Multispecies macrozoobenthic seasonal bioturbation effect on sediment erodibility

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MULTISPECIES MACROZOOBENTHIC SEASONAL BIOTURBATION EFFECT ON SEDIMENT ERODIBILITY

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Abstract

Bioturbation in estuarine environments describes all sediment reworking processes implied in sediment transport. However, modelling at large spatial and temporal scales remains a challenge because of the need to consider the fauna at the community level, and because animal behaviour is highly seasonal. Bioturbation processes can be linked to the activity of organisms, based on the principle of energy ecology, linking the metabolic rate to the erodibility of a sediment colonised by benthic fauna. This study investigates this postulate by evaluating the erodibility parameters of a sediment subjected to: i) the bioturbation under seasonal temperature variations; ii) the joint bioturbation of different species. The experimental design consisted of: i) three temperature levels (winter, spring and summer), ii) two species combined (*Cerastoderma edule* and *Macoma balthica*; *Scrobicularia plana* and *Hediste diversicolor*; *Corophium volutator* and *Peringia ulvae*) at 4 different relative densities. Two successive experiments were carried out on the same individuals: measurement of oxygen consumption of fauna then measurement of the erodibility of the colonised sediment in a flume. The oxygen consumption confirmed that the metabolic rate is a good model of the fauna respiration, regardless of species. The erosion results indicated that the metabolic rate in the case of the fluff layer is an interesting descriptor for 1) the assessment of the bioturbation under variable temperatures and 2) the integration of the two different bioturbator species that could co-occur in the same habitat. In contrast, the effect of bioturbation on the mass erosion threshold seems to be more related to the bioturbation processes than to the metabolic rate. Bioturbation models of the fluff layer using metabolic rate is a promising tool for modelling the effects of faunal communities on sediment transport at the scale of an estuary and over the long term, even projected in the context of global warming.

Highlights

- Temperature influences the effect of bioturbation on sediment erodibility by regulating physiological metabolism.
- The erosion of the fluff layer is positively linked to the total metabolic rate, without consideration of the species.
- The mass erosion threshold is negatively impacted by some species, without consideration of their metabolic rate.

Keywords

Bioturbation, respirometry, erosion, erodibility, metabolic rate, intertidal, mudflat, estuaries, benthos

Manuscript

1 Introduction

Measuring the interaction between fauna and their environment on a large scale using generic models is necessary to better understand complex coastal and estuarine ecological systems (Carleton Ray and McCormick-Ray, 2013) and to make visible the feedback loops at work within the habitats they contain, including small-scale effects (Ettema and Wardle, 2002; Hewitt et al., 2005; Thrush et al., 2003). In particular, the impact that benthic fauna can have on sediment transport via its erodibility is an element to consider when describing the morphodynamics of an estuary. However, this impact is rarely taken into account in numerical hydro-morpho-sedimentary models [the recent work of Brückner et al is a case in point (Brückner et al., 2021)], because the fauna is considered more as an 'end user' of a habitat rather than an element in the feedback loop as a community of species interacting with each other and with the environment.

Indeed, many benthic species are considered to be ecosystem engineers (Jones et al., 1994), and play a crucial role in the formation, transformation and maintenance of habitats. Bioturbation covers all the mechanical and biological processes by which ecosystem engineers can modify sediment and its erodibility. This includes actions such as digging galleries, stirring up sediments and mixing sediment layers (Jones et al., 1997; Kristensen et al., 2012; Le Hir et al., 2007; Meysman et al., 2006). Historically, studies of the effects of bioturbation on sediment erodibility have been carried out for isolated species and the best proxy was defined by the density or biomass of the species at the time of measurement.

The species chosen are generally frequently found in intertidal areas, such as *Macoma balthica* (Paarlberg et al., 2005; Widdows and Brinsley, 2002; Widdows et al., 2000), *Cerastoderma edule* (Andersen et al., 2010; Dairain et al., 2020a, 2020b; Li et al., 2017; Rakotomalala et al., 2015; Widdows et al., 1998), *Hediste diversicolor* (de Deckere et al., 2001), *Scrobicularia plana* (Kristensen et al., 2013; Orvain, 2005; Soares and Sobral, 2009), *Peringia ulvae* (Andersen et al., 2005, 2002; Orvain et al., 2003), *Corophium volutator* (de Deckere et al., 2000).

To describe the effects of bioturbation on the scale of an estuary-type environment over the long term, it is necessary to consider a community of species rather than isolated species, and to take account of the seasonal variation in species activities. It is therefore necessary to use a biological descriptor that is adapted to the physiological or functional diversity of the species while reflecting the seasonal cycles in order to describe the bioturbation mechanisms involving different species over time.

Based on the principle that bioturbation is the result of an individual's activity as much as its morphology and physiological state, and that this activity requires energy which results from its metabolism, the sum of the metabolisms of a population, or even a community, appears to be a relevant indicator for assessing the effects of bioturbation on sediment erodibility. According to Brown's definition, "metabolism is the biological processing of energy and materials" (Brown et al., 2004). For heterotrophic organisms, the metabolic rate is assimilated to respiration, the basis of their energy transformation (Brown et al., 2004).

The metabolic rate has been modelled as the Standard Metabolic Rate, which varies as a function of body mass and temperature (Allen et al., 2005; Brey, 2010). Although the rigid mechanistic interpretation of individual energy scaling laws and their larger-scale effects by the metabolic theory of ecology (MTE) is widely debated and partly overcome (Glazier, 2022), the increase in metabolic rates with size and temperature remains one of the fundamental general trends observed in living things. Metabolic theories are therefore widely used as a mechanistic basis for models of ecological dynamics at all scale levels (Posfai et al., 2017). The dependence of metabolic rates on temperature makes these models particularly useful in terms of predicting the functioning of ecosystems subject to seasonal variations but also potentially under the effect of global warming (Huey and Kingsolver, 2019).

Studies have explored the possibility of defining the effects of bioturbation of isolated species on sediment erodibility using the energy balance rather than the traditional descriptors of biomass, density or size of individuals (Cozzoli et al., 2018). The energy approach proposes the use of metabolic rate, i.e. the amount of energy expended by an organism for its survival, as a parameter to model bioturbation effects in an environmental energy balance (Cozzoli et al., 2021; Lehuen and Orvain, 2024).

An attempt at multi-species modelling describing facilitated erosion of the biogenic matrix was made by integrating such “metabolic respiration rate” (Cozzoli et al., 2019). Even though this approach was performed for several bioturbators, calculations were only applied to separate single-species datasets until now. Another study mixed some benthic species, but only the erosional effects of the sediment

structural layer were described (de Smit et al., 2021a). Because of the number of interactions that may exist between species, the effects of species may vary according to their behavioural functions. All these effects may therefore add up, cancel each other out or not affect the same factors, depending on their nature or the nature of the interactions between the species themselves.

In this study, we propose to explore these various aspects in a multifactorial protocol. Firstly, we use metabolic rate as a biological descriptor of fauna to explain the effects of bioturbation from an energetic point of view, by measuring the respiration rate of the individuals used to check the suitability of the SMR model. Secondly, we take into account the variability of faunal activity as a function of temperature and its impact on the effects of bioturbation on sediment erodibility, by exposing individuals on sediment to three temperature levels corresponding to the seasonal cycle during a period of bioturbation before measuring erodibility. Thirdly, we measure the effects of bioturbation on sediment erodibility of several species combined in the same sediment simultaneously, and at different relative densities, in order to assess the impact of interactions between species on bioturbation. These species were paired according to their functional groups to study various cases of interactions.

2 Material and Methods

2.1 Biological models

The species selected were based on the communities observed in intertidal areas of estuaries in north Atlantic, such as the Seine estuary or Schelde estuary, choosing the more frequent and ubiquitous ones (Figure 1A). This study proposes to evaluate combined bioturbation effects of those six emblematic species by defining three species duos to explore the following questions (Figure 1B):

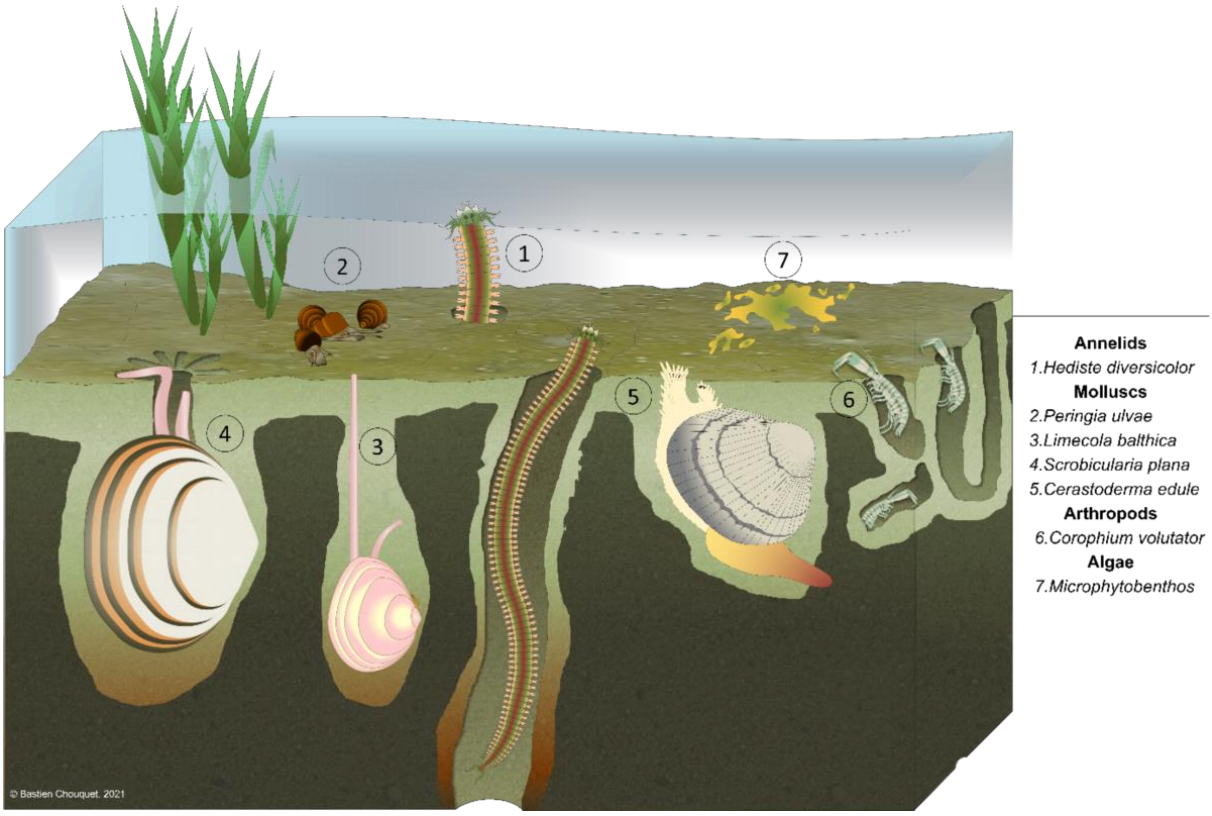
1. *Cerastoderma edule* and *Macoma balthica*: do these two species that look alike have same bioturbation effect, even though they do not have the same feeding behaviour? They both create a biogenic layer on the first few centimetres of sediment and can play a role in both types of erosion (fluff and mass erosion). However, *C. edule* is strictly a suspension feeder, whereas *M. balthica* is a mixed suspension and deposit feeder at low tide, influencing the water-sediment interface more directly. The two species are known to facilitate each other and cohabit (Bocher et al., 2007; Montserrat et al., 2009; Ysebaert et al., 2003) and are cited together to describe communities in the EUNIS habitat A2.24 : Polychaete/bivalve-dominated muddy sand shores (A2.241/MA5251, A2.242/MA5252, A2.243/MA5253) and A2.31 : Polychaete/bivalve-dominated mid estuarine mud shores (A2.312/MA6224, A2.313/MA6225) (European Environment Agency, 2023).
2. *Scrobicularia plana* and *Hediste diversicolor*: The question is “does the cohabitation of species mitigate antagonistic bioturbation effects?”. Those two species are known for their antagonistic effects on the deep structure of the sediment: *H.diversicolor* is a biostabilizator,

S. plana is a bed destabilizator. These antagonistic effects were observed *in situ* during experiments carried out on enclosures enriched with one or the other species, after one week under winter conditions and at the end of summer (Morelle et al., 2024). They also both create traces on the sediment surface (bioresuspension), but *S. plana* also generates pseudo-faeces when filtrating water (biodeposition). By definition, this duo is the least suitable for unifying a model without taking into account the bioturbation functional group. They live and often co-exist in mud or sandy-mud, frequently anoxic under 1 cm depth (EUNIS habitat A2.313/MA6225).

3. *Corophium volutator* and *Peringia ulvae*: can the effect of two surface-mobile deposit feeders on erosion parameters be equated? *C. volutator* and *P. ulvae* have similar influence on a very fine upper layer by crawling over the sediment-water interface for capturing microphytobenthic biofilms. They can be found in the same type of habitats, sheltered estuaries with muddy-sand or sandy-mud sediment, classified EUNIS A2.243/MA5253 and A2.312/MA6224.

Based on the theoretical frame of Brown and Allen (Allen et al., 2005; Brown et al., 2004), the individual metabolic rate *I* was expressed as function of the individual body size (M) and the temperature (T): $I \approx r_0 M^b . e^{-Ek/T}$. The equation was adjust the parameters $r0$, b and Ek for each species to the Standard Metabolic Rate (SMR) of aquatic invertebrates model of Brey (Brey et al., 2010). *Itot* [$mW.m^{-2}$] is thus the sum of basal metabolic rate of all individuals in the sample (details in Supplementary data 2.1).

A



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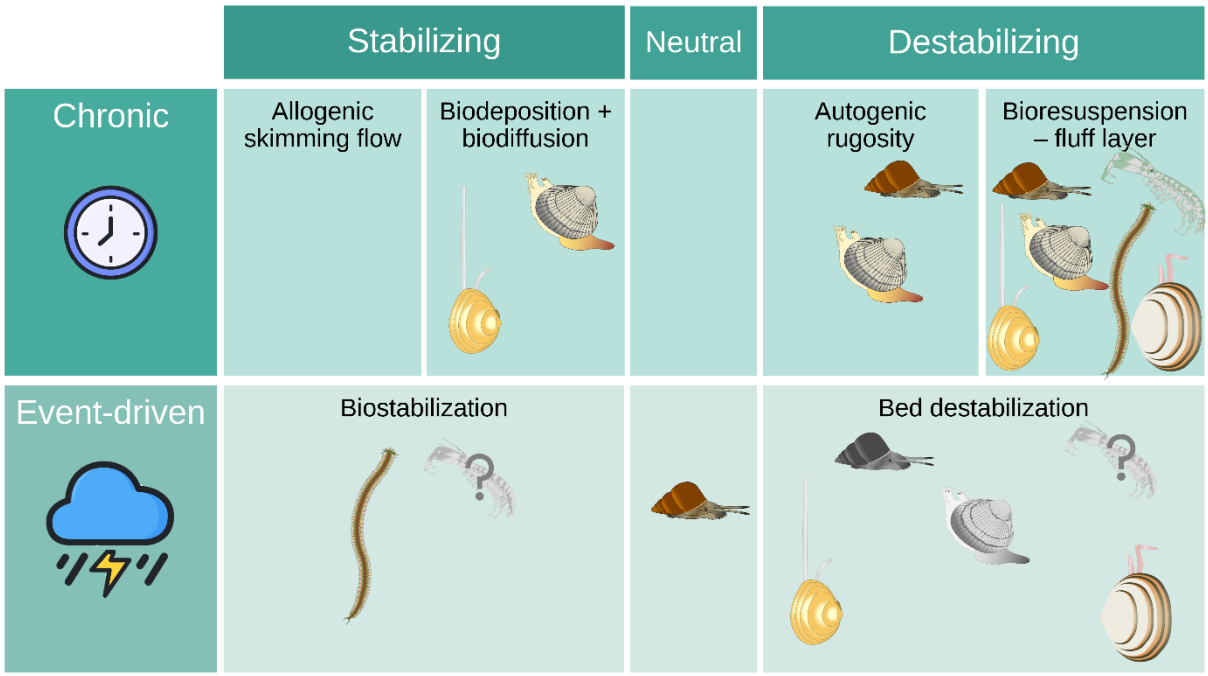

147 *Figure 1 A: Fauna models used in their sediment. B: Classification of species according to the*
148 *different effects of bioturbation on sediment characteristics (references in Supplementary data 2.1,*
149 *SuppFig 2.B and SuppTab 2.C).*

2.2 Sediment and animal collection

The Schelde estuary, a macrotidal coastal estuary, situated between The Netherlands and Belgium, is split in two main parts, named Westerschelde (south part) and Oosterschelde (north part). Due to anthropological transformations, the Oosterschelde is no longer fed by Schelde freshwater (Louters et al., 1998) (Figure 2).

A muddy and a sandy sediment were collected in the Westerschelde (mud in Groot Buitenschoor D50 = 20.69 µm; silt fraction 85.79 % < 63 µm; sand in Rilland D50 = 158.83 µm; silt fraction 3.53 % < 63 µm), wet-sieved at 5mm and defauned 48h in a freezer, then wet-sieved at 1mm to remove fauna and larger debris. Each sediment grain-size profile was characterized with a Mastersizer 2000 (Malvern Instruments Ltd., Malvern, UK). A 50%-50% vol mix was made (D50 = 67.99 ± 14.17 µm; silt fraction 48.81 ± 3.21 % < 63 µm), and let settle for two weeks to reduce the water content (33.30 % ± 0.78 %). The water content, density, grain-size composition and organic matter were monitored all along the experiment (details of sediment characteristics in Supplementary data 2.2 SuppFig 2.E, SuppTab 2.D).

Species were collected either in Oosterschelde or Westerschelde; *C. edule* in Oesterdam and in Den Inkel; *H. diversicolor* in Haven Rattekaai; *C. volutator* in Haventje Ellewoutsdijk; *S. plana* and *M. balthica* in Den Inkel; *P. ulvae* in Nolleweg. Individuals of each species were sorted to create batches of size classes, and a sub-sample of each class were used to measure length, fresh weight, dry weight, Ash Free Dry Weight (gAFDW) and define conversion coefficients that were used to define sample populations experiment (results in Supplementary data 2.2). The rest of the individuals were placed in the acclimatized mesocosms (thermoregulation).

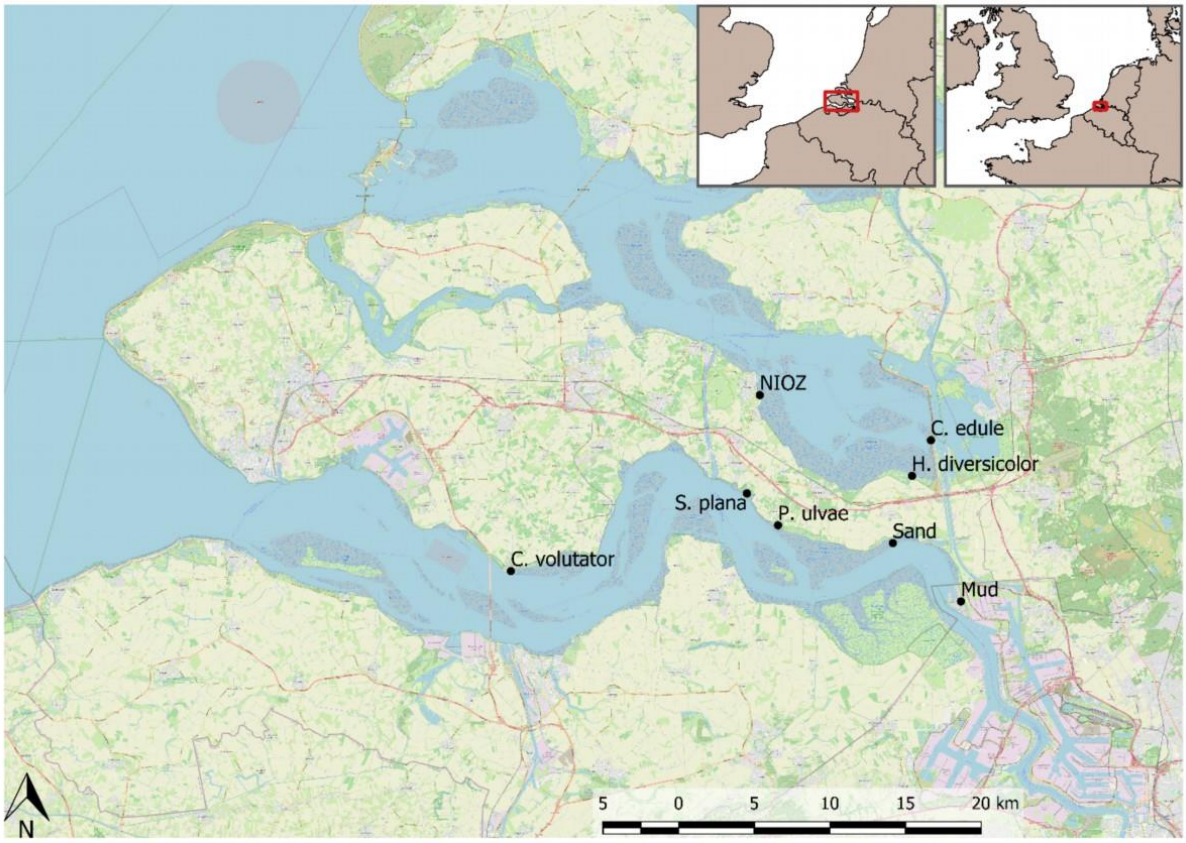

Figure 2 Maps of sampling location for each species and sediment.

2.3 Experimental design

The design of the experiment was built to measure the erodibility properties of the sediment for combined species and at varying temperatures (Figure 3A). Biological samples consisted in 3 duos of species of fixed body size, with 4 levels of relative densities for a global stable metabolic rate and a control. Experiments were run at three levels of temperatures that would represent winter, spring and summer (setpoint 10, 15, 20°C) (details in Supplementary data 2.4 SuppTab 2.E and SuppFig 2.L, M). Two replicates were made for each condition.

Measurement started with a respiration measurement of the biological samples in filtered sea water (salinity 31) at control temperature. Then fauna samples were settled in an incubation core of muddy sediment with a smoothed surface in a mesocosm under a tidal rhythm (Figure 3C) with controlled temperature for a bioturbation period. The colonized sediment cores were then used in an erosion measurement in flume, made with filtered sea water at room temperature.

Depending on the erosion measurement sequence (3 hours of measurement and cleaning with one flume, Figure 3B), the bioturbation duration varied from 6h to 18h, with an adapted set-up for *Corophium volutator* and *Peringia ulvae*, to ensure their presence on the sample bearer. The fauna was in this case put in a waiting mesocosm, and installed directly on the sample bearer for bioturbation, resulting to the absence of seawater during the bioturbation period (Figure 3C).

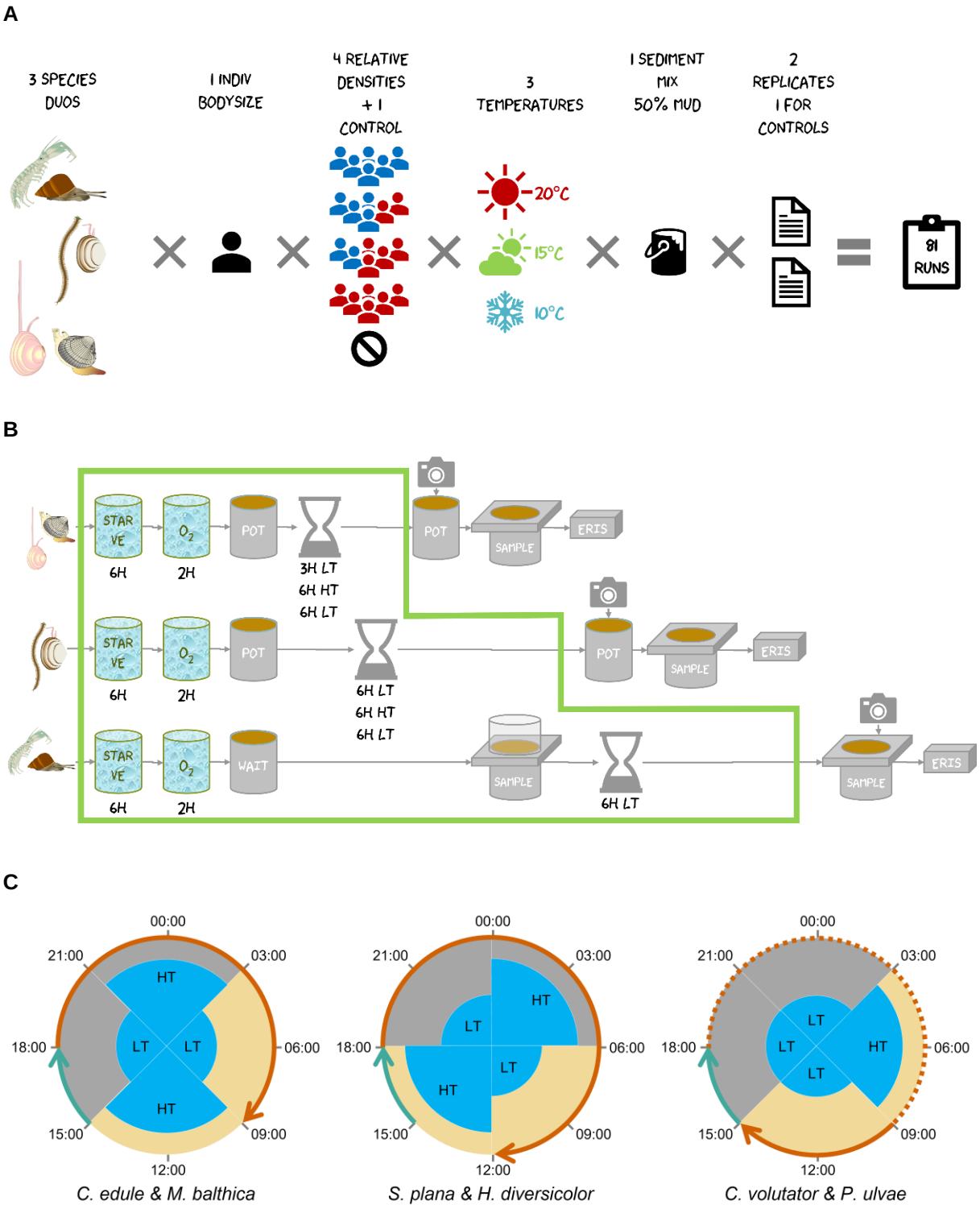

Figure 3 A: Experimental design. B: Measurement's chronology. LT: low tide, HT: high tide, O_2: respiration chamber, pot: incubation core, sample: sample bearer for the erosion flume, ERIS: erosion flume. The green frame represents the steps with a controlled temperature. C: Mesocosms tidal rhythm for each duo. The blue arrow represents the respiration measurement and the installation in the pot, the red arrow the bioturbation phase, the red dotted line the holding period of C. volutator and P. ulvae in a dedicated mesocosm prior to installation on sample bearer.

2.4 Experimental measurements

2.4.1 Respiration measurements

Selected animals for each sample were individually weighted or measured then put in filtered sea water for 6h to starve, in order to reduce metabolic consumption due to digestion and O_2 side consumption by faeces. The sample pools were then placed in a hermetic respiration chamber (V = 1.5L) with stirring. The oxygen concentration [µmol.L^{-1}] was measured during 2h using a PyroScience FireStingO2 sensor, without light nor human presence. In the measurement sequence, 3 periods visually without disturbance were selected to calculate 3 slopes of a linear regression, summarized as mean and standard deviation as the respiration rate [µmolO_2.s^{-1}]. Based on (Brey et al., 2010) the respiration rate was converted into metabolic rate $Itot_{respi}$ [mW] with the oxycalorimetric coefficient 468 J/mmolO_2, and divided by the surface of the flume for consistency [mW.m^{-2}].

The mean respiration chamber temperature was used to calculate a mesocosm metabolic rate $Itot_{meso}$ for the sample surface of flume [mW.m^{-2}]. In addition, given the water temperature was not controlled during the flume experiment, the mean water temperature in the flume was used to calculate a flume $Itot_{flume}$ [mW.m^{-2}]. When *Itot* is mentioned, the same treatment was made with the three metabolic rates.

2.4.2 Sediment erodibility analyses

ERIS is a unidirectional flume designed by Ifremer to measure the erodibility of non-cohesive and cohesive sediments. The mass erosion threshold and the erosion flux are calculated from the turbidity in response to increasing shear stress. The shear stress is modulated by different flow velocities in a closed channel. Details about flume set up are in (Guizien et al., 2012; Le Hir et al., 2008; Orvain et al., 2014b). Erosion experiment run by steps with current velocity from 0 to 91 cm.s^{-1} in 14 steps lasting 5 to 8 min, for a total of 2 hours measurement. The bed shear stress (*BSS* or τ [Pa]) was converted from the current velocity based on (Guizien et al., 2012), without accounting for sediment bed roughness, and turbidity measurement was converted into resuspended mass calculated on the sample surface, M_{erod} [g.m^{-2}]. Every current step was defined, and fluff or mass erosion steps were identified visually. Every step was summarized with mean of hydrological conditions, and the 95th centile of the M_{erod}. The critical BSS_{mass} [Pa] was calculated as the value of the *BSS* corresponding to M_{erod} = 0 on the linear regression on the mass steps. The Q_{fluff} was determined as the 95th centile of M_{erod} at the last fluff erosion step before mass erosion was visible (details in Supplementary data 2.4 SuppFig 2.N).

2.4.3 Data analysis

Respiration measurement results were compared to the metabolic rate $Itot_{meso}$ calculated with the mesocosm temperature. Both variables were normalized with a Box-cox transformation (function

AID::boxcoxnc, with $y = (x+\lambda_2)^{\lambda}/\lambda$), and a correlation was calculated to assess the adequacy of the Brey model to account for fauna activity. An one-way ANCOVA was made with the metabolic rate based on respiration measurement as dependant variable and $Itot_{meso}$ as covariate, with two factors: 1) duos to ensure experimental conditions does not create differences between species; 2) temperature conditions that reflect also the global sequence of experiments (details in Supplementary data 2.4 SuppFig 2.I).

Both bioturbation parameter Q_{fluff} and erosion parameter BSS_{mass} were normalized with a Box-Cox transformation and used as dependant variable in a one-way ANCOVA with the metabolic rate ($Itot_{meso}$) as covariate, and temperature or duos as factor to assess the species dependency of erosion parameters to the general metabolic rate. A linear regression of each transformed erosion parameter was conducted regarding the metabolic rate of the two species in the duos separated to evaluate their relative bioturbation role.

The validity of ANCOVAs were verified by evaluating the normality of the sub-groups per factors, the independence of covariant and factors was tested with ANOVA and the homogeneity of regression slopes for each sub-group was checked. Post-hoc tests were made for testing validity conditions (homogeneity of variance, normality and homoskedasticity of residues, outliers). Models and post hoc tests were conducted with packages broom (tidy, glance, augment (Robinson et al., 2023)), performance (compare_performance (Lüdecke et al., 2021)), rstatix (Shapiro-Wilk, Levene, ANOVA & ANCOVA (Kassambara, 2023)), lmtest (Harrison-McCabe test) and emmeans (Estimated marginal means of linear trends (Lenth et al., 2023)). All data processing was conducted in R version 4.3.0.

3 Results

3.1 Respiration measurements

The overall oxygen consumption was measured for *C. edule & M. balthica* at 0.0012±0.0007 $\mu molO_2.s^{-1}$ (n = 27), *S. plana & H. diversicolor* at 0.0008±0.0006 $\mu molO_2.s^{-1}$ (n = 26) and *C. volutator & P. ulvae* at 0.0004±0.0004 $\mu molO_2.s^{-1}$ (n = 27), corresponding to respectively 0.03±0.02 $x10^{-4}$ $\mu molO_2.s^{-1}.gAFDW^{-1}$; 0.06±0.04 $x10^{-4}$ $\mu molO_2.s^{-1}.gAFDW^{-1}$ and 0.28±0.33 $x10^{-4}$ $\mu molO_2.s^{-1}.gAFDW^{-1}$, and 88±50; 55±44 and 27±31 $mW.m^{-2}$ (details in Supplementary data 3.1 SuppTab 3.A). The metabolic rate based on respiration rate measurements, $Itot_{respi}$, was normalized with a Box-Cox transformation (λ = -1.280 and λ_2 = 100), as well as $Itot_{meso}$ calculated at the mesocosm temperature (λ = 0.3 and λ_2 = 1).

The metabolic rate $Itot_{respi}$ [$mW.m^{-2}$] was plotted against the modelled $Itot_{meso}$ (Figure 4A). The dataset with *C. volutator & P. ulvae* showed correlation between $Itot_{meso}$ calculated and the measured $Itot_{respi}$ (R^2 = 0.512****) with a slope significantly different than the two other duos, *C. edule & M. balthica* (R^2 = 0.683****) and *S. plana & H. diversicolor* (R^2 = 0.551****). The global regression was considered

representative enough of the global link between the two variables (R^2 = 0.571****). The global slope, like that of *C. edule & M. balthica* and *S. plana & H. diversicolor*, had a value slightly below the identity line (i.e. the diagonal), but with a higher intercept, meaning that a low $Itot_{meso}$ underestimates $Itot_{respi}$, while a high $Itot_{meso}$ overestimates it. For *C. volutator & P. ulvae*, $Itot_{meso}$ systematically underestimates $Itot_{respi}$, meaning that the individuals were more active than expected.

The ANCOVA results of $Itot_{respi}$ transformed ~ $Itot_{meso}$ transformed + Duo + Temperature ($F_{(2,65)}$ = 6.64, p = 0.002, Figure 4B, details in Supplementary data 3.1 SuppTab 3.B, C) show that there was no significant effect of the duos on $Itot_{respi}$ but a significant effect of the temperature, in particular the medium temperature that would lead to a lower $Itot_{respi}$ value.

Note that for all the ANCOVAs performed in the study, the $Itot_{meso}$ covariate has a significant relationship with the factors, either duos or temperature, as these factors are used to define $Itot_{meso}$. The violation of this hypothesis is accepted because of its very nature: $Itot_{meso}$ is defined independently of any measurement, the ANCOVA results would then indicate whether duos or temperature have additional effects to those expected and taken into account by $Itot_{meso}$ (metabolism more active than basal for example).

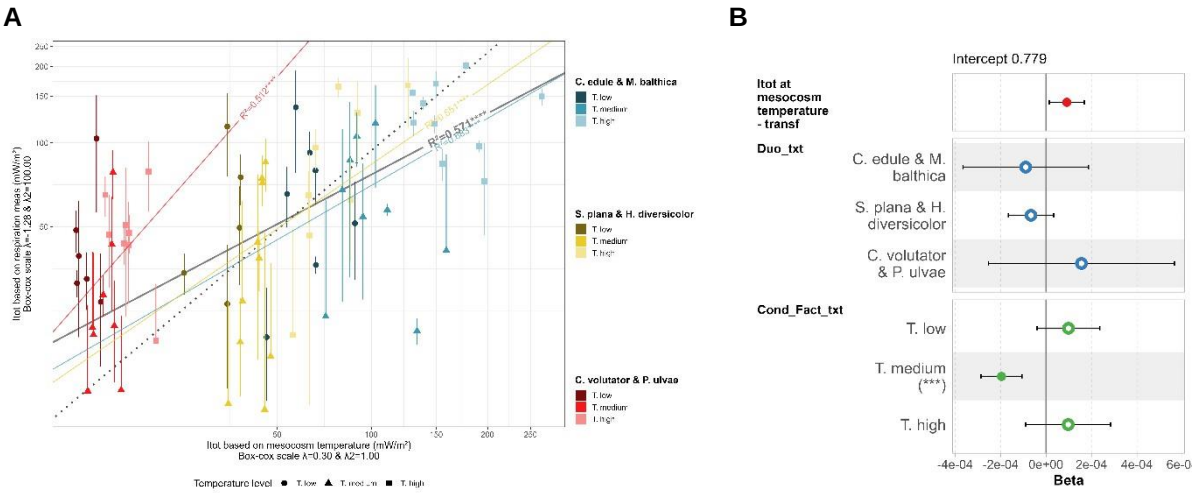

Figure 4 A: $Itot_{respi}$ [mW.m^{-2}] vs $Itot_{meso}$, with standard deviation and its regression line for each duo (corresponding colours) and in grey for all data combined, the grey dotted line represents the identity relation. Note that the scales are Box-Cox transformed, and the regression lines were made on transformed data. B: ANCOVA results for $Itot_{respi}$ transformed ~ $Itot_{meso}$ transformed + Duo + Temperature. Filled dot are p-value ≤ 0.1 and empty dot are p-value > 0.1.

3.2 Erodibility analysis

3.2.1 Erosion data treatment

All erosion runs made on ERIS flume were treated similarly to determine when the fluff layer erosion and mass erosion occurred (Figure 5). Fluff layer erosions were observed mainly from the seventh to the eleventh step of bed shear stress BSS = 0.81±0.53 Pa corresponding the shear velocity U* = 2.67±0.87 cm.s^{-1}. Mass erosion occurred mainly between the eleventh and the fourteenth steps of bed

shear stress BSS = 1.73±0.74 Pa, i.e. a shear velocity of U* = 4.01±0.87 cm.s^{-1} (details in Supplementary data 3.2.1 SuppTab 3.D).

The temperature of the water in the flume was significantly higher than in the mesocosm, leading to a $Itot_{flume}$ systematically higher than the $Itot_{meso}$ (details in Supplementary data 2.4 SuppTab 2.E and SuppFig 2.L). For the erosion results, the three ways of calculation of metabolic rate were examined.

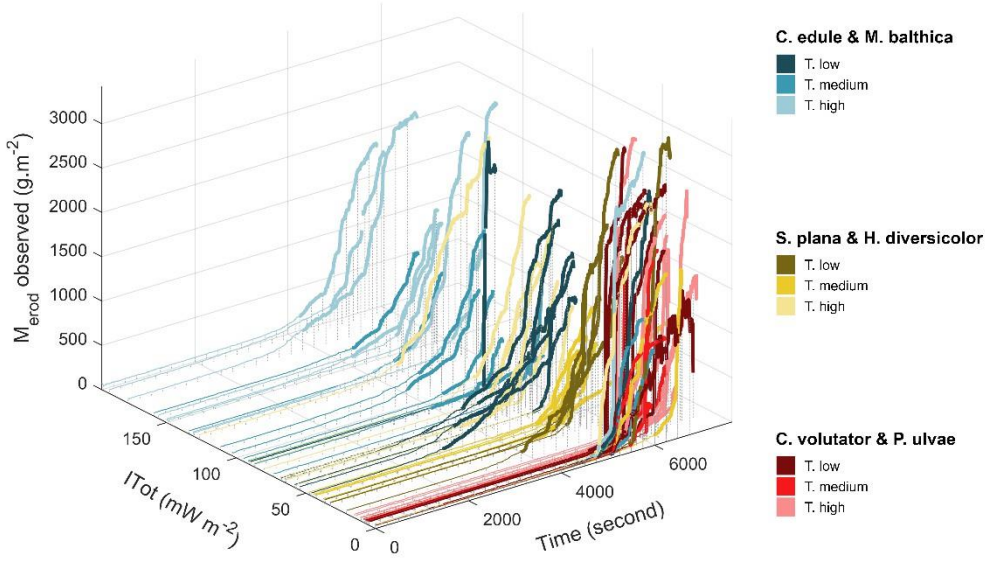

Figure 5 Erosion M_{erod} *(g.m^{-2}) vs time (s) and mesocosm metabolic rate (*$Itot_{meso}$ *[mW.m^{-2}]). The thick solid lines represent the steps identified as mass erosion steps. The various colours represent the different combination of species and temperature.*

3.2.2 Fluff layer erosion

The estimated fluff layer quantity (Q_{fluff} [g.m^{-2}]) showed a high dispersion in regard of any of the three metabolic rate of the sample (Figure 6). Q_{fluff} was measured for controls at 66+/-14 g.m^{-2} (n = 14), *C. edule & M. balthica* at 118+/-57 g.m^{-2} (n = 25), *S. plana & H. diversicolor* at 84+/-39 g.m^{-2} (n = 23) and *C. volutator & P. ulvae* at 73+/-22 g.m^{-2} (n = 24). Q_{fluff} was normalized by a Box-Cox transformation (λ = -1.07 and λ_2 = 100).

A linear model of transformed Q_{fluff} versus *Itot* showed a low value of indicator R², the $Itot_{flume}$ being with the best (R^2 = 0.204****), followed by $Itot_{meso}$ (R^2 = 0.177****), $Itot_{respi}$ (R^2 = 0.084**) being the lowest (Figure 6). An ANCOVA was conducted on Q_{fluff} transformed as a dependent variable, with $Itot_{meso}$ as covariant and temperature as factor ($F_{(2,82)}$ = 0.21, p = 0.8, Figure 7-A1, details in Supplementary data 3.2.2 SuppTab 3.E, H). There was no significant effect of duos but a significant effect of the metabolic rate (p<0.1). The positive value of the global slope indicates that the higher the metabolic rate, the more fluff layer is created and resuspended.

An ANCOVA was conducted on Q_{fluff} transformed as dependent variable, with $Itot_{meso}$ as covariant and duos as factor ($F_{(3,81)}$ = 0.22, p = 0.88, Figure 7-A2, details in Supplementary data 3.2.2 SuppTab

3.F, H). There was no significant effect of duos but a significant effect of the metabolic rate ($p<0.1$). The positive value of the global slope indicates that the higher the metabolic rate, the more fluff layer is created and resuspended.

A linear regression of Q_{fluff} as a function of the two metabolic rates of each species within duos has an R^2 similar to overall $Itot_{meso}$ ($R^2 = 0.177$***, n = 86, Table 1). The slopes for the two species are similar and positive but not significant for the *C. edule & M. balthica* and *S. plana & H. diversicolor* duos. This could suggest that the two duos of species contribute equally to the formation of the fluff layer. The slopes for the duo *C. volutator & P. ulvae* have confidence intervals that are too wide to be considered conclusive (details in Supplementary data 3.2.2 SuppFig 3.K SuppTab 3.I)

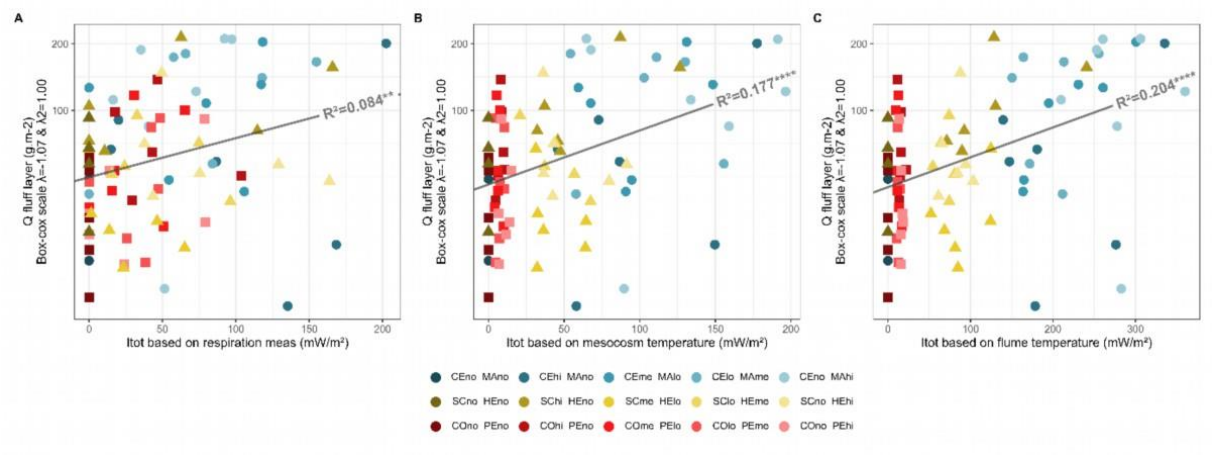

Figure 6 Fluff layer quantity (Q_{fluff} [$g.m^{-2}$]) vs the different metabolic rate evaluation [$mW.m^{-2}$]: based on the measured respiration rate $Itot_{respi}$ (A), the Itot with the mesocosm temperature $Itot_{meso}$ (B) and the Itot with the flume temperature $Itot_{flume}$ (C) and their regression line. Note that the y scale is Box-Cox transformed, and the models were made on transformed data.

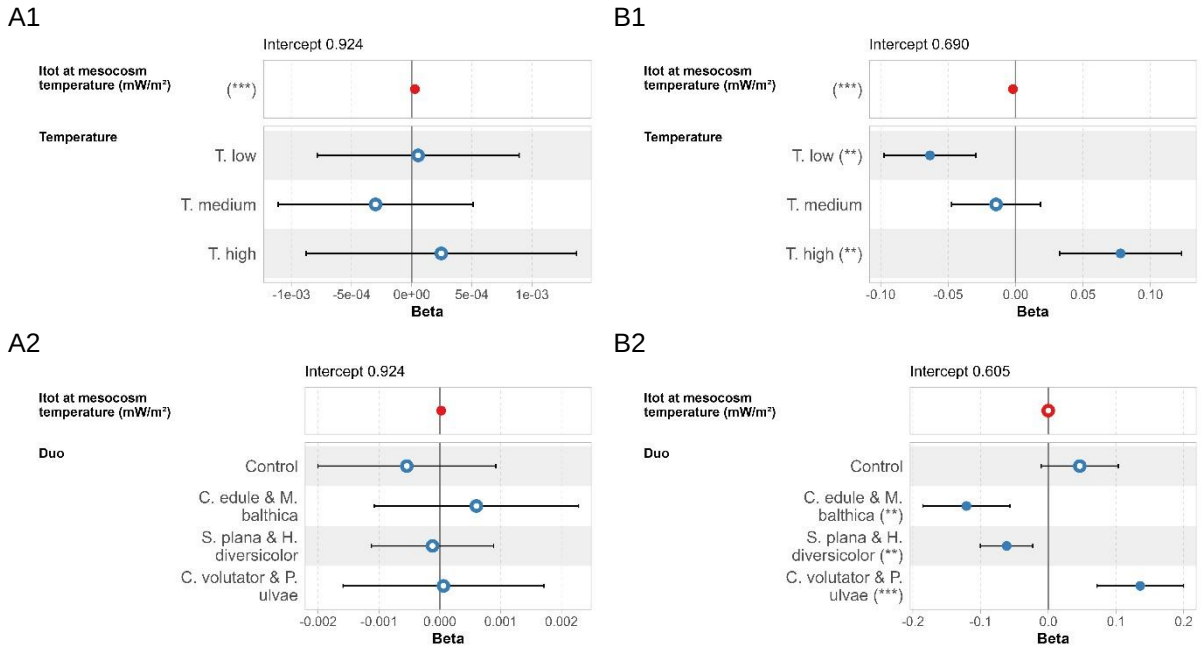

Figure 7 Right column: results for transformed Q_{fluff} - A1) ANCOVA model using the temperature as factor and the $Itot_{meso}$ as covariant; A2) ANCOVA model using the duos as factor and the $Itot_{meso}$ as covariant; Left column: results for transformed BSS_{mass} - B1) ANCOVA model using the temperature as

factor and the $Itot_{meso}$ as covariant; B2) ANCOVA model using the duos as factor and the $Itot_{meso}$ as covariant. Filled dot are p-value ≤ 0.1 and empty dot are p-value > 0.1.

Table 1 Linear regression estimates for each species $Itot_{meso}$ *($y = Intercept + \beta_{S1}.S1 + \beta_{S2}.S2$)*, with 95% confidence interval in all experiments and by duos separated for Q_{fluff} and BSS_{mass}.

	Intercept	β_{S1}	β_{S2}	R^2	N
Fluff layer : Q_{fluff}					
All	$9.24e^{-01}$ [$9.23e^{-01}$, $9.25e^{-01}$]	$2.67e^{-05}$ [$6.85e^{-06}$, $4.65e^{-05}$]	$2.94e^{-05}$ [$1.29e^{-05}$, $4.59e^{-05}$]	0.177***	86
C. edule & M. balthica	$9.25e^{-01}$ [$9.21e^{-01}$, $9.30e^{-01}$]	$8.53e^{-06}$ [$-3.92e^{-05}$, $5.62e^{-05}$]	$2.43e^{-05}$ [$-1.36e^{-05}$, $6.23e^{-05}$]	0.089	25
Control	$9.24e^{-01}$ [$9.22e^{-01}$, $9.25e^{-01}$]	-	-	-	14
C. volutator & P. ulvae	$9.23e^{-01}$ [$9.20e^{-01}$, $9.27e^{-01}$]	$3.44e^{-04}$ [$-2.04e^{-04}$, $8.92e^{-04}$]	$-9.87e^{-06}$ [$-4.10e^{-04}$, $3.90e^{-04}$]	0.168	24
S. plana & H. diversicolor	$9.24e^{-01}$ [$9.21e^{-01}$, $9.27e^{-01}$]	$4.03e^{-05}$ [$-1.38e^{-05}$, $9.44e^{-05}$]	$4.98e^{-06}$ [$-6.03e^{-05}$, $7.03e^{-05}$]	0.144	23
Mass erosion threshold : BSS_{mass}					
All	$6.73e^{-01}$ [$6.32e^{-01}$, $7.14e^{-01}$]	$-1.87e^{-03}$ [$-2.74e^{-03}$, $-1.01e^{-03}$]	$-1.33e^{-03}$ [$-2.05e^{-03}$, $-6.08e^{-04}$]	0.262****	84
C. edule & M. balthica	$4.56e^{-01}$ [$3.08e^{-01}$, $6.04e^{-01}$]	$4.78e^{-04}$ [$-1.11e^{-03}$, $2.07e^{-03}$]	$7.63e^{-05}$ [$-1.19e^{-03}$, $1.34e^{-03}$]	0.023	25
Control	$6.52e^{-01}$ [$5.87e^{-01}$, $7.17e^{-01}$]	-	-	-	13
C. volutator & P. ulvae	$4.93e^{-01}$ [$3.54e^{-01}$, $6.33e^{-01}$]	$3.37e^{-02}$ [$1.33e^{-02}$, $5.41e^{-02}$]	$2.75e^{-02}$ [$1.25e^{-02}$, $4.25e^{-02}$]	0.434**	23
S. plana & H. diversicolor	$5.73e^{-01}$ [$4.67e^{-01}$, $6.80e^{-01}$]	$-1.69e^{-03}$ [$-3.59e^{-03}$, $2.06e^{-04}$]	$7.32e^{-04}$ [$-1.56e^{-03}$, $3.02e^{-03}$]	0.299*	23

3.2.3 Mass erosion

The threshold for mass erosion bed shear stress (BSS_{mass} [Pa]) showed a high dispersion in regard of any of the three different ways to evaluate the metabolic rate of the sample (Figure 8). BSS_{mass} was measured for controls at 1.40+/-0.51 Pa (n = 14), *C. edule & M. balthica* at 0.84+/-0.36 Pa (n = 25), *S. plana & H. diversicolor* at 1.00+/-0.34 Pa (n = 23) and *C. volutator & P. ulvae* at 1.88+/-0.73 Pa (n = 24)

A linear model of BSS_{mass} versus *Itot* showed a low value of indicator R^2, the $Itot_{flume}$ being with the best (R^2 = 0.339****), followed by $Itot_{meso}$ (R^2 = 0.252****), $Itot_{respi}$ (R^2 = 0.046·) being the lowest (Figure 8). An ANCOVA was conducted on BSS_{mass} transformed as dependent variable, with $Itot_{meso}$ as covariant and temperature as factor ($F_{(2,80)}$ = 7.76, p = 0.0008, Figure 7-B1, details in Supplementary data 3.2.3 SuppTab 3.K, N). There was a significant effect of the metabolic rate but also a significant effect of the temperatures (p<0.1). In detail, the low temperature had significant negative effect on the BSS_{mass}, when high temperature has a significant positive effect (a negative effect lowers the erosion threshold and therefore increases erodibility). These results showed that the temperature has supplementary effect than the one from the metabolic activity of the fauna.

An ANCOVA was conducted on BSS_{mass} transformed as dependent variable, with $Itot_{meso}$ as covariant and duos as factor ($F_{(3,79)}$ = 8.39, p<0.0001, Figure 7-B2, details in Supplementary data 3.2.3

SuppTab 3.L, N). There was no significant effect of the metabolic rate but significant differences between three duos ($p<0.1$). In detail, the duos *C. edule & M. balthica* and *S. plana & H. diversicolor* had significant negative effects not significantly different on the BSS_{mass}, when the *C. volutator & P. ulvae* have a significant positive effect compared to the controls. These results showed that independently of the metabolic rate in the range of this experiment, the duo *C. edule & M. balthica* would destabilize the sediment more than *S. plana & H. diversicolor*, and that *C. volutator & P. ulvae* could have a stabilizing effect compared to an abiotic sediment.

The linear regressions of BSS_{mass} as a function of the two metabolic rates of each species within the duos had a R^2 similar to that of the $Itot_{meso}$ as a whole (R^2 = 0.262****, n = 84, Table 1). The slopes of the two species are significantly similar and negative for all duos. However, the duo *C. edule & M. balthica* showed almost no effect for both species, without significance, and *S. plana & H. diversicolor* showed a slightly asymmetric effect, slightly positive for *H. diversicolor* and negative for *S. plana*, but without significance. Slopes for *C. volutator & P. ulvae* are significantly positive, slightly higher for *C. volutator*, but with very wide confidence intervals (details in Supplementary data 3.2.2 SuppFig 3.R SuppTab 3.O).

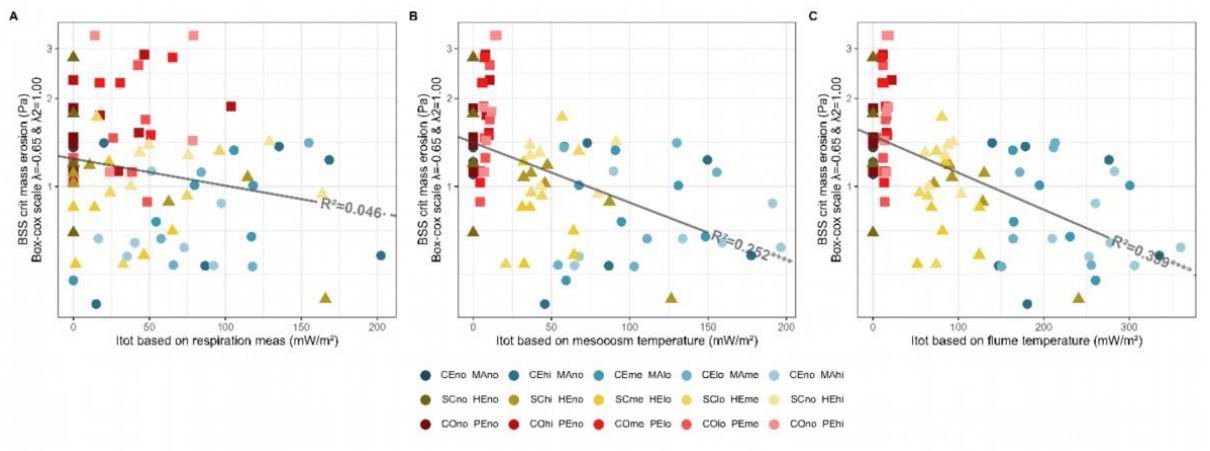

Figure 8 Critical bed shear stress (BSS_{mass} [Pa]) vs the different metabolic rate evaluation [$mW.m^{-2}$]: the measured respiration rate $Itot_{respi}$ (A), the Itot with the mesocosm temperature $Itot_{meso}$ (B) and the Itot with the flume temperature $Itot_{flume}$ (C) and their regression line. Note that the scales are Box-Cox transformed, and the models were made on transformed data.

4 Discussion

4.1 Metabolic rate and physiologic state of individuals

By measuring the respiratory rate of the animals in each sample, we sought to verify the relevance of the basal metabolic rate model and achieve the first objective of the study. However, the results showed a high variability, which can be attributed primarily to the experimental conditions that could affect the physiological state of animals or their behaviour.

Firstly, small mobile fauna such as *C. volutator* and *H. diversicolor* were unable to bury themselves during the respiration measurement (only water in the chamber). They were therefore forced to swim actively in the stirred water, which is not entirely representative of a natural activity. For comparison, the respiration rate of *H. diversicolor* showed results 10 to 25 times higher than obtained by Galasso (Galasso et al., 2018) (see Supplementary data 2.1 SuppTab 2.B). This may explain the differences observed in the slopes by duos in Figure 4, as the measurement conditions were relatively optimal for molluscs but lead to a higher respiration level for the others due to the stress induced by the measurement.

Secondly, the ANCOVA showing a significant difference for medium (spring) temperature is also the result of the experimental conditions. Measurements at this temperature were carried out at the beginning of experiments using animals recently taken from the natural environment and placed in a mesocosm at a temperature very close to the temperature of the environment at the time of sampling (see Supplementary data 2.4 SuppFig 2.L). The individuals were therefore in a state of minimal stress and in a physiological state as close as possible to their natural state. As the experiment progressed, the fauna was collected over a period of two months, with some individuals being kept in the mesocosm for the duration of the experiment and others being sampled shortly before the experiment. Noticeably, this period was marked by a heat wave - which was reflected in the temperature of the flume water - and may have had an effect on the physiological state of the animals that were taken last. Furthermore, no tests were carried out on the animals after the erosion had been measured, to assess possible parasitism or the state of their energy reserves, for example. This was partly due to a technical impossibility, as many of the animals were swept away by the current and destroyed by the circulation in the pump.

All those experimental biases explain the variability in respiration measurements, and explain the performance of the correlation with the basal metabolic rate model. But overall, the metabolic rate model is sufficiently valid for all species combined. The *Itot* parameterization is broad in its classification, separating the invertebrate phylogenetic tree into "only" 19 categories, here *C. edule*, *M. balthica* and *S. plana* were calculated with the same parameters. This is a good point for generalization and simplification that could be useful from a modelling point of view.

4.2 Temperature effect on bioturbation activity

The second objective of this study was to assess the effect of temperature variation on metabolism and its consequence on bioturbation and sediment erodibility. Respiration measurements showed that the animals used throughout the experiment were not in the same physiological state, hence the interest in comparing erodibility results with $Itot_{respi}$ and $Itot_{meso}$. It should be noted that the temperature in the protocol affects not only the animals but also the sediment. A positive correlation was observed between temperature and sediment erodibility (decrease in BSS erosion threshold, increase in erosion flux), although empirical studies have not ruled out the nature of the relationship between the two variables

(Grabowski et al., 2011). In an ANOVA using controls alone according to temperature, there was no significant difference for any of the erodimetry parameters between the 3 temperature levels, but a shift was observed reflecting a facilitation of erosion with increasing temperature, more pronounced for the summer temperature (see Supplementary data 3.2.1 SuppFig 3.E).

There were three methods of calculating the metabolic rate, which we have chosen to present, although the metabolic rate based on mesocosm temperature ($Itot_{meso}$) remains our reference. The use of respiration data ($Itot_{respi}$) added a significant degree of uncertainty and variability, the origin of which is mostly experimental. As the erodimetry results are also subject to biases that create variability, we chose not to use the respirometry results as a reference for the statistical tests, but only to validate that the metabolic rate model was relevant, as it is a tool for functional modelling of the environment.

On the other hand, displaying the results with the metabolic rate calculated with the temperature in the flume ($Itot_{flume}$) serves several purposes. Firstly, this result highlights the need to design experimental protocols that do not introduce biases of this magnitude. Indeed, we should have worked in erodimetry with water at a temperature similar to the mesocosm, or best in a climatic room, but technical limitations prevented us from doing so. The better performance of the model with flume temperature is probably a mathematical artefact, as the range of $Itot_{flume}$ values is wider than with $Itot_{meso}$, without the erosion parameter being modified.

However, the difference in temperature between the mesocosm and the flume raises the question of the speed of thermal adaptation of these species, which originate from the intertidal zone and thus experience considerable variations in environmental conditions over the course of a day. Settling in the sediment can buffer the variations in temperature, but feeding, particularly by filtering, puts the individual in close and immediate contact with water whose temperature can vary. If we were to consider the rapid change in temperature as a thermal shock, then Brey's model would no longer be appropriate, because it models a static metabolism, not a dynamic one. In general, metabolic models are defined under long-term stable temperature conditions, but are unable to reproduce thermal stress. On the other hand, we could consider that this type of variation is of the order of magnitude that these organisms experience daily. What are the kinetics of adaptation of the different species to these dynamic variations remains to be clarified.

Moreover, being a linear relationship limited by bounds, metabolic models exclude any possibility of extrapolation outside the observed range. Recent *in situ* observations have shown that the activity and therefore the magnitude of the bioturbation effects can vary according to the season, with a range of low temperatures well below those examined in this study (Morelle et al., 2024). In winter, *H. diversicolor* appears to maintain its stabilizing effect, while *S. plana* no longer has a significant effect. It was hypothesized that the abiotic winter conditions have a greater effect on sediment transport than the biological effect due to reduced biological activity in winter.

Finally, there is the question of what bioturbation is being measured. The experimental protocol of this study was designed to measure mainly the result of the integration of a period of bioturbation, rather than the immediate bioturbation that may occur during the measurement. This is due to the time difference between these two phases (more than 6h of bioturbation, and less than 2h for erodimetry), particularly regarding the fluff layer. The mechanisms of chronic bioturbation are linked to the living and feeding environment as well as the tidal cycle. A grazing epibenthic species will produce surface traces associated with its crawling time at low tide (Orvain and Sauriau, 2002), whereas a suspension-feeding endobenthic species will produce an immediate and continuous biogenic layer at high tide. We can see the role that the dynamics of metabolic adaptation could also play in the effects of bioturbation on bed erodibility, for example with “fight or flight” strategies such as sinking into sediments in inhospitable conditions, as Zhou showed in the case of a heat wave (Zhou, 2023).

4.3 Effects of species combination bioturbation on sediment erodibility

4.3.1 Fluff layer resuspension

The erosion of the fluff layer appears to be explained by the metabolic rate of the fauna present in the sediment, whatever the species. However, this result must be qualified by the discrepancy of the results. This is because Q_{fluff} determination is an indirect method that inherently involves a high degree of uncertainty. It depends on the height and duration of the erosion measurement steps, with threshold effects which, depending on the decision to attribute a step to fluff or mass, can significantly vary the Q_{fluff} value (Dairain et al., 2020b). In addition, the fluff layer is created in the incubation core, which is transferred to the sample bearer for erosion measurement, producing disturbances on the sample that were minimized as much as possible, but could not be totally avoided.

The Q_{fluff} was normalised by a Box-Cox transformation with a λ close to -1, *i.e.* an inverse transformation. The linear regression of the transformed data then corresponds to a linear relationship for the raw data. The choice of defining a simple linear relationship was intended to highlight the relationship between the two parameters, without over-interpreting it given the variability of the results. The relation between $Itot_{meso}$ and Q_{fluff} is probably more modelled by an asymptotic von Bertalanffy relationship, as could have been observed for *C. edule* (Lehuen and Orvain, 2024), and used in other studies like for *P. ulvae* (Orvain and Sauriau, 2002), for *S. plana* (Orvain, 2005), or *M. balthica* (Willows et al., 1998).

The results of the study of (Cozzoli et al., 2018), with *C. edule*, *M. balthica*, *S. plana*, *H. diversicolor* and *C. volutator* isolated, showed some similar scales of results for Q_{fluff} but with a quicker dynamic (critical fluff BSS lower) and global asymptotical with a clearer trend (details in Supplementary data 3.2.1 SuppFig 3.F). This trend difference may be mainly due to the fact that there were made on different flumes and with a different way to prepare the sediment, as shown by the records of controls, and as seen in a meta-analysis of erodibility studies (Lehuen and Orvain, 2024).

Overall, the presence of metabolic energy explains the creation of an easily erodible sedimentary layer, which can be attributed to the bioturbation action of the fauna present. Although the results are very noisy, they suggest that metabolic rate is an interesting way of describing surface bioturbation phenomena and a generic model could be sought, which could facilitate the integration of these processes in sediment transport models.

4.3.2 Mass erosion

Bioturbation can modify the constitutive layer of sediments, facilitating or hindering mass erosion at high bed shear stress: *S. plana* was observed as a deep destabilizing species, reducing the critical threshold of mass erosion (Orvain, 2005); on the other hand, a stabilizing effect was attributed to the worm *H. diversicolor* (Passarelli et al., 2014). The processes involved take place in subsurface sediment and are closely linked to the history of settlement of the individual in the sediment.

The results of this study tend to indicate that the metabolic rate is not a suitable descriptor for assessing the effects of bioturbation on sediment mass erodibility. Despite very noisy results, the ANCOVA did not show a statistical link between metabolic rate and mass erosion threshold, but did show significant differences depending on the species duos. On the one hand, *C. edule & M. balthica* and *S. plana & H. diversicolor* would have a destabilising effect, more marked for *C. edule & M. balthica*, on the other hand, *C. volutator & P. ulvae* duo appears to have a stabilizing effect.

In the case of *S. plana & H. diversicolor*, it appears that the destabilising effect of *S. plana* is more pronounced than the stabilising effect of *H. diversicolor* in the experiment temperature range. Although the results seem to indicate that *S. plana* and *H. diversicolor* have antagonistic effects on sediment erodibility, the number of experiments performed did not allow us to distinguish them significantly. (Morelle et al., 2024) observed *in situ* at summer conditions this antagonistic effects of the two species. However, this study does not provide any information on the hydrodynamic conditions during the measured bioturbation period. It is likely that these conditions were of the order of chronic effects rather than the strong hydrodynamic conditions associated with mass erosion. As de Smit observed (de Smit et al., 2021a, 2021b), the behaviour of *H. diversicolor* could be modified by the presence of other species in the sample, preventing the stabilization effect from being significantly expressed. This interacting mechanism should be described with further details.

As far as the *C. edule & M. balthica* duo is concerned, the effect of mass destabilisation is generally little or no highlighted in the literature for these two species (see Supplementary data 2.1 SuppFig 2.C SuppTab 2.C). An analogy could be made between *M. balthica* and *S. plana* and therefore on its effects, for a smaller species but installed less deeply. However, in the case of *C. edule*, its impact on erodibility relates more to the surface, and is generally linked to its movements and the generation of intrinsic roughness (Dairain et al., 2020b). In our experimental conditions, the presence of *C. edule*, and to a lesser extent *M. balthica*, generated fragilities on the sediment surface during transfers from the cores to the sample bearer in the flume, which may have facilitated mass erosion. These fragilities also

519 exposed the individuals to the currents, causing *C. edule* to sink into the sediment during phases of
520 strong currents, facilitating mass erosion.

521 Finally, for *C. volutator* & *P. ulvae*, these two species live on the surface of sediment. *P. ulvae* was
522 already identified as a bioturbator not able to change the mass erosion critical threshold (Orvain, 2005;
523 Orvain et al., 2003). In addition, there were no observation of effect of *C. volutator* on mass erosion by
524 (Grant and Daborn, 1994). It is important to note that the experimental methodology for *C. volutator* &
525 *P. ulvae* was different to the others duos. Their bioturbation period was made in the absence of high
526 tide, it was not possible for *C. volutator* to dig a gallery, which it did in the flume as soon as it was put in
527 the water, as observed in (De Backer et al., 2010). In addition, the bioturbation phase took place in the
528 sample bearer and not in the incubation core, thus eliminating a disturbance phase present in all the
529 measurements of the other two duos. This was a limitation of this protocol which, due to the design of
530 the flume, did not allow equivalent treatment for surface and sub-surface species.

531 4.4 Toward a community erosion model

532 This study illustrates the potential importance of missing data when modelling the bioturbation effects
533 on sediment erodibility. However, due to several biases and experimental limitations, the data set was
534 noisy enough to prevent modelling of the bioturbation effect of combined species on erodibility that could
535 be incorporated into HMS models.

536 Nevertheless, our results suggest that this route is sufficiently relevant for the fluff layer erosion to
537 be pursued with this type of experiment, with fewer factors and more controlled conditions to guarantee
538 a higher degree of accuracy. An assessment of the impact of temperature on the effects of bioturbation
539 on sediment erodibility for isolated species, taking into account the kinetics of metabolic adaptation is
540 clearly required. According to (Kooijman, 2010), metabolic adaptation to a new temperature is rather
541 slow (days to weeks). However, intertidal animals are subject to very wide temperature conditions, so
542 they should have a range of metabolic functions that allow them to adapt. In any case, the *Itot* calculation
543 is only applicable in the range of temperatures valid for the organism.

544 The metabolic rate is a good descriptor to link the fauna activity to the chronic bioturbation effect, but
545 is not adequate to combine several species as a community considering mass erosion (event-driven
546 effects), regardless of their type of bioturbation activity. A simple categorisation were made by depth of
547 living for fauna in (Cozzoli et al., 2018) for example. Indeed, the variety of bioturbation processes and
548 their impact on sediment erodibility shows that the question of metabolic energy alone may be
549 insufficient, and may explain the level of dispersion of the results obtained in the present study.
550 Moreover, the experimental conditions in the bibliography used to classify these species were very
551 diversified, depending on the sediment types, the measurement methods, or the mesocosm conditions
552 (presence/absence of microphytobenthic biofilm for instance) and bioturbation behaviours and
553 acclimation.

Among the many methodological differences in all the existing studies, one aspect seems key: the presence or absence of MPB biofilm on the sediment surface. Deposit feeder species have often been classified as destabilizing, either chronically or event-driven, because they graze biofilm, which has a strong stabilising effect (Andersen et al., 2002; de Deckere et al., 2000; Orvain et al., 2014a, 2004; van Prooijen et al., 2011). The effects measured in laboratory experiments without MPB do not take into account a key element of *in situ* conditions. In the environment, the properties of the sediment on the surface are the result of a synergy between the bioturbating fauna and the MPB, with the former altering the effects of the latter. There is therefore often a discrepancy between laboratory and *in situ* results, to say it roughly: in the laboratory we measure the characteristics of the sediment itself (unless intended inoculation), in the field the characteristics of the MPB biofilm (Andersen et al., 2010, 2005; Orvain et al., 2004).

5 Conclusion

This study aimed at revealing how macrozoobenthic communities and temperature could modify the sediment erodibility parameters. By coupling two species, we showed that the metabolic rate was an interesting descriptor for modelling sediment transport at the community scale for the creation of fluff layer. The effects of bioturbation on mass erosion appeared to require another information rather the metabolic rate, information that the bioturbation functional group could provide, even if the destabilizing effects on the constitutive layer of sediment seemed to dominate, at least in the absence of MPB. The kinetics of metabolic acclimatisation still need to be explored to determine how reactive the individual might be, in order to settle the question of how metabolic rate is taken into account in a model. The effect of fauna and their bioturbation activity regarding the temperature condition through the metabolic rate is a prerequisite to model at large spatial and temporal scales the impact of fauna on their habitat, and especially to integrate this process into hydro-morpho-sedimentary models of ecosystems such as estuaries.

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Figure 1 A: Fauna models used in their sediment. B: Classification of species according to the different effects of bioturbation on sediment characteristics (references in Supplementary data 2.1, SuppFig 2.B and SuppTab 2.C).

Figure 2 Maps of sampling location for each species and sediment.

Figure 3 A: Experimental design. B: Measurement's chronology. LT: low tide, HT: high tide, O_2: respiration chamber, pot: incubation core, sample: sample bearer for the erosion flume, ERIS: erosion flume. The green frame represents the steps with a controlled temperature. C: Mesocosms tidal rhythm for each duo. The blue arrow represents the respiration measurement and the installation in the pot, the red arrow the bioturbation phase, the red dotted line the holding period of C. volutator and P. ulvae in a dedicated mesocosm prior to installation on sample bearer.

Figure 4 A: $Itot_{respi}$ [$mW.m^{-2}$] vs $Itot_{meso}$, with standard deviation and its regression line for each duo (corresponding colours) and in grey for all data combined, the grey dotted line represents the identity relation. Note that the scales are Box-Cox transformed, and the regression lines were made on transformed data. B: ANCOVA results for $Itot_{respi}$ transformed ~ $Itot_{meso}$ transformed + Duo + Temperature. Filled dot are p-value ≤ 0.1 and empty dot are p-value > 0.1.

Figure 5 Erosion M_{erod} ($g.m^{-2}$) vs time (s) and mesocosm metabolic rate ($Itot_{meso}$ [$mW.m^{-2}$]). The thick solid lines represent the steps identified as mass erosion steps. The various colours represent the different combination of species and temperature.

Figure 6 Fluff layer quantity (Q_{fluff} [$g.m^{-2}$]) vs the different metabolic rate evaluation [$mW.m^{-2}$]: based on the measured respiration rate $Itot_{respi}$ (A), the Itot with the mesocosm temperature $Itot_{meso}$ (B) and the Itot with the flume temperature $Itot_{flume}$ (C) and their regression line. Note that the y scale is Box-Cox transformed, and the models were made on transformed data.

Figure 7 Right column: results for transformed Q_{fluff} - A1) ANCOVA model using the temperature as factor and the $Itot_{meso}$ as covariant; A2) ANCOVA model using the duos as factor and the $Itot_{meso}$ as covariant; Left column: results for transformed BSS_{mass} - B1) ANCOVA model using the temperature as factor and the $Itot_{meso}$ as covariant; B2) ANCOVA model using the duos as factor and the $Itot_{meso}$ as covariant. Filled dot are p-value ≤ 0.1 and empty dot are p-value > 0.1.

Figure 8 Critical bed shear stress (BSS_{mass} [Pa]) vs the different metabolic rate evaluation [$mW.m^{-2}$]: the measured respiration rate $Itot_{respi}$ (A), the Itot with the mesocosm temperature $Itot_{meso}$ (B) and the Itot with the flume temperature $Itot_{flume}$ (C) and their regression line. Note that the scales are Box-Cox transformed, and the models were made on transformed data.

Table list