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Temporal variability of intertidal benthic metabolism under emersed conditions in an exposed sandy beach (Wimereux, eastern English Channel, France)

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Abstract

Benthic community metabolism during emersion was measured in a three-year survey by monitoring CO_2 fluxes in benthic chambers on an exposed sandy beach of the eastern English Channel (Wimereux, France). The three-year chronology of variations in benthic metabolism was characterised by a high variability around a low value for gross community primary production (GCP: 17.47 ± 40.85 mgC m^{-2} h^{-1}, mean ± SD) and community respiration (CR: 1.66 ± 1.97 mgC m^{-2} h^{-1}, mean ± SD). Although benthic metabolism remained low most of the time, some high values of primary production and respiration were occasionally detected. High primary production rates (up to 213.94 mgC m^{-2} h^{-1} measured at the end of summer) matched with the development of *Euglena* sp., together with the occurrence of phytoplanktonic species on the sediment, whereas high community respiration rates were detected at the end of spring on *Phaeocystis* sp. foam deposits. Community respiration was positively correlated with bacterial abundance, suggesting that CR was mainly supported by microfauna.

Keywords: Intertidal environment; Benthos; Primary production; Respiration; *Phaeocystis* sp. bloom

1. Introduction

Sandy beaches are the most widely distributed intertidal habitat, dominating both temperate and tropical shores. Numerous sand beaches have been investigated around the world in terms of faunal community structure and development (e.g. Gray and Rieger, 1971; Eleftheriou and Nicholson, 1975; Whitlatch, 1977; Dexter, 1992; Bachelet and Dauvin, 1993, Lercari et al., 2002). However, less is known about their role in the carbon cycling, in relation to

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primary production and respiration. The degree of exposure of a beach to wave action largely determines sediment particle size and it has a dominant effect on animal and algal communities. The biomass of microphytobenthos is higher in sheltered, muddy habitats than in exposed sandy habitats. Thus, sandy tidal flats are considered to be less productive than estuarine habitats (Plante-Cuny, 1984; MacIntyre et al., 1996).

For some subtidal habitats, studies have shown the contribution of phytoplankton sedimentation to benthic chlorophyll-a biomass (Josefson and Hansen, 2003) and its incorporation into the benthic food web (Josefson et al., 2002). Although active phytoplankton could be deposited, only a few studies have suggested that such cells could contribute to benthic primary production (Sundbäck et al., 1996).

In the eastern English Channel and the Southern Bight of the North Sea, intense pelagic spring blooms are composed of *Phaeocystis* sp. (Prymnesiophyceae, Gentilhomme and Lizon, 1998, and references therein). This species is characterised by the development of gelatinous colonies leading to accumulations of mucilaginous aggregates (foam) on the sea surface and on the beach (Lancelot, 1995). The impact of this foam has been studied mainly on phyto-and zooplankton populations (Lancelot, 1995; Becquevort et al., 1998). In the intertidal benthic habitat, its incorporation into the food web (Cadée, 1996) and its influence on macrofaunal populations and mineralisation processes in estuarine sediments (Desroy and Denis, 2004) have been investigated. To our knowledge, nothing is known on its impact on intertidal benthic community metabolism.

The aim of this study was to determine whether the benthic metabolism (community primary production and community respiration) of an exposed sandy beach of the eastern English Channel was low throughout a three-year survey, or whether it could be affected by events such as *Phaeocystis* sp. foam deposits, leading to high primary production or respiration rates.

2. Methods

A three-year survey (from April 2000 to May 2003) of intertidal benthic metabolism was conducted in Wimereux (eastern English Channel, France, Fig. 1). The study area is a typical hydrodynamically exposed (western exposition) sandy beach submitted to a semi-diurnal megatidal regime (spring tidal range >8 m). The study site was located in the higher part of the beach between mean high water of neap tides and mean tide level where the sediment is characterised by medium size sand (median grain size 0.20 mm).

During the survey, 48 measurements of benthic metabolism (community primary production and

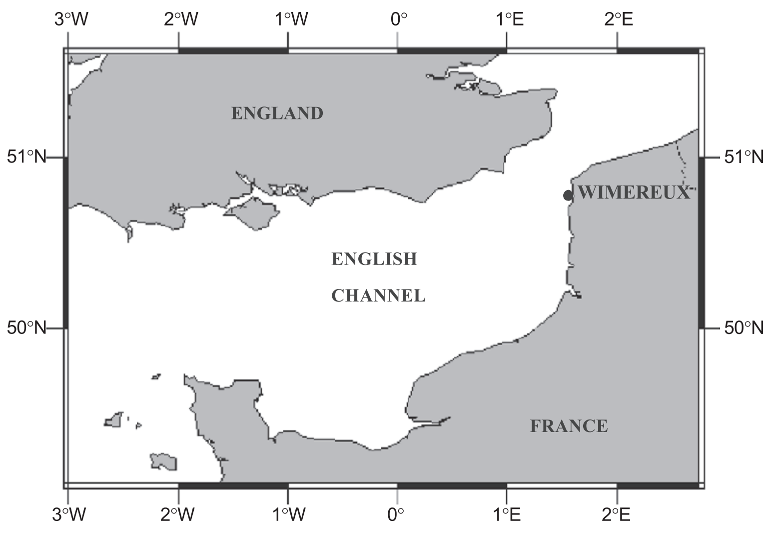

Fig. 1. Location of the study site along the coast of the eastern English Channel.

community respiration) were performed by monitoring the change in CO_2 concentration in a benthic chamber, as described in Migné et al. (2002). The chamber consisted in a Perspex dome fitted on a stainless steel ring (pushed into the substratum to a depth of 10 cm) and connected to a closed circuit of CO_2 analysis. The sediment surface covered was 0.126 m^2, the volume of trapped air was about 25 L. Experiments were carried out at ambient light and in darkness in order to estimate net community primary production (NCP) and community respiration (CR), respectively. Measurements were made around local noon, when microalgae were light-saturated. CO_2 flux was calculated through a regression analysis of CO_2 concentration against time during light or dark incubations. Fluxes were expressed at the community level (mgC m^{-2} h^{-1}). The dark incubation rate obtained on a given date was added to measurements from individual light incubations to determine gross community primary production (GCP=NCP+CR). Since the intertidal system appeared to be homogeneous at a small spatial scale, considering both primary production and respiration (Davoult et al., 2004), no replication was made for metabolism measurements.

Additional measurements of CO_2 exchanges were carried out on spring *Phaeocystis* sp. foam deposits. One additional measurement was carried out in 2001, and two in 2002 as well as in 2003. In 2002 and 2003, these measurements were performed simultaneously with measurements on bare sediment, using two benthic chambers.

Sediment chlorophyll-a content was determined for each primary production measurement (i.e. both on bare sediment and foam-covered places during *Phaeocystis* foam occurrence). Plastic cores (1.9 cm^2, 3 replicates) were pushed into the sediment within the chamber down to a depth of 1 cm and sediment samples were stored in the dark at $-20°C$. Chlorophyll-a concentrations were determined by spectrophotometry following Lorenzen (1967) and expressed in terms of chlorophyll-a per surface unit (mg Chl-a m^{-2}).

Sediment was also sampled (as described before for chlorophyll-a) for bacterial abundance determina-

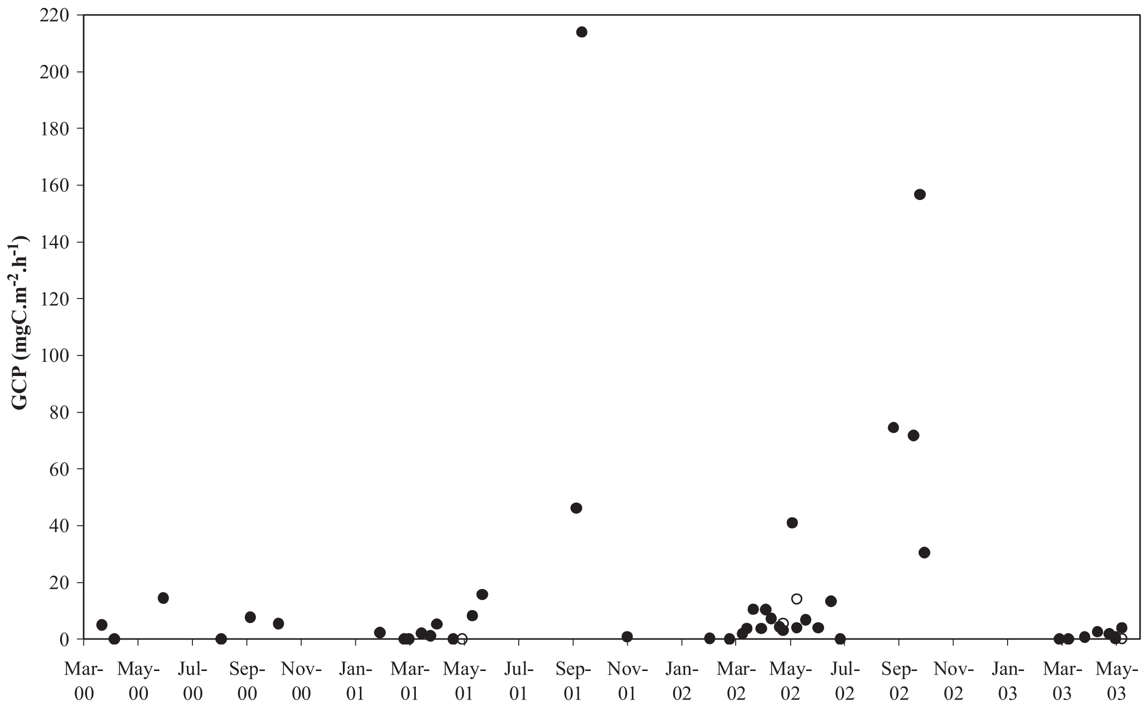

Fig. 2. Gross community production (GCP in mgC m^{-2} h^{-1}) measured at Wimereux from April 2000 to May 2003. Open dots correspond to measurements made in foam-covered places.

tion. Bacterial numbers were determined by epifluorescence direct counting following Chevaldonné and Godfroy (1997) and Artigas (1998).

3. Results

The three-year chronology of variations in benthic metabolism was characterised by a high variability around a low value for gross community primary production (mean ± SD=17.47 ± 40.85 mgC m^{-2} h^{-1}, Fig. 2) and community respiration (mean ± SD=1.66 ± 1.97 mgC m^{-2} h^{-1}, Fig. 3). However, high GCP rates were measured, the highest being on 26 September 2001 (213.94 mgC m^{-2} h^{-1}). High assimilation numbers (ratio of GCP to Chl-a biomass) were calculated on 21 June 2000 (20.66 mgC mgChl-a^{-1} h^{-1}), on 20 and 26 September 2001 (16.68 and 19.83 mgC mgChl-a^{-1} h^{-1}, respectively) and on 16 May and 5 September 2002 (4.46 and 4.55 mgC mgChl-a^{-1} h^{-1}, respectively) whereas assimilation number remained low throughout the three-year survey (2.43 ± 4.67 mgC mgChl-a^{-1} h^{-1}).

No GCP was detected on foam deposits in 2001 (0.00 mgC m^{-2} h^{-1} on 17 May). In May 2002 and 2003, GCP differed slightly on foam and on bare sediment but the trend in the shift was different for the two years; in 2003 GCP was lower on foam deposits than on bare sediments; in 2002 it was the opposite. Each year, CR was higher on foam deposits than on bare sediment (Fig. 3). The correlation between respiration and bacterial abundance (including three measurements made on foam-covered places in May 2001 and 2002) was significant ($r=0.579$, $p<0.01$, $n=17$). Both highest CR and bacterial abundances were measured on foam during spring 2001 and 2002.

4. Discussion

Benthic microalgal production rates calculated here (17.47 ± 40.85 mgC m^{-2} h^{-1}, mean ± SD) are in accordance with those reported in the literature for intertidal sandy habitats (14–35 mgC m^{-2} h^{-1}, Rasmussen et al., 1983; 5–35 mgC m^{-2} h^{-1}, Varela

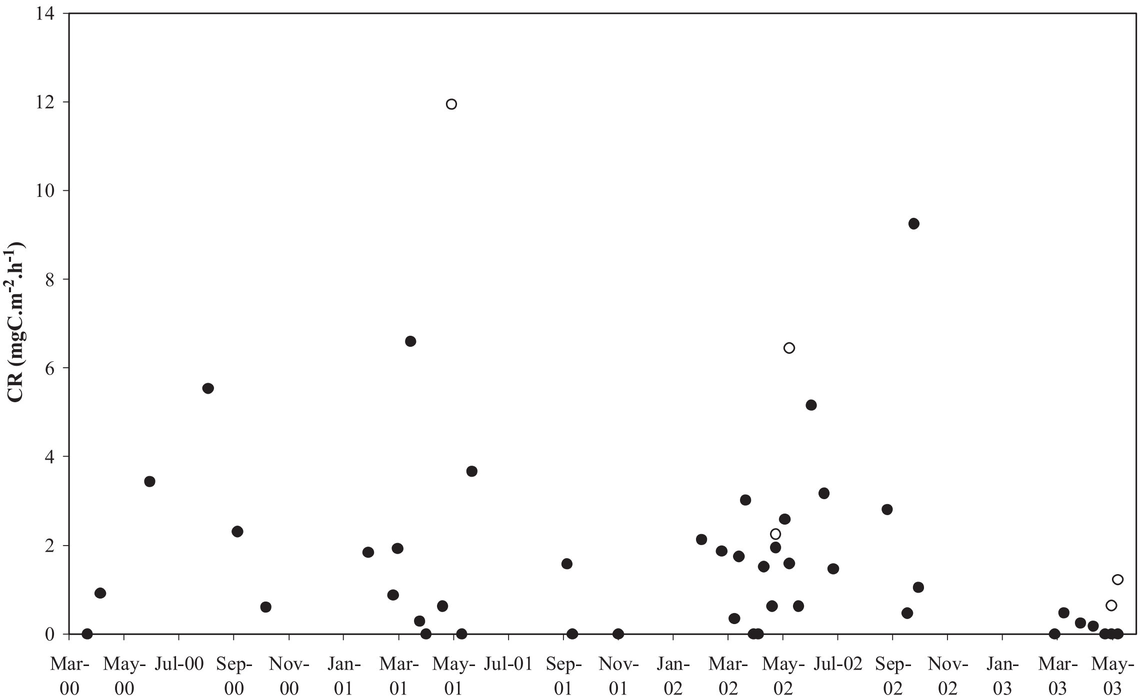

Fig. 3. Community respiration (CR in mgC m^{-2} h^{-1}) measured at Wimereux from April 2000 to May 2003. Open dots correspond to measurements made in foam-covered places.

and Penas, 1985). Mean community respiration on the study site was ten times lower than CR measured using the same method in a close sheltered area, the Bay of Somme (Davoult et al., 2004). As fauna on exposed sandy beaches is known to be poor (Eleftheriou and Nicholson, 1975; Dexter, 1992) because of stresses and weak organic carbon inputs, community respiration is expected to be low. The correlation observed between respiration and bacterial abundance suggested that CR was mainly supported by microfauna, as it was shown for most marine habitats, including the subtidal (Piepenburg et al., 1995) and intertidal (Schwinghamer et al., 1986; Cammen, 1991).

Although benthic metabolism remained low most of the time, some high values of primary production were occasionally detected. For some dates (e.g. 26 September 2001), GCP measured on the beach of Wimereux (Fig. 2) was above the highest value measured in the Bay of the Somme (122.8 mgC m^{-2} h^{-1}, together with a Chl-a concentration of 228 mg m^{-2}, Davoult et al., 2004). One of these high primary production values was also characterised by a high assimilation number (19.8 on 26 September 2001). Sediment samples made on this date for cell observations showed that the microalgal population was dominated by the genus *Euglena* (several million cells per cm^2). Brotas and Catarino (1995) found a high *Euglena* abundance in early October in the Tagus Estuary and pointed out that it corresponded to a higher assimilation number for the community. Although our study site was highly exposed, calm conditions (i.e. weak wind and/or not from the west) may allow dense populations of *Euglena* to develop at the end of summer, leading to high primary production and assimilation numbers. The high abundance measured on 26 September 2001 was indeed found after a moderate wave action due to a weak wind (<7 m s^{-1}) over the five days preceding the measurements. Nevertheless the order of magnitude of assimilations numbers found in this study is higher than those calculated by Brotas and Catarino (1995), even with *Euglena*. In our study, the occurrence on the sediment of marine phytoplanktonic species (*Navicula* sp., *Cylindrotheca* sp., *Paralia* sp., *Odontella* sp., *Raphoneis* sp.) usually observed in the coastal waters of the study area (Lefebvre and Barbet, 2003) could explain high assimilation numbers. Cahoon and Cooke (1992) indeed pointed out that average assimilation numbers for benthic algae were much lower than those for phytoplankton.

High community respiration rates were measured at the end of the spring phytoplanktonic bloom when *Phaeocystis*-derivated foam appeared. Becquevort et al. (1998) showed the role of bacteria in the degradation of *Phaeocystis*-derived organic matter: both specific biomass and growth rate of particle-attached bacteria are very high during *Phaeocystis* blooms. Since community respiration was correlated with bacterial abundance, the high CR and bacterial abundances measured on foam deposits might be due to microbial activity during *Phaeocystis* degradation. *Phaeocystis*-attached bacteria were deposited with foam and their high degradation activity was measured as high CR levels. Together with bacteria, some active photosynthetic cells may have been deposited in foam, leading to non-negligible primary production measurements, sometimes higher than on bare sediment. Nevertheless, comparisons between measurements made on foam were hazardous because of the difficulty in estimating the amount of foam enclosed in the chamber. Although the whole surface was covered by foam, its height changed from day to day, sometimes several centimetres. Since foam formation occurs under specific windy conditions (Lancelot, 1995), the amount of foam deposited on the beach is directly dependent on the wind speed and direction that control foam formation and deposit on the beach, respectively. Contrary to the conditions allowing *Euglena* sp. to develop, foam accumulations need favourable west winds to reach the beach and to settle. Foam formation and persistence vary from year to year, mainly depending on spring storm intensity, but also on absolute spring abundance of *Phaeocystis*, which has recently been shown to be significantly correlated with the North Atlantic Oscillation (NAO; Seuront and Souissi, 2002). The increase in community respiration being related to the amount of foam transported to the beach, its magnitude varies at a daily scale during the bloom, and at an inter-annual scale. Although the impact of foam was weak at an hourly scale, it can be significant for global carbon fluxes at a larger spatial scale, since foam deposits occur all along the coats of the eastern English Channel.

As mentioned by Shaffer and Onuf (1985), estimating monthly and annual production rates from single measurements is contentious because of a high patchiness in space and time in most environments. It is indeed hazardous in our study site because of the high variability induced by the exposed conditions and the particular events (*Euglena* development and *Phaeocystis* occurrence). Nevertheless, such a brief event as *Phaeocystis* foam deposits should not be missed in the estimation of total metabolism of exposed sandy beaches in the eastern English Channel and southern bight of the North Sea.

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