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Relevance of macrozoobenthic grazers to understand the dynamic behaviour of sediment erodibility and microphytobenthos resuspension in sunny summer conditions☆

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ABSTRACT

The quantification of overall microphytobenthos productivity should include the export of biomass from the intertidal zone during high tides, which implies refined estimates and concepts of erosion parameters. For the first time, the export of microphytobenthic cells was assessed over an intertidal mudflat in the Marennes-Oléron Bay, France, during a complete spring/neap tide modulation. In the summer of 2008, resuspension rates of chl-*a* exported only reached 2.5% of the standing stock of benthic diatoms on each day. Sedimentary factors failed to explain any variation regarding bed and microphytobenthos erodibility. During the early fluff layer erosion phase, there were negative effects of grazing activities exerted by motile infauna (*Peringia ulvae*) on erosion fluxes of chl-*a*, while there was a related positive correlation with pheopigment proportion. The erosion process plays an important role in this vegetal–herbivore interaction by reinforcing the decline of the microphytobenthic biomass and provoking a catastrophic shift to mass erosion after a sequence of several days of co-occurring intense grazing by snails and chl-*a* decline. During mass erosion, the biofilm decline explained the variations of sediment erodibility, with a marked negative correlation between bound extracellular polymeric substance (EPS) proteins and critical threshold for bed erosion, in contrast with the commonly observed positive influence of EPS secretion on bed resistance. The complex nature of the effects of EPS by microphytobenthos must be further investigated to unravel their complex role in bioengineering sediments. The increase of protein proportion in EPS could provide specific properties related to hydrophilic features. Nevertheless, the level of grazing pressure by *P. ulvae* should be so intense that the top-down control must explain this original finding, since there was a positive correlation of proteins in EPS and snail density that could be related to mucus secretion (as a constitutive part of the EPS pool).

1. Introduction

In intertidal soft-sediment habitats, the microorganisms developing at the sediment–water interface form a consortium within a microphytobenthos (MPB) biofilm that is generally controlled by the physical environment. However, this biota also mediates physical processes as bioengineers (see Orvain et al., 2014-in this issue for details about potential interactions between microorganisms making the consortium). All microorganisms living upon bare intertidal mudflats can enter the pelagic food web, and can serve as food items for zooplankton and benthic suspension-feeders (Herman et al., 2000). Given the value of ecological processes in estuarine ecosystems and the level of human disturbance in these areas (shellfish exploitation, fisheries, littoral modification, watershed water discharge, accumulation of pollutants, eutrophication, etc.), it is of primary importance to understand the natural processes that govern their dynamics, and especially microphytobenthos resuspension. It remains an important challenge to quantify and model the complex dynamics and fates of matter and energy fluxes between sediment habitats and the water column, and to provide models predicting the overall functioning of intertidal ecosystems.

Benthic diatom resuspension into the water column is directly related to hydro-sedimentary dynamics, which is affected by Bed Shear Stress (BSS) itself, depending on the intensity of tidal currents and wind-induced waves. The erosion fluxes depend also on sediment

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erodibility, which is defined as the resistance of the sediment to erosion, a highly variable parameter in space and time (Tolhurst et al., 2003). The changes in bed erodibility result not only from complex interrelationships between sediment properties, bioturbation activities by macrofauna, and microphytobenthic biofilms especially in summer (Herman et al., 2001; Orvain et al., 2004; Thrush et al., 2012; Wood and Widdows, 2002); but also from events like direct rainfall, especially in winter (Pilditch et al., 2008; Tolhurst et al., 2008b). In more detail, the MPB could play a role as a sediment stabiliser, either by secreting EPS (exopolymeric substances), via binding properties, or by forming an armouring biofilm over the sediment surface (Tolhurst et al., 2003) in close association to the 3D-microstructural assemblage of microorganisms within the biofilm (de Brouwer et al., 2005). When biofilms are saturated with benthic diatoms, destabilising factors can also be imputed to some EPS fraction when they reinforce water retention of sediments by acting like sponges, or when they promote bacteria degradation of the biofilm, and disruption of the biofilm (Orvain et al., 2003; Yallop et al., 2000). The latter phenomenon probably remains rare in the field, but is easily induced in lab controlled conditions when processes responsible for MPB removal like resuspension and grazing by macrofauna are removed and biofilm thickness is increased (Tolhurst et al., 2008a).

There are many processes that could explain the nature of biostabilisation, but many still require further investigation, such as the effects of tidal variation along a spring/neap tidal cycle, which have not previously been described in literature. Simple projection on the observation of the short-term dynamics of MPB biomasses (Blanchard et al., 2002) suggested that resuspension of benthic diatoms should be important in the Marennes-Oléron Bay when shifting from spring tides to neap tides during the early spring or in summer, i.e. when microphytobenthos blooms develop, and when phytoplankton biomass remains low (Blanchard et al., 2002; Guarini et al., 2008). EPS-induced bioengineering of sediments must therefore be exacerbated in these conditions. The temporal patterns of MPB development and resuspension vary extremely depending on the spring/neap tidal cycle phase, seasonal patterns, and meteorological events (Orvain et al., 2012). The variability in light exposure and temperature at various temporal scales (hour–day–month–year) interrelate with an already complex network of interactions, so that MPB via sediment biostabilisation can be considered to be an ecosystem engineer resulting in idiosyncratic responses of the ecosystem's functions (Tolhurst et al., 2003) due to several feedback mechanisms especially with benthic fauna (Murphy and Tolhurst, 2009; Weerman et al., 2011). There is still a necessity to unravel the drivers of MPB and sediment erodibility, to be able to predict their erosion in natural settings where hydrodynamic drivers are now being predicted with improving accuracy.

The main objectives of the present study were to understand the sediment and biofilm parameters most able to control bed and microphytobenthos erodibility, and to quantify how these were affected by the tidal cycle. In addition, it was intended to assess whether the microphytobenthic resuspension net export could be predictable as a function of tidal and light conditions. To enhance the ability to detect effects of tidal regime, the experiment was conducted during 13 subsequent days, during high and low degrees of light exposure (see Table 1). If MPB and associated EPS alone were the most important factor in driving sediment erodibility, a consistent response to tidal effects would be expected to be seen (i.e. bottom-up effects). If grazing by macrofauna was the most important, strong dependence upon snail abundance and/or pheopigment, in addition to a lack of tidal influence, would be expect to be seen (i.e. top-down effects). In the present study, sediment and MPB erodibility parameters (critical BSS for erosion and erosion rates) were measured at the end of each diurnal low-tide of a 13-day period. These erodibility descriptors were compared to an exhaustive set of biofilm properties: MPB (chl-*a* concentration in the 1st mm, and the 1st cm, EPS carbohydrates, and proteins), bacteria, macrofauna, and sediment parameters. Recent studies on sediment erodibility used miniaturised techniques measuring critical threshold for erosion like cohesive strength meter (CSM) and magnetic particle induction (MagPI) to better unravel biologically mediated effects on physical processes in relation to patchiness and rapid changes over emersion periods (Lubarsky et al., 2012). Despite their convenience for rapid evaluation of bed adhesion and binding properties of EPS, these tools are not appropriate for quantifying erosion rates, especially when examining the chl-*a* resuspension, and to evaluate the sediment export by erosion forces. A classical flume study in the field remains appropriate to assess sediment and chl-*a* erosion rates. Besides, recent methodological advances have enabled more precise quantitative studies of sediment erodibility and the evaluation of bed erodibility. These are due to the refinements of bed sheer stress and roughness quantification, which are applied upon experimented sediments giving systematic estimates during each independent experiment. In addition, a new optimized procedure for EPS extraction has been developed to avoid contamination by cell-internal EPS (Takahashi et al., 2009), and a thorough description of EPS, including protein contents, has consequently been carried out.

2. Material and methods

2.1. Study site and environmental descriptors

The Marennes-Oléron Bay, France, consists of vast intertidal areas lined by a semi-diurnal macrotidal regime (tidal range of 6 m). Within

Table 1
Values of the different erodibility parameters measured at the end of emersion during 13 days in July 2008 (*SE*: standard error).

July	Critical threshold for chl-*a* fluff layer erosion (Pa)	Chl-*a* erosion rate (μg.m^{-2}.s^{-1})	Critical threshold for sediment mass erosion (Pa)	Sediment erosion rate (mg.m^{-2}.s^{-1})	Chl-*a* erosion rate (μg.m^{-2}.s^{-1})
	Fluff layer erosion		*Mass erosion*		
14	0.57	0.23	3.87	6.61	0.68
15	1.59	0.42	4.72	88.5	0.86
16	1.81	0.50	4.58	9.3	1.00
17	2.52	0.75	5.87	155.3	1.24
18	2.06	0.28	8.39	90.5	0.81
19	1.96	0.74	4.70	87.9	1.72
20	4.45	0.37	8.33	77.7	0.82
21	0.81	1.15	2.20	27.7	0.50
22	1.53	0.20	3.70	60.5	1.21
23	1.42	0.08	8.69	28.4	0.68
24	1.06	0.13	5.62	47.8	0.81
25	0.60	0.29	1.36	79.0	0.79
26	2.79	0.39	5.70	95.7	1.56
Mean	*1.78*	*0.42*	*5.21*	*72.4*	*0.98*
SE	*0.78*	*0.22*	*1.68*	*28.5*	*0.26*
% of error	*43.8*	*52.0*	*32.2*	*39.4*	*27.1*