Modelling the effects of macrofauna on sediment transport and bed elevation: Application over a cross-shore mudflat profile and model validation

Francis Orvain[a, b, *], Pierre Le Hir[d], Pierre-Guy Sauriau[c], Sébastien Lefebvre[e]

[a] Université de Caen, FRE3484 BioMEA – CNRS, Esplanade de la Paix, B.P. 5186, 14032 Caen Cedex, France
[b] CNRS, UMR 7208 BOREA, Muséum d'histoire naturelle, CRESCO, 38 Rue du Port Blanc, 35800 Dinard, France
[c] LIENSs, CNRS, Université de la Rochelle, 2 rue Olympe de Gouges, 17000 La Rochelle, France
[d] IFREMER, Centre de Brest, laboratoire DYNECO, BP 70, 29280 Plouzané, France
[e] Université de Lille 1 Sciences et Technologies – CNRS, UMR 8187 Laboratoire d'Océanologie de Géosciences, Wimereux Marine Station, 28 av. Foch, 62930 Wimereux, France

*: Corresponding author : Francis Orvain, email address : francis.orvain@unicaen.fr

Abstract:

The effects of 2 functional groups of bioturbators have been predicted in terms of long-term impact on erodability: (1) one superficial mobile deposit-feeder, the gastropod *Hydrobia ulvae*; and (2) one endobenthic deposit-feeder, the bivalve *Scrobicularia plana*. Different scenarios of morphodynamical cross-shore 1DH/1DV model were performed to simulate the equilibrium profile of an intertidal mudflat under tide and wave forcings. This process-based model for erosion is able to simulate multiphasic sequential resuspension, by discriminating various erosion behaviour like benthos-generated fluff-layer erosion (BGFL) and general bed loosening and burrowing activity in deep layers. The results were analysed and compared to examine the long-term effect of macrofauna after 14 years. It reveals that the impact of the bivalve *S. plana* is very significant after only 4 years of simulation while the effect of the gastropod *H. ulvae* is negligible in terms of sediment transport even after 14 years. More generally, this reveals the strong impact of stationary endobenthic bioturbators that induces a high downward shift of the upper shore while the effects of superficial motile bioturbators remain very low. This impact is mainly due to the effect of endobenthic species in deep layers associated to burrowing activities and their consequences on the bed erosion, but the production of a fluff layer by surface grazer like *H. ulvae* at the sediment surface can be neglected. The importance of macrofauna mediation of bed erodability is discussed in this study by comparing the activities of the two functional groups of bioturbation on the general functioning of intertidal mudflats. The model outcomes (transferred in a 1DV framework) were in close agreement with the measured results of flume data at 3 different bathymetric levels of the mudflat over the cross-shore profile. This validation step revealed that model of sediment transport under influence of biota effects does not need further refinements at the upper shore where *S. plana* dominates the species assemblage, whereas there is still a need to include further formulations of biota effects to simulate the erosion experimental results at the lower shores where other molluscs and Annelids significantly contribute to the species assemblage.

Keywords : modelling ; sediment dynamics ; erodability ; bioturbation ; macrofauna ; biota ; sediment stability

1. Introduction

The effects of microphytobenthos, macrofauna and marine vegetation on sediment erodability have been widely described in literature (see the review by Le Hir et al., 2007). Macrofauna effects are very complex even for a single species and also greatly vary both in time and space. Epibenthic deposit-feeders living on bare intertidal mudflats have systematically been reported to increase erodability of surficial cohesive sediments through bed material pelletisation, the production of large amount of easily-resuspended pseudofaeces by bivalves and surface tracking (Willows et al., 1998; Wood and Widdows, 2002; Orvain, 2005; Le Hir et al., 2007, van Prooijen et al. 2011). This process is mediated by the formation of a "biogenic" fluff layer (BGFL) that is easily resuspended before the bed erosion (Willows et al., 1998; Orvain et al., 2003; Orvain, 2005). The surface sediment can be covered by a layer that is actively reworked by macrofauna in relation to their feeding behaviour, while deep layers are more resistant to erosion because of consolidation and the absence of reworking macrofauna. Those deep layers can also be affected by animal activity when the species inhabit deep burrows. The erosion behaviour differs from the surface layer to the deep layers according to the vertical position in the sediment matrix (Orvain et al., 2003; Orvain, 2005; van Prooijen et al., 2011)

A biogenic fluff layer is generated by the macrozoobenthos and has its own specific behaviour in terms of erodability that differs from that of the sediment bed itself (BGFL in Fig. 1). In sediment budget models (Orvain et al., 2003; Orvain, 2005), this fluff layer is a specific compartment of sediment with a low critical erosion threshold (T_{bio}) and its production is based on biological activities and feeding behaviour (crawling activities and biodeposit production). The biological activities at the sediment surface are thus responsible for multiphasic resuspension (Orvain et al., 2003) with first the fluff layer erosion followed by the bed erosion. These refinements of sediment erosion in a process-base model have been recently added in another model structure (van Prooijen et al., 2011) to revisit the analysis of anterior data that quantified the density effects of another bioturbator, like the bivalve *Macoma balthica* (Willows et al., 1998) and the cockle *Cerastoderma edule* (Ciutat et al., 2006).

Some species can also have an additional effect by the presence of deep burrows that destabilise subsurface sediments and lead to bed erosion. For example, the bivalves *Scrobicularia plana* can have the two potential effects (pseudofaeces creation at the surface contributing to the generation of a BGFL and modification of the bed erosion by creating burrows in subsurface sediments) while the gastropod *Hydrobia ulvae* only contributes to the formation of a BGFL (i.e. the tracks of the snail and faecal pellets; Andersen, 2001; Orvain et al., 2003; Fig. 1). This is also the case for the bivalve *Macoma balthica* (van Prooijen et al., 2011).

Previous experiments have been performed to quantify and model the bioturbation effects of the two species *S. plana* and *H. ulvae* (Orvain et al., 2003; Orvain, 2005). Fieldwork has also confirmed that these two species are very active in the control of bed erodability in the Marennes-Oléron Bay (Orvain et al., 2007). In the present study, these well documented biological processes and parameterised erosion function have been taken into account in a one-dimensional cross-shore model framework (1DH/1DV) in an attempt to examine long-term effects of these species on bed elevation of intertidal mudflats after 14 years. The effects of the two destabilizers were analysed in large-scale applications to understand the long-term effects on morphology of mudflats. A validation exercise of erosion laws was also carried out to test the model conceptualization and parameterization to better illustrate the potential improvement that can be done in future model developments. On the basis of modelling tools that exist now, the aim of the present study is to develop a pioneering strategy to improve representation of benthic processes in future models of sediment

transport as well as trophic food webs implying exchanges between benthic and pelagic compartments, for which the process-based models could be appropriate.

2. Material and methods

2.1. Model design and variables

A cross-shore morphodynamical model of an intertidal mudflat (Brouage in the Marennes-Oléron Bay) was used to evaluate the change of the equilibrium profile of the bed elevation with a time-step of 10 seconds. This model is a streamlined version of the SIAM 3D along a horizontal axis across a theoretical mudflat (Waeles et al., 2004). Navier-Stokes equations were solved for computing currents and wave propagation is calculated by solving a wave energy equation.

The model solved the Navier-Stokes equations describing the conservation of momentum and the viscous shear stress:

$$\frac{\partial \rho U}{\partial t} + \frac{\partial (\rho u w)}{\partial z} = -\frac{\partial p}{\partial x} + \frac{\partial}{\partial z}(\tau_{xy})$$

(1)

Viscous shear stress reads the following equation:

$$\tau_{xy} = \rho \upsilon \frac{\partial u}{\partial z},$$

(2)

where U = the mean velocity (m.s^{-1}), p = pressure (kg.m^{-1}.s^{-1}), t = time (s), u = the horizontal component of the current velocity vector (m.s^{-1}), w = the vertical component of the current velocity vector (m.s^{-1}), x is the horizontal co-ordinate (m), z is the vertical co-ordinate (m), υ is the kinematic viscosity of the suspension (10^{-6} m^2.s^{-1}) and ρ = the water density (kg.m^{-3}). Turbulent closure used the turbulent viscosity (and diffusivity) concept following the mixing length theory. The turbulent viscosity (N$_z$) and diffusivity (K$_z$) were corrected by a damping factor, which was calculated from the Richardson number Ri (see Cugier and Le Hir, 2002 for a detailed description).

The sediment transport module solves an advection-dispersion equation for the mass-conservation of suspended mud (Le Hir et al., 2011) modified by to include a bed-erosion term (Q_E in kg.m^{-2}.s^{-1}) and a bioresuspension term (Q_E^{bio} in kg.m^{-2}.s^{-1}) as in Orvain et al. (2003):

$$\frac{\partial C}{\partial t} + U \cdot \left(\frac{\partial C}{\partial z}\right) + Ws\frac{\partial C}{\partial z} = K \cdot \frac{\partial^2 C}{\partial z^2},$$

(3)

where C is the concentration of suspended sediment by mass (kg.m^{-3}). The bed shear stress (τ_0) was represented by means of a uniform Nikuradse roughness height k$_s$ of 1 cm.

Boundary conditions are determined by bed exchanges. Sediment source is the sum of 2 erosion terms $(Q_E + Q_E^{bio})$ and sediment sink is the deposition term Q_D. The 3 deposition and erosion terms were calculated at every time-steps. The detailed equations and parameters for the calculation of bed erosion and bioresuspension are presented in Orvain et al. (2003) and Orvain (2005).

The bathymetry was recomputed at all implemented time-steps and directly results from the net difference between Q$_D$ – Q$_E$ – Q$_E$^{bio}. The muddy sediment was transported in suspension (see Le Hir et al, 2011 for the equations of motion) with deposition and erosion represented with Krone and Partheniades formulas (Q$_D$ and Q$_E$). Biological activities were included by taking into account a BGFL with its own behaviour in terms of production and erosion Q$_E$^{bio} (i.e bioresuspension). This is the first time that this cross-shore model including effects of

macrozoobenthos is described. The 2 erosion processes were actively computed on each implementation.

There is a bed load that is directly eroded from the upper layer of the sediment and a small quantity of sediment that is indirectly resuspended by being first manipulated by bioturbators (through the BGFL). First, the bed-erosion term Q_E was calculated from the Partheniades law for consolidated sediments:

$$Q_E = E_0 \times \left(\frac{\tau_0}{\tau_{ce}} - 1 \right) \text{ when } \tau_0 > \tau_{ce}; \quad Q_E = 0 \text{ when } \tau_0 < \tau_{ce},$$

(4)

where E_0 is the erosion rate (2.5×10^{-5} kg.m^{-2}.s^{-1}) and τ_{ce} the critical shear stress for erosion or "abiotic" erosion threshold (0.5 Pa). For bed erosion, the concept of active layer is used to allow further erosion down to the base of the active layer by dividing the timestep dt in a series of smaller time steps dt1 (the time of eroding the layer at a given rate). If the total quantity of sediment that could be eroded is higher than the quantity of sediment comprised in the first superficial layer, the sediment in this layer in question is fully exported toward the water column, and the erosion rate of the next remaining layer that must be eroded more in depth, is eroded only during the amount of time dt1 that is diminished because of the time already used to erode the first layer. Density effects of *Scrobicularia plana* clearly modified the critical bed shear stress for bed erosion in benthic flume due to their burrowing activity in deep layers of the sediment matrix (Orvain, 2005). Based on these experimental results of and associated model parameterisation, a biotic effect related to *S. plana* bioturbation (animal density n in ind.m^{-2}) was included to modify the critical threshold for bed erosion :

$$\tau_{ce} = 0.35 \times \exp^{-0.0478 \times n} + 0.15$$

(5)

This equation represented the destabilising influence of the siphon activity on surface and subsurface of sediments (several centimetres in depth) was confirmed on the field where dense populations of *S. Plana* are present (Orvain *et al.*, 2007). By applying this equation, the critical BSS for erosion free of biological activities (when *n=0*) was set at 0.5 Pa and could reach the lowest value of 0.15 Pa in case of very dense *S. Plana* populations.

BGFL was than created at the upper bed layer (the production flux is $\mathbf{Q}_P^{bio}$) and the quantity of sediment was determined by animal activities. This parameter was necessary to quantify bioresuspension term ($\mathbf{Q}_E^{bio}$). In fact, $\mathbf{Q}_P^{bio}$ is equal to 0 at all layers except at the surface layer where biodeposits are produced. This term is included in Eq. 4 to guarantee mass-conservation.

The complete biological module including bioturbation effects was given in Orvain et al. (2003). In this model, there was a specific layer of sediment that included a BGFL created by the animal activities (tracks, biodeposits in fig. 1). For the sake of mass-conservation, the sediment was taken from the upper layer of the simulated bed and supplied the sediment in BGFL (A_t in kg.m^{-2}):

$$\frac{\partial \text{BGFL}}{\partial t} = Q_P^{bio} - Q_E^{bio}$$

(6)

This surface compartment comprised only one layer and the thickness of this layer is implemented at each time-step by considering a constant sediment concentration of this loose material (ρ_{BGFL}=100 kg.m^{-3}). Sediment from the water column never returns directly to the BGFL (even if resuspended) and settling sediment is not added to the fluff layer but returns to the „normal„ sediment.

Before calculating the bioresuspension term ($\mathbf{Q}_E^{bio}$), the BGFL production term is calculated ($\mathbf{Q}_P^{bio}$). The 2 bioturbators successively contribute to supply sediment from the upper layer of the bed to this BGFL compartment.

For *Hydrobia ulvae*, the equations for track production were used to compute the resulting suspended particular matter in the water column. In the first version of the model (Orvain *et al.*, 2003), the parameters differed according to the state of the sediment-water interface (emersion/immersion, dry sediment density, chl *a* content, day/night, behavioural features), the activity of animals widely fluctuating in nature and experiments. We considered a constant dry sediment density (600 kg.m^{-3}), and we tested a scenario with a constant activity of bioturbation at the interface (except that bioturbation activity was set to 0 during flood and ebb periods of the high tides because snails are resuspended in such conditions and are unable to graze the sediment at the surface). The values of the parameters were given to consider that the snails were always covered by water (as in runnels from the Brouages mudflat), on illuminated sediments without chl *a* and without variation of the crawling snail density. In these conditions, the tracking and grazing activities are maximal (Orvain and Sauriau, 2002; Haubois *et al.*, 2005). Track production (in kg.m^{-2}.s^{-1}) was computed by the following equations:

$$Q_P^{bio} = n \times \phi \times BGFL_{max} \times a \quad \text{and} \quad \phi = 1 - \frac{BGFL}{BGFL_{max}},$$

$$(7)$$

where $BGFL_{max}$ is the maximum (0.0169 kg.m^{-2}), *a* is the fraction of sediment area covered by tracks (unitless), *n* is the snail density (ind.m^{-2}), *a* is the individual snail crawling rate (2.54 x 10^{-9} m².s^{-1}.ind^{-1}). Due to overlapping feeding areas, the effect is non-linear with density of the animals or bioturbation timesteps as showed in past studies on *Hydrobia* crawling behaviour (Orvain and Sauriau, 2002; Orvain *et al.*, 2003; Orvain, 2005).

For *Scrobicularia plana*, BGFL was constituted by biodeposits that are easily resuspended (faeces and pseudofaeces in Fig. 1). During the parameterisation of this formulation by a direct comparison to data from flume experiments (Orvain, 2005), the production rate of pseudofaeces was considered as a linear function of animal density and bioturbation time. Contrary to *Hydrobia ulvae* bioturbation, this means that there was no saturation process in the BGFL production provoked by a lack of spatial coverage by bioturbated sediments (see Orvain, 2005 for a detailed explanation of the mechanism). For *S. plana* and contrary to observation made on other tellinids, like *Macoma balthica* in the model by van Prooijen *et al.* (2011), we did found such linearity with animal density within the range observed on the field while a lack of linearity was observed for he bivalve *M balthica*. This could be explained by differing feeding behaviour between *M. balthica* and *S. plana* in terms of overlapping of reworked layers (for instance, we can imagine a higher feeding radius siphon extension for *M. balthica*, a higher limitation of siphon activity at the sediment surface due to interaction with microphytobenthic biofilm, or different spatial small-scale aggregations that are not randomly distributed...), but it can also be related to the different vertical position of *Scrobicularia plana* within the sediments and they could also expel high amounts of sediment coming from deep layers, by avoiding to rework an already bioturbated material. They sometimes expel some deep oxygen-reduced sediments and they are likely to avoid to consume their own pseudofaeces. During the parameterization step of this function by minimisation of resuspended erosion rates (model versus observed data), we also found that the bioturbation activity and BGFL production continued to develop during immersion phases and even at high current velocities. Observations of bivalve behaviour during flume experiments suggested that a direct bioresuspension remained active during the immersion and flood periods and this linear relationship was retained even during immersion periods (Orvain 2005). This could be ascribed either to active filtration of the suspended particulate matter (SPM) in the water column during immersion periods with their siphons or to bivalves sucking up the surface sediments at the entrance to their burrows (and in deeper reduced layers). There was a high diversity of feeding behaviours observed during flume experiments. The retained equation was as follows:

$$Q_P^{bio} = n \times b,$$
<div align="right">(8)</div>

where b is the coefficient of creation of pseudofaeces set to a value of $4,12.10^{-12}$ kg.ind^{-1}.s^{-1} by using parameters from Orvain (2005) and by considering the averaged length size L=12,65 mm of *Scrobicularia* populations on the field study in Orvain *et al.* (2007).

Finally, the additional erosion term (Q_E^{bio} in kg.m^{-2}.s^{-1}) was used to calculate the precocious resuspension of BGFL:

$$Q_E^{bio} = \alpha \times \text{BGFL} \times \left(\frac{\tau_0}{\tau_{bio}} - 1 \right) \text{ when } \tau_0 > \tau_{bio}, \text{ else } Q_E^{bio} = 0$$
<div align="right">(9)</div>

This sediment compartment in the model has its own specific critical threshold for erosion (τ_{bio}) that remained contant in different experimental conditions (Orvain *et al.*, 2003; Orvain, 2005). The erosion rate depended on sediment mass in snail tracks that is easily resuspended (i.e. BGFL in kg.m^{-2}). The parameter α was a specific coefficient for the erosion of BGFL (1.5×10^{-4} s^{-1}). Most of the time, bioresuspension can occur alone (when $\tau_0 > \tau_{bio)}$ but the 2 resuspension exports Q_E and $\boldsymbol{Q_E^{bio}}$ can also co-occur when the shear stress is in excess compared to the critical bed shear stress of the „normal" sediment (when $\tau_0 > \tau_{ce)}$. Similarly to the original 1DV process-based model (Orvain et al. 2003), we incorporated a variation of the critical shear stress in relation to the sediment quantity remaining attached to the bed (A_t) :

$$\tau_{bio} = \tau_{bio}^{up} + \delta \frac{A_{t=0} - A_t}{A_{t=0}}$$
<div align="right">(10)</div>

With δ = 0.744 Pa (coefficient rate of increase of τ_{bio} according to the quantity of bioturbated sediment remaining at the sediment surface). The maximum value of τ_{bio} at the beginning of erosion of the BGFL is 0.12 Pa.

The deposition of suspended sediment on the upper bed layer was determined by local shear stress and the settling velocity of the particles. The deposition term Q_D (kg.m^{-2}.s^{-1}) was calculated by reading Krone formulation:

$$Q_D = w_s C \left(1 - \frac{\tau_0}{\tau_{cd}} \right) \text{ when } \tau_0 > \tau_{cd}; \quad Q_D = 0 \text{ when } \tau_0 < \tau_{cd},$$
<div align="right">(11)</div>

where w_s is the settling velocity (mm.s^{-1}) and τ_{cd} the critical BSS for deposition (= 0.1 Pa). The settling velocity was assigned a high value (0.5 mm.s^{-1}) to account for flocculation processes. The upper layer of sediment received this sediment flux and this layer thickness is calculated by setting the sediment concentration to a value of 100 kg.m^{-3}.

The settling velocity depended on the relative density of the resuspended particles, and also on the degree of aggregation that is determined by suspended sediment concentrations (see Le Hir *et al.*, 2011 for more details).

The sediment module was a multilayer model where the sediment bed was divided into several layers with varying thickness.

2.2. Scenario conditions

Boundary conditions consisted of a sinusoidal tide elevation (4-m range) and a steady concentration of suspended sediment during flood periods. The computational grid was a one layer 1DH cross-shore channel with a 100 m horizontal resolution. The daily values of external SPM supplied were the same for all scenarios. In other studies simulating the impact of benthic organisms on the geomorphology of mudflats, sand-mud morphodynamical

models were used (Waeles *et al.*, 2004; Paarlberg *et al.*, 2005; Borsje *et al.*, 2008). This degree of complexity is not necessary for simulating the Brouages mudflat ecosystem since the flats contain only mud (Le Hir *et al.*, 2000).

The simulation of the wave signal (Fig. 2) was based on a 1-year survey of wave height in the Marennes-Oléron Bay (Monbet *et al.*, 2006). For the sake of simplicity, the signal was described by a sequence of computed waves. During fall and winter we considered a wave regime (10 cm height, 3 s period), but storms (lasting during 12 hours every 10 days), the wave regime changed (40 cm height ; 5 s period). During spring and summer, wave regime was modified, with a normal regime (5 cm height ; 3 s period) and storms (15 cm ; 4 s).

The consolidation was not accounted for in the model but a 4-m muddy sediment layer of relatively compact sediments (600 kg.m^{-3} dry density) was considered over the rigid bottom. The natural heterogeneity of the bedforms could not be taken into consideration in the cross-shore model. The initial slope of the simulated flat was low (5 km long for 4-m difference between the low and high tides). The simulations were designed to represent the natural processes occurring on the top of the ridges where compact sediments are always found. The Brouages flats are easily drained through the fine network of runnels. Due to the limited resolution of the model, we could not represent the different erosion and deposition fluxes between the crests of the ridges and the runnels that are always covered by running seawater. Lab studies clearly show the importance of sediment dryness, which not only determine the bed-erosion rate but also control the bioturbation activities and their consequences on erosion rates (Orvain and Sauriau, 2002; Orvain *et al.*, 2003; Orvain, 2005). Flume experiments in runnel systems clearly indicated that bed erosion was facilitated in runnel systems, but unfortunately, the actual model development cannot still allow us to integrate sediment erosion and transport in runnel and ridges simultaneously. To avoid an overestimating of the fluxes, we preferred simulating the bioturbation activities by assuming compact sediments everywhere since aerial-photo analysis revealed that ridge is the dominant sediment bed form by covering 2/3 of the Brouages flat (Sauriau, pers. comm.).

Scenarios were established to assess the effects of the different biological community structure that were observed during field investigation (Bocher *et al.,* 2007; Orvain *et al.,* 2007). Regarding their natural distribution along the shore, the densities of the 2 studied species depended on the bathymetric level in the model (Table 1). High-tide levels are dominated by the presence of *S. plana* while the snails *H. ulvae* are more evenly spatially distributed. First, effects of the gastropod *H. ulvae* were compared to those of *S. plana* on a realistic community structure. The simulations were then performed to include the impact of seasonal trends on the activity of *S. Plana* (biodeposition) and the effect of the pelletisation on the bioresuspended material (Table 3). Simulations were set up either to examine the absence of fauna (n=0; only Eq. 4 is integrated for erosion), *S. Plana* effect on sediment erosion (Eqs. 5, 6, 8 and 9) or *H. ulvae* effect (Eq. 6, 7, 9 and 10)

Scenario DH-1: This is the abiotic run (n=0 in all nodes of the grid for *H. ulvae* and *S. plana*).

Scenario DH-2: This run considers the bioturbation activities of *S. plana* but only the direct subsurface destabilising effect was considered (Eq.6).

Scenario DH-3: This run takes into account all bioturbation activities of *S. Plana* (Eqs. 5, 6, 8 and 9). Compared to scenario 2, the surface influence of the bivalve on the sediment erodability has been added by including the production and the erosion of biodeposits (BGFL in Fig. 1).

Scenario DH-4: This run considers all bioturbation activities of *S. plana*. Compared to scenario 3, 20% of the biodeposits were considered as faecal pellets in the model with a higher settling velocity (Andersen, 2001; Andersen and Pejrup, 2002). The settling velocity of

bioresuspended material has been set to a high value of 5 mm.s^{-1} in Eq. 11 instead of 0.5 mm.s^{-1} for mud particles.

Scenario DH-5: This run simulates all bioturbation activities of *S. plana* as scenario 3. This time, its activity was affected by a seasonal component, with a peak of physiological activity between June and August. The destabilising effects due to burrows were assumed to exist during the entire year, since the formation of burrows does not depend on the activity level of the animal but only on its presence within the sediments. During periods of activity, biodeposit production rates were set equal to the baseline reference of scenario 2 (Eq. 10) and were decreased during cold seasons according to a sinusoidal curve with a minimum activity (close to zero) during the 3 winter months (December, January and February).

Scenario DH-6: This run takes into account the bioturbation activities of *H. ulvae* (Eqs. 6, 7, 9 and 10).

Scenario DH-7: This run simulates the bioturbation by *H. ulvae*. Compared to scenario 6, this simulation considered a differentiation of the faecal pellets in the model with a higher settling velocity in Eq. 11 (Andersen, 2001; Andersen and Pejrup, 2002). As in scenario 5, the settling velocity of bioresuspended material was ten-fold higher than mud particles.

2.3. Validation of erosion laws

In parallel of the large scale application, a direct confrontation of erosion functions of the model was carried out by comparing model outcomes to field flume experiments. Winter data were chosen (to avoid any potential interference with microphytobenthic biofilm that could affect flume measurements in summer). These experiments were performed by analysing the spatial variability of bed erodabity along the same cross-shore profile over intertidal mudflats of the Marennes-Oléron Bay (Orvain *et al.*, 2007).

The direct confrontation of the erosion functions (in a 1DV model framework) to flume experiments was performed to evaluate the validity of the erosion functions in Eqs. 4-11, the realism of the multiphasic erosion that was simulated in the present paper and also the eventual lack of the model outcomes to identify the potential model refinements that are needed in the future to better describe biota effects. The same erosion functions than the cross-shore model along with parameter sets (and conditions in Table 1) were tested in terms of validity. Critical bed shear stress was of 1 Pa on intermediate levels (station 2) and reached 2.5 Pa at the lower shore (station 3), with respect to the sediment concentration measured at these 2 sites (550 kg.m^{-3} at station 2 and 743 kg.m^{-3} at station 3). One of the main conclusions of the original study were that the sediment was more resistant to bed erosion when shifting from the upper to the lower shore, however, when the sediment is loosened by burrowing activities of endobenthic bioturbators like *S. Plana*, the critical bed shear stress is drastically reduced. Only biota effects by *S. Plana* can provide a reasonable explanation for the very low critical shear stress for bed erosion observed in this study at high bathymetric level , since the measured sediment concentration reached the same extent (643 kg.m$^{-3)}$ at the end of exposure period than on the 2 downward stations (Orvain et al. 2007).

For this validation exercise, the evaluation of each erosion type was tested separately and also simultaneously in various model runs to better differentiate the respective contribution of biotic versus abiotic factors to sediment transport. To simulate flume experiments, we exactly transferred the same erosion laws along with their associated parameter sets than in similar conditions to the 1DH/1DV cross-shore model (Eqs. 4-11). In this 1DV streamlined version of the model, the pelagic compartment was not vertically discretized but a cumulative mass of resuspended sediment was considered to mimic flume experiments (advection was neglected). The sediment compartment was split up into 3 layers, by differentiating the main

sediment matrix from a surface layer (whose sediment balance was set up by bed erosion and deposition). Deposition could occur in the surface layer with a variable thickness and this active layer can be resuspended by reducing the erosion rate of the underlying sediment compartment, in proportion. The pelagic compartment was considered as a single layer, implying a depth-averaged approach. The BGFL compartment was constituted by a sediment input coming from the sediment compartment by following the production laws used for BGFL production. The thickness of this compartment was variable and the sediment concentration of this sediment is set to 100 $kg.m^{-3}$ as in the cross-shore model. The thickness of this BGFL compartment was subject to a sediment output when BGFL erosion occurred. The hydrodynamic forcings were given by the measured sequence of bed shear stress that was imposed to the field-collected sediment during flume experiments.

3. Results

3.1. Model outcomes

Equilibrium profiles of all simulations stabilized in less than 4 years (Figs. 3 and 4). Bed elevation profile of the abiotic simulation conserved an almost uniform slope. This result clearly differed from anterior simulation with this model (Waeles *et al.*, 2004; Le Hir *et al.*, 2007). This is only caused by the choice that was made concerning the initial cross-shore slope which was close to the equilibrium profile. The limited changes of bathymetric profile must be considered only as an artefact due to the initial conditions. Similar to results of Le Hir *et al.* (2007), a typical equilibrium profile under wave action was obtained with a small progradation of high-shore levels and a small downward shift of the mid-shore levels and below. The wave decay towards the upper shore induced by bottom dissipation was apparent since erosion was slightly greater at the most offshore point. There was a mud accumulation at high-shore levels that increased bed elevation by 10-20 cm after 14 years of simulation. At these locations, the seasonal component of wave effects was not apparent since bed elevation increased progressively (Fig. 3A). Nonetheless, the bed elevation was subject to a seasonal component. Deposition occurred during spring and summer and erosion occurred during fall and winter. The model response for the whole year showed less variation (an increase of only 5 cm after 14 years of simulation). Seasonal variation in bed elevation increased with the offshore distance (Fig. 4A).

Local destabilising effects of *Scrobicularia plana* on critical threshold for erosion were very pronounced at the high-shore levels with a downward shift of 40 cm after 14 years (Figs 4A-B and 5A). In response, the slope was steepened around upper shore levels where *S. Plana* was present (scenario DH-2, Fig. 3B). The difference in bed elevation was 50 cm between the abiotic simulation and the *S. plana* simulation (scenario DH-3, Fig. 4A). The dissipation effects of the bottom that reduced wave effects in the abiotic scenario (scenario DH-1, Fig. 3A) were completely smothered because of the downward shift of the flat caused by biological influences (Fig. 3B). This process resulted in a net seasonality of bed elevation variation (Fig. 4A) that was not apparent without *S. plana*, even on the most inward location. The effect of bivalves on bed elevation diminished with offshore distance but the drastic modification of bed profile at the upper shore levels implied a modification of erosion-deposition cycles at mid-shore levels and below (Fig. 4A), even if bivalves were absent at these locations. This indirect effect of *S. plana* induced a downward shift of ca. 25 cm at intermediate levels and 15 cm at the most offshore point (Fig. 4A). At these locations, the seasonal range of bed elevation was reduced because of the general downward shift and the higher slope of the profile.

The inclusion of biodeposit formation induced a greater tendency towards the downward shift (ca. 10 cm) across transect (scenario DH-3, Fig. 3C). The pattern of net erosion was mainly

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driven by burrowing behaviour of the bivalve but BGFL contributed up to ca. 15% of bed elevation decrease (Fig. 4B). The influence of *Hydrobia ulvae* was limited to the BGFL erosion rate and this bioturbation activity altered to a lesser extent bed elevation than *S. plana* did (scenario DH-6, Fig. 5A). The effect of *H. ulvae* (less than 5 cm of downward shift all along transect) almost could be neglected since equilibrium profile was very close to the abiotic simulation (scenario DH-1, Fig. 3A). An increase of the settling velocity of the resuspended material still decreased the differences compared to the abiotic scenario (number DH-7, Fig. 5B).

The inclusion of seasonal variation in pseudofaeces formation related to temperature effects (scenario DH-6) did reduce to a small extent the decrease of bed elevation due to *Scrobicularia plana*. The difference due to this seasonal variation of the biodeposition explained only 5% of the biological effect. This is equivalent reducing BGFL formation by 33%. The simulation accounting for pelletisation of 20% of biodeposits (scenario DH-7) gave rise to a similar effect. These refinements affected the model so little that the long-term results can be considered not sensitive either to the pelletisation effect on settling velocity (Fig. 6A) nor to the seasonal variation of pseudofaeces production (Fig. 6B).

3.2. Validation of erosion laws

The flume experiments data of the study by Orvain *et al.* (2007) were used by comparing model outcomes to measurements at 3 different bathymetric levels (station 1 at the upper shore on fig. 7A, station 2 at an intermediate bathymetric level on fig. 7B and station 3 at the lower shore on fig. 7C). Resuspension data clearly indicated that the multiphasic erosion laws (with distinction of precocious BGFL and bed erosion) were necessary for a good realism of erosion kinetics and only process-based models for sediment transport work well when considering biota effects. This is especially the case on the lower shores (stations 2 and 3, Figs. 7B and 7C). On station 1 (Fig. 7A) and 3 (Fig. 7C), there were 2 different measurements of erosion curves at 2 different emersion times. The first experiment was performed at the beginning of the emersion period (sediment samples were taken immediately after water exposure and inserted in the flume to perform erosion experiment immediately on board on the site). In such condition, there was no BGFL production that was observed on the field (smooth surface without biogenic irregularities) and only bed erosion occurred. In fact, The BGFL is systematically eroded during tidal immersion, implying a smooth sediment surface after tidal water removal. Biological effects progressively develop during the exposure period with irregularities appearing at the surface of sediment. However, biota effects caused by burrowing activities of endobenthic species in deep layers remain always active whatever the tidal sequence. During the exposure period, there was a development of a BGFL, with tracks and pseudofaecal mounds that gradually covered the surface areas. Bioturbation time is a relevant parameter in the model to determine the quantity of sediment in the BGFL. The second experiment that was performed at the end of emersion period clearly indicated that there was precocious BGFL erosion (Fig. 7B and 7C). In the model, it was necessary to include the additional quantity of sediment eroded during the BGFL erosion phase to reproduce well the measured data.

The multiphasic layer erosion on station 1 was less obvious than on lower stations because the 2 processes related to biota effects (i.e. BGFL and bed erosion) become difficult to distinguish when *S. Plana* population is very dense (Orvain, 2005). In fact, the critical shear stress for the two each erosion types is very close for high densities (Orvain, 2005). In this case, it was clear that bed erosion occurred rapidly since there was no supply-limited erosion at high bed shear stress (Orvain, 2005). At the upper shore, the model outcomes were differentiated to better display the contribution of each process at the 2 different times (bed erosion alone at the beginning of emersion period and association of the 2 erosion types at the end of emersion period). At this bathymetric level, bed erosion was drastically modified by *S. plana* effect because of the bed loosening that implied a change of the critical bed

shear stress (Orvain *et al.,* 2007). This observation was made in a previous lab study (Orvain, 2005). When considering the bed erosion alone, the resuspended model outcomes were in good agreement with flume data at the beginning of emersion period. This was related to the absence of a BGFL at sediment surface in this condition. The confrontation between model outcomes after a 6h bioturbation duration (i.e. equivalent to the emersion period on the field) revealed that the model reproduced well the flume data obtained at the end of emersion, when we incorporated the additional BGFL production/erosion during this period. Finally, the model simulated well both processes, by discriminating biota effects on bed erosion at the beginning of emersion period and the additional BGFL erosion that was essential to simulate well the flume data at the end of emersion. At the upper shore, the model was fully valid to reproduce the 2 different biota effects and there is no need to integrate other fauna effects at this bathymetric level.

At station 2 (i.e. the intermediate bathymetric level, Fig. 7B), there was a bed erosion registered at the beginning of erosion without any BGFL erosion. As for station 1, we obtained a very close agreement between bed erosion simulation and flume data at the beginning of emersion period. By contrast, experimental results at the end of emersion revealed a clear BGFL erosion with the typical erosion kinetics with a supply-limited erosion along with an asymptotic plateau observed in terms of cumulative erosion mass at high bed shear stresses (before bed erosion). However, even if there was a relatively dense population of *Hydrobia ulvae* at this location (2500 ind.m^{-2}), the model outcome displayed that only a very small quantity of sediment was involved in BGFL erosion when *H. ulvae* is considered as a single bioturbator in the model (after 4 hours of emersion period). The model of BGFL erosion is not valid at station 2 since the modelled resuspension rate was extremely low compared to the measured BGFL erosion rate at the end of emersion period. In fact, the sediment surface was hardly modified by the presence of *H. ulvae* tracks (i.e. BGFL). There was a clear lack in the model validity in this case. For now, we only have calibrated erosion laws for *H. ulvae* and *S. plana* in the model and this appears insufficient to simulate properly the BGFL erosion measured at station 2. This emphasizes the needing to incorporate other biota effects in further model improvements and especially other molluscs like *Abra* (*tenuis* and *nitida*), *Macoma balthica* and *Cerastoderma edule* and, above all, the annelids *Hediste diversicolor* and *Aphelochaeta marioni* that was dominant at this location (see Orvain et al. 2007 for details of macrofauna assemblages). We have searched for the condition required to obtain a good agreement between measurement and model outcomes. We must consider a quantity of sediment involved in the BGFL erosion (Fig. 7B, line d) equivalent to a numerical density of 2500 *S. Plana*.m^{-2} to obtain a good resemblance with measured BGFL erosion (the real density of juvenile *S. Plana* was only of 57 ind.m^{-2} at this location).

At the lower shore (illustrated by station 3 results), erosion kinetics were measured only at the end of emersion, but, at this location too, the model outcomes cannot work well when only 1 erosion type was simulated. It must be recognised that, once again, a process-based model with a multiphasic erosion (precocious BGFL and subsequent bed erosion) was appropriate to simulate properly the measured data (Fig. 7C). Similarly to station 2, the contribution of *H. ulvae* can be neglected in terms of BGFL production/erosion, when comparing model results with only *H. ulvae* BGFL erosion to the measured eroded mass. This time, a BGFL production/erosion equivalent to the numerical density of 1500 *S. Plana*.m^{-2} (during 3 hours) is suitable to reproduce well the observation (while there is no *S. Plana* found on this site). Once again, the 2 dominant annelids *Hediste diversicolor* and *Aphelochaeta marioni* and the bivalve *Macoma balthica* must be responsible for this BGFL action. The model must be revisited in the future by incorporating the feeding behaviours of these 3 species.

4. Discussion and conclusions

Most studies related to interactions between biota and sediment concluded that there was a strong dependence of erodability on the macrozoobenthos activity. To our knowledge, published modelling studies that involve macrozoobenthos effects did not account for long-term morphodynamical processes but investigated limited periods lasting at most 1 year (Wood and Widdows, 2002; Paarlberg *et al.*, 2005; Lumborg *et al.*, 2006, Borsje *et al.*, 2008). The influence of bioturbation activities on the quantity of sediment in the BGFL is higher for *Scrobicularia plana* than for *Hydrobia ulvae* on compact sediments where only BGFL erosion occurred. So, higher amounts of sediment were released in the water column by the bivalves than by the snails on compact sediments (Fig. 3A, 3B and 3C). The differences between both species were largely amplified in softer sediments (Fig. 3D, 3E) because of the supplementary burrowing activity of the bivalves that deeply affected the sediment bed by modifying the value of the critical BSS for erosion.

The impact of the bivalve *Scrobicularia plana* on the bed geomorphology was very significant after 4 years of simulation (Figs. 4 and 5) while the effect of the gastropod *Hydrobia ulvae* was negligible even after 14 years of simulation (Fig. 6). More generally, this revealed the strong impact of stationary species that induces a high downward shift of the upper shore while the effects of mobile species remain very low. This impact was mainly due to the effect of this bivalve in deep layers and its consequences on bed erosion. This result confirms the study by Wood and Widdows (2002) who found similar effects of another bivalve (*Macoma balthica*) on bed elevation profile.

The present study clearly indicates the importance of endobenthic bivalves such as *Scrobicularia plana* to explain the fate of bed elevation profile of an intertidal mudflat, by confirming laboratory and field experiments. By destabilising surface and deep layers of sediment, the endobenthic bivalve *S. plana* can drastically enhance the erosion fluxes at the upper-shore levels of the Brouages mudflats. The local sediment bed elevation at the upper-shore levels were mainly driven by the burrowing activity of the sedentary bivalves with a very marked impact on the long-term scale. In these locations, the model predicted a difference of 0.5 m in the bed elevation after 4 years.

This phenomenon provoked an indirect effect on the geomorphological dynamics of the whole transect since the mid-shore and low-shore levels that were not affected by the presence of *Scrobicularia plana* were subject to enhanced erosion rates too. This is due to the reduction of the dissipation effects on the wave actions and the decrease of bathymetric level at the upper shore in response to local biological activities. There are other modelling studies demonstrating unexpected local variation of bed erodability determined by the erosion-deposition cycle at other areas of the basins. For instance, Wood and Widdows (2002) obtained similar indirect effects of the bivalve *Macoma balthica*, which altered erodability of the intermediate mudflats, subsequently affecting bed level profile on the upper shore in return. Similar effects were attributed to the saltmarsh at the upper shore in Le Hir *et al.* (2007). Another example is illustrated by Lumborg et al. (2006) who modelled the effect of the surface activity of *Hydrobia ulvae* leading to modify the bed shear strength of sediments that were prone to erosion. This process is very similar to the BGFL erosion modelled in the present study. They obtained unexpected findings since they concluded that "the modelling results suggest that the presence of large numbers of the destabilising mudsnail *H. ulvae* results in higher net accumulation on the intertidal mudflat investigated". This paradox was explained by the fact that the sheltered areas received strong inputs of sediment coming from other parts of the tidal basin. This process was reinforced by the protection of the microphytobenthic biofilm in these locations and by the high settling velocities of aggregates eroded from the tidal flats in relation to pelletisation by *H. ulvae*. This unexpected result was so drastic that they obtained a net deposition (integrated over the whole basin) with *H. ulvae*

impacts exceeding the abiotic situation. The process in question is exactly the same in the present paper: the mediation of sediment erodability by benthic organisms have local effects on the bed level that can in return affect the BSS profile all over the investigated areas by many ways (such as a reduction of the dissipation effects of wave actions, an enhancement of desiccation processes…etc), but this is *S. plana* that is involved instead of *H. ulvae* in Marennes-Oléron bay. This could create indirect biological effects even in places where benthic organisms were absent. The measurements of settling velocities of aggregates eroded from the tidal flat also showed that the pelletisation by *H. ulvae* had a strong influence on the settling velocity (Andersen and Pejrup, 2002). We considered this effect in the present paper but, in our conditions, we did not have the same findings since this process was insignificant in the Brouages mudflat. This should be related to the different configuration of the basin with less sheltered areas than in of Kongsmark intertidal mudflat of Andersen and Pejrup (2002).

Macrofauna activities have large long-term effects, mainly because this biological component occurs throughout the year. Salt marshes also have considerable effects on the geomorphology of the mudflat because of the persistence of these plants in winter (Le Hir *et al.,* 2007). In contrast, the seasonal trend in the development of the microphytobenthic biofilms implies that local stabilisation does not have large long-term effects. One problem of including the macrofauna effects is the high variability induced by fauna, partly due to the biodiversity but also to the diversity of influences. Even if the exercise remained difficult, the present paper shows that using "functional groups" and process-based model are very convenient to simulate the effect of fauna and to discriminate the effect of different species. This enabled us to distinguish the species-effect and the effects of different types of bioturbation activity (burrowing activities, BGFL erosion). For instance, the present study clearly states that, whatever the species in question, BGFL erosion remained limited in explaining variability of morphology of mudflats compared to burrowing activity. A process-based model (with the help of functional groups) appears very useful to elucidate the effects of different species. The biodiversity on mudflats is relatively low and these processes must be more thoroughly investigated to consider other species. The effects of crustaceans and annelids are yet not integrated in sediment transport models.

A long-term morphodynamical exercise revealed the lack of MPB effects on bed elevation after 14 years even if a four-fold increase of critical BSS was attributed to MPB. This is due to the seasonal pattern of benthic diatoms and especially the lack of stabilising effects at the critical periods of October when waves regulate the elevation profile and explain the general inter-annual trends. In contrast, the seasonal pattern does not regulate macrozoobenthos impact on bed elevation because the main impact of macrozoobenthos was constant throughout the year. As shown on the field (Orvain *et al.,* 2007), the presence of burrows in surface sediments always affects bed erodability, even in case of low temperature, and this process is thus considered constant throughout the year in the model. Seasonality can be related to a purely variation in the population of bivalves. In fact, the seasonal peaks of macrozoobenthos are generally observed during fall and early winter (Sauriau *et al.,* 1989; Bocher *et al.,* 2007; Orvain *et al.,* 2007) and inclusion of such seasonality would still amplify the impact of these species on long-term bed elevation. In contrast, the ecophysiological activities of macrozoobenthos such as tracking or biodeposition can be affected by strong seasonal patterns, since these animal activities are mainly regulated by temperature. We have included such a seasonal variation in the biodeposit production and track production. In contrast to the microphytobenthos impact on bed destabilisation, the seasonality of the process does not change the conclusions of the study because the part of bed variability explained by the BGFL production remains weak compared to the burrowing activity.

To conclude, the intense bioturbation activity could avoid the natural accretion of mudflats in the Marennes-Oléron Bay by many interrelated ways. By extending our conclusions, we can also imagine that *Scrobicularia plana* bioturbation activity could actually explain why there is

no colonisation of sediment by persistent microphytobenthic biofilm over the upper shore of these mudflats (Guarini *et al.*, 1998). At the upper shores, persistent biofilm of microphytobenthos and biostabilising is often considered as a pioneering status before the development of a saltmarsh. After extrapolating, we can thus reasonably assume that high bioturbation rate and associated erosion regularly destabilised the sediment, hence limiting the development of a saltmarsh plant field at these locations. The development of a saltmarsh has pioneering stages with development of microphytobenthic mats, which cannot take place on the upper shores because of the too intense reworking of sediment and regular erosion (see the second part of the discussion). Accretion of mudflats and salt marshes generally provides a natural coastal defence, by serving to dissipate energy from high tides and waves (Le Hir *et al.*, 2007). The extension of saltmarsh is a result of a positive-feedback loop since the dissipation of energy by the plants themselves provides the favourable conditions for a reinforcement of colonization. When high bioturbation rates induce a very pronounced erosion of the bed at the upper shore, limiting the extension of saltmarsh produces a lack of defence against tidal energy, amplifying the process of bed erosion further. A future challenge will be to produce sediment transport models able to include all interactions between biological components (microphytobenthos, macrozoobenthos, saltmarsh plants) with a rising sea level. Sand/mud mixture are now better considered in the sediment consolidation and sediment transport (Le Hir *et al.*, 2011), but there is a need to understand the combined effects of sand/mud mixture and biota effects. For instance, *Scrobicularia plana* is a drastic destabilizer in pure mud but this impact can shift from the status of sediment destabilizer to the one of sediment stabilizer when sediment becomes dominated by sand (Soares and Sobral, 2009).

To do this, sediment transport models must simulate multiphasic erosion and hydrodynamic modification caused by vegetation. Discrimination between multiple layers with specific erosion features constitutes the most original feature of the present model. The validation exercise (Fig. 7) that was carried out by direct confrontation to field flume data clearly displayed that the process-based model with multiphasic layers was required to properly take into account biota effects. We obtained very reasonable agreement between model outcomes and flume experiments at the upper shore concerning BGFL and bed erosion. The model works very well to simulate the biota effects at the highest bathymetric levels where the macrozoobenthic assemblage is dominated by *Scrobicularia plana*. Concerning lower shores, the validation revealed that the model was well conceptualised for simulating erosion data but the parameter sets for BGFL erosion (related to feeding behaviour of surface deposit-feeders) must be improved to incorporate the effects of other species. This validation procedure confirms that the gastropod *Hydrobia ulvae* hardly contributes to the BGFL erosion and to sediment transport in nature, but that other species must be more essential. However, on the lower shores, the macrozoobenthic assemblage is more diversified and there is a need to improve the erosion functions associated to BGFL production/erosion to incorporate properly the effects of Polychets like *Hediste diversicolor* and *Aphelochaeta marioni* and, to a lesser extent other mudflat bivalves (like *Abra*, *Cerastoderma*, *Macoma*...). This is necessary to consider simultaneous macrofauna effects of different destabilizers because of the wide variety of bioturbation types (e.g. surface trackers, subsurface destabilizers). Published data clearly shows the succession in time of the 2 erosion types that must be accounted for (Orvain *et al.*, 2003; Orvain, 2005; Orvain *et al.*, 2007) and the validation procedure (Fig. 7) displays that the developed model realistically simulates the erosion of bioturbated sediments. This model design and development has been recently used by van Prooijen *et al.* (2011) model *Macoma balthica* bioturbation by revisiting anterior data (Willows *et al.,* 1998) by using the same concept of BGFL production/erosion that was developed in the anterior development of the actual model (Orvain *et al.*, 2003; Orvain, 2005). Even though the main effects must be attributed to the impact of endobenthic species loosening the sediment beds, it remains very crucial to keep these refinements with the concept of fluffy layer production/erosion for improving sediment transport model. This will help us to amend the sediment transport model, especially at low and intermediate

bathymetric levels. Surface activities and feeding behaviour implied in the BGFL production must be better understood to provide one day a model of sediment transport under influence of climate change (Wood and Widdows 2003) and more especially when the objective is to simulate the microphytobenthos exportation in the water column. By following a step-by-step approach, we must incorporate multispecies assemblages of macrozoobenthos to improve the validity of this model of sediment transport before being able to adapt modelling tools to the exchange between benthic and pelagic compartments in terms of organic matter (like microphytobenthos) and food item distribution in the food web.

For this reason, there is a divergence of interest between a sedimentologist and a biologist, when modelling the "biota effects" at sediment-water interface, must be considered in the definition of a modelling strategy that depends on the objectives of the study in question. Actually, the impact of different bioturbators on the ecosystem will thus be completely different depending on the aims of the study and the processes in question. If the prime objective is to analyse the impact of macrofauna on sediment budget, only processes that are likely to change long-term erosion-sedimentation of the first centimetre are relevant (and endobenthic bioturbators must be considered in priority). For instance, the present study clearly displays that the sediment transport as well as bed elevation on a mudflat must take into account the effects of endobenthic bioturbators such as the bivalves *Scrobicularia plana* and can neglect bioturbation by small surface grazers such as *Hydrobia ulvae*. However, we must restrict our conclusion to the objective of the study in question, which consisted in evaluating the impact on sediment transport. Concerning other biological processes, all processes that affect short-term surface erosion fluff layer production caused by surface deposit-feeders like *H. ulvae* should be relevant to better describe microphytobenthic biofilm variations because of their very rapid spatial coverage of sediment surface (and especially feeding behaviour, top-down regulation of microphytobenthos, spatial microheterogeneity and benthic microalgae exportation rates from sediment bed towards the water column). We must also admit that the evaluation of *H. ulvae* impact on sediment transport is not fully understood and could still be underestimated, because this species could also affect bed roughness, especially when high abundances can cover wide areas of intertidal mudflats by robust shells that must largely interfere with the evaluation of "skin" roughness. This issue cannot be elucidated for now since it remains very difficult to state about the contribution of minute bioturbation effects compared to neglected bedforms and geological effects in 1m height-difference ridge/runnel systems, including desiccation, compaction and continuous flow in runnels.

Acknowledgements

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Tables

Table 1. Density of *Hydrobia ulvae* and *Scrobicularia plana* (ind m^{-2}) as a function of the bathymetric level in the 1DV/1DH model (simplification based on data from Bocher et al. (2007)).

Bathymetric level	Critical shear stress for bed erosion (Pa)	*Hydrobia ulvae* density	*Scrobicularia plana* density
$L > 4.95$ m	0.5	0	0
4.2 m ≤ L ≤ 4.95 m	0.15 (Eq. (6))	1000	850
4 ≤ L ≤ 4.2	0.15 (Eq. (6))	2500	850
2 m ≤ L ≤ 4 m	1	2500	0
1 m ≤ L ≤ 2 m	2.5	1000	0

Table 2. Description of the cross-shore 1DV/1DH model scenarios (Fig. 3, Fig. 4, Fig. 5 and Fig. 6).

Abiotic run	Biotic runs		Biotic conditions
	Scrobicularia plana	*Hydrobia ulvae*	
Scenario DH-1	Scenario DH-2	/	With only effect of bioturbation on bed erosion (no BGFL production/erosion)
	Scenario DH-3	Scenario DH-6	With total bioturbation effect (including also BGFL erosion)
	Scenario DH-4	Scenario DH-7	With pelletisation effect (on settling velocity)
	Scenario DH-5	/	With seasonal effect (on BGFL production/erosion)

Figures

Figure 1. Schematical diagram of the bioturbation activities exerted by 2 destabilizers. The snail *Hydrobia ulvae* inhabits the surface sediments where it can float (in runnels or in the seawater column), crawl and graze over the microphytobenthic biofilm, be inactive or bury itself in deeper layers. This gastropod, by creating tracks during its foraging activities, produces a Benthos-Generated Fluff Layer (BGFL) that is easily resuspended. The bivalve *Scrobicularia plana* inhabits the subsurface sediments. The entrance of its burrow is bioturbated by the active elongated siphon that sucks up surface sediments. The pseudofaecal mounds are released by this siphon at the surface of the sediment and produce a biogenic fluff layer that is resuspended precociously as well as snail tracks. Lower amounts of faeces are also produced over the surface by the other exhaling siphon. This species can also modify the strength of resistance of deep layers of sediment via its burrowing activity and the destructuration of deeper sediments. The drawing on the right is borrowed from Eisma et al. (1997) who represented another bivalve *Macoma balthica* which have similar bioturbating influence and belongs to the same superfamily of Tellinids. The notations Eq. 8 and Eq. 10 refers to processes represented by model equations in the text.
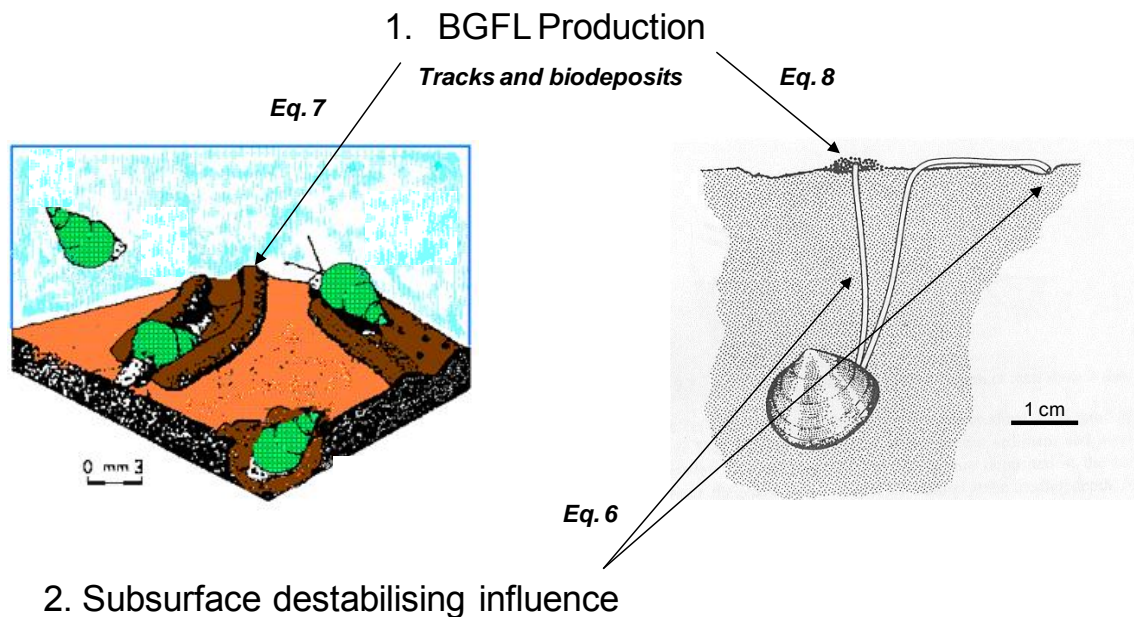

Figure 2. One-year survey of the wave height in the Marennes-Oléron bay (taken from Monbet et al., 2006). The wave forcing for simulation over 14 years was based on this measured signal.
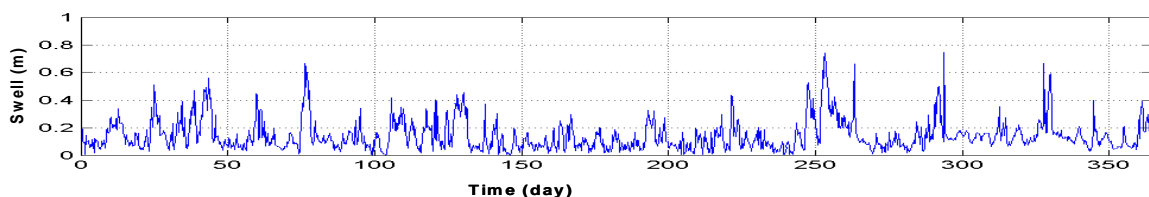
Figure 3. Simulation of the bed elevation (1DH/1DV cross-shore model) without *Scrobicularia plana* (A) and with effects of 850 ind.m^{-2} on upper shore (B and C). Two simulations were compared: B) only with the effects on bed destabilisation (scenario DH-2) and C) with all effects of bivalve activity i.e. by including also BGFL resuspension (scenario DH-3)
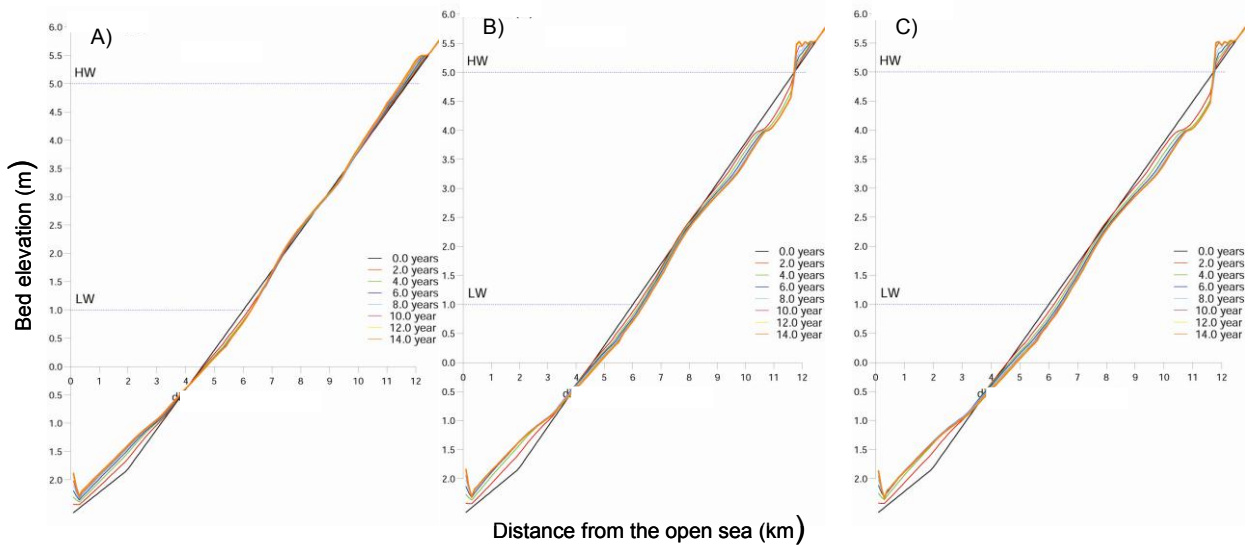

Figure 4. Dynamics of the bed elevation at 3 levels of the intertidal mudflat (lower, intermediate and upper shores): a) comparison between the control run (scenario DH-1 in solid) and the run with the single effect of *Scrobicularia plana* on destabilisation by burrows (scenario DH-2 in dashed line); b) comparison between the run with the single effect of *S. plana* on destabilisation by burrows (scenario DH-2 in dashed line) and the run with an additional effect due to the pseudofaeces erosion (scenario DH-3 in solid)
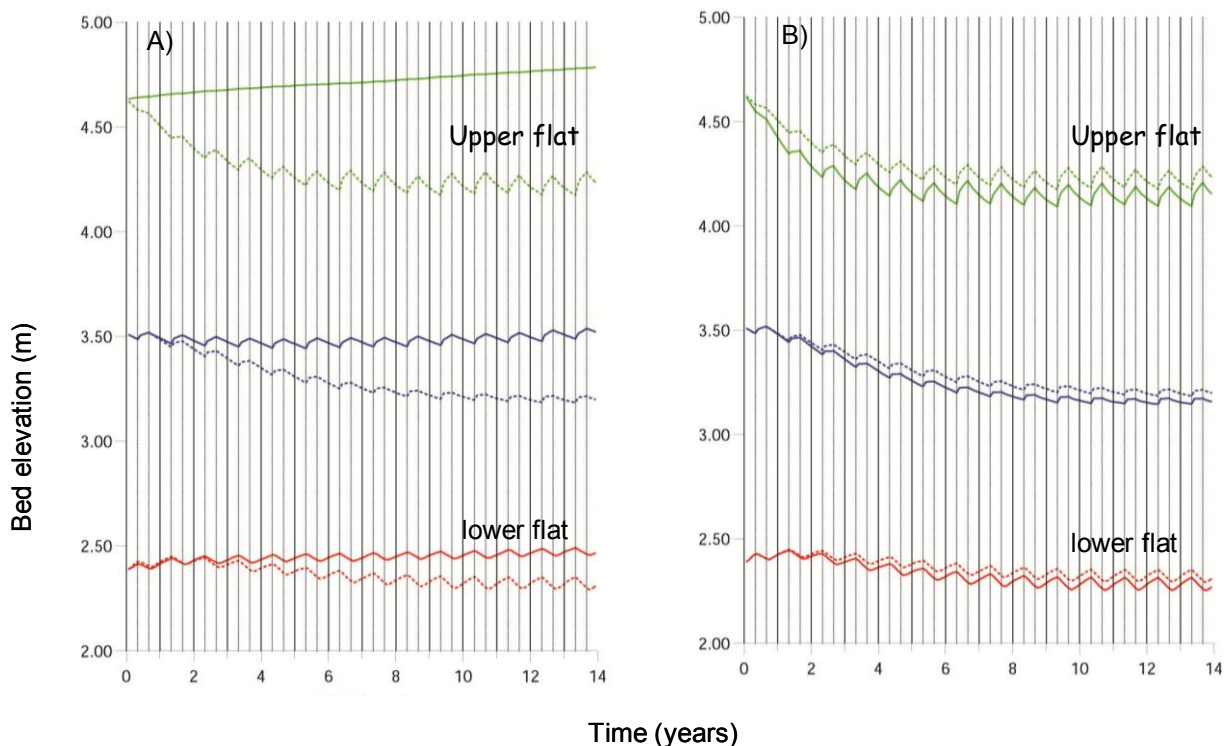
Figure 5. Simulation of the bed elevation given by the 1DH/1DV cross-shore model: A) with effects of *Hydrobia ulvae* on bed erodability (scenario DH-6) and B) also including a pelletization of 20% of the biodeposits (scenario DH-7)
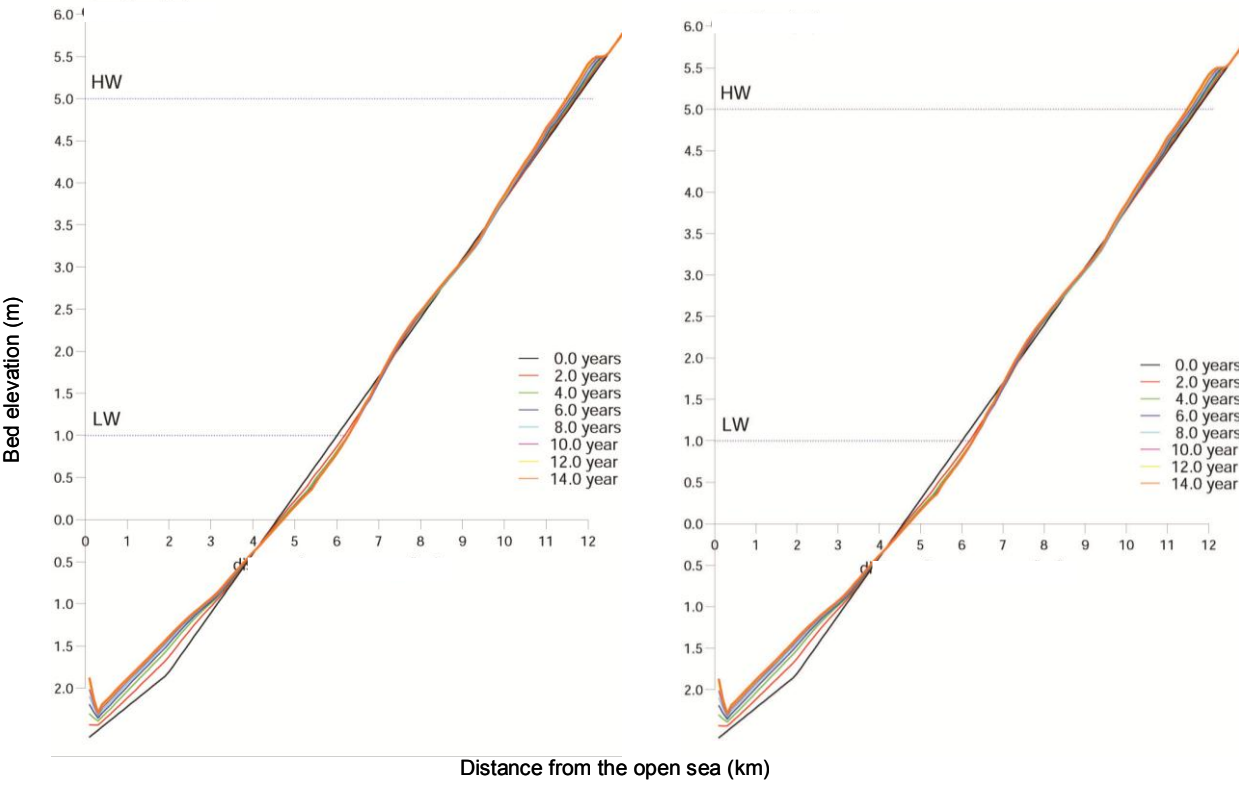
Figure 6. Additional effects of pelletisation and seasonality on bioturbation effects of *Scrobicularia* and impact on the bed elevation at 3 levels of the shore: a) This figure compared scenario DH-2 simulating *Scrobicularia* effects without accounting for BGFL production (solid) with scenario DH-4 simulating BGFL production but in this case 20% of the biodeposits were pelletized (dashed line) b) This figure compared DH-scenario 2 (solid) to scenario 5 considering a seasonal pattern of pseudofaeces production (dashed line).
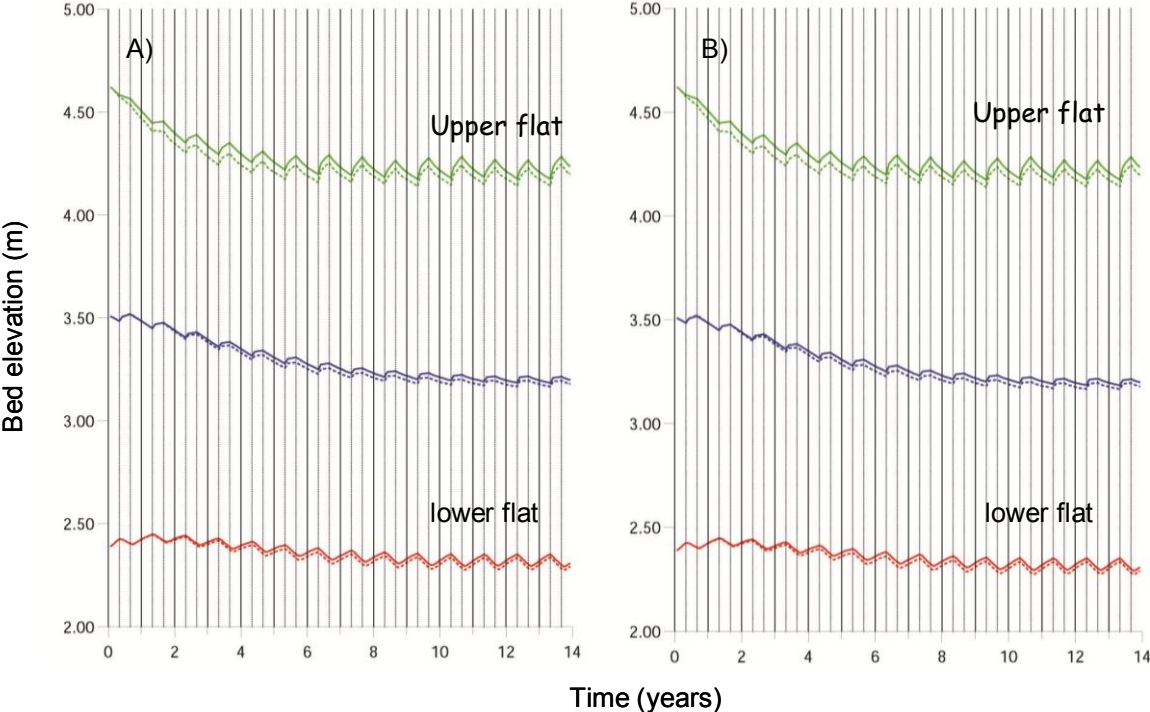
Figure 7. Time kinetics of the suspended sediment mass during the erosion experiments of Orvain et al. (2007). The thin lines represent the flume measurement data and the solid lines are 1DVmodel outcomes. The different velocity steps are separated with vertical dashed lines. The associated bed shear stresses in Pa are given at top. The 3 diagrams compared at 3 bathymetric levels (the corresponding bathymetric level of the model, L, is given on the diagrams in reference to Table 1), several runs of the 1DV model of sediment transport to flume experiment data (at stations 1, 2 and 3 of the original data in Orvain et al. 2007). Several model outcomes were displayed to better discriminate the contribution of each erosion functions (See Table 1 for model conditions).