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Bacterial dynamics in a microphytobenthic biofilm: A tidal mesocosm approach☆

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ABSTRACT

In intertidal mudflats, during low tide exposure, microphytobenthos (MPB) migrate vertically through the surface sediment and form, with the heterotrophic bacteria, a transient biofilm. Inside this biofilm, multiple interactions exist between MPB and bacteria. These micro-organisms secrete a wide range of extracellular polymeric substances (EPS), which are major components of the biofilm matrix. In this study, we used a tidal mesocosm experiment in order to decipher the interactions of the MPB–EPS–bacteria complex within the biofilm. We tried to determine if the EPS could control bacterial activities and/or production and/or richness according to the age of the biofilm and to the immersion/emersion period. The dynamics of biomasses of MPB and prokaryotes, the bacterial production, the hydrolysis of predominating organic constituents in the dissolved organic carbon (DOC) pool (i.e., carbohydrates and polypeptides), and the bacterial structure were studied in relation to the different EPS fractions (carbohydrates and proteins: colloidal and bound) dynamics during 8 days. Our experiment had emphasized the influence of the environmental conditions (light, immersion/emersion) on the interactions within the biofilm and also on the effects on biofilm aging. Bacterial production was always inhibited by the bound EPS-carbohydrate, especially during low tide. Our results suggest that the concentration and composition of EPS had a major role in the bacterial/MPB interactions: these interactions can be either positive or negative in order to regulate the productive phases of MPB and bacteria.

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1. Introduction

Intertidal mudflats are highly productive ecosystems associated with estuaries and semi-enclosed bays. In Western Europe, these geomorphological structures are mostly devoid of macrophytes, but nevertheless exhibit high primary productivity due to the presence of microphytobenthos (MPB) mainly composed of epipelic diatoms (MacIntyre et al., 1996; Underwood and Kromkamp, 1999). Many works on mudflats also demonstrated that the bacterial production showed high rates, especially in summer and autumn (Cammen, 1991; Hamels et al., 2001; Pascal et al., 2009; van Duyl and Kop, 1990) and bacterial abundance may be equivalent to billions of cells by mL of mudflat sediment (Pascal et al., 2009; Smith and Underwood, 1998).

During low tide exposure, MPB migrate vertically through the sediment to the surface and form with the heterotrophic prokaryotes, a transient biofilm (Consalvey et al., 2004; Herlory et al., 2004). Inside this biofilm, multiple interactions exist between MPB and prokaryotes (Makk et al., 2003). The MPB and prokaryotes secrete a wide range of extracellular polymeric substances (EPS) which are major components of the biofilm matrix. Epipelic diatoms secrete 30–60% of photoassimilated carbon as EPS into the surrounding sediment (Middelburg et al., 2000; Smith and Underwood, 2000; Underwood et al., 1995). These EPS are rich in polysaccharides, proteins, proteoglycans, lipids and many other compounds expressed at different contents (Chiovitti et al., 2003; Pierre et al., 2010, 2012; Underwood et al., 2004). The types of EPS are related to the location and/or environmental conditions which affect food webs, the primary production of this ecosystem, and sediment properties (Underwood and Paterson, 2003). Polymer chemistry and surface properties of EPS affect coagulation and aggregation (Bhaskar

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et al., 2005), pore water content (Potts, 1994) and ion binding (Chin et al., 1998). Furthermore, EPS can act as a kind of glue stabilizing whole sediments and help mitigate surface sediment losses (Decho, 2000; Lubarsky et al., 2010; Stal and de Brower, 2003; Sutherland et al., 1998; Underwood and Paterson, 2003). EPS are also involved in the motility system and substratum adhesion of epipelic diatoms (Higgins et al., 2003; Stal and Défarge, 2005; Wustman et al., 1997). EPS consist of two fractions: colloidal and bound EPS. Recently, Takahashi et al. (2009) have optimized a protocol for bound EPS extraction and proposed an innovative method (Dowex) to extract EPS without any contamination by internal compounds. Bound EPS are especially rich in deoxy sugars compared to other fractions, but deoxy sugars are known to be an unfavorable substrate for bacteria that select other sources of carbon like glucose (Giroldo et al., 2003).

Concerning the interaction between MPB and prokaryotes, the photosynthetically fixed carbon by the MPB is transferred towards bacteria in few hours, translating a quick use from sources of labile carbon, possibly including EPS (Cook et al., 2007; Goto et al., 2001; Middelburg et al., 2000; Underwood and Paterson, 2003). Bellinger et al. (2009) showed, in a ^{13}C-tracer study of estuarine biofilms, that the photosynthetically fixed carbon by the biofilm community was incorporated within 4 h into diatom intracellular storage carbohydrates, extracellular polysaccharides, and into Gram-negative bacterial PLFAs (phospholipid fatty acids) through heterotrophic utilization of EPS.

On mudflats, correlative studies of algal, bacterial, and enzymatic activity suggest that some degree of algal–bacterial coupling does occur (Haynes et al., 2007). Moreover, Yallop et al. (2000) found a significant correlation between MPB biomass and bacterial production. In Marennes-Oléron bay, a survey conducted in 2008 revealed contrasting results according to the season (Orvain et al., 2014-this issue). In summer, there was a high level of correlation between bacteria and MPB biomasses coinciding with a secretion of colloidal EPS and a high proportion of bound EPS-protein (~10%). In winter, the MPB biomass was higher and there was an opposition between phases of MPB growth and bacterial growth that seems to be related to a high secretion rate of bound EPS and the absence of EPS-protein at this season. A potential role of inhibition caused by bound EPS-carbohydrates was evoked, but such an assumption must be verified in controlled conditions.

Bacteria play an active role in the production of dissolved organic carbon (DOC) from particles particularly originating from primary production via exoenzymatic activities (Hoppe, 1984; Smith et al., 1992). In mudflat sediment, hydrolysis process and the extracellular enzyme activities of bacteria can convert bound EPS into colloidal EPS (Hanlon et al., 2006). Bacteria can produce exoglucanases such as the glucosidase enzymes in order to cleave the α- and β-linkages of combined carbohydrates (Sutherland, 1999) and exopeptidases such as the leucine amnipeptidase to hydrolyze polypeptides and proteins (Gonzales and Robert-Baudouy, 1996). Nevertheless, the regulation of these activities depends on the composition of the organic matter (type and quantity of compounds) and environmental conditions (pH, temperature, ions) which can induce, inhibit, or suppress them (Boetius and Lochte, 1994, 1996; Chróst and Overbeck, 1990). However in the case of nutrient deficiency, MPB is in competition with bacteria and the growth of bacteria remains limited (Waksman and Butler, 1937). In spite of strong levels of organic matter in muddy sediments, a correlation between algal production and exoenzymatic activities of bacteria was highlighted during field studies (Hanlon et al., 2006; van Duyl et al., 1999) and during experimentation on diluted sediment (Goto et al., 2001; Haynes et al., 2007; Thornton et al., 2010). Concerning the structure of the bacterial community, some studies suggest that algal–bacterial coupling in estuarine sediments is likely to involve particular taxa rather than a response from the entire bacterial community (Amin et al., 2012; Bellinger et al., 2009; Hanlon et al., 2006; Haynes et al., 2007).

Mudflats are highly dynamic environments (MacIntyre et al., 1996; Underwood and Kromkamp, 1999). Multiple variables are at play and complex ecological relationships may mask the signal associated with the interactions of the MPB–EPS–bacteria complex. Owing to the possibility of achieving a good balance among control, realism and generality (Kemp et al., 2001; Petersen et al., 2003), mesocosms are well suited for the study of interspecific interactions within the biofilm. Mesocosms have proven to be appropriate tools to study the impact of nutrient deficiency and biofilm age on the composition of EPS secreted by the microorganisms (Blanchard et al., 2001; Orvain et al., 2003; Staats et al., 2000b).

In our study, the use of tidal mesocosm provides a limited quantity of sediment, in which environmental factors (such as temperature, light, predators, and tides) can be well-controlled. Our experimental system allows us to study the interaction within the biofilm age (composition and concentration of EPS secreted by microorganisms) and the immersion/emersion period. The biomasses of algae and prokaryotes, the bacterial production, the enzymatic activity rates by bacterial communities (i.e., α- and β-glucosidase and the aminopeptidase) and the bacterial diversity were followed as well as the dynamics of the EPS (colloidal and bound) during 8 days in this tidal mesocosm.

2. Materials and methods

2.1. Sampling area and experimental mesocosm

We first collected a large amount of sediments (1 m^3) from the Esnandes mudflat located in the northern part of the Aiguillon Bay, France (46°15′18.00″N, 1°8′30.20″W). The sediment was sieved by hand, without adding seawater and using 1 mm sieve, to exclude macrofauna (i.e., grazers). Two weeks later, in similar tidal conditions, we collected fresh sediments from the same site (only the top 2 mm surface sediment, in areas with visible biofilms — i.e. 10 m^2). Ten liters of enriched sediment was brought back to the lab and this fluid superficial sediment was immediately filtered to remove macrofauna and applied on four sediment plates (20 × 30 cm), with eight nylon nets (100 μm mesh size, Buisine, France) over the surface (not lens tissues). Two folds of nylon nets were put over the surface of each plate and exposed to artificial lights during 24 h. On the following day, the top net was collected and mixed in 5 L of artificial seawater. Microphytobenthic algae settled rapidly and the supernatant was discarded after 10 min to keep 50 mL of the pellet containing a concentrated mixture of MPB. This mixture was immediately used as an inoculum that was added to 20 L of sediment collected from the previously-prepared sediment (and from which water content was measured one day before). Eighty four milliliter of water per liter of sediment was precisely added to the inoculum in order to match the water content of superficial sediment in the field (i.e., 65%) (Orvain et al., 2014-this issue). The enriched sediment was mixed and a layer of 1 cm was deposited in each experimental core (height: 15 cm; diameter: 5 cm) over a sub-layer of 20 cm of compact sediment without MPB (i.e. the same sediment stock that was previously prepared but without the addition of inoculum).

Cores were maintained in experimental mesocosm connected to a recirculating filtered seawater system, with a tidal simulation (2 tides per day), at a temperature of 20 ± 1.3 °C and a light (993 ± 300 μmol m^{-2} s^{-1}), dark regime of 12 h and 12 h, respectively. Monitoring of irradiance (Licor captor) and air, air/water and sediment temperatures (Hobo captor) was made during all the mesocosm experiments (8 successive days) (Fig. 1). Salinity of the sea water was measured 4 times during the experiment (Fig. 1).

One 6 h-daytime air exposure period and one 6 h-night time air exposure were reproduced in the mesocosm between 9 AM and 3 PM and 9 PM and 3 AM respectively. Outside these times, sediments were covered with seawater in the light during the day (from 3 PM to 9 PM) and in the dark during the night (from 3 AM to 9 AM). The sampling was done each day at the end of high night tide (7:30 AM), at the beginning (10:30 AM) and the end (1:30 PM) of low day tide and beginning of high day tide (4:30 PM). For each sampling, three individual cores

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