



Modelling the effect of *Cerastoderma edule* bioturbation on microphytobenthos resuspension towards the planktonic food web of estuarine ecosystem



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ABSTRACT

Microphytobenthos (MPB) represents an important food source for primary consumers in estuarine ecosystems and the availability of MPB as food items results from complex physical, chemical, and biological interactions. In Baie des Veys (Lower Normandy, France), the common cockle *Cerastoderma edule* constitutes the major bioturbator in the ecosystem in terms of biomass. In this ecosystem, cockle bioturbation is a key process regulating the MPB erosion flux in the water column. This bivalve intensely modifies the top layer of the sediment by increasing the sediment erodibility and the fluxes of suspended chlorophyll *a* through the valve movements. More precisely, cockle bioturbation destabilizes the sediment surface by creating a biogenic layer that is easily eroded with tidal hydrodynamic forces. Associated MPB can then be exported to the water column to fuel higher trophic levels of the planktonic food web. The aim of this study was to develop a numerical model that reproduces the export of MPB associated to the biogenic layer erosion. Kinetics of suspended MPB, in response to increasing stress, were obtained from flume experiments in lab controlled conditions and *in situ* natural conditions. Following this, the suspended MPB were analyzed to respectively parameterize the model by (1) a calibration approach, and (2) an independent validation. The analysis has highlighted that the higher the biomass of cockles, the higher the MPB resuspension rates. Our model consistently reproduces the tendency encountered in laboratory analysis and with *in situ* natural conditions. During the validation, a small site-specific lack of adjustment was identified, but, among the macrozoobenthic community, the model can be significantly improved by considering the bioturbation activities of another ecosystem engineer, *Pygospio elegans*. This study thus provides reliable estimates of the daily food availability from benthic primary consumers in an estuarine system where cockles dominate the bioturbating assemblage. This model can be inserted in various model designs (0D, 1D-vertical or 3D).

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1. Introduction

Numerical modelling represents a useful tool to overcome complexity and temporal variations of marine ecosystems. It has been used to reproduce physical transport on tidal flat temporal pattern in estuarine system (e.g. Toorman, 2002). Such complex models simulate the temporal pattern of tidal flats through hydrodynamic disturbances which integrate sediment suspension and circulation (Cancino and Neves, 1999; Chao et al., 2008; Clarke and Elliott, 1998; Warner et al., 2008). Moreover, sediment erosion may also be mediated by biological activities (Kristensen et al., 2012; Orvain

et al., 2012; Widdows and Brinsley, 2002; Willows et al., 1998; Wood and Widdows, 2002). Biology can affect the sediment properties through faunal bioturbation process described by the same authors. Bioturbation is a key process in coastal system and greatly modifies the physical properties of the sediment (Andersen et al., 2010; Ciutat et al., 2006). Macrofauna bioturbation can stabilize or destabilize the sediment depending on the species. Macrozoobenthos changes the erodibility of the sediment. This process of ecosystem functioning has been modelled by simulating the bioturbation effect of macrofauna on sediment stability (Orvain, 2005; Orvain et al., 2003; Willows et al., 1998). Orvain et al. (2012) have validated a model of bioturbation effect of two macrofauna species (*Scrobicularia plana* and *Peringia ulvae*) on sediment erodibility. They stated that the effect of bioturbation on sediment properties remains a species-specific process. Moreover, Kristensen et al.

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(2012, 2013) clearly showed that faunal erosion impacts must preferably be evaluated in biomass units when developing bioturbation/erosion laws, however erosion laws remain species-specific (Kristensen et al., 2012; Orvain et al., 2012). Species such as the bivalve *S. plana* have strong erosion impact in the sediments they inhabit while *P. ulvae* have strong surface effects, especially when compared in biomass unit. *P. ulvae* also have strong grazing effects on microphytobenthic biofilms (Orvain, 2005; Orvain et al., 2014) and the important surface area can be rapidly covered, even by one single individual (Orvain et al., 2012).

Moreover, the study of the benthic autotrophic compartment has also been modelled with special focus on the role of microphytobenthos (MPB) resuspension and the dynamics of its biomass (Guarini et al., 2008; Mariotti and Fagherazzi, 2012). Export of MPB in the water column is a key process that maintains the biofilm development and avoids the saturation of MPB development in the sediment (Blanchard et al., 2001). A realistic simulation of resuspension of MPB biofilm can be obtained only if this process is not associated to the strong erosion of the underlying sediment (Guarini et al., 2008). The mass bed erosion is a strong event that has a too drastic influence on chlorophyll *a* biomass dynamics to let develop the biofilm at a sustainable equilibrium state. The model developed by Guarini et al. (2008) represents detachment process that continually and moderately affects the benthic marine MPB biofilms under low hydrodynamic forces. In nature, such chronic detachment of benthic microalgae can be assumed to be equivalent to the commonly named “fluff layer erosion” by Shimeta et al. (2002) and Orvain et al. (2003), mainly related to bioturbation activities (Orvain et al., 2004). Mariotti and Fagherazzi (2012) have developed a model of growth and resuspension of MPB biofilm development under hydrodynamic disturbances. The chronic detachment of MPB biofilm was integrated in a simple manner in the model, which corresponds to the resuspension of MPB described by Guarini et al. (2008). They have also integrated the erosion of the sediment in the model, which occurs in a case of high hydrodynamic forcing, and traditionally considered as “bed erosion” (type Ib or type II erosion, according to the definition by Amos et al. (1992). Mariotti and Fagherazzi (2012) have pointed out that the intensity, the frequency of hydrodynamic disturbances, and the time scale dynamic of MPB growth are decisive factors for MPB temporal pattern.

The common cockles (*Cerastoderma edule*) move in their environment and rework the sediment particles, modifying the chemical and physical properties of their habitats (Hedman et al., 2011). There is some controversy about the effect of this species on sediment erodibility. The destabilizing (Ciutat et al., 2006, 2007) or stabilizing (Andersen et al., 2010) effect of cockles has been counteracted. Nonetheless, Andersen et al. (2010) have highlighted the stabilizing effect of MPB biofilm, such as other studies have found in absence of fauna (Sutherland et al., 1998; Underwood and Paterson, 1993). Also, they explained the lack of destabilizing effect of cockles in their results as the direct consequence of the entirely buried position of cockle during the experiments. They then stated that the position of the cockle in the sediment can increase the bed roughness. Otherwise, species-specific behaviour such as filtration, valve movement, and burying activity, common to the cockle, disturbs the sediment and leads to the erosion of sediment at a lower shear stress as compared to an undisturbed sediment. Experiments conducted by Jonsson et al. (2005) also support the assumption that cockles directly consume a part of suspended algal matter, playing a key role by disturbing turbulence in the benthic boundary layer. Cockles can thus be considered as an engineer species that physically disturbs sediment and water column allowing MPB availability in the ecosystem.

To the best of our knowledge, there is a dearth of modelling the export of MPB in the water column associated to sediment erosion

due to macrofaunal bioturbation. We need to bridge the gap between modelling the chronic detachment of MPB and the fluff layer erosion in a bioturbated system, to better evaluate the role of these ecosystem engineers. The purpose of this study was to assess the predictability of MPB erosion by using bioturbation/erosion laws that have only been used in the past for modelling sediment transport (Orvain et al., 2012) in a bioturbated system. More specifically, we aimed at refining the way to model the ‘chronic’ fluff layer erosion and the associated MPB under the bioturbation action of the bivalve *C. edule* in the Baie des Veys (Normandy-France), where this species drastically dominates the wild macrofaunal community (Ubertini et al., 2012). The objective of this study was to model the erosion rate of MPB in response to various body sizes and densities of cockles and thereby determine the food availability of benthic primary producers for the cockles and associated suspension-feeders in estuarine ecosystems. The model of fluff layer erosion has been parameterized with experimental data by following a 2-step approach: (1) calibration of erosion parameters related to bioturbation on the basis of experimental data in controlled lab conditions, cockle density and body size, and (2) validation performed with *in situ* data from three locations in the Baie des Veys (Normandy-France). The validation step was conducted without readjusting the parameters to assess the model fitness to independent *in situ* data. The residuals between modelled and observed data were computed to discuss fitting adjustment.

2. Data

2.1. Laboratory experiments

Experiments were conducted to determine the effects of cockle bioturbation on the resuspension rates of microphytobenthic biofilm in the water column. Density effect of juveniles (0.25–1.4 cm) and adult cockles (2.2–2.7 cm) were experimented. Erosion was conducted with the Erodimeter flume. Details of the functioning of the flume are explained in Le Hir et al. (2008). The device allowed the imposition of controlled bed shear velocities (u^* ca 1.40–4 cm s⁻¹) on sediment cores of microphytobenthos and cockle culture. Tested velocities were incrementally increased every 5 min, constituting the forcing factor for the model developed later. Probes connected to the flume recorded continually: (i) the flow discharge; (ii) the pressure upstream and downstream the sediment core; (iii) the turbidity; and (iv) the suspended Chlorophyll *a* biomass (calibrated with the fluorimetry). Following the method of Guizien et al. (2012), the bed shear stress (τ_f , Pa or kg m⁻¹ s⁻²) was calculated. The recorded fluorescence was also converted in quantity of chlorophyll (Chl a_{probe} , $\mu\text{gChl } a \text{ L}^{-1}$) in the water column. Chl a_{meas} , which represents the quantity of eroded chlorophyll *a* per unit of area ($\mu\text{gChl } a \text{ m}^{-2}$) was deduced with the product of chlorophyll *a* concentration ($\mu\text{gChl } a \text{ L}^{-1}$) and the volume of the Erodimeter (L) over the surface of the core (m²). Water was sampled at 3 different flows (1.65, 2.97, 3.94 cm s⁻¹), was filtered with Whatman filters (GF/C 47 mm), and treated to determine the concentration of suspended matter (in g L⁻¹) and the concentration of suspended chlorophyll *a* (in $\mu\text{g L}^{-1}$).

2.2. Chlorophyll *a* correction

Studies conducted by Jonsson et al. (2005) have shown direct consumption of a part of suspended matter exported in the water column by cockles. A high resolution camera was placed over the sediment cores during the erosion experiments. Time during which an active filtration occurred (t_{fil} , s) was then deduced from siphon movement. Given that cockles filtered a certain quantity of suspended chlorophyll *a* during the experiments, the filtration

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