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► To cite this version:

Amélie Lehuen, Francis Orvain. A cockle-induced bioturbation model and its impact on sediment erodibility: A meta-analysis. *Science of the Total Environment*, 2024, 912, pp.168936. 10.1016/j.scitotenv.2023.168936 . hal-04356296

HAL Id: hal-04356296

<https://hal.science/hal-04356296>

Submitted on 20 Dec 2023

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6 A cockle-induced bioturbation model and its 7 impact on sediment erodibility: A meta- 8 analysis.

9 Abstract

10 Modelling the dynamics of an estuary and the evolution of its morphology requires a process-based
11 description not only of the physical processes, but also of the influence of benthic fauna on sediment
12 characteristics at ecosystem scale. A meta-analysis was tested as an approach for modelling the effect
13 of bioturbation exerted by the cockle *Cerastoderma edule* on sediment erodibility. Six different erosion
14 flume datasets were collected to ensure a broad range of experimental conditions including bed shear
15 stress, population characteristics, and sediment composition. First, a model was built to describe the
16 biogenic fluff layer created by *C. edule* activity in relation to (i) bioturbation activity using the population
17 metabolic rate [$\text{mW}\cdot\text{m}^{-2}$] as a proxy for faunal metabolic energy, and (ii) the silt content [%] of the
18 sediment. Second, different erosion models were compared by testing parameterization steps
19 incorporating both erosion of the fluff layer and/or mass erosion of the sediment bed. Structural
20 differences in the flumes and in the preparation of samples in the six different datasets makes it difficult
21 to propose a single model that satisfactorily simulates all the data and encompasses both types of
22 subsequent erosion, that of the fluff layer and that of the underlying consolidated bed. However, a
23 generic model is proposed for the surficial fluff layer erosion covering a moderate range of bed shear
24 stress (<1 Pa). This study shows that including several datasets covering a wide range of environmental
25 conditions is a key to the robustness of this model, and that new insights can be gained by integrating
26 the complexity of sediment features. We expect that this two-part model can be used in broad contexts

27 in terms of cockle populations, estuarine habitats, and climatic conditions and can combined with various
28 hydro-morpho-sedimentary models that include these biological effects.

29 Highlights

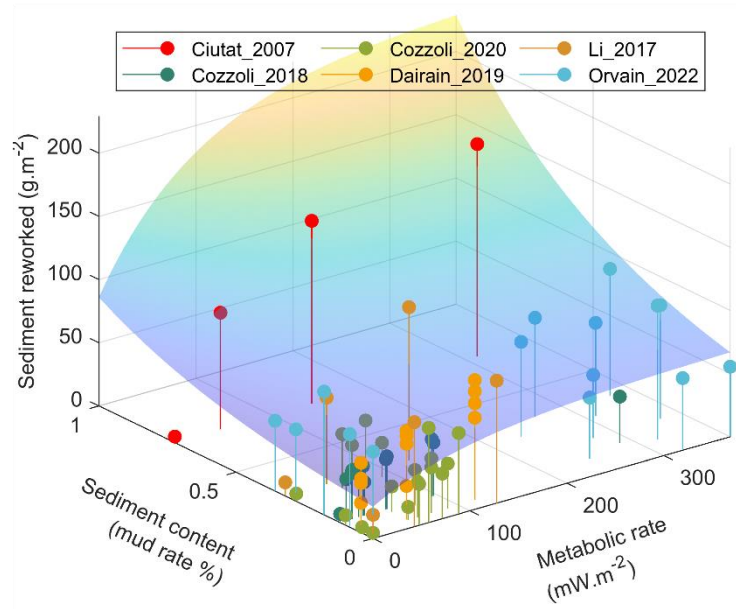
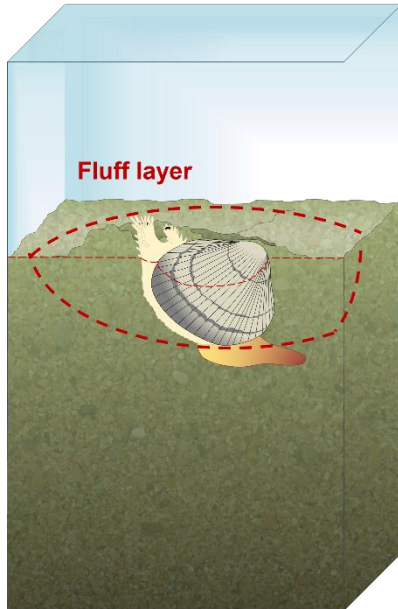
- 30 • 6 erodibility studies were used to parametrize a generic model of the bioturbation effect of
31 the cockle *Cerastoderma edule*.
- 32 • A model of the fluff layer made by cockles' bioturbation is proposed using the metabolic rate
33 and the silt content.
- 34 • This model simulates sediment resuspension at moderate bed shear stress, whatever flume,
35 population or sediment.
- 36 • It is more difficult to fit a model reliable for simulating sediment resuspension at high bed
37 shear stress.

38 Keywords

39 Model, *Cerastoderma edule*, erosion, erodibility, bioturbation, metabolic rate, sediment transport,
40 hydrosedimentary processes

41 Graphical abstract

Model of reworked sediment quantity by bioturbation (fluff layer)



42

43 Manuscript

44 1 Introduction

45 An estuary is an ecosystem at the interface of a river and the ocean, an ecotone through which
46 energy and material flows both upstream and downstream and where a haline front creates a mobile
47 turbidity maximum that shifts with the tide. The extent of the tidal regime defines the range of physico-
48 chemical parameters of the estuary (salinity, flooding time, sediment texture, etc.), which intrinsically
49 define different habitats such as salt marshes, sand banks, and intertidal mudflats (Dronkers and van
50 den Berg, 2023). This mosaic of habitats is very diverse and highly productive, and provides a variety
51 of ecosystem services including natural resources, possible recreational activities, as well as regulation
52 services including nutrient transfer, eutrophication, coastline protection, reducing flood risks,
53 greenhouse gas sequestration, cultural services, and other socio-economic benefits (Barbier et al.,
54 2011).

55 Although the physical phenomena that drive sediment transport in an estuary still need to be refined,
56 some hydro-morpho-sedimentary (HMS) models are well established and are increasingly accurate and
57 process based (Baas et al., 2013; Diaz et al., 2020; Grabowski et al., 2011; Grasso et al., 2015; Le Hir
58 et al., 2011). HMS factors are physical habitat-defining parameters, on which lifetraits and lifespans of
59 biological communities fully depend (Herman et al., 2001; Ysebaert and Herman, 2002). In particular,
60 sediment properties and hydrological parameters have direct impacts on the activity and spatial
61 distribution of macrozoobenthos, with sediment pools representing food sources, habitats, refuges and
62 nurseries. The grain size distribution of the sediment, represented by the median grain size and the silt
63 content ($< 63 \mu\text{m}$), play a particular role in explaining variations in macrozoobenthic communities
64 (Degraer et al., 2006; Thrush et al., 2005).

65 Conversely, benthic bioturbators are ecosystem engineering species (Jones et al., 1994), which have
66 the ability to actively modify their immediate environment by moving particles, either by foraging for food
67 or by other behaviours involving mobility. Many HMS models of sediment transport neglect the relevance
68 of biological factors such as bioturbation in the control of sediment transport, in particular sediment
69 erosion even though it has been demonstrated via two main approaches. On one hand, a reductionist
70 laboratory approach, studies using process-based models of sediment transport, with controlled abiotic
71 parameters, isolated bioturbating species and a design with few factors (Cozzoli et al., 2020; Dairain et
72 al., 2020b; Le Hir et al., 2007; Orvain, 2005; Orvain et al., 2012; Paarlberg et al., 2005; van Prooijen et
73 al., 2011; Wood and Widdows, 2002). On the other hand, a global *in-situ* approach can be applied,
74 integrating the complete structure of the sediment, the presence of micro-algae and the biological
75 community present, often in order to isolate the most contributory species or to focus on one species in
76 particular (Harris et al., 2015; Joensuu et al., 2018; Li et al., 2021; Needham et al., 2013, 2013; Shi et
77 al., 2020).

78 Depending on the behaviour of species, different processes take place which can also be expressed
79 at different magnitudes depending on the environmental conditions (Andersen et al., 2002; Orvain et al.,
80 2007; Widdows and Brinsley, 2002). Many flume experiments have been conducted to evaluate the
81 impact of different species on sediment resuspension (e.g. Andersen et al., 2010; Orvain et al., 2003;
82 Widdows et al., 1998). The variety of sediments, temperatures and feeding conditions, either
83 circumstantial or experimental factors, have a wide range of results (Amos et al., 1992; Andersen, 2001;
84 Soissons et al., 2019; Widdows et al., 1998). The list of environmental factors likely to modify the extent

85 of sediment bioturbation and its impact on erodibility includes: (i) physical factors such as the water
86 content of the sediment, the emersion time (Orvain et al., 2003), the sediment consolidation status
87 (Orvain et al., 2003; Orvain and Sauriau, 2002), the sediment grain size composition (Ubertini et al.,
88 2015) and (ii) the biological variables that reflect interspecific interactions, such as the biomass of
89 microphytobenthic chl *a* as food resources (Andersen et al., 2010; Dairain et al., 2020b; Orvain et al.,
90 2004) or contamination by parasitic pathogens (Dairain et al., 2020a).

91 The common cockle *Cerastoderma edule* (Linnaeus, 1758) has been widely studied as a
92 destabilising biodiffusor living in rather transitional areas of the foreshore and subject to medium currents
93 (Cozzoli et al., 2014; Herman et al., 1999), typically marine salinity values (> 30 PSU) and that prefers
94 fine sands (Cozzoli et al., 2014; Ubertini et al., 2012). Its broad distribution around the Atlantic (Hayward
95 and Ryland, 1995) and the economic interest for fishermen has made it a good target model organism
96 to investigate flow/sediment/organism interactions (Eriksson et al., 2017; Soissons et al., 2019).

97 This bivalve *C. edule* causes surface reworking of the sediment and sediment erosion by valve
98 movements and feeding. These movements create a layer with a low erosion threshold called the
99 sediment fluff layer (Ciutat et al., 2007; Cozzoli et al., 2020, 2019; Dairain et al., 2020b; Orvain et al.,
100 2003). Conversely, it can have a stabilising effect on sandy sediments by promoting biodeposition linked
101 to filtration feeding and can increase the silt content by incorporating particles in the top centimetres of
102 sediment (Donadi et al., 2014; Li et al., 2017; Soissons et al., 2019). Bio-stabilisation has also been
103 reported to promote colonisation by microphytobenthos, which has an additional stabilising effect
104 (Andersen et al., 2010; Rakotomalala et al., 2015; Sutherland et al., 1998).

105 Erosion studies generally measure the effect of biomass or of the density of *C. edule* on sediment
106 resuspension. However, the body size of each individual cockle is also an important factor, because the
107 roughness created by the presence of the shell disrupts the surface of the sediment (Dairain et al.,
108 2020b). Sediment reworking is also linked to the behavioural activity of cockles (valve movement,
109 feeding, burrowing, etc.) which can be affected by physical factors such as temperature and
110 physiological metabolism but which can be weakened by pathogen infection (Dairain et al., 2020a; Zhou
111 et al., 2022).

112 Metabolic rate appears to be a good proxy to assess the activity of an individual (Brown et al., 2004).
113 The mass specific respiration rate (MSR) developed by Brey (Brey, 2010) firstly to assess respiration at

114 the level of a population or community, includes population density, mean body size and temperature.
115 Several studies have used the metabolic rate specifically to assess sediment erodibility under the
116 influence of bioturbation (Cozzoli et al., 2020, 2019, 2018), by converting the biomass and density of a
117 biota into an energy flux per unit surface area.

118 In this study, we revisited existing datasets from laboratory flume experiments through a meta-
119 analysis with two main goals: (1) to aggregate different experimental conditions to extend the set of
120 biological conditions (biomass, density and individual body size) and to explore the interacting role of
121 sediment characteristics, in particular silt content, which mediates the influence of the bioturbator on
122 bed erodibility; (2) to use the MSR rate to characterise the biological factor, to reflect the activity of the
123 organism that results in bioturbation at different temperatures, thus seasonality. Modelling bioturbation
124 processes on the basis of these parameters enables them to be integrated into the description of
125 hydrodynamic sediment transport processes. In particular, by reflecting two aspects of biological activity
126 - the variation of bioturbation activity with season and sediment type - this model allows application on
127 a wider temporal and spatial scale, an element missing for the HMS modelling approach, which prevents
128 from assessing the long-term impact of bioturbation on coastal or estuarine morphology.

129 2 Materials and methods

130 All data processing was conducted in R version 4.2.2 (2022-10-31 ucrt) and Matlab 2021a.
131 Significance levels are $p < .0001$ with “****”, $p < .001$ with “***”, $p < .01$ with “**”, $p < .05$ with “*”.

132 2.1 Metabolic rate

133 The metabolic rate was estimated in this study by the mass specific respiration rate (MSR) of aquatic
134 invertebrates developed by Brey (Brey, 2010), by using a spreadsheet tool that implements an artificial
135 neural network. The spreadsheet requires as variables: (1) individual body mass in J, (2) temperature
136 in K, (3) depth in the water column, (4) taxonomic definition, (5) mobility mode (sessile, crawler, elective
137 or permanent swimmer/floater), (6) alimentation mode (carnivorous versus other modes), (7) type of
138 vision ('yes or no' defined as possession of image-forming eyes *sensu* (Seibel and Drazen, 2007), i.e.
139 a better optical sense than merely being able to distinguish light from dark), and (8) the starved state of
140 the animal (yes or no). The bivalve *C. edule* is classified as Mollusca 1, is sessile, not carnivorous and
141 has no vision.

142 MSR was calculated using the average energy density $21.4469 \text{ J.mgAFDW}^{-1}$ (Brey et al., 2010), a
143 depth of 1 m for intertidal species, and by default not starved. MSR was converted from [J/J/day] to
144 [mW.ind⁻¹]. The MSR_{tot} is defined (MSR*Density, [mW.m⁻²]), as the total metabolic energy of the
145 sample.

146 2.2 Erosion data

147 Erosion data were collected from six studies of *C. edule* performed in different experimental
148 conditions with different recirculating flumes.

149 The first dataset came from an experiment that used an annular flume (Ciutat et al., 2007). The
150 muddy sediment (72.3 % <63 μm), sampled from the Tamar estuary (southwest England), was
151 maintained as found in the field and inserted directly into the flume. All measurements were performed
152 at 15 °C in a climate-controlled room, with an alternating day/night regime, and the fauna was maintained
153 for 24 h in the flume and then for 24 h in sinusoidal cycles of current velocity to mimic tidal cycles before
154 erosion was measured. Fed with phytoplankton (*Isochrysis galbana*) the fauna was set up at 3 density
155 levels and a control (47.06 to 311.76 ind.m⁻²; 25.41 to 168.35 gAFDW.m⁻²). Current velocity ranged from
156 5 to 50 cm.s⁻¹ in 12 steps each lasting 15 to 50 min. The set comprised 4 runs, including 1 control run.

157 The second study used an annular flume (Cozzoli et al., 2018). Only data concerning the bivalve *C.*
158 *edule* was selected. The muddy sand sediment (12 % < 63μm) was defaunated, homogenised and
159 wetted so it would settle and consolidate in the flume. The flumes were placed in a climate-controlled
160 room at 18 °C, filled with filtered marine water, and the fauna bioturbation time was 48 h. The
161 experimental setup crossed 3 individual body sizes and 4 densities (3 in the case of large bivalves;
162 12.74 to 382.17 ind.m⁻²; 1.03 to 117.72 gAFDW.m⁻²). Current velocity ranged from 10 to 35 cm.s⁻¹ in 6
163 steps each lasting 20 min. Each combination was performed with 2 replicates and one control prior to
164 each body size, giving a total of 28 runs including 6 control runs.

165 The third dataset was taken from a study also made using an annular flume (Cozzoli et al., 2020).
166 The sediment parameter comprised 4 percentage silt contents (0-28 % <63 μm), obtained by mixing
167 defaunated, homogenised and wetted sediment that was allowed to settle and consolidate in the flume.
168 The flumes were placed in a climate-controlled room at 18 °C, filled with filtered marine water, and the
169 fauna bioturbation time was 48 h. The fauna factor comprised 4 combinations of sizes of individual

170 cockles and density (33.16 to 530.52 ind.m⁻²) to maintain the same total biomass (19.1 gAFDW.m⁻²).
171 Current velocity ranged from 5 to 30 cm.s⁻¹ in 7 steps each lasting 20 min. Each combination was
172 performed with two replicates and a control prior to each run, giving a total of 28 runs performed, plus
173 32 controls.

174 The fourth dataset was extracted from an experiment using a one-way flume, ERIS (Dairain et al.,
175 2020b). The slightly muddy sand sediment (4.4% <63 µm) was obtained by mixing defaunated,
176 homogenised and concentrated sediments, and filled in cores. The mesocosm was filled with filtered
177 marine water at a field temperature of 12 °C with a semi-diurnal tidal cycle (one diurnal emersion phase),
178 and the fauna bioturbation time was 6 days. The experimental design had 4 factorial parameters:
179 mesocom with or without phytoplankton (*Isochrysis galbana*), with or without microphytobenthos (MPB)
180 enrichment, 2 physiological states of fauna: parasitised and unparasitised, and 2 density levels (314.38
181 to 785.95 ind.m⁻²; 22.02 to 55.05 gAFDW.m⁻²) plus a control. Current velocity ranged from 0 to 72.5
182 cm.s⁻¹ in 20 steps each lasting 5 min. Each combination was made with 3 replicates, giving a total of 36
183 runs, including 12 controls.

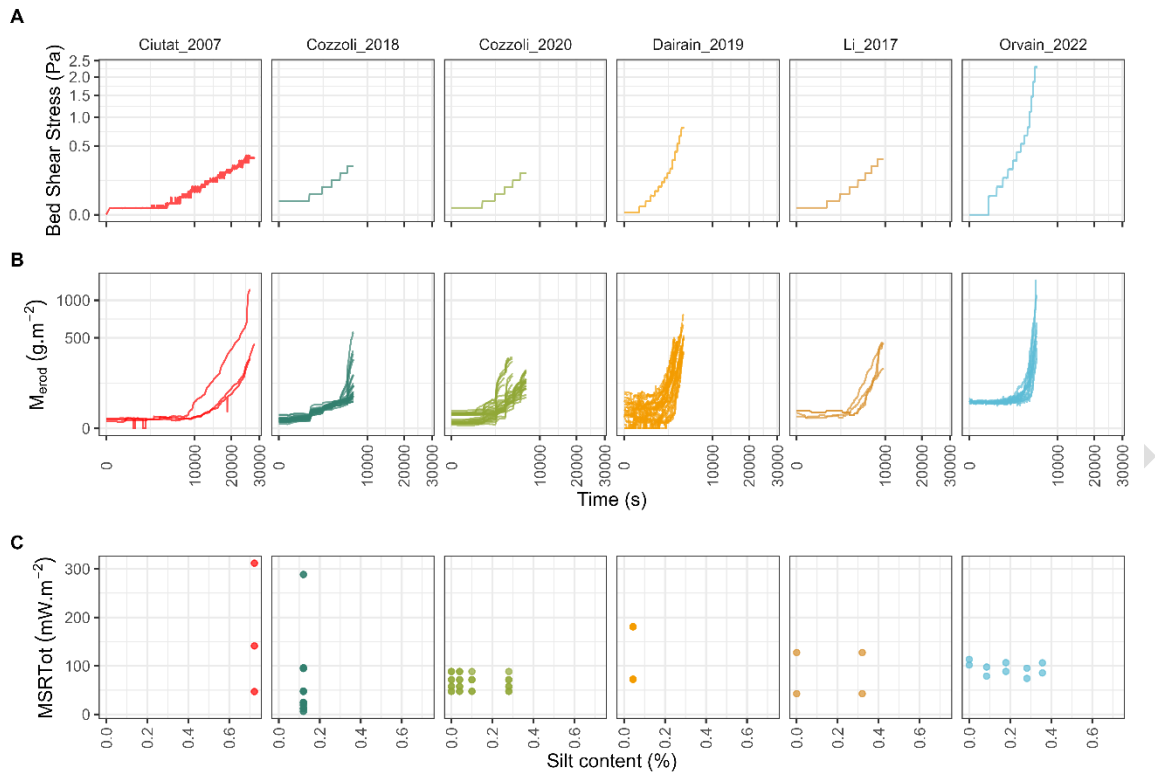
184 The fifth dataset was collected from an experiment using an annular flume (Li et al., 2017). The
185 sediment had 2 levels of silt content (0 % and 32 % <63 µm), obtained by mixing defaunated,
186 homogenised and wetted sediment poured into the flume and allowed to consolidate. The flumes were
187 placed in a climate room at 15 °C, filled with filtered marine water, and the fauna bioturbation time was
188 48 h. The fauna had 2 density levels (228 to 686 ind.m⁻²; 14.1 to 42.24 gAFDW.m⁻²). Current velocity
189 ranged from 5 to 40 cm.s⁻¹ in 8 steps each lasting 20 min. The results are the average of 3 replicates of
190 each run and 3 controls for each density, giving a total of 6 mean runs, including 2 controls. These data
191 were retrieved by graphic analysis using the Matlab "digitize" function (Sanchez, 2006).

192 The sixth dataset originated from an experiment made by F. Orvain (2022, unpublished) using a one-
193 way flume, ERIS. The sediment parameter had 5 levels of silt content (0 to 36 % <63 µm), obtained by
194 mixing defaunated, homogenised sediments, and filled in cores. The fauna was settled in cores and
195 measurements were made immediately after in filtered sea water at 14.96±1.27°C (bioturbation time
196 was 0 day). The fauna factor was 2 combinations of individual size (juveniles and adults) and densities
197 to keep the same total biomass (157.19 to 471.57 ind.m⁻²; 33.2 to 36 gAFDW.m⁻²). Current velocity
198 ranged from 0 to 83 cm.s⁻¹ in 14 steps each lasting 5-8 min. Each combination was made with 1
199 replicate, giving a total of 15 runs, including 5 controls.

200 The dataset that combined the experimental results of the 6 aforementioned studies consisted of 149
 201 time series, 91 with fauna, and 58 control experiments. The dataset contained two types of BSS ranges
 202 linked to the two types of flumes, with ERIS (Dairain_2019 and Orvain_2022) reaching values up to 10
 203 times higher than annular flumes. In terms of erosion measurement time, the Ciutat_2007 experiments
 204 lasted around 8 h, those of Cozzoli_2018, 2020, and Li_2017 lasted 2 h, and those of Dairain_2019 and
 205 Orvain_2022 lasted 1h30. Only the Ciutat_2007 set had a high silt content (72%), the other sets were
 206 all in the same range, from 0 to 36%, for a total of 12 levels. The biological ranges were fairly well
 207 distributed, MSR_{tot} varied on 33 levels, from 6.23 to 368.33 mW.m⁻², on 3 temperature levels, from 12
 208 to 18°C. The bioturbation duration prior to erosion measurement was highly dependant of the experiment
 209 from none in Orvain_2022 to 6 days in Dairain_2019 (Table 1, Figure 1).

210 *Table 1. Characteristics of the experimental set-up for each dataset. BSS: bed shear stress.*

	Ciutat _2007	Cozzoli _2018	Cozzoli _2020	Dairain _2019	Li_2017	Orvain _2022
Type of flume	Annular	Annular	Annular	One way flume	Annular	One way flume
Current speed (cm.s⁻¹)	5 – 50	10 – 35	5 – 30	0 – 72.5	5 – 40	0 – 83
BSS (Pa) max	0.370	0.249	0.183	1.65	0.326	2.29
Sample surface (m²)	0.17	0.157	0.157	0.0016	0.157	0.0016
Water volume (L)	46	31.4	31.4	21	31.4	21
Plateaus length (min)	15-50	20	20	5	20	5-8
Plateaus nb	12	6	7	20	8	14
Nb records	7,289	6,686	13,768	29,757	1,245	16,836
Temperature (°C)	15	18	18	12	15	15
Silt content (%)	72.3	12	0 – 28	4.4	0 & 32	0 – 36
Sediment preparation	Natural	Decanted	Decanted	Moulded	Decanted	Moulded
Bioturbation time	24 h	48 h	48 h	6 days	48 h	0 h
Biological density (ind.m⁻²)	47.1 – 311.8	12.7 – 382,2	33.2 – 530.5	314.4 – 786	228 – 686	157.2 – 471.6
Biological biomass (gAFDW.m⁻²)	211.8 – 1402.9	1 – 117.7	19.1	22 – 55.1	14,1 – 42.2	33.2 – 36

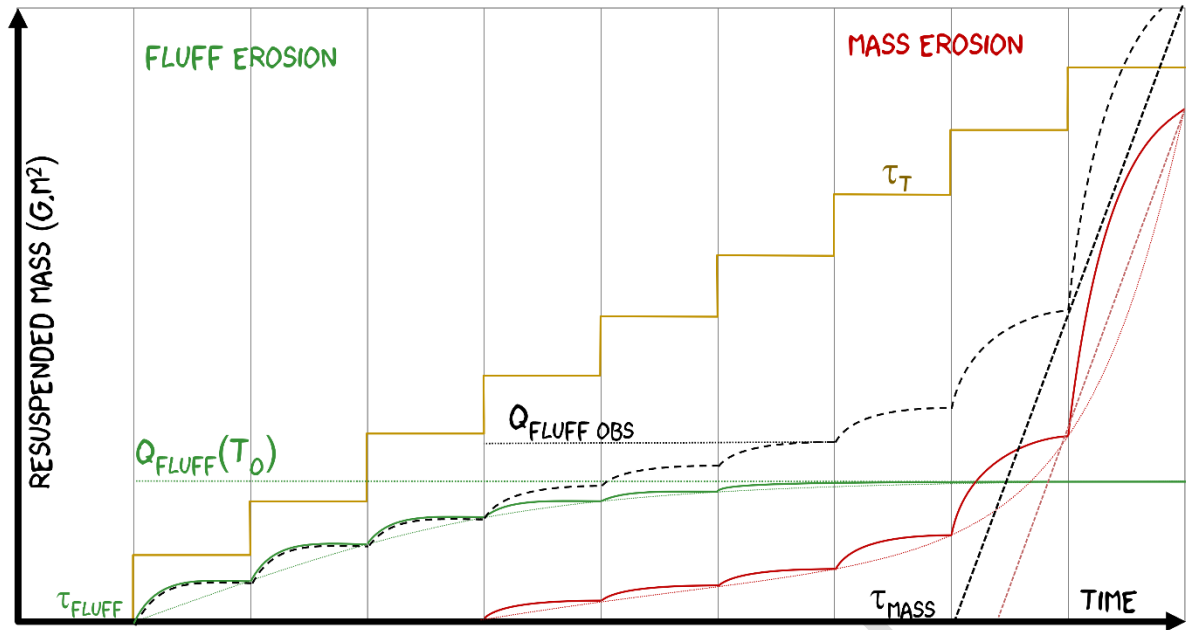


211

212 *Figure 1. A: Bed sheer stress (BSS [Pa]) time scheme for each experiment, B: Resuspended mass*
 213 *(M_{erod} [g.m⁻²]) versus time for each experiment and C: the metabolic rate calculated ($MSRT_{tot}$ [mW.m⁻²])*
 214 *versus the sediment silt content [%] for each experiment.*

215 2.3 Data treatment

216 The bed shear stress (BSS or τ [Pa]) for every run of each study was determined using their
 217 respective published estimates (Figure 1), and each turbidity measurement was converted into
 218 Resuspended mass calculated on the sample surface, M_{erod} [g.m⁻²]. Every current step was defined, and
 219 fluff or mass erosion steps were identified visually. Every step was summarised by its mean hydrological
 220 conditions, and the 95th centile of the M_{erod} . The Q_{fluff_obs} was determined as the 95th centile of M_{erod} at
 221 the last fluff step before mass erosion became visible (Figure 2). The critical τ_{mass} [Pa] was calculated
 222 as the intercept of the best linear regression between U^* and M_{erod} among mass steps as $M_{erod} = aU^* + b$
 223 thus $U^* = -b/a$ with $M_{erod} = 0$.



224

225 Figure 2. Sketch of erosion processes in the fluff layer erosion (green line), mass erosion (solid red
 226 line) and the parameters used. The dashed black line represents the addition of the two processes, the
 227 M_{erod} measured in the experiment. The straight dashed black line represents the linear regression of the
 228 mass erosion steps that determined the critical mass erosion threshold (τ_{mass} [Pa]).

229 2.4 Model building

230 2.4.1 Erosion model

231 The model erosion was based on several works including two by Orvain et al. (2003, 2012) that
 232 consider the erosion flux as the result of three processes (Equation 1).

$$233 \text{ Equation 1 } \frac{dM_{erod}}{dt} = E_{fluff} + E_{mass} - D$$

234 where E_{fluff} is the fluff erosion rate, E_{mass} is the mass erosion rate and D the deposition flux, all [$g \cdot m^{-2} \cdot s^{-1}$]. For this study, we did not use the deposition flux for process simplification, the measured M_{erod}
 235 were considered as the result of the equilibrium between resuspension and deposition. The fluff erosion
 236 rate was based on Orvain's model development (Orvain et al., 2003) and expressed as Equation 2.
 237

$$238 \text{ Equation 2 } E_{fluff}(t) = \alpha \cdot Q_{fluff}(t - dt) \cdot \left(\frac{\tau_t}{\tau_{fluff}(t)} - 1 \right) + o \text{ and } E_{fluff} = 0 \text{ if } \tau_t < \tau_{fluff}$$

239 where α is a kinetic erosion coefficient [s^{-1}] integrating the Q_{fluff} erodible amount of sediment, which
 240 varies in dt . The parameter τ_{fluff} [Pa] represents the BSS threshold (critical τ) when fluff erosion starts,
 241 known to be at low level. τ_t [Pa] is the dynamic BSS, the physical forcing variable that was applied on
 242 the sample at time t [s]. $Q_{fluff}(t - dt)$ is the remaining quantity of fluff layer (result of faunal activity reworking

243 the sediment) for the previous time interval. It was assumed that the amount of M_{erod} just before mass
 244 erosion (Q_{fluff_obs}) was a good proxy for the quantity of fluff layer generated on the sample before erosion
 245 began, called $Q_{fluff}(t_0)$ [$g \cdot m^{-2}$] (Figure 2). We assumed that $Q_{fluff}(t_0)$ can be expressed as a function of
 246 biological and sediment factors (Equation 3).

247 *Equation 3* $Q_{fluff}(t_0) \sim BioFact * SedFact$

248 where *BioFact* is MSRTot [$mW \cdot m^{-2}$], *SedFact* stands for the silt content [%]. The biological part of this
 249 equation was chosen as a von Bertalanffy function, as its adequacy has been demonstrated in several
 250 studies describing this kind of process for other bioturbators like the gastropod *Peringia ulvae* or the
 251 bivalve *Macoma balthica* (Orvain and Sauriau, 2002; van Prooijen et al., 2011; Willows et al., 1998). For
 252 cockles it was used in models that specifically simulate microphytobenthos resuspension (Rakotomalala
 253 et al., 2015). In the latter study, the best minimised function was linear, as was the case for another
 254 bivalve, *Scrobicularia plana* (Orvain, 2005). Adding a sediment component to the model required
 255 exploring various mathematical functions without an *a-priori* (linear, von Bertalanffy) so as to adjust the
 256 quantity of sediment contained in an easily eroded fluff layer, and the dependence of this variable (Q_{fluff})
 257 on abiotic factors (*SedFact*) (Supplementary Data 2.4.1).

258 The mass erosion rate is the expression of bed load erosion, as described in previous studies e.g.
 259 (Orvain et al., 2012), in line with the Partheniades formula for cohesive beds (Partheniades, 1965)
 260 (Equation 4).

261 *Equation 4* $E_{mass}(t) = E_0 \cdot \left(\frac{\tau_t}{\tau_{mass}} - 1 \right)$ and $E_{mass} = 0$ if $\tau_t < \tau_{mass}$

262 where E_0 is the erosion rate [$g \cdot m^{-2} \cdot s^{-1}$], τ_{mass} [Pa] represents the BSS threshold (critical τ) when mass
 263 erosion starts, and τ_t [Pa] the BSS applied to the sample at time t [s]. E_0 was made to vary as a function
 264 of biological factors and optionally as a function of the sedimentary factor (Equation 5, Supp Data 2.4.1).

265 *Equation 5* $E_0 \sim E_{0ab} * BioFact (* SedFact)$

266 where E_{0ab} is the abiotic erosion rate [$g \cdot m^{-2} \cdot s^{-1}$], a function of sediment conditions, which was then
 267 modulated by biological conditions. In the same way, τ_{mass} is expressed as an abiotic $\tau_{mass0ab}$ potentially
 268 modified by biological factors and optionally by sedimentary factors (Equation 6, Supp Data 2.4.1).

269 Equation 6 $\tau_{mass} \sim \tau_{mass0ab} * BioFact (* SedFact)$

270 2.4.2 Model adjustment

271 The model was adjusted using the Simplex method in Matlab by minimising the ordinary least
272 squares criterion (Sum of Squares Error). The model adjustment minimisation was made by the Matlab
273 function `fminsearchbnd` (D'Errico, 2006), the boundaries being defined to ensure a realistic outcome for
274 each parameter. The initial conditions for solving the `fminsearch` were optimised by using combinations
275 of several values of each adjusted parameter. The adjustments to the model were made in five steps
276 (Figure 3):

277 **I. Creation of the fluff layer:** This modelled process describes the biological effect of sediment
278 reworking prior to erosion through the creation of an easily eroded fluff layer, due to the
279 activity of surface fauna. $Q_{fluff}(t_0)$ was **globally** adjusted (all observations fitted together)
280 (Equation 3) based on Q_{fluff_obs} extracted from all the runs (Figure 2). The model with the best
281 fit was selected by comparing 6 mathematical functions (Supp Data 2.4.1).

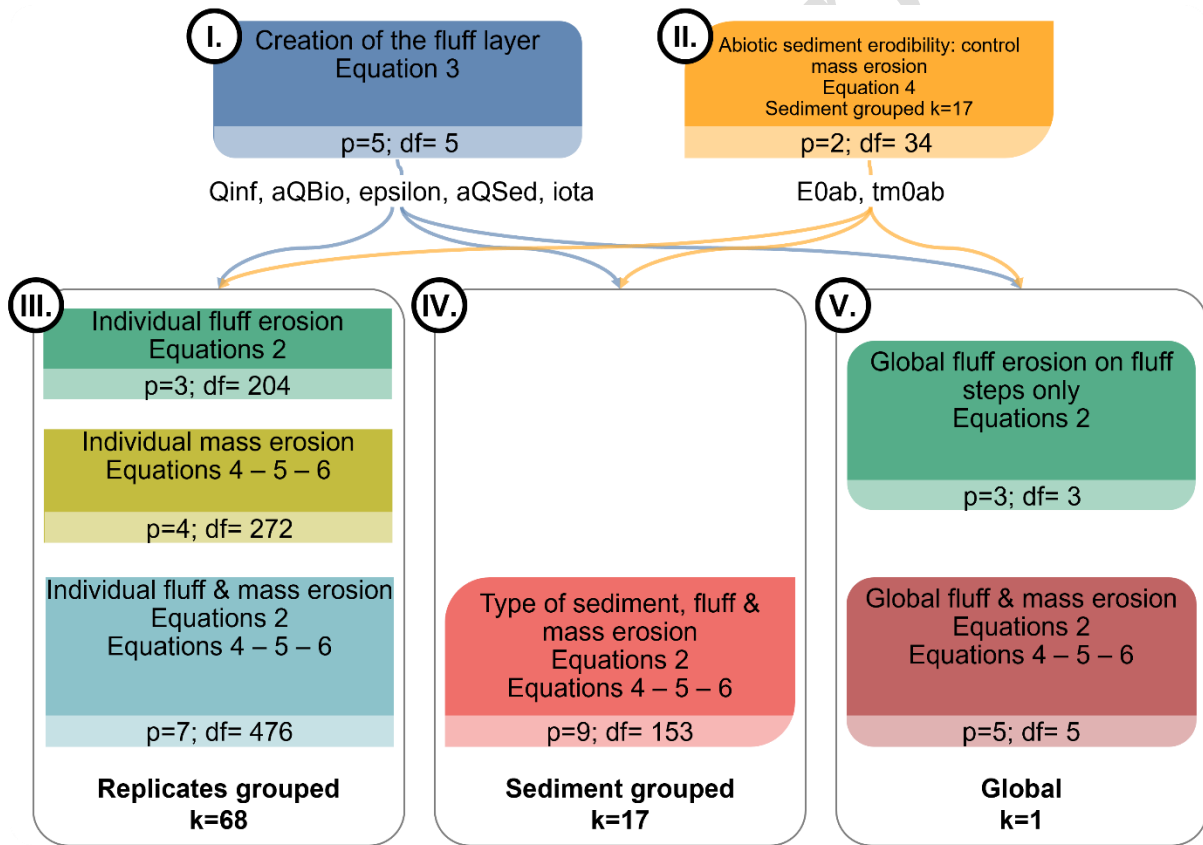
282 **II. Abiotic sediment erodibility: control mass erosion:** This model made it possible to calibrate
283 differences in sediment properties linked to their content, preparation, and the experimental
284 set up. Controls from all studies were selected and grouped **in series of sediment types**
285 (including phytoplankton & MPB conditions for Dairain_2019, independently of the biological
286 conditions, i.e. a total of 17 different adjustments). Each pool was adjusted on mass erosion
287 parameters (Equation 4). Each adjustment parameter (E_{0ab} and $\tau_{mass0ab}$) was then associated
288 with its corresponding biological run.

289 **III. Individual fluff & mass erosion:** This adjustment enabled us to determine whether combining
290 the two types of erosion processes would improve model performance. The comparison of
291 **individual** adjustments (grouped in replicates: the same conditions for sediment and fauna,
292 a total of 68 different adjustments) using (i) the fluff equation (Equation 2), (ii) the mass
293 equation (Equation 4), (iii) the fluff and mass equations combined (Equation 2 & Equation 4:
294 Equation 1). These adjustments used the $Q_{fluff}(t_0)$ (I.) and the control (II.) adjustment
295 parameters as fixed parameters.

296 **IV. Sediment type, fluff & mass erosion:** The aim of this model was to fit the data more globally
297 by grouping them according to the type of sediment, to only evaluate the capacity of the
298 biological factor to account for the effects of bioturbation. Adjustments were made with fluff

299 and mass combined (Equation 2 & Equation 4: Equation 1) **per series of sediment types**
 300 using model parameters **I.** and **II.** as fixed parameters. The mass parameters were adjusted
 301 taking the fauna into account with Equation 5 and Equation 6.

302 **V. Global fluff & mass erosion:** This trial evaluated how the erosion processes can be fitted in a
 303 more global model by assuming that the mass erosion related to sediment variability is
 304 accounted for in the control **II.** parameters. The effects of bioturbation on mass erosion were
 305 thus generalised to all the runs. The mass parameters were adjusted by taking the fauna
 306 into account with Equation 5 and Equation 6. The **global** adjustments made with the fluff
 307 and mass combined (Equation 2 & Equation 4: Equation 1) were compared with those made
 308 with fluff erosion **on fluff steps** (Equation 2) using the **I.** and **II.** parameters as fixed
 309 parameters.



310

311 *Figure 3. Scheme of the adjustments made, p is the number of parameters, k the number of sub-*
 312 *groups, and df represents the degree of freedom as $p \cdot k$.*

313 2.4.3 Model validation

314 The models were evaluated with the help of graphic visualisation and compared using model
315 validation indexes calculated on the $y = x$ relationship (diagonal) between the observed and modelled
316 data.

317 The root mean squared error (RMSE) represents the standard deviation of the residuals, equivalent
318 to σ when the estimator is unbiased. This criterion defines the extent of data scattering around the
319 regression line. This non-standardised index is equivalent to its standardised counterpart R^2 . Expressed
320 in the same units as the response variable, this index can be normalised (nRMSE) with respect to the
321 range of the response variable, which makes it possible to compare models of different datasets. The
322 lowest RMSE indicates the best fit, but for an equivalent reading such as R^2 , nRMSE is transformed as
323 $1 - \text{nRMSE}$, hence the closer to 1 the better.

324 The Akaike information criterion (AIC), (Akaike, 1974) makes it possible to compare models with
325 different numbers of parameters, i.e. to use as few parameters as necessary, the smaller AIC the better
326 the fit. AICc is a second-order (or small sample) AIC with a correction for small sample size. The
327 Bayesian Information Criterion (BIC) is interpreted as the AIC, with a higher penalty given to the number
328 of parameters.

329 When necessary, post-hoc tests were performed on the observed and predicted data to assess the
330 quality of the selected model: a Durbin-Watson test was used to evaluate the autocorrelation of
331 residuals, which ranged from zero to four, where a value of 2.0 indicates zero autocorrelation. Values
332 below 2.0 indicate a positive autocorrelation, and values above 2.0 a negative autocorrelation. Second,
333 the Harrison-McCabe statistic was used to check whether the residuals were homoscedastic or
334 heteroscedastic.

335 3 Results

336 High resolution figures showing the main results and complementary figures are in the
337 supplementary data file, model result parameters Supplementary Table 3.A, and validation scores in
338 Table 2 and in Supp. Table 3.B.

339 3.1 Model pre-adjustments

340 3.1.1 Creation of the fluff layer (I.)

341 The model was selected by analysing the model validation indexes, with nRMSE=0.806 (Figure 4,
342 modelled-observed plot in Supp. Fig 3. B). The equation with coefficient values obtained by fitting
343 methods, includes two terms (in brackets): a biotic one related to metabolism and an abiotic one that
344 varies with the silt content of the sediment.

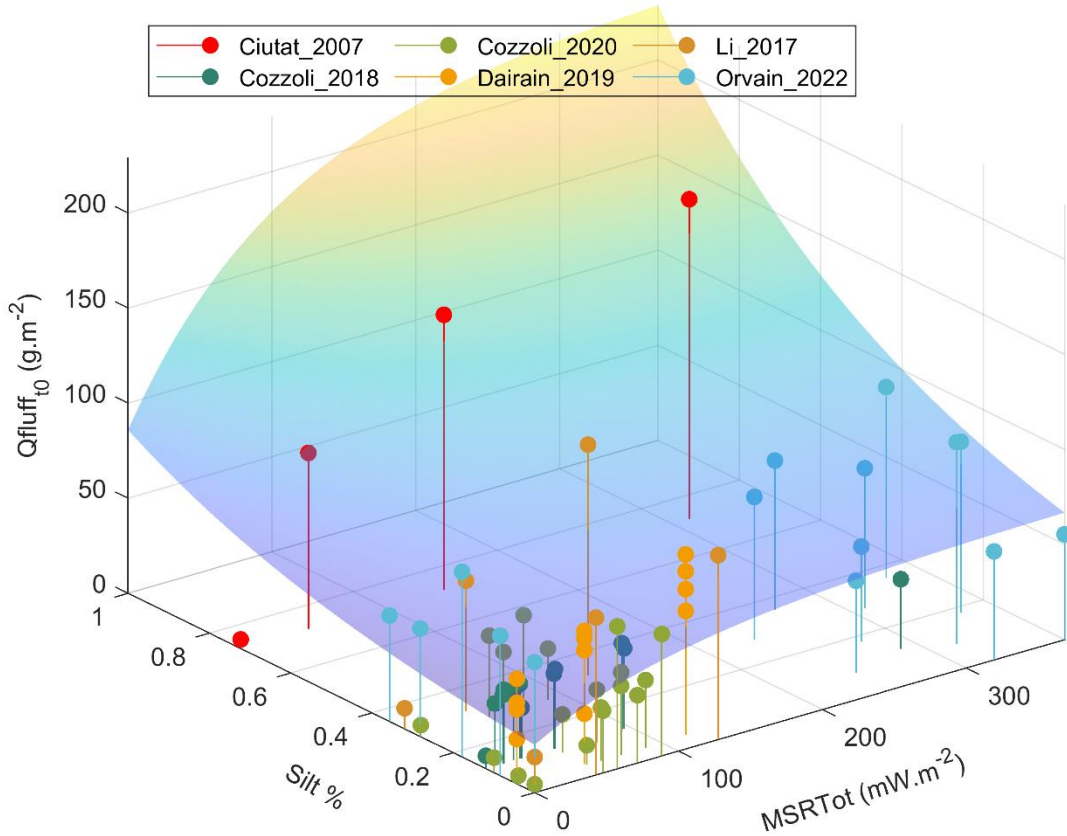
$$345 \quad Q_{fluff}(t_0) = [Q_{inf} \cdot (1 - e^{(-a_{Bio} \cdot MSR_{tot}t)}) + \varepsilon] \cdot [e^{(a_{sed} \cdot \%Silt t)} + t]$$

$$346 \quad \text{with } Q_{inf} = 20.163; a_{Bio} = 0.01; \varepsilon = 11.837; a_{sed} = 1.815; t = 1.12$$

347 Overall, the model tended to slightly underestimate the quantity of eroded fluff layer (Figure 4). The
348 bioturbation model went up to 200g.m⁻², representing eroded material up to 1 mm in height assuming a
349 sediment concentration of 200kg.m⁻³. This order of magnitude therefore seems realistic. The von
350 Bertalanffy curve for biological factors represented a plateau similar to an asymptotic quantity, meaning
351 that, above a certain biological energy rate, the bioturbation activity reworks sediment that has already
352 been reworked but without affecting the erodibility of the sediment in old tracks (see Orvain and Sauriau,
353 2002, for details concerning this mechanism). The curve of eroded material as a function of silt content
354 gradually increased with an increase in silt content. The model showed a slight increase in $Q_{fluff}(t_0)$ fitting
355 when the silt content increased in the absence of biota, accounting for a kind of “abiotic fluff layer”
356 comprised of erosion aggregates detached from the bed matrix whose detachment was not caused by
357 macrofaunal activity. The model that only included the biological effect (Supp. Data 2.4.1, Equation 3.1)
358 performed less well (nRMSE = 0.481) than when the sediment factor was included. The dataset by
359 Ciutat_2007 appeared to drive a substantial part of the adjustment, but this effect did not seem to
360 compromise the quality of overall parameterization too much, since, according to a Durbin Watson test
361 (Supp. Data 3.1.1), the data were not affected by any strong autocorrelation.

362

I.



363

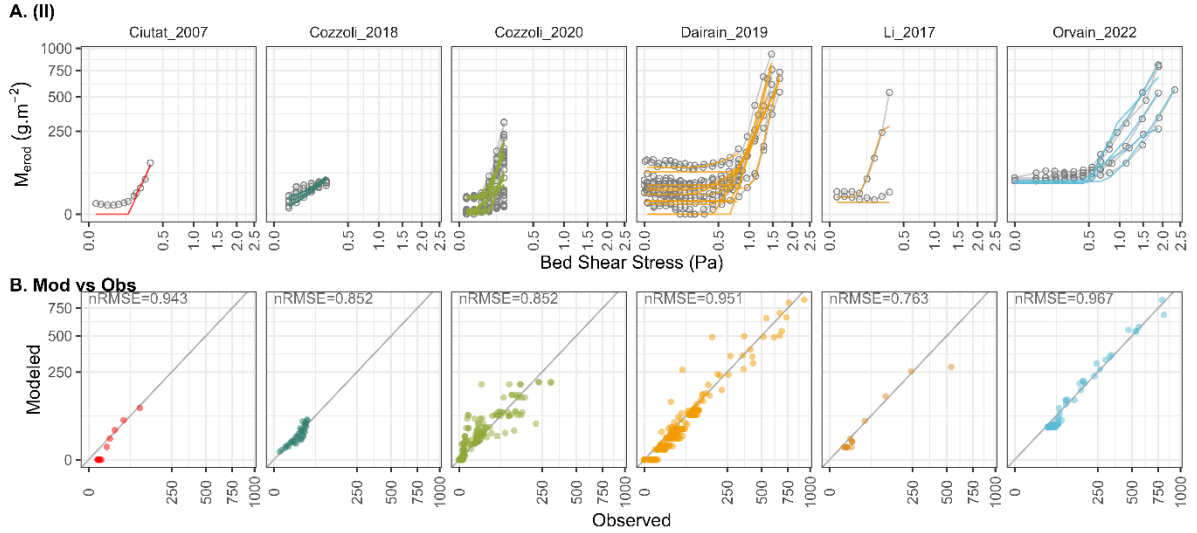
364 *Figure 4. Observed Q_{fluff_obs} values for MSR_{tot} ($mW \cdot m^{-2}$), (%) silt content and its validated $Q_{fluff}(t_0)$*
 365 *modelled surface.*

366 **3.1.2 Abiotic sediment erodibility: control mass erosion (II.)**

367 The control set of 58 runs was subdivided into 17 pools each containing one to eight replicates of
 368 the same sediment condition (Figure 5, 3D plots in Supp. Fig 3. D, M_{erod} vs time plots in Supp. Fig 3. D).
 369 Modelled erosion was satisfactory with a global nRMSE of 0.966 with two parameters:

370
$$E_{mass}(t) = E_{0ab} \cdot \left(\frac{\tau_t}{\tau_{mass0ab}} - 1 \right) \text{ and } E_{mass} = 0 \text{ if } \tau_t < \tau_{mass}$$

371 The Dairain_2019 and Orvain_2022 datasets were the most involved in driving the adjustment
 372 process, since they were the runs with the highest BSS (Figure 1). The Cozzoli_2020 dataset was not
 373 well simulated, was either under or over-estimated depending on the replicates, but the observed data
 374 showed high variability in the same sediment conditions. No particular pattern was observed between
 375 the parameters and the silt content (Supp. Fig 3. E), underlining the difficulty of comparing data from
 376 different flume experiments. In Cozzoli_2018 and 2020, mass erosion started at the beginning of the
 377 run when the BSS was low (respectively $\tau_{mass} = 6 \cdot 10^{-11}$ and [0.018 to 0.105] Pa).



378

379 *Figure 5. A: Erosion data from control experiments in grey and model II in colours; B: Predicted*
 380 *versus observed data, the grey line represents the 1:1 line. Note that x and y axis are in square root*
 381 *scale.*

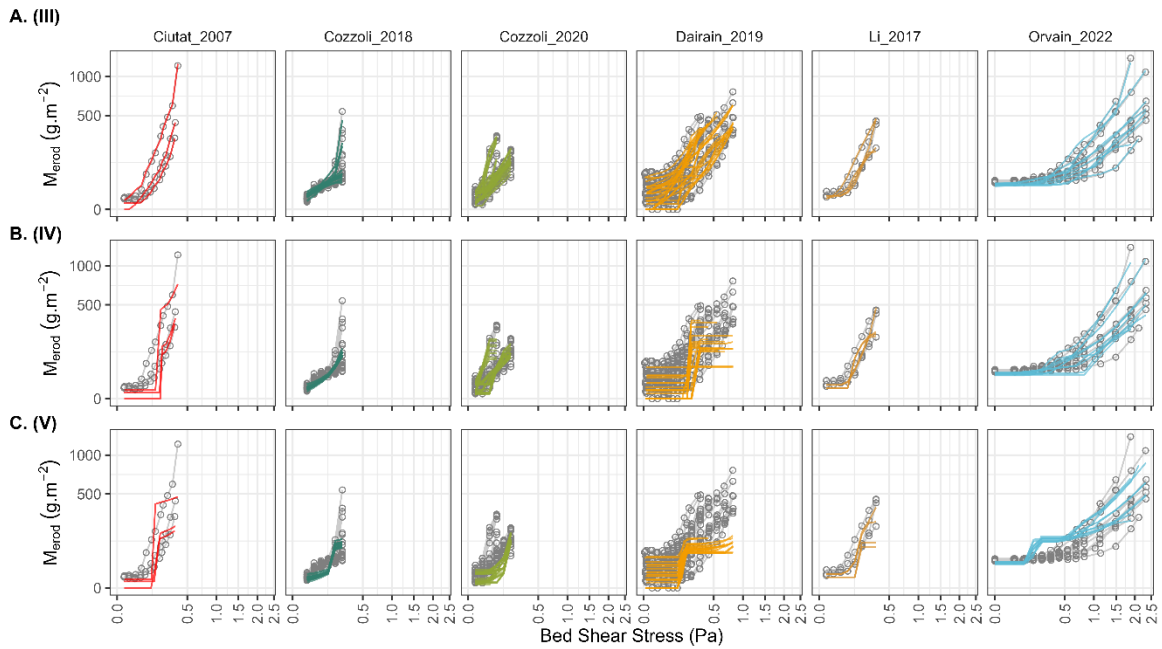
382 3.2 Individual fluff & mass erosion (III.)

383 The grouped datasets were adjusted to the groups of replicates (k=68) using the fluff layer erosion
 384 model (Supp. Fig 3.I & L), the mass erosion model (Supp. Fig 3.J & M) and the combined fluff & mass
 385 erosion models (Figure 6 & Figure 7 A, Supp. Fig 3.K & N). Although the fluff and mass erosion models
 386 were individually efficient (respectively nRMSE = 0.966 and 0.974), the two models combined gave the
 387 best fit (nRMSE = 0.981). However, the fluff & mass model required 5 parameters, of which 3 were
 388 dedicated to fluff erosion (Q_{fluff} parameters being pre-fitted in I.) and 2 to mass erosion (control
 389 parameters E_{0ab} & $\tau_{mass0ab}$ being pre-fitted in II.).

$$390 E_{fluff}(t) = \alpha \cdot Q_{fluff}(t - dt) \cdot \left(\frac{\tau_t}{\tau_{fluff}} - 1 \right) + o \text{ and } E_{fluff} = 0 \text{ if } \tau_t < \tau_{fluff}$$

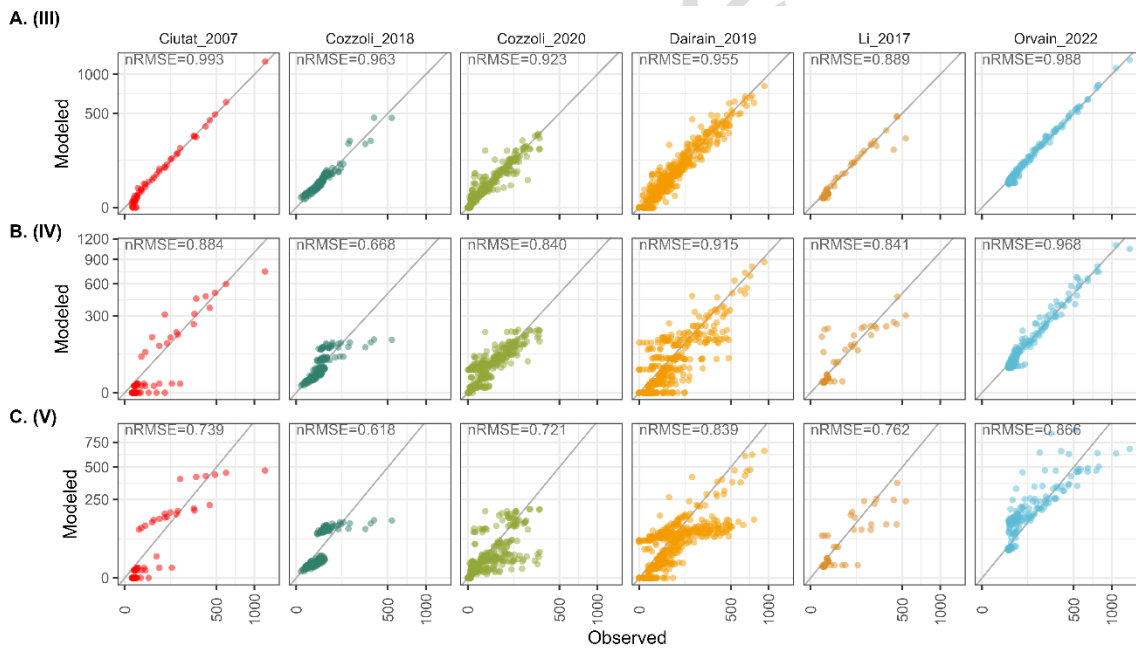
$$391 E_{mass}(t) = \alpha_{EBio} \cdot E_{0ab} \cdot \left(\frac{\tau_t}{\alpha_{TBio} \cdot \tau_{mass0ab}} - 1 \right) \text{ and } E_{mass} = 0 \text{ if } \tau_t < \tau_{mass}$$

392 Specifically, the fluff model performed relatively well in all runs, the best being obtained with the
 393 Orvain_2022 dataset, which covered a wide range of silt contents. The mass model performed less well
 394 for Cozzoli_2018. Considering the studies individually, both models were generally fit less than the fluff
 395 & mass mixed model, which was particularly efficient in simulating the 2-part aspect of the curve (Figure
 396 2). It is noteworthy that, when evaluated visually, mass erosion started sooner than expected, partly due
 397 to the $\tau_{mass0ab}$.



398

399 *Figure 6. Erosion data from data experiments in grey and fluff and mass models in colours,*
 400 *respectively A: model III, B: model IV, C: model V. Note that x and y axis are in square root scale. Control*
 401 *data are not included for the sake of clarity.*



402

403 *Figure 7. Modelled versus observed data, respectively A: model III, B: model IV, C: model V. The*
 404 *grey line represents the 1:1 line. Note that x and y axis are in square root scale. Control data are not*
 405 *included for the sake of clarity.*

406 3.3 Type of sediment, fluff & mass erosion (IV.)

407 The fluff & mass adjustment was made by pooling data with similar sediment conditions rather than
 408 by replicates, the number of different conditions was reduced from 68 to 17 values, the global nRMSE

409 = 0.957 (Figure 6 & Figure 7 B, Supp. Fig 3.M & S). The model required 7 parameters, of which 3 were
 410 dedicated to fluff erosion (Q_{fluff} parameters being pre-fitted in I.) and 4 were used for mass erosion
 411 (control parameters E_{0ab} & $\tau_{mass0ab}$ being pre-fitted in II.).

$$412 \quad E_{fluff}(t) = \alpha \cdot Q_{fluff}(t - dt) \cdot \left(\frac{\tau_t}{\tau_{fluff}} - 1 \right) + o \text{ and } E_{fluff} = 0 \text{ if } \tau_t < \tau_{fluff}$$

$$413 \quad E_{mass}(t) = \alpha_{EBio} \cdot E_{0ab} \cdot \left(\frac{\tau_t}{\tau_{mass0ab} \cdot (\alpha_{TBio} \cdot e^{(BioFact \cdot b_{TBio}) + oo})} - 1 \right) \text{ and } E_{mass} = 0 \text{ if } \tau_t < \tau_{mass}$$

414 The general aspect of the model showed a “trigger” effect of erosion, with a too sudden increase in
 415 M_{erod} , except in Orvain_2022 and Cozzoli_2018. The Ciutat_2007 dataset showed that the global aspect
 416 did not match observations. The $\tau_{mass0ab}$ was low in every run, meaning that even if the modelled fluff
 417 and mass erosion equation was used, the solution led to mass erosion starting right at the beginning of
 418 the experiment.

419 3.4 Global fluff & mass adjustment (V.)

420 The fluff & mass global adjustment was made by pooling all the data, the global nRMSE = 0.911
 421 (Figure 6 & Figure 7 C, Supp. Fig 3. Q & T). The model required 5 parameters, of which 3 were dedicated
 422 to fluff erosion (Q_{fluff} parameters being pre-fitted in I.) and 2 were used for mass erosion (control
 423 parameters E_{0ab} & $\tau_{mass0ab}$ being pre-fitted in II.).

$$424 \quad E_{fluff}(t) = \alpha \cdot Q_{fluff}(t - dt) \cdot \left(\frac{\tau_t}{\tau_{fluff}} - 1 \right) + o \text{ and } E_{fluff} = 0 \text{ if } \tau_t < \tau_{fluff}$$

$$425 \quad E_{mass}(t) = \alpha_{EBio} \cdot E_{0ab} \cdot \left(\frac{\tau_t}{\alpha_{TBio} \cdot \tau_{mass0ab}} - 1 \right) \text{ and } E_{mass} = 0 \text{ if } \tau_t < \tau_{mass}$$

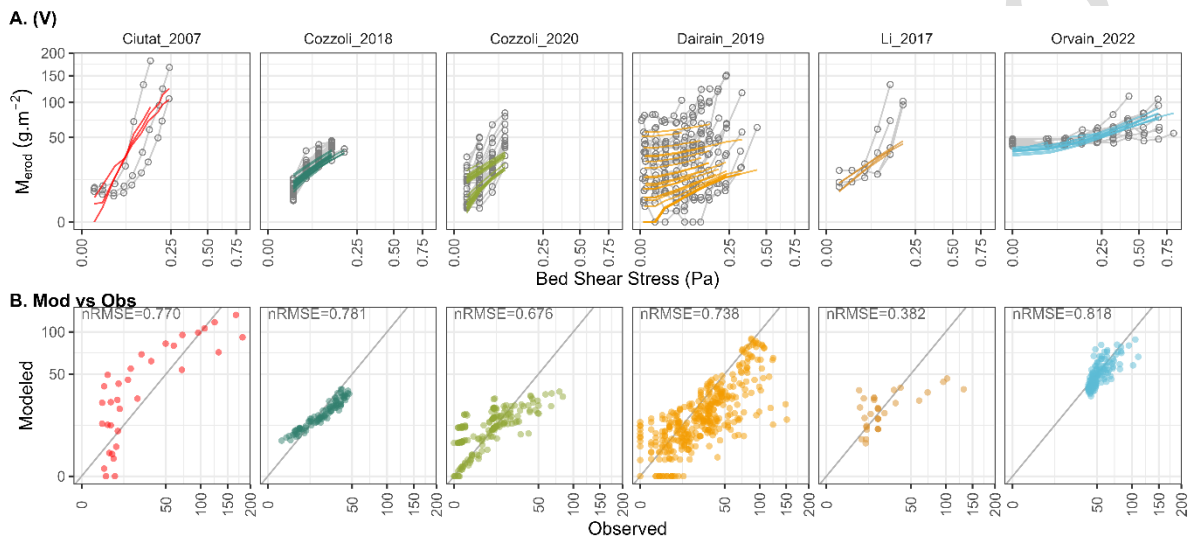
426 Mass erosion started slightly later than in the sediment types, i.e. closer to the observed levels.
 427 Except in Orvain_2022 and Li_2017, the M_{erod} level reached a plateau after mass erosion started. The
 428 Orvain_2022 study showed a clear fluff sequence before mass erosion. In Dairain_2019, erosion was
 429 underestimated, which was also the case in Ciutat_2007.

430 **3.5 Global fluff adjustment (V.): the selected model**

431 The global fluff adjustment was made by pooling all the data and removing all the steps identified as
 432 mass erosion steps. The global nRMSE = 0.868 (Figure 8, Supp. Fig 3. V & W). The model required 3
 433 fluff erosion parameters (Q_{fluff} parameters being pre-fitted in I.).

434
$$Q_{fluff}(t_0) = [20.163 \cdot (1 - e^{-0.01 \cdot MSR_{tot}}) + 11.837] \cdot [(e^{(1.815\% \cdot Silt)} + 1.12)]$$

435
$$E_{fluff}(t) = 6.877 \cdot 10^{-6} \cdot Q_{fluff}(t - dt) \cdot \left(\frac{\tau_t}{0.014} - 1\right) + 0.005 \text{ and } E_{fluff} = 0 \text{ if } \tau_t < \tau_{fluff}$$



436

437 *Figure 8. A: Erosion data from data experiments in grey and fluff model V in colours; B: Predicted*
 438 *versus observed data, the grey line represents the 1:1 line. Note that x and y axis are in square root*
 439 *scale. Control data are not included for the sake of clarity.*

440 *Table 2: Models validation scores.*

Model	Records	AICc	RMSE	nRMSE	df	Parameters	Pools
I. Creation of the fluff layer	68	629	24.281	0.806	5	5	1
II. Abiotic sediment erodibility	28,593	276,580	29.049	0.966	34	2	17
III. Individual fluff erosion	75,581	754,456	34.304	0.966	204	3	68
III. Individual mass erosion	75,581	733,400	29.874	0.974	272	4	68
III. Individual fluff & mass erosion	75,581	703,551	24.557	0.981	476	7	68
IV. Type of sediment, fluff & mass erosion	75,581	729,758	48.230	0.957	153	9	17
V. Global fluff & mass erosion	75,581	883,666	80.136	0.911	5	5	1
V. Global fluff erosion on fluff steps	49,292	419,134	16.583	0.868	3	3	1

441

442 3.6 Other parameterization tests

443 The whole process of this study was designed to obtain - as exhaustively as the technical limits
444 permitted - the most generic model. To this end, model fitting in Matlab was done using Parallel for-Loop
445 (parfor) with the Parallel Computing Toolbox™, which makes it possible to explore several combinations
446 of conditions; a loop on a wide range of initial conditions were set up to ensure the “fminsearch” function
447 found the best minimum. Only relevant results are shown here, but some unsuccessful tests are worth
448 mentioning.

- 449 1. The consolidation state of the fluff layer and varying resistance to sediment was accounted for
450 in one test, by allowing the τ_{fluff} and τ_{mass} to evolve with time during the ongoing erosion
451 process (Orvain et al., 2003). To this end, at each time interval, the critical threshold of the
452 sediment was modified according to the quantity of sediment that remained not eroded. The
453 τ_{fluff} equation was tested based on the Q_{fluff} remaining at each dt (Supp. Table 3, Equation
454 7). This addition had the effect of inverting the erosion curve in some runs/steps, revealing
455 an exponential rather than an asymptotic trend. For the τ_{mass} , three equations were based
456 on the total amount of eroded sediment (because there is no ‘remaining’ quantity), with the
457 possibility of having different curve shapes (Supp. Table 3, Equation 8). One seemed rather
458 promising when adjusting the control runs, but increased the complexity of adjusting the
459 biological runs.
- 460 2. To deal with the sediment variability, a global adjustment of control runs was made by
461 adjusting E_0 and τ_{mass} using the silt content (Supp. Table 3, Equations 9 and 10). The silt
462 content was the sediment factor chosen because it was the only factor present in all the
463 datasets we collected. In the combination of equations (Supp. Table 3, Equation 8 was not
464 included), the model was only able to fit the ERIS datasets (Orvain_2022 and Dairain_2017),
465 while the other simulations showed no mass erosion at all.
- 466 3. In order to limit the number of parameters adjusted simultaneously and to manage differences
467 in magnitude between fluff and mass erosion, the global fluff model was used as a source of
468 input parameters for the global mass erosion adjustment. However, with the exception of the
469 Orvain_2022 dataset, the model showed no mass erosion.

- 470 4. The fluff model was tested without the alpha parameter, which could be considered as
471 buffering the parameterized Q_{fluff} . However, the result was a complete failure.
- 472 5. All processes were tested with density (ind.m^{-2}) and biomass (g.m^{-2}) as BioFact. Density was
473 systematically less adequate than the other, the biomass being equivalent in results than the
474 MSRTot, mainly due to the narrow range of temperatures in the dataset, even though
475 MSRTot showed a global best performance.

476 4 Discussion

477 4.1 What the modelling process revealed

478 Individual erosion adjustments are useful to evaluate the performance of different types of models
479 (fluff layer, sediment mass and their combination), removing the experimental dispersion that could
480 jeopardise the model readings. The model that simulated mass erosion performed well, along with the
481 model that simulated fluff layer erosion alone; however, the version that mixed fluff layer and mass
482 erosion was clearly the most reliable. Although improving the model by mixing the two processes
483 requires more parameters, doing so makes it possible to distinguish the two processes and give more
484 applicability to different measurement conditions (Orvain, 2005; Orvain et al., 2003). In fact, the two
485 processes are based on equations with different profiles (Figure 2), and the observed profiles can only
486 be rendered by combining them, as long as the experiment reaches a sufficiently high BSS.

487 The choice of using the metabolic rate in this type of exercise, over and above its interest in
488 describing bioturbation processes in the context of the Metabolic Theory of Ecology (Brown et al., 2004),
489 is that it allows different experimental designs to be combined. Indeed, the different sample surfaces
490 are an important driver in the choice of the size and number of individuals installed. As (Cozzoli et al.,
491 2020) showed, density and biomass information alone are not sufficient to describe the effect of
492 bioturbation of the cockle on the sediment. In addition, the measurements were taken at different
493 temperatures, which, although within a fairly low range (12 to 18°C), can have an effect on the activity
494 of the individuals in the sample. With a view to modelling in extrapolated temperature ranges, while
495 remaining within the tolerance range of the species, it is possible with the metabolic rate to take account
496 of these variations in activity, which may be reflected in sediment reworking.

497 The individual fluff & mass models used the adjustment of $Q_{\text{fluff}}(t_0)$, an estimate of the quantity of
498 sediment reworked by the fauna. As the observation of this quantity of sediment was indirect and rather
499 empirical, the performance obtained was fairly good. This estimate uses two generic descriptors that
500 are interesting from a biological point of view. On the one hand, the type of sediment is known to have
501 an impact on the bioturbatory activity of *C. edule*, as well as on many species of benthic macrofauna,
502 and silt content is known to be a good indicator of this (Carss et al., 2020). On the other hand, the
503 metabolic rate can express bioturbation as an energy flow transmitted to the sediment, which enables
504 comparisons between the effects of individuals with different body sizes and potentially different species.
505 The development of the model by Cozzoli et al (Cozzoli et al., 2018) concerning $Q_{\text{fluff}}(t_0)$, did not take
506 any dependency on the composition of the sediment into consideration, but was a linear function of the
507 faunal factor (i.e. the metabolic rate). That kind of relation cannot account for a well-known process: the
508 surface saturation effect, the fauna at some point reworking the same sediment, hence the choice of a
509 von Bertalanffy relationship (Orvain and Sauriau, 2002). The quality of the model that simulates erosion
510 of the fluff layer could still be improved by collecting more data, paying particular attention to the
511 intermediate values in the range of the chosen factors. The same model would also benefit from a less
512 indirect method of measurement, such as topographic measurement of the reworked sediment from a
513 smoothed surface, to estimate the volume of the fluff layer more precisely and to reinforce the process-
514 based approach. This bioturbation model (and not erosion) is the first step towards the construction of
515 a community-scale bioturbation model that uses the metabolic rate to describe surficial bioturbation
516 effects and sediment-water column interactions (Maire et al., 2008).

517 The models that simulated fluff layer and sediment mass erosion were also based on adjustments
518 made on control data, which gave significantly different parameters for Equation 4. We did not find a
519 satisfactory solution when we applied the mass erosion equation globally, even when we attempted to
520 include a silt content dependence function. This result means that the silt content was not an appropriate
521 descriptor to define the erodibility of the sediment prepared in these flume studies. In fact, the description
522 of sediment features requires numerous parameters (particle size distribution, water content, sediment
523 density) and their vertical distribution, information which is not systematically collected during flume
524 experiments. Moreover, the procedure used to prepare the sediment also considerably modifies
525 sediment characteristics such as the state of consolidation and its vertical structure. For instance, the
526 experiment conducted by (Ciutat et al., 2007) was designed to maintain the natural state and stratified

527 layers of the natural field sediments to the greatest possible extent, whereas the other experiments
528 included major modifications, such as defaunation, mixing, sieving and removal of biofilm, and the
529 sediment was introduced into the flume by letting it decant in water (Cozzoli et al., 2020, 2018; Li et al.,
530 2017) or moulded in a container (Dairain et al., 2020b).

531 However, as it stands, the individual fluff & mass model cannot be used to describe bioturbation and
532 erosion processes. The generalisation of the model via the adjustment by sediment conditions only
533 allowed us to focus on biological factors. The model that combined all the sediment conditions led to a
534 diminishing performance, but the reduction in the degree of freedom was significant (from 408 to 136)
535 for only two additional parameters. The performance of the Dairain_2019 dataset was poor during fitting
536 of the model, which must be due to the fact that the biological parasitism factor was clearly responsible
537 for reduced bioturbation activity. For now, such information could not be included in the model, because
538 it was not available in the other papers.

539 The global fluff & mass parameterization was undertaken based on the hypotheses that 1)
540 adjustment of the control sediment conditions accounted for all sediment and flume variability, 2) the
541 biological factors were satisfactorily described by the metabolic rate. The model performance
542 diminished, but with a massive reduction of degree of freedom (from 136 to 7). Nevertheless, the model
543 failed to satisfactorily describe erosion over time, its success varied with the dataset, and still used the
544 control parameters (vector of length 17) as inputs. This model is thus not sufficiently global nor
545 sufficiently efficient to be considered fully generic and reliable in diverse HMS models and estuaries.

546 Our final proposal is a global model, without mass erosion, developed by combining the creation of
547 a surficial fluff layer (the Q_{fluff} model) and its erosion. The Q_{fluff} model is a new insight as it accounts for
548 the metabolic activity of the species studied *C. edule*, and its response to the type of sediment using a
549 meta-analysis approach. In previous *C. edule* model studies, only fauna density indices or sediment
550 factors were considered (Dairain et al., 2020b; Rakotomalala et al., 2015). The model developed by
551 (Cozzoli et al., 2019) includes a metabolic rate approach, model sediment resuspension versus the
552 metabolic rate and the BSS, but does not adjust the erosion pattern kinetics (and especially the effect
553 of time dt). As the biological effect had already been described, erosion of the fluff layer was then simple
554 and robust to fit globally at the scale of the meta-analysis. This model was designed to be introduced in
555 an HMS model to refine the modelling of sediment transport, with the conversion of biomass and density
556 to MSR via Allen's equation (Allen et al., 2005). With that aim in view, the combination of fluff and mass

557 processes also appears to be mandatory to be sure all the biological effects are properly incorporated
558 in sediment transport models.

559 4.2 A recommendation for improving flume experiments

560 Problems with the general adjustment of bioturbation and fauna effect on erodibility are mainly
561 encountered in the case of cohesive sediments. Sand erosion is less complex to model, and requires
562 fewer parameters to describe. On the other hand, cohesive and mixed sediments are intrinsically
563 complex to characterise. It is thus necessary to work on bioturbation issues, taking care to describe the
564 sediment used as precisely as possible. Working in collaboration with sedimentology scientists would
565 also ensure factors or parameters that could be decisive in terms of model development are not
566 neglected (Grabowski et al., 2011; Le Hir et al., 2011; Mitchener and Torfs, 1996; Tolhurst et al., 2005).

567 When measuring the effects of bioturbation, the practice to measure the control immediately before
568 measuring the biological sample, and to use the control to keep only the biological effect, like in the
569 study by (Cozzoli et al., 2020), appears to be very efficient. However, this is technically impossible in
570 the case of one-way flumes like ERIS, for which the same sediment bed cannot be redeposited to be
571 experimented twice.

572 Measuring the actual BSS requires further study. Flume calibration is generally performed on a
573 smooth surface, but this does not account for the autogenous roughness effects of the individuals
574 present on the sample (Friedrichs et al., 2000). As soon as the cockle scratches the surface of the
575 sediment, it modifies the hydraulic conditions, and hence BSS. In fact, the degree of roughness does
576 not remain the same over the course of the flume experiment, but changes throughout the erosion
577 ongoing process, all the more so as a bioturbator fauna is present (Dairain et al., 2020b). The ERIS is
578 equipped for upstream/downstream measurement of the pressure in the flume, enabling the difference
579 in pressure to be used to measure a 'rough' BSS that is more representative of dynamic reality. What is
580 more, BSS calibration does not account for variations in the height of the water column during erosion,
581 which can vary unchecked when the flume is driven by the upper surface of the water. When only the
582 fluff layer is involved, these effects can be considered negligible, but this remains to be proven when
583 mass erosion is involved. In addition, the autogenic bioturbation effects are not taken into account in a
584 annular flume built nowadays (Dombroski and Crimaldi, 2007).

585 The choice of flume equipment is also decisive. The annular flume is efficient for fluff erosion, but
586 cannot be used to investigate mass erosion. The ERIS flume can handle both types of erosion, thanks
587 to its powerful pump, but there are many experimental biases, especially because of the small size of
588 the sediment sample. It would be useful to perform experiments that more closely resemble the kinetics
589 of annular flume experiments, with fewer but longer steps, to observe a clearer equilibrium. CSMs
590 (Tolhurst et al., 1999), for example, are better designed for mass erosion than other devices. Inter-
591 calibration of the different methods is necessary, and in the meantime, accurate distinction of the two
592 types of erosion is not possible. We need to better define whether it is possible to observe both types of
593 erosion in a single experiment (Tolhurst et al., 2000; Vardy et al., 2007; Widdows et al., 2007).

594 In addition, the flumes used in these experiments are of two types, both of which are unidirectional,
595 among a wide possibilities of flumes, either in lab or in-situ (Tolhurst et al., 2009). There are also
596 oscillation channels, or wave channels, which more closely reproduce the complex hydrodynamic
597 conditions and turbulence field that could occur in the field. Examples include wave mesocosms
598 (Infantes et al., 2021), wave channel for *in-situ* or lab cores (de Smit et al., 2021), and portable channel
599 for in-situ measurements (de Smit et al., 2020). Comparative measurements between the two types
600 show that the results are not equivalent depending on the type of instrument used (Jepsen et al., 2004,
601 2012), thus preventing pooling data from unidirectional and oscillatory flumes.

602 Some flumes make it possible to use sediment taken directly *in-situ* (as in (Ciutat et al., 2007)),
603 keeping its natural structure, which makes erodimetry measurements more realistic. It is also possible
604 to carry out *in situ* measurements directly using flume designed for this purpose. However, in this case,
605 the biological parameters are less well controlled, which makes modelling more complex. Most
606 laboratory prepared sediment are highly altered, but clarify the results depending on biological factor,
607 which are still delicate to analyse. To our knowledge, no comparative study has been carried out to
608 assess the difference in results using the same sediment in its natural state and defaunated and
609 prepared in the laboratory.

610 The procedure for preparing the samples also needs to be more clearly defined. Indeed, depending
611 on the objective of the experiment, attention needs to be paid to different factors: the sediment
612 preparation method as mentioned above, but also the fauna bioturbation phase. If we consider the
613 genesis of the fluff layer, the time spent by the fauna on the sample and its history are both crucial as is
614 accurate biometric measurement of all individuals. Knowledge of a tidal rhythm, the temperature of the

615 environment, and the duration of bioturbation, as distinct from the duration of settlement or even
616 acclimation, is also essential when defining the Q_{fluff} . If bioturbation lasts long enough or if the density
617 of fauna is high enough to reach saturation of the reworked surface before measurement, it is no longer
618 possible to assess the mediation of sediment erodibility by biological organisms. On the other hand, the
619 activities of many animals differ radically depending on the moment of the tide. Consequently, it is
620 necessary to define bioturbation activity during alternating daily fluctuations with immersion and
621 emersion phases. The cockle has a wide range of individual behaviours including filtering with open
622 siphons, burial when the current becomes too strong. The fluff layer involves a direct bioresuspension
623 process for cockles with an immediate effect linked to valve movements at the surface, and cockles are
624 less active at low tide. The fluff layer produced by cockles is completely different from the fluff layer
625 (mainly tracks) created by the model gastropod *Peringia ulvae* species, for which the first models of the
626 fluff layer were developed during emersed periods (Orvain et al., 2003), providing alternate phases in
627 long term simulations (Orvain et al., 2012): (i) emersion periods showing accumulation of the quantity
628 of sediment in the fluff layer over time and (ii) immersion periods with a potential reduction in the quantity
629 of sediment because the animals do not crawl when they are covered in water and the resuspension
630 rate and bed shear stress are high enough.

631 In addition, treatment of the sediment and the condition of the mesocosm can affect the presence or
632 absence of microphytobenthos (MPB), which has a role in the bioturbation process (Andersen et al.,
633 2010; Dairain et al., 2020b; Orvain et al., 2004). On one hand, MPB form biofilm made of
634 exopolysaccharides (EPS) which reinforces cohesiveness and/or reduces the roughness of the
635 sediment surface, which can limit erosion (Andersen et al., 2010; Sutherland et al., 1998). On the other
636 hand, MPB is a source of food for different species, in particular *C. edule*, which can cause resuspension
637 of sediment through its efforts to access MPB (Rakotomalala et al., 2015).

638 Further, when the metabolic rate is used rather than historical descriptors, experimental temperature
639 becomes a factor that needs to be controlled, and even studied as a dedicated factor to be thoroughly
640 investigated. Indeed, if we assume that bioturbatory activity is linked – among other things – to the basal
641 activity of the individual and hence to temperature, then for the same pool of individuals, Q_{fluff} must vary
642 with variations in temperature. In the present study, temperature was not a factor, and it was not possible
643 to compare the temperatures of the different datasets, as the biomasses were not equivalent. Having
644 said that, further research is required to explore the effect of temperature and its influence on

645 bioturbation and related processes, and many questions require close collaboration with specialists in
646 the metabolism of benthic fauna. Taking temperature into account is also useful when considering the
647 seasonality of benthic macrofauna activities. Biomass and population density vary significantly
648 throughout the year, but so does their metabolism. How do these factors influence bioturbation activity
649 over the course of a year?

650 5 Conclusion

651 The aim of this study was to propose a sediment erosion model including *Cerastoderma edule*
652 bioturbation. The first step was to develop a model for the creation of the biogenic (fluff) layer linked to
653 cockle bioturbation activity. However, it was not possible to combine the processes of fluff layer erosion
654 and mass erosion in a single generic model. We therefore propose a model that focusses only on erosion
655 of the fluff layer, but incorporates creation of the fluff layer model as a function of the metabolic rate and
656 silt content. We provide a general model for measurements made using different equipment, under a
657 wide range of conditions. The model is therefore a first step in the process-based modelling of fluff
658 erosion. In addition, the use of the metabolic rate means that temperature can be incorporated in the
659 model, enabling questions of bioturbation activity to be developed over the course of the seasons, not
660 only from a demographic point of view, but also in terms of physiological status.

661 ACKNOWLEDGEMENTS

662 The authors are grateful to the following researchers who gave permission to use their data: Aurélie
663 Ciutat, Francesco Cozzoli, Tjeerd Bouma and Baoquan Li.

664 The authors acknowledge anonymous reviewers for their valuable comments and suggestions.

665 FUNDING

666 This research was supported by the *Region Normandie* (A. Lehuen's PhD) and by the *Office Français*
667 *pour la Biodiversité* (the MELTING POTES project).

668 CREDIT AUTHOR STATEMENT

669 **A. Lehuen:** Conceptualisation, Methodology, Formal analysis, Writing - Original Draft, Funding
670 acquisition; **F. Orvain:** Conceptualisation, Methodology, Validation, Formal analysis, Resources, Writing
671 - Reviewing & Editing, Supervision, Project administration, Funding acquisition

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915 Reference list

916 Figure 1. A: Bed shear stress (BSS [Pa]) time scheme for each experiment, B: Resuspended mass
917 (M_{erod} [$\text{g}\cdot\text{m}^{-2}$]) versus time for each experiment and C: the metabolic rate calculated (MSRTot [$\text{mW}\cdot\text{m}^{-2}$])
918 versus the sediment silt content [%] for each experiment.

919 Figure 2. Sketch of erosion processes in the fluff layer erosion (green line), mass erosion (solid red
920 line) and the parameters used. The dashed black line represents the addition of the two processes, the
921 M_{erod} measured in the experiment. The straight dashed black line represents the linear regression of the
922 mass erosion steps that determined the critical mass erosion threshold (T_{mass} [Pa]).

923 Figure 3. Scheme of the adjustments made, p is the number of parameters, k the number of sub-
924 groups, and df represents the degree of freedom as $p*k$.

925 Figure 4. Observed $Q_{\text{fluff_obs}}$ values for MSRTot ($\text{mW}\cdot\text{m}^{-2}$), (%) silt content and its validated $Q_{\text{fluff}}(t_0)$
926 modelled surface.

927 Figure 5. A: Erosion data from control experiments in grey and model II in colours; B: Predicted
928 versus observed data, the grey line represents the 1:1 line. Note that x and y axis are in square root
929 scale.

930 Figure 6. Erosion data from data experiments in grey and fluff and mass models in colours,
931 respectively A: model III, B: model IV, C: model V. Note that x and y axis are in square root scale. Control
932 data are not included for the sake of clarity.

933 Figure 7. Predicted versus observed data, respectively A: model III, B: model IV, C: model V. The
934 grey line represents the 1:1 line. Note that x and y axis are in square root scale. Control data are not
935 included for the sake of clarity.

936 Figure 8. A: Erosion data from data experiments in grey and fluff model V in colours; B: Predicted
937 versus observed data, the grey line represents the 1:1 line. Note that x and y axis are in square root
938 scale. Control data are not included for the sake of clarity.

939

940 **Table list**

941 Table 1. Characteristics of the experimental set-up for each dataset. BSS: bed shear stress.

942 Table 2: Models validation scores.

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