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Multispecies macrozoobenthic seasonal bioturbation effect on sediment erodibility

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 with non-linear effects of macrofauna functional trait interactions. 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 synergistic bioturbation of different species. The experimental design consisted of: i) three temperature levels (winter, spring and summer), ii) three types of species duos (*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 resuspension 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 sediment erosion threshold cannot be easily modelled by using the metabolic rate and the classification in functional groups is required. 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 sediment 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

Graphical abstract
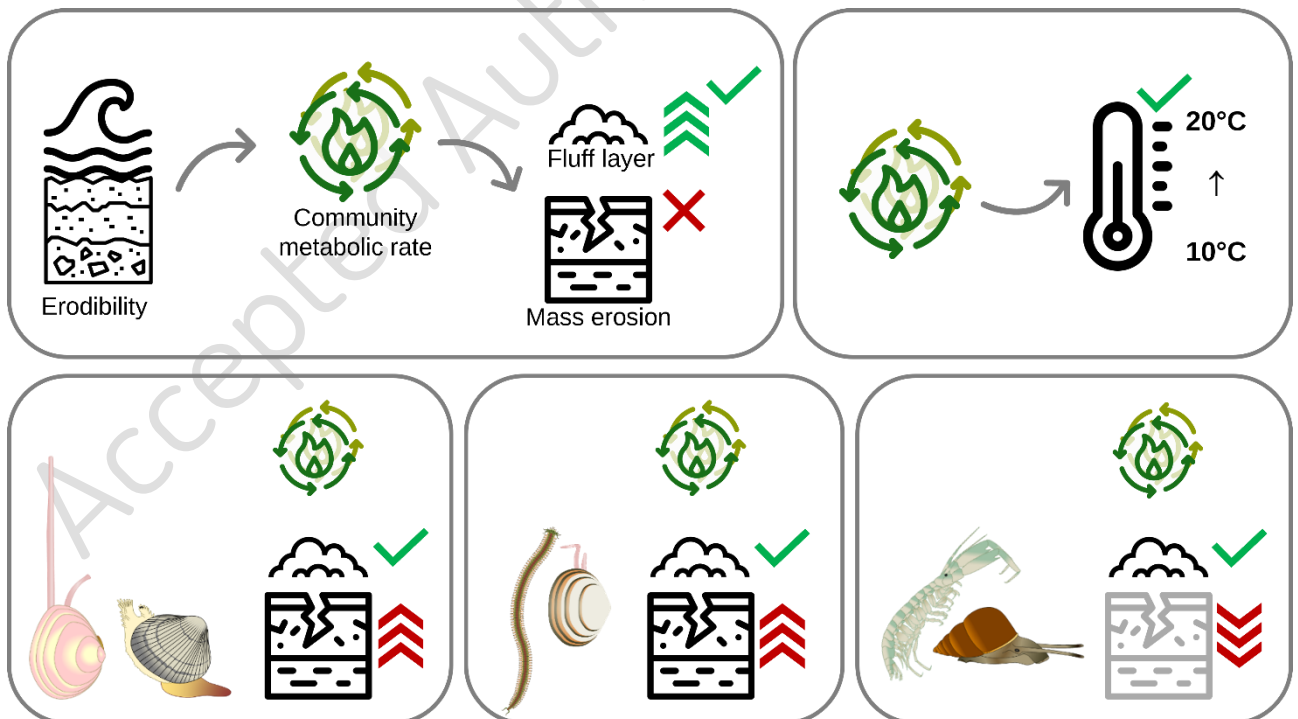
Manuscript

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 (HMS) models (the recent work of Brückner et al. (2021) is a case in point), 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 some of 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). From an erosion point of view, two kinds of processes can be distinguished: the fluff layer erosion, a biogenic reworked layer eroded under chronic conditions, and the mass sediment erosion, happening under dynamic events, such as winter storms (Orvain et al., 2003). 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 (Cozzoli et al., 2018).

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 (SMR), 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 the metabolic rate, that is to say the quantity of energy spent 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 sediment 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 and the non-linear effects that may exist between species, this is a challenge to unravel the interacting benthic processes at a multi-species level. All these effects may therefore add up, cancel each other out or not affect the same factors, depending on their life traits 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 the 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 took 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 measured 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 bioturbation effect of species using the sum of their metabolic rate. These species were associated according to their functional groups to study various cases of interactions.

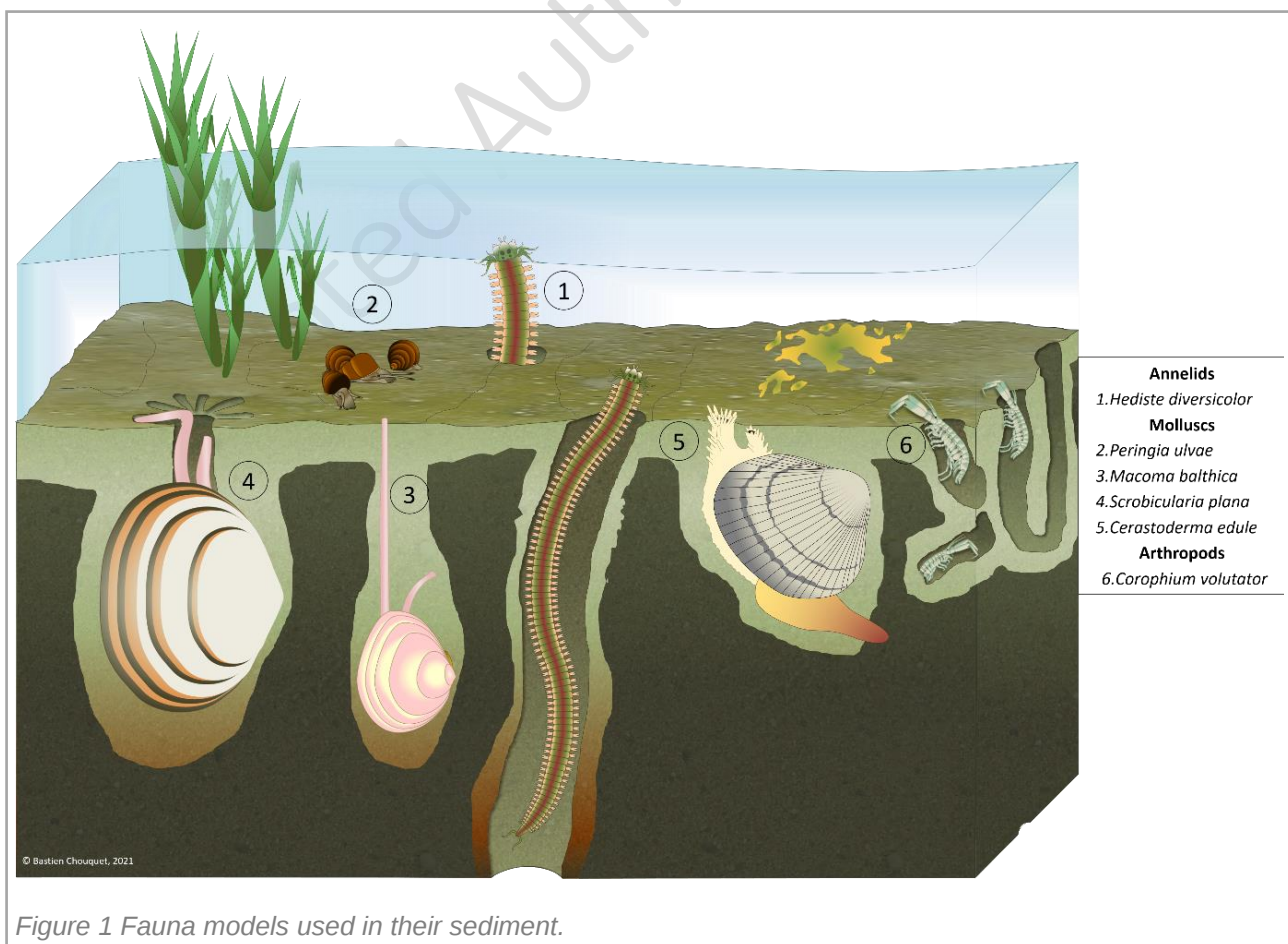## 2 Material and Methods

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 1). This study proposes to evaluate combined bioturbation effects of those six emblematic species by defining three species duos:

1. *Cerastoderma edule* and *Macoma balthica*: They both create a biogenic layer on the first few centimetres of sediment and can play a role in both types of erosion -fluff layer and mass sediment erosion- (*C. edule:* Ciutat et al., 2007; Dairain et al., 2020b; Li et al., 2017; *M. balthica:* de Smit et al., 2021a; van Prooijen et al., 2011; Widdows et al., 1998). 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 coexist (Bocher et al., 2007; Montserrat et al., 2009; Ysebaert et al., 2003).

2. *Scrobicularia plana* and *Hediste diversicolor*: Those two species are known for their antagonistic effects on the deep structure of the sediment: *H.diversicolor* is a biostabilizator (Cozzoli et al., 2019; Fernandes et al., 2006; Passarelli et al., 2012), *S. plana* is a bed destabilizator (Kristensen et al., 2013; Orvain et al., 2005; Soares and Sobral, 2009). 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 tracks on the sediment surface, but *S. plana* also generates pseudo-faeces when filtrating water.

3. *Corophium volutator* and *Peringia ulvae*: *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 (*C. volutator:* Cozzoli et al., 2019; de Deckere et al., 2000; *P. ulvae:* Kristensen et al., 2013; Orvain et al., 2014b; Orvain and Sauriau, 2002).

Based on the theoretical frame of Allen et al. (2005) and Brown et al. (2004), the individual metabolic rate *(I)* was expressed as function of the

Figure 1 Fauna models used in their sediment.

Legend:
Annelids
1.Hediste diversicolor
Molluscs
2.Peringia ulvae
3.Macoma balthica
4.Scrobicularia plana
5.Cerastoderma edule
Arthropods
6.Corophium volutator

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individual body size (M) and the temperature (T): $I \approx r_0 M^b \cdot e^{-Ek/T}$. The equation was adjusted for the parameters $r0$, b and Ek for each species to the SMR of aquatic invertebrates model of 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).

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) (Table 1).

Muddy and sandy sediments 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. 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 in Supplementary data 2.2).

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 (Table 1 Coordinates of animal and sediment sampling sites). 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).
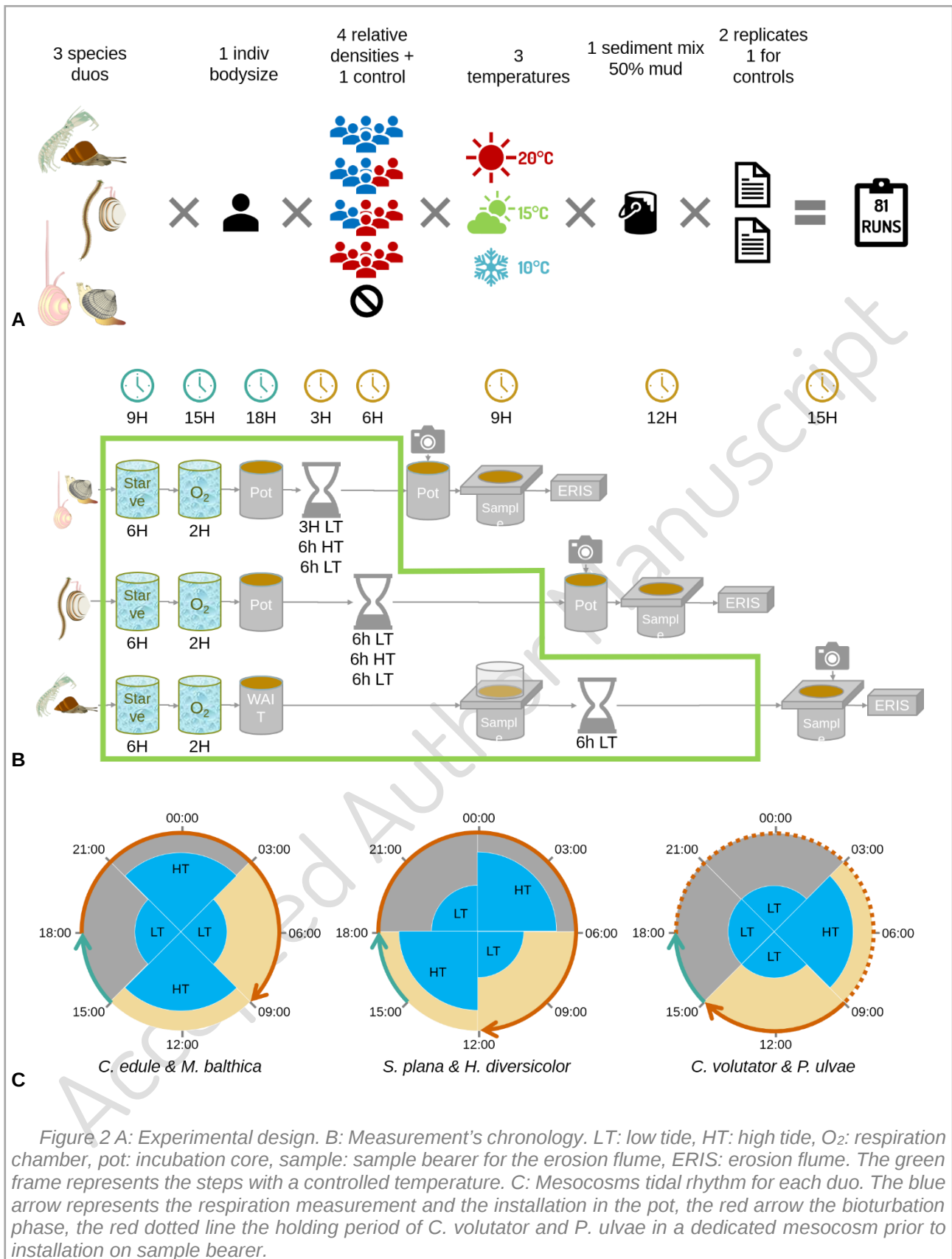
2.3   Experimental design

The design of the experiment was established to measure the erodibility properties of the sediment for combined species and at varying temperatures (Figure 2A). 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). Two replicates were made for each condition.

Experiments started with a respiration measurement of the biological samples in filtered sea water (salinity 31) at controlled temperature. Then, the faunal samples were deposited into a muddy sediment core for incubation. The sediment surface was smoothed and set into a tidal mesocosm (Figure 2C) with controlled temperature for a bioturbation period. A 12h day light is set up in the mesocosm, and there was no microphytobenthos (MPB) inoculated to the surface.

Table 1 Coordinates of animal and sediment sampling sites (decimal degree WGS84)

Species	Latitude	Longitude	Name	Country
C. edule	51.460569	4.219271	Oesterdam	Netherlands
H. diversicolor	51.439567	4.200713	Haven Rattekaai	Netherlands
C. volutator	51.386035	3.818547	Haventje Ellewoutsdijk	Netherlands
S. plana	51.430484	4.043624	Den Inkel	Netherlands
M. balthica	51.430484	4.043624	Den Inkel	Netherlands
P. ulvae	51.41137	4.072761	Nolleweg	Netherlands
NIOZ	51.488869	4.057137	Yerseke	Netherlands
Mud	51.364531	4.245363	Groot Buitenschoor	Belgium
Sand	51.399782	4.181586	Rilland	Netherlands

Figure 2 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.

Depending on the erosion measurement sequence (3 hours of measurement and cleaning of the flume, Figure 2B), the bioturbation duration varied from 6h to 18h, with a setup adapted for *Corophium volutator* and *Peringia ulvae*, to ensure their presence on the surface of the sample. In this case, the fauna was placed in a waiting mesocosm, and installed directly on the sample holder, resulting in the absence of seawater during the bioturbation period. (Figure 2C).

The incubation cores were then transferred in a sample bearer for the erosion measurement in flume, producing disturbances on the sample that were minimized as much as possible, but could not be totally avoided. The erosion measurement was conducted with filtered sea water at room temperature, which was 7.44 ± 3.75 °C higher than mesocosm temperature (details in Supplementary data 2.4).

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 secondary consumption of O_2 by faeces. The sample pools were then placed in a sealed respiration chamber (V = 1.5L) under agitation. The oxygen concentration [µmol.L^{-1}] was measured for 2h using a PyroScience FireStingO2 sensor, without light or human presence. From the recordings of the measurements, 3 visually disturbance-free periods were selected to calculate 3 slopes of a linear regression, summarized as mean and standard deviation of respiratory rate [µmolO$_2$.s^{-1}]. Based on Brey et al. (2010), the respiration rate was converted to metabolic rate $Itot_{respi}$ [mW] with the oxycalorimetric coefficient 468 J/mmolO$_2$ and divided by flume area 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, the mean water temperature in the flume was used to calculate a flume $Itot_{flume}$ [mW.m^{-2}].

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 critical threshold for mass sediment erosion and the erosion flux were calculated from the turbidity in response to increasing bed shear stress. The bed shear stress is modulated by different flow velocities in a closed channel. Details about flume setup are in Guizien et al. (2012), Le Hir et al. (2008), Orvain et al. (2014b). The erosion experiments were carried out in stages with a current velocity from 0 to 91 cm.s^{-1}. The experimental sequence contained 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. Turbidity measurement was converted into resuspended mass calculated on the sample surface, M_{erod} [g.m^{-2}]. Every current step was defined, and fluff layer or mass sediment erosion steps were identified visually, since a bed failure appears during the mass sediment erosion. 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 sediment erosion steps. The fluff layer quantity eroded, named Q_{fluff}, was determined as the 95th centile of M_{erod} of the last fluff erosion step before mass sediment erosion (details in Supplementary data 2.4).

Given the erodimetry measurement duration (2 hours) compared to that of bioturbation (at least 6h), the metabolic rate based on the temperature of the mesocosm ($Itot_{meso}$) was the reference biological parameter. The metabolic rate based on respiration rate measurements, $Itot_{respi}$, and on flume temperature ($Itot_{flume}$) are also displayed for comparison.

2.4.3 Data analysis

Respiration measurement results, $Itot_{respi}$, were compared to the metabolic rate $Itot_{meso}$ calculated

with the temperature of the mesocosm. 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 effectiveness of the Brey's model in accounting for fauna activity. An one-way ANCOVA was made with the metabolic rate based on respiration measurement $Itot_{respi}$ 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).

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 to test the effect of the metabolic rate ($Itot_{meso}$), as covariate, and temperature or duos as controlled factors. 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 was verified by evaluating the normality of the sub-groups per factor (with a Shapiro-Wilk test) and the homogeneity of regression slopes for each sub-group was checked (with a Harrisson-Mac Cabe test). 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.
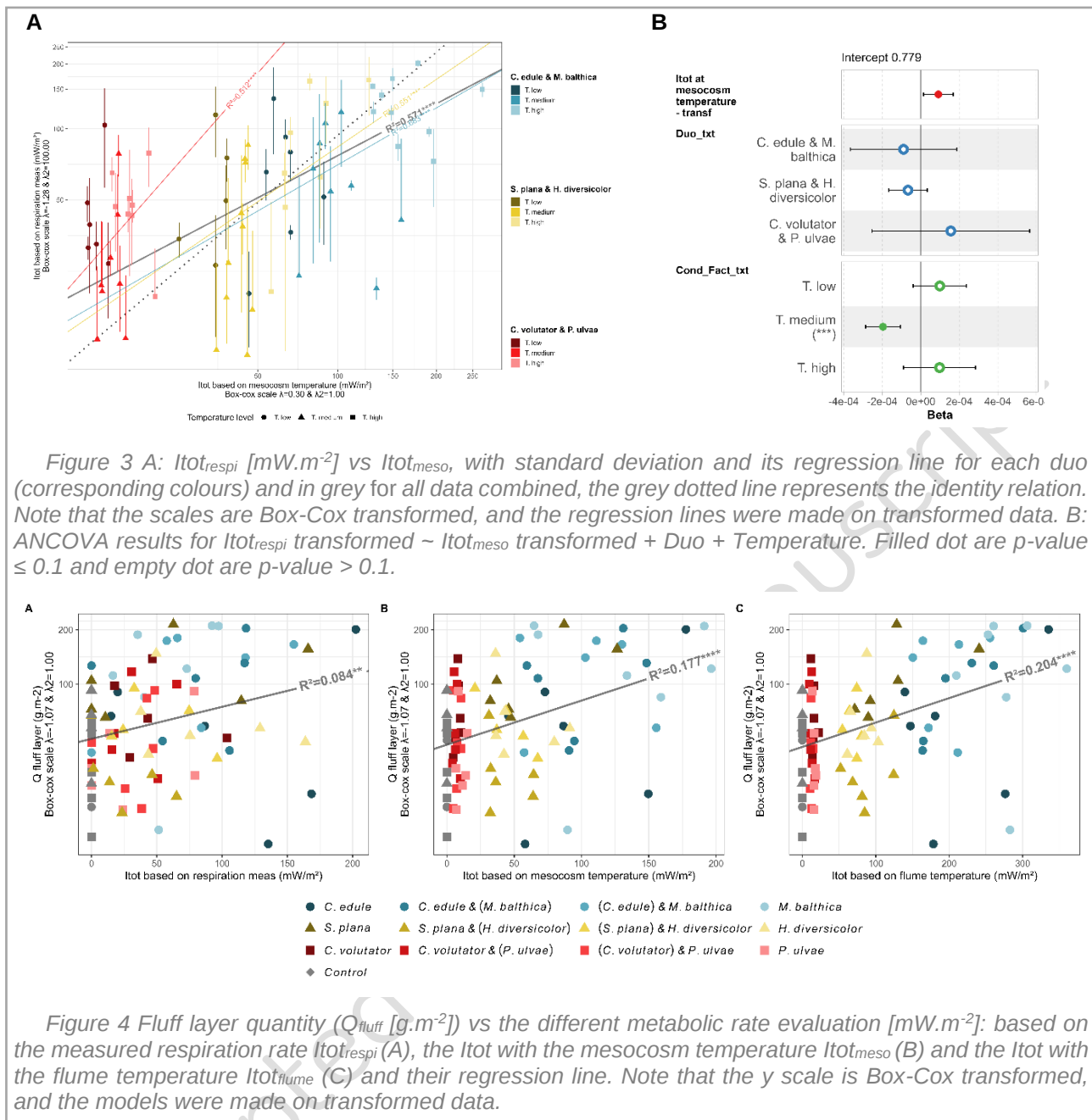
3 Results

3.1 Respiration measurements

The overall oxygen consumption was measured for *C. edule & M. balthica* at 0.03 ± 0.02 x10^{-4} $\mu molO_2.s^{-1}.gAFDW^{-1}$ (88 ± 50 mW.m^{-2}, n = 27), *S. plana & H. diversicolor* at 0.06 ± 0.04 x10^{-4} $\mu molO_2.s^{-1}.gAFDW^{-1}$ (55 ± 44 mW.m^{-2}, n = 26) and *C. volutator & P. ulvae* at 0.28 ± 0.33 x10^{-4} $\mu molO_2.s^{-1}.gAFDW^{-1}$ (27 ± 31 mW.m^{-2}, n = 27). The metabolic rate calculated from the measured respiration rate $Itot_{respi}$ was normalized with a Box-Cox transformation (λ = -1.280 and λ_2 = 100), as well as $Itot_{meso}$ calculated with 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 3A). The dataset with *C. volutator & P. ulvae* showed a significant level of correlation between $Itot_{meso}$ calculated and the measured $Itot_{respi}$ (R^2 = 0.512****) with a slope significantly different from 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 relationship between the two variables (R^2 = 0.571****). The overall slope, like that of *C. edule & M. balthica* and *S. plana & H. diversicolor*, had a value slightly lower than the identity line (i.e. the diagonal), but with an ordinate originally higher, meaning that a weak $Itot_{meso}$ underestimates $Itot_{respi}$, while a high $Itot_{meso}$ overestimates it. For *C. volutator & P. ulvae*, $Itot_{meso}$ systematically underestimated $Itot_{respi}$, 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 3B) show that there was no significant effect of duos on $Itot_{respi}$ but a significant effect of the temperature, in particular the medium

Figure 3 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 4 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.

temperature which would lead to a lower *Itot$_{respi}$* value.

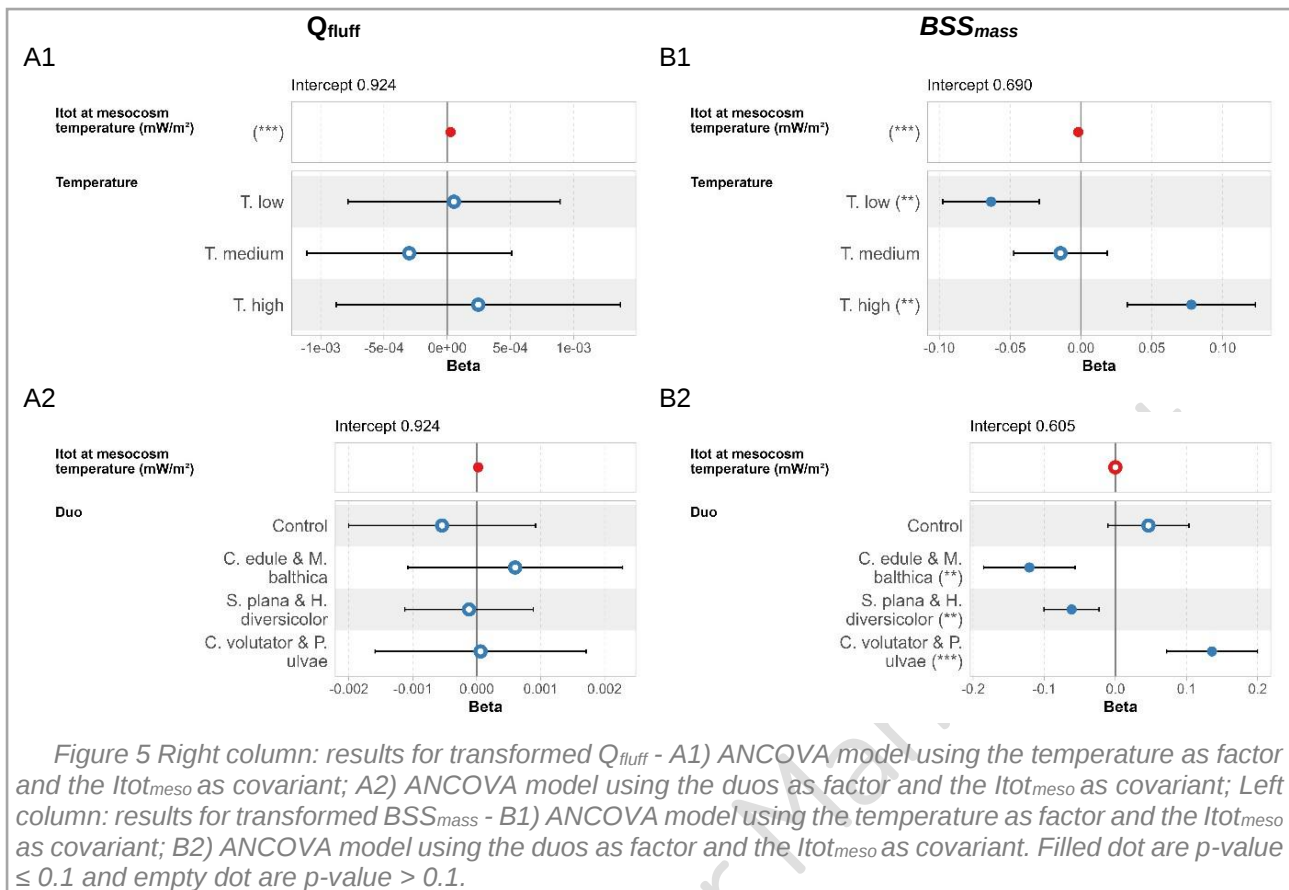## 3.2   Erodibility analysis

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 sediment erosion occurred. Fluff layer erosions were observed until the bed shear stress BSS reached the critical threshold of 0.81 ± 0.53 Pa (U* = 2.67 ± 0.87 cm.s^{-1}). The mass sediment erosion critical threshold BSS was of 1.73

± 0.74 Pa (U* = 4.01 ± 0.87 cm.s^{-1}). 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$_{meso}$*.

3.2.2   Fluff layer erosion

The estimated quantity of sediment in the fluff layer (Q$_{fluff}$ [g.m^{-2}]) showed a high dispersion for the three metabolic rates of the sample (Figure 4). Q$_{fluff}$ was estimated 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}

Figure 5 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.

(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 R², the $Itot_{flume}$ being with the highest (R^2 = 0.204****), followed by $Itot_{meso}$ (R^2 = 0.177****) and finally $Itot_{respi}$ (R^2 = 0.084**; Table 2). An ANCOVA was conducted on Q_{fluff} transformed as a dependent variable, with $Itot_{meso}$ as covariant and as factor either the temperature ($F_{(2,82)}$ = 0.21, p = 0.8, Figure 5-A1) or duos ($F_{(3,81)}$ = 0.22, p = 0.88, Figure 5-A2). For both ANCOVAs, there was a significant effect of the metabolic rate (p<0.1), but no significant effect of the factor. The positive value of the global slope indicates that the higher the metabolic rate, the more the fluff layer was created and resuspended.
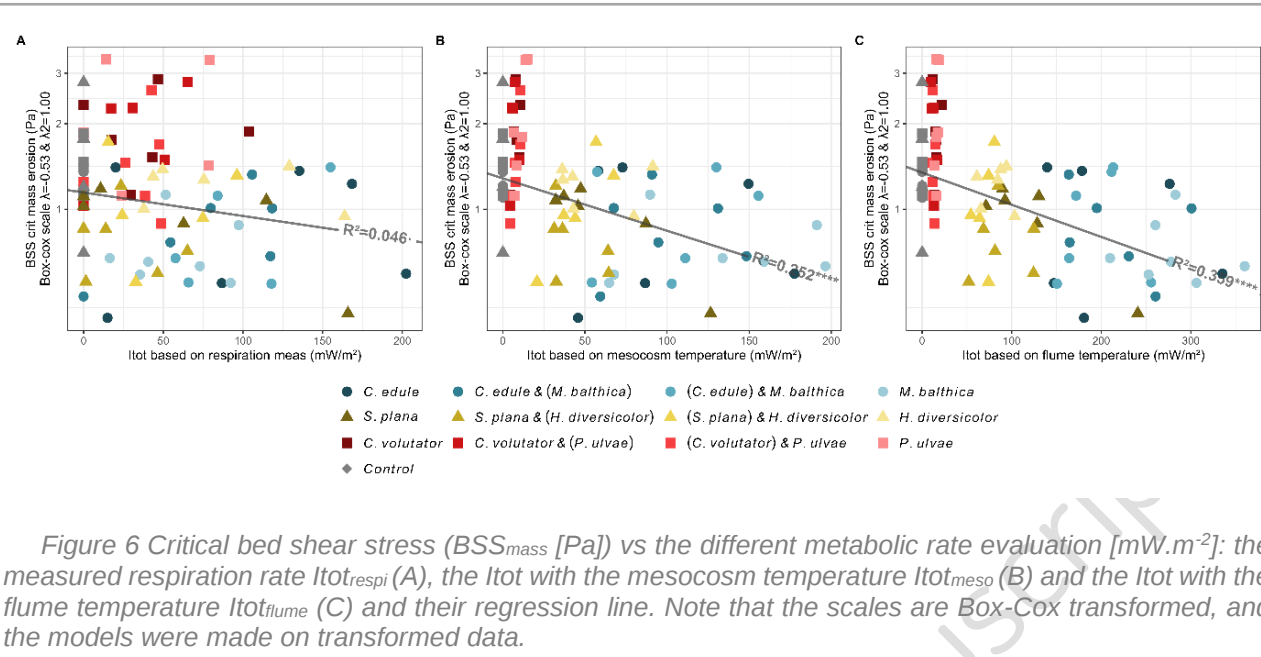
A linear regression of Q_{fluff} as a function of the two metabolic rates of each species within duos (R² = 0.177***, n = 86, Table 2) indicates that the slopes for the two species were not significantly different for the *C. edule & M. balthica* and *S. plana & H. diversicolor* duos. This could suggest that the two

species contributed equally to the formation of the fluff layer. The slopes for the duo *C. volutator & P. ulvae* had confidence intervals that were too wide to be considered conclusive (details in Supplementary data 3.2.2).

3.2.3   Mass sediment erosion

Regarding the mass sediment erosion, the critical threshold for bed shear stress (BSS_{mass} [Pa]) showed a high dispersion whatever the way of evaluating the metabolic rate (Figure 6). 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 R², the $Itot_{flume}$ being with the highest (R^2 = 0.339****), followed by $Itot_{meso}$ (R^2 = 0.252****) and $Itot_{respi}$ (R^2 = 0.046·) being the lowest (Figure 6). The ANCOVA conducted on BSS_{mass} with $Itot_{meso}$ as the covariant, revealed that the temperature effect

Figure 6 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.

was significant ($F_{(2,80)}$ = 7.76, p = 0.0008, Figure 5-B1) as well as the duos ($F_{(3,79)}$ = 8.39, p<0.0001, Figure 5-B2). There was a significant effect of the metabolic rate in the ANCOVA with temperature as factor.

In detail, the low temperature had significant negative effect on the *BSS$_{mass}$*, while high temperature has a significant positive effect (a negative effect lowers the erosion threshold and therefore increases erodibility). The duos *C. edule*

& M. balthica and *S. plana & H. diversicolor* had significant negative effects on *BSS$_{mass}$*, compared to the controls but without difference between them, while the *C. volutator & P. ulvae* had a significant positive effect compared to controls.

The linear regressions of *BSS$_{mass}$* as a function of the two metabolic rates of each species within the duos (R² = 0.262****, n = 84, Table 2) indicated that the slopes of the two species were not significantly different for all duos together. However, the duo *C.*

Table 2 Linear regression estimates for each species Itot$_{meso}$ (y = Intercept + β_{S1}.S1 + β_{S2}.S2), with 95% confidence interval in all experiments and by duos separated for Q$_{fluff}$ and BSS$_{mass}$.

	Intercept	β_{S1}	β_{S2}	R²	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
Control	9.24e^{-01} [9.22e^{-01}, 9.25e^{-01}]	-	-	-	14
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
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 sediment 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
Control	6.52e^{-01} [5.87e^{-01}, 7.17e^{-01}]	-	-	-	13
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
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

edule & M. balthica showed an absence of effect for both species, while *S. plana & H. diversicolor* showed a slightly asymmetric effect, positive for *H. diversicolor* and negative for *S. plana*, but without significance. Slopes for *C. volutator & P. ulvae* were significantly positive, slightly higher for *C. volutator*, but with very wide confidence intervals (details in Supplementary data 3.2.2).

4 Discussion

4.1 Metabolic rate and physiologic state of individuals

This study was designed to answer the question of whether metabolic rates can predict some ecological functions and in particular the influence of bioturbation on sediment erodibility. This experiment represents a useful intermediate step to better scaling up this process from the local, monospecific scale to the field scale, where non-linear effects systematically occur between species (Schenone et al., 2019).

By measuring the respiratory rate of the animals in each sample, we sought to verify the relevance of the basal metabolic rate given by the Brey's model. 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. We decided to acclimate animals during a two weeks period at 3 different temperatures before measurements, to be sure that the results were not influenced by the recent past on the field.

Indeed, the ANCOVA showed a significant difference for the medium (spring) temperature. 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). 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 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. One recommendation for future studies could be to conduct such experiments at different seasons to avoid a significant difference between the temperature tested and the actual temperature in the field. However, this may entail another limitation, since the animals must be in a comparable physiological state, which is never the case at different seasons. We have chosen to maintain homogeneity in terms of physiological state, but this required acclimatisation. We recommend that the duration of the acclimation period be reduced as much as possible (~3 days) if similar studies are investigated. A long incubation period of animals in laboratory breeding affects the physiological state of individuals too drastically and this can considerably affect the quality of the results. It would be interesting to conduct experiments to find out if an incubation period is really necessary before testing the effect of temperature in particular, in terms of metabolism.

There is also other bias related to metabolism measurement and respiration rate. For instance, the 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. This observation could explain why the modelled metabolic rate overestimated the respiration rate for these two

species (Figure 3). 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).

All those experimental biases explain the variability in respiration measurements, and explain the performance of the correlation with the basal metabolic rate model. Despite all these limits, the metabolic rate model is sufficiently valid for all species combined (R^2 = 0.571****). 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. Despite all the limits developed in terms of methods, we consider that the experiment is still valid and can help to gain new insights in the interesting question of whether metabolic rates can predict some ecological functions.

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. 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, 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 for the summer temperature (see Supplementary data 3.2.1). The mass sediment erosion results confirmed that the temperature has supplementary effect than the one

from the metabolic activity of the fauna, linked to abiotic processes, which is not visible for the fluff layer erosion, more related to biologic processes. The relationship between temperature and sediment properties could explain this but the interaction with other biota like bacteria or the presence of microorganisms must also interfere (Le Hir et al., 2007).

There were three methods of calculating the metabolic rate, which we have chosen to present. 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 best 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. This raises the question whether the rate of bioturbation depends on a temperature felt almost immediately or whether the rate of bioturbation responds primarily to a temperature experienced over the previous few days. We recommend to test this question before performing studies on the effect of temperature on bioturbation activity. The species originate from the intertidal zone where they experience considerable variations in environmental conditions over the course of a day. Settling from the water column to the seafloor can buffer temperature variations, but feeding, particularly by filtration, puts the individual in close and immediate contact with water whose temperature can vary quicker. 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 and 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 on a daily basis. The question of what are the kinetics of adaptation of different species to these dynamic variations remain to be clarified.

Furthermore, being a linear relationship limited by bounds, metabolic models exclude any possibility of extrapolation outside the recorded range. Recent *in situ* observations have shown that the activity and therefore the magnitude of the bioturbation effects can vary seasonally, with a range of low temperatures much lower than 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.

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. The choice of defining a simple linear relationship between Q_{fluff} and $Itot_{meso}$ 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 best 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). 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 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 sediment erosion

Bioturbation can modify the constitutive layer of sediments, facilitating or hindering mass sediment erosion at high bed shear stress. 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 did not show a statistical link between metabolic rate and the critical threshold for mass sediment erosion, but did show significant differences depending on the species duos, despite very noisy results. 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.

As far as the *C. edule & M. balthica* duo is concerned, the effect of mass sediment destabilisation is generally little or no highlighted in

the literature for these two species (see Supplementary data 2.1). 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*, near the surface of the sediment generated fragilities on the surface during transfers from the cores to the sample bearer in the flume, which may have facilitated mass sediment erosion more than the direct effects of the bioturbation.

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 sediment 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, with experimental design more adequate than what was done in this study. Assessing the interaction between these two antagonistic species remains a challenge, because in the field they coexist, but maybe not very locally, because these two species show a high degree of patchiness that is difficult to take into account when scaling up processes to propose a modelling approach (Thrush et al., 2003;

Weerman et al., 2010). Synergistic effects of the interaction of species with very different functional traits have been described (see for example, although in different contexts, de Smit et al., 2021a; Schenone et al., 2019).

Finally, *C. volutator & P. ulvae* live on the surface of sediment. *P. ulvae* was already identified as a bioturbator not able to change the mass sediment erosion critical threshold (Orvain, 2005; Orvain et al., 2003). In addition, there were no observation of effect of *C. volutator* on mass sediment erosion by Grant and Daborn (1994). It is important to note that the bioturbation period was made in the absence of high 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 the water, as observed in De Backer et al. (2010). In addition, the bioturbation phase took place in the sample bearer and not in the incubation core, thus eliminating a disturbance phase present in all the measurements of the other two duos. This was a limitation of this protocol which, due to the design of the flume, did not allow equivalent treatment for surface and sub-surface species. As a result, the apparent stabilizing effect of the duo is doubtful. In any case, this difference was only very subtle and was probably more an experimental artefact than a bioturbation effect.

Besides the various limitations of the mass sediment erosion results, the data showed that, unlike the fluff layer erosion, the metabolic rate is not a suitable descriptor for assessing the effects of bioturbation of several species taken together, when analysing the critical threshold for mass sediment erosion.

4.4 Toward a community bioturbation model

The results of this study showed that the metabolic rate is an adequate tool to model effects of bioturbation on chronic erosion (fluff layer

erosion), in a range of temperature corresponding to the seasonal variations, and for any species considered. However, the data set was too noisy to propose a detailed mathematical function simulating the bioturbation effect of combined species on erodibility that could be incorporated into HMS models.

Nevertheless, our results suggest that this modelling approach is sufficiently relevant to be pursued with this type of experiment, with fewer factors and more controlled conditions to guarantee a higher degree of accuracy. Our data have the advantage to make a step forward a generalized model combining several species together, by confirming that using a metabolic rate seems to be good way of generalising and predicting ecological functions when exploring multi-species interactions. An assessment of the impact of temperature on the effects of bioturbation on sediment erodibility for isolated species, by taking into account the kinetics of thermal adaptation is clearly required. According to Kooijman (2010), metabolic adaptation to a new temperature is rather slow (days to weeks). However, intertidal animals are subject to very wide temperature conditions, so they should have a range of metabolic functions that allow them to adapt. In any case, the *Itot* calculation is only applicable in the range of temperatures valid for the organism.

In addition, scaling up to a community level implies considering also 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). On the contrary, fauna can also create a biodeposition of organic matter (pseudo-faeces and faeces), that can facilitate the biofilm development, hence stabilizing the sediment

surface (Lohrer et al., 2004; Richard et al., 2023; Soissons et al., 2019). For the deposit feeder, the food availability is also a factor that can affect the activity, thus having an effect on bioturbation effects (Orvain and Sauriau, 2002). Modelling the bioturbation effects on sediment transport at a community level thus should include MPB presence in further studies.

The metabolic rate is a good descriptor to link the fauna activity to the chronic bioturbation effect, but is not adequate to combine several species as a community considering mass sediment erosion (event-driven effects), regardless of their type of bioturbation activity. At least, the distinction between stabilisers and destabilizers is still obvious. A simple categorisation can also be made by depth of living for fauna as made by Cozzoli et al. (2018) for example. Indeed, the variety of bioturbation processes and their impact on sediment erodibility shows that the question of metabolic energy alone is insufficient. Bioturbation functional groups have until then described the different processes impacting particles movement and biogeochemistry (Kristensen et al., 2012), but functional groups concerning sediment erodibility are still to be refined, especially as antagonistic processes can occur for the same species depending on the environmental conditions (Kristensen et al., 2013; Li et al., 2017).

5 Conclusion

This study aimed at revealing how the assemblage of species in the macrozoobenthic communities and temperature could modify the sediment erodibility parameters. By coupling two species in the same samples, 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 sediment 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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Reference list

Figure 1 Fauna models used in their sediment.

Figure 2 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 3 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 4 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 5 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 6 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

Table 1 Coordinates of animal and sediment sampling sites (decimal degree WGS84)

Table 2 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}.