Journal of Sea Research 92 (2014) 2–5

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Introductory paper

Ecology of intertidal microbial biofilms: Mechanisms, patterns and future research needs

Carl Van Colen [a,*,1], Graham J.C. Underwood [b,2], João Serôdio [c,3], David M. Paterson [d,4]

[a] Ghent University, Marine Biology Research Group, Krijgslaan 281-S8, B-9000 Ghent, Belgium
[b] School of Biological Sciences, University of Essex, Colchester, Essex CO4 3SQ, UK
[c] Departamento de Biologia and CESAM — Centro de Estudos do Ambiente e do Mar, Universidade de Aveiro, Campus de Santiago, 3810-193 Aveiro, Portugal
[d] Scottish Oceans Institute, School of Biological Sciences, University of St Andrews, KY16 8LB, UK

1. Introduction

There is a continual struggle in ecology to improve our understanding of the complex interactions that take place between organisms and their surroundings at the genetic, species, community and ecosystem level. These interactions, and the transfer of material and energy that they support, drive the functional capacity of any ecosystem (Solan et al., 2012). Intertidal soft-sediments of temperate estuaries and shallow coastal lagoons are ranked among the most productive marine ecosystems (Heip et al., 1995) and are critical habitats in determining the sediment transport balance between the terrestrial and marine realm. On intertidal sand and mudflats, microbial biofilms, that are complex agglomerates of prokaryotes and microbial eukaryotes like diatoms, protozoa and fungi (Decho, 2000), are instrumental to both processes by affecting sediment stability through the secretion of extracellular polymeric substances (EPS) (Underwood and Paterson, 2003) and by regulating the energy transfer through the benthic food web as a major food source for herbivore consumers (Herman et al., 2000). Autotrophic diatoms are major components of the biofilms and contribute significantly to estuarine primary production (i.e. 29–314 g C $m^{-2} \cdot yr^{-1}$; Underwood and Kromkamp, 1999), thereby supplying energy resources to biofilm consumers and their predators, while the heterotrophic prokaryotes are the primary remineralizers of organic matter. The exposure to highly variable and often extreme conditions is a regulating feature of estuarine conditions that determines biofilm properties. For example, UV radiation (Mouget et al., 2008; Waring et al., 2007), dessication and change in temperature and salinity (Coelho et al., 2009; Rijstenbil, 2005) during emersion; and hydrodynamic forces and sediment transport associated with currents and waves during submersion (Van Colen et al., 2010a; Widdows et al., 2004), have survival implications for the structure and functioning of biofilms and therefore require adaptation mechanisms such as the vertical migration exhibited by diatoms (Brotas et al., 2003; Consalvey et al., 2004; Jesus et al., 2006).

As an introduction to this special issue, we summarize the current knowledge of the mechanisms that underpin the dynamics in properties and functionality of tidal flat biofilms. This review therefore elaborates on (1) microbial interactions and the production of EPS, (2) photophysiological stress responses, and (3) mechanisms of benthos–pelagic coupling, including the role of grazer interactions, which are all instrumental to the spatio-temporal dynamics of microbial biofilms. In addition, we identify future research needs that will help to further unravel the aforementioned physiological processes and ecological interactions, thereby enhancing our ability to better assess the functional capacity of tidal flats.

2. Microbial interactions and the production of EPS

Marine benthic diatoms and bacteria produce many different EPS, mainly heteropolymers that are rich in glucose and galactose (Bellinger et al., 2005, 2009; Hoagland et al., 1993). The production of these molecules is highly variable (e.g. Pierre et al., 2014-this volume) and is moderated by environment factors (e.g. light and nutrient stress; Staats et al., 2000; Underwood, 2002; Underwood and Paterson, 2003), rhythms of vertical migration (Hanlon et al., 2006; Perkins et al., 2001; Smith and Underwood, 1998) and interactions between microbial taxa (Bruckner et al., 2011; Grossart et al., 2005; Vanelslander et al., 2009).

There is a rapid transfer of fixed carbon from photosynthesis into EPS, and then into heterotrophic organisms (Bellinger et al., 2009; Cook et al., 2007; Goto et al., 2001; Middelburg et al., 2000; Moerdijk-Poortvliet et al., 2014-this volume; Oakes et al., 2010; Perkins et al., 2001; Smith and Underwood, 1998). Smaller polysaccharides and other algal-derived carbohydrates are rapidly degraded by bacteria under aerobic conditions, followed by the utilization of larger colloidal and more insoluble EPS constituents (Giroldo et al., 2003; Goto et al., 2001; Haynes et al., 2007; Hofmann et al., 2009), and EPS carbon has been tracked into the phospholipid fatty acids (PLFA) (Bellinger et al., 2009; Gihring et al., 2009; Middelburg et al., 2000) and RNA (Taylor et al., 2013) of various bacterial groups. Correlations are also found between enzyme activity rates (e.g. β-glucosidase), changes in concentrations of various sediment carbohydrate fractions (Bhaskar and Bhosle, 2008; Haynes et al., 2007; Hofmann et al., 2009; McKew et al., 2011),

---

[*] Corresponding author.
E-mail address: carl.vancolen@ugent.be (C. Van Colen).

[1] Carl Van Colen is a post-doctoral research fellow in Marine Ecology at the Research Group of Marine Biology, Ghent University, Belgium.

[2] Graham Underwood is a Professor of Marine and Freshwater Biology at the University of Essex, UK.

[3] João Serôdio is an Assistant Professor in the Department of Biology of the University of Aveiro, Portugal.

[4] David Paterson is a Professor in Coastal Ecology at the University of St Andrews, UK.

http://dx.doi.org/10.1016/j.seares.2014.07.003
1385-1101/

and shifts in the bacterial community (Hanlon et al., 2006; Haynes et al., 2007; Orvain et al., 2014-this volume-a). There is some evidence of benthic diatoms utilizing carbohydrates from their environment (de Brouwer and Stal, 2002; Smith and Underwood, 2000), though is not clear whether diatoms can utilize EPS directly, or benefit in some other way from enhanced bacterial activity within biofilms (Bruckner et al., 2011; Croft et al., 2005; Taylor et al., 2013).

The production of a mixture of labile and more refractory carbon sources by diatom biofilms, and the links between autotrophic and heterotrophic activity provide a fertile situation for microbe–microbe interactions in intertidal sediments (Agogué et al., 2014-this volume). Most of this research has so far been on aerobic pathways of carbon flow that take place in the surface sediments near the sediment–water interface. To gain more insight in the microbial biotic interactions that drive the cycling of organic matter in tidal flat sediments, the biogeochemical links between diatom carbon production and anaerobic cycles that generally take place at greater depth require further investigation (McKew et al., 2013).

3. Coping with light stress

The highly variable environmental conditions of the intertidal environment are a likely cause of damage to the photosynthetic apparatus of biofilm microalgae, mainly through the accumulation of reactive oxygen species (ROS; Roncarati et al., 2008; Waring et al., 2010). High levels of ROS are a major cause of photoinhibition, causing a reduction in photosynthetic yield and primary productivity, mainly due to the inactivation of photosystem II protein D1 (Nishiyama et al., 2006). The high capacity of microphytobenthos to cope with high light stress has been hypothesized to result from the combined action of two types of photoprotective processes: (1) a particularly effective operation of the xanthophyll cycle, shown to occur in estuarine diatom species (Lavaud et al., 2007; Serôdio et al., 2005), and (2) vertical migration, a form of behavioral photoprotection unique to microphytobenthos, consisting in the regulation of light exposure by active cell movements within the light gradient of the sediment photic zone (Admiraal, 1984; Consalvey et al., 2004; Serôdio et al., 2006).

The effects of vertical migration on biofilm photophysiology have attracted a growing interest (Consalvey et al., 2004; Jesus et al., 2006; Mouget et al., 2008; Perkins et al., 2010; Waring et al., 2007). More recently, this topic has been approached through manipulative studies based on the application to biofilms of specific inhibitors of the main photoprotective processes, the xanthophyll cycle (Lavaud et al., 2002) and vertical migration (Cartaxana et al., 2011). Taking advantage of the possibilities offered by chlorophyll fluorescence imaging, allowing the simultaneous monitoring of a large number of samples, the use of inhibitors makes it now possible to evaluate the contribution of the two processes to biofilm-level photoprotection, as well as to estimate rates of photoinhibition (Serôdio et al., 2012). Despite the advantage of allowing the study of intact biofilms, approaches based on PAM fluorometry can only provide indirect evidence on the underlying biochemical processes. More direct and valuable information on the efficiency of photoprotection and on the extent of photoinhibition can be obtained by the quantification of the xanthophyll cycle pigments (Cartaxana et al., 2011) and of the protein D1 (Cartaxana et al., 2013; Domingues et al., 2012).

4. Grazer interactions and benthos–pelagic coupling

In the past, hydrodynamic stress was generally considered to drive the sediment transport (i.e. erosion versus accretion of particles) in tidal flat systems with the organisms having a fairly passive role in response to physical forcing. The classic book by Vogel (1994) helped change this perception and more recently the way in which many phyla of organisms both adapt to and moderate flow has become much clearer. For example, microbial biofilms enhance sediment adhesion and stability by increasing the erosion threshold through the production of EPS which traps and binds particles together (Stal, 2010). The understanding has also recently developed that the material that is eroded from the bed (primary particles, flocs and organic material) varies with the structural nature of the interface and the microbial assemblages that colonize it (Wiltshire et al., 1998). The critical thresholds of biofilm resuspension differ among microorganisms (Dupuy et al., 2014-this volume; Mallet et al., 2014-this volume) and the resuspended microorganisms may determine pelagic food web functioning (Montanié et al., 2014-this volume).

Stable isotope and fatty acid studies indicate that certain infaunal invertebrates (Moens et al., 2014-this volume), fish (Carpentier et al., 2014-this volume; Como et al., 2014-this volume) and shorebirds (Bocher et al., 2014-this volume; Cheverie et al., 2014-this volume; Lucia et al., 2014-this volume) feed substantially upon biofilm carbon resources, either directly or indirectly through predation on benthic invertebrates that rely on microbial biofilms for their diet, e.g. polychaetes, bivalves and crustaceans. These grazing activities disrupt and concurrently render the biofilm more susceptible to erosion (Orvain et al., 2014-this volume-b). In addition, infaunal invertebrates may also affect biofilm stability indirectly through bioturbation and bioirrigation activities that alter bacterial and diatom communities (Gilbertson et al., 2012) which are instrumental to the production of EPS (Hubas et al., 2013; Lubarsky et al., 2010). Moreover, the effect of biofilms on benthos recruitment success through the mediation of larval settlement (Harder et al., 2002; Van Colen et al., 2009) and growth of juvenile recruits (Van Colen et al., 2010b) has been demonstrated. Activities of these recruits, in turn, affect the spatio-temporal dynamics of biofilms (Weerman et al., 2011). Hence, the population dynamics and spatial distribution of macrobenthos are often tightly coupled to the spatio-temporal dynamics in biofilm biomass (De Backer et al., 2010; Van Colen et al., 2008, 2012). While organisms may thus modify the erosive process, those that have particularly strong effects on structuring the ecosystem are known as “ecosystem engineers” (Jones et al., 1994). Recently, the possibility that organism may “work together” to create beneficial conditions, affecting the erosion threshold of depositional habitats, has been proposed and termed “cooperative ecosystem engineering” (Passarelli et al., 2014-this volume). This improved and more holistic understanding of the bio-physical interactions and bentho-pelagic coupling in tidal systems helps addressing the natural complexity of the habitat and is to be encouraged. The variety of interactive mechanisms described above makes the understanding of the erosion process and related sediment dynamics a greater, and much more detailed, challenge than previously realized but the consequence will be a far clearer perception of benthic–pelagic coupling and system ecology (Saint-Béat et al., 2014-this volume).

5. Conclusion

Insights in the complexity of interactions that influence microbial biofilms, as reviewed above, would not have been achieved without the development of new technologies, both laboratory and field based, to support it, and the study of biofilm properties and processes across research disciplines (e.g. ecology, taxonomy, physiology). Consequently, such multidisciplinary studies should be stimulated, together with the development of new technologies, in order to enhance our understanding of the mechanisms that drive the dynamics of microbial biofilms in tidal flats, and their associated ecosystem functions. A major challenge remains to develop better methods that enable the quantification of key compounds within microbial biofilms, especially in the thin photic layers of the biofilm where light stress conditions take place.

Investigation of the mechanisms that drive the spatio-temporal dynamics of microbial biofilms clearly has a high socio-economic value, given the important ecosystem services delivered by biofilms, i.e. high rates of organic matter production resulting from photosynthesis that