3.31 and $12.39 \pm 2.81 \text{ g}_{\text{AFDW}} \text{ m}^{-2}$ respectively). Finally, changes in salinity might have affected the microphytobenthic community composition as commonly observed in estuarine gradients (see for example Sahan et al., 2007). The increase in microalgae biomass in freshwater seepage could then

coincide with changes in the species composition or dominance, species with a wide tolerance to salinity being favoured. This would be consistent with the intermediate disturbance hypothesis which predicts that a moderate increase in the intensity of a disturbance releases resources that can enhance the local density of populations (Connell, 1978). However, for the present this must remain speculative. Interactions between fauna, microflora and sediment are indeed complex and complementary studies would be necessary to evaluate the main factors affecting the small-scale spatial variability of microphytobenthic biomass.

The impact of *Enteromorpha* spp. development was far more important. The community gross primary production was much higher in sediment covered by the macroalgal mat than in bare sediment. The magnitude of the difference varied seasonally; the greatest difference was observed in April with a gross primary production increase more than twelve fold with respect to the control point. This was not only explained by the high biomass of the algal mat but also by the higher productivity of the community with macroalgae compared to the one of bare sediment (Fig. 5c). The macroalgal mat also increased the community respiration (more than eight fold with respect to the control point in April) and led to a shift in its seasonal trend with a maximum occurring sooner (on the 31st of May instead of 29th of June according to the sinusoidal fits). Previous studies on the accumulation of macroalgae on the sediment have shown a negative effect both on microbenthic photosynthesis (by shading; Sundbäck et al., 1990) and sediment aerobic respiration (by decreasing O₂ availability below the macroalgae; Corzo et al., 2009). Nevertheless, both total benthic community primary production and respiration could be enhanced by the accumulation of ephemeral green macroalgae as has already been shown with different experimental approaches (Corzo et al., 2009 and references therein). Furthermore, physiological activity of ephemeral macroalgae changed seasonally and their net effects on the benthic community metabolism were expected to change accordingly (Hubas and Davout, 2006). When physiologically active, macroalgae became the major autotrophic component of the benthic community. Macroalgae lying at the surface of the sediment benefitted from better light conditions than microphytobenthos inside the sediment and the productivity was enhanced. As suggested by Sundbäck and McGlathery (2005), microphytobenthos might also not be outcompeted by overlying macroalgae owing to a combination of shade adaptation and good nutrient availability through an efficient recycling of nutrients within the sediment. When macroalgae decayed, the respiratory activity of the associated biota was enhanced. The impact of the ephemeral macroalgae development was also expected to vary at the inter-annual scale. Indeed, the amount of accumulated macroalgae varied from year to year as a consequence of inter-annual variations of environmental conditions. Total benthic primary production and respiration were measured on macroalgal mats and bare sediments simultaneously (during *Enteromorpha* spp. development, accumulation and decaying) in the Roscoff Aber bay during the years 2003 (Hubas and Davout, 2006) and 2007 (the present survey). The effect on total benthic primary production was comparable (with an increase in GPP up to ten times in 2003) but the effect on total benthic respiration was greater in 2003 when the increase in CR reached twenty times. Primary production of dense algal mats was self-limited due to self-shading whereas the respiration of decaying algal mats and the associated biota (mainly bacteria) was directly linked to the amount of algae.

5. Conclusions

This study demonstrated different effects of two widespread phenomena altering intertidal sediments (freshwater seepages and

ephemeral macroalgae proliferation) on the benthic community biomass and metabolism in a small bay. Freshwater seepage had a clear localised effect by increasing meiofauna and microalgae biomasses and enhancing the total benthic metabolism without changing its seasonal trend. Ephemeral macroalgae proliferation was characterised by the temporal variation of its effects linked to the seasonal variation of the macroalgae physiology that led to a shift in the seasonal trend of the benthic metabolism. Thus, changes in meiofauna biomass and in community metabolism depended on the time period considered. The development of macroalgae first increased meiofauna biomass and above all the benthic primary production. When macroalgae decayed, the benthic community respiration was enhanced. These results highlight the need for a better understanding of the spatial and temporal variability in benthic metabolism which is required to give reliable whole-system estimates.

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