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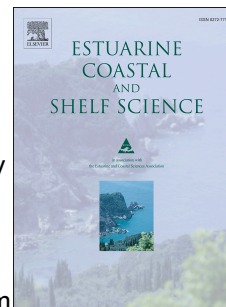
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**Francesco Cozzoli:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Visualization, Writing -original draft.

**Tatiana Gomes da Conceição:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology.

**Jeroen Van Dalen:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology.

**Xiaoyu Fang:** Conceptualization, Writing - review & editing.

**Vojsava Gjoni:** Conceptualization, Writing - review & editing.

**Zhan Hu:** Writing - review & editing.

**Laura M. Soissons:** Writing - review & editing.

**Brenda Walles:** Writing - review & editing.

**Peter M.J. Herman:** Writing - review& editing,

**Tom Ysebaert:** Writing - review & editing.

**Tjeerd J. Bouma:** Conceptualization, Writing- review & editing, Funding acquisition, Project administration.

1 **Biological and physical drivers of bio-mediated sediment resuspension: a flume study**  
2 **on *Cerastoderma edule***

3 Francesco Cozzoli<sup>a,b,c,†</sup>, Tatiana Gomes da Conceição<sup>b</sup>, Jeroen Van Dalen<sup>b</sup>, Xiaoyu Fang<sup>d</sup>,  
4 Vojsava Gjoni<sup>a</sup>, Peter M. J. Herman<sup>e,f</sup>, Zhan Hu<sup>g,h,§</sup>, Laura M. Soissons<sup>b,i</sup>, Brenda Walles<sup>j</sup>,  
5 Tom Ysebaert<sup>b,j</sup>, Tjeerd J. Bouma<sup>b</sup>

6 <sup>a</sup> Dipartimento di Scienze e Tecnologie Biologiche ed Ambientali, University of the Salento – 73100 Lecce,  
7 Italy

8 <sup>b</sup> Department of Estuarine and Delta Systems. Royal Netherlands Institute of Sea Research (NIOZ) and Utrecht  
9 University – 4401 NT Yerseke, The Netherlands

10 <sup>c</sup> Research Institute on Terrestrial Ecosystems (IRET) - National Research Council of Italy (CNR) via Salaria  
11 km 29.3 – 00015 Monterotondo Scalo (Roma), Italy

12 <sup>d</sup> Marine Biology Research Group, Department of Biology, Ghent University – 9000 Ghent, Belgium

13 <sup>e</sup> Department of Hydraulic Engineering, Delft University of Technology – 2628 CN, P.O. Box 5048 2600 GA,  
14 Delft, The Netherlands

15 <sup>f</sup> Deltares – P.O. Box 177 2600 MH, Delft, The Netherlands

16 <sup>g</sup> School of Marine Science, Sun Yat-sen University – 510275 Guangzhou, China

17 <sup>h</sup> Southern Laboratory of Ocean Science and Engineering (Guangdong, Zhuhai) – Zhuhai 519000, China

18 <sup>i</sup> MARBEC, Univ. Montpellier, CNRS, Ifremer, IRD – Sète, France

19 <sup>j</sup> Wageningen Marine Research, Wageningen University and Research – P.B. 77, 4400 AB Yerseke, The  
20 Netherlands

21 <sup>†</sup>**Corresponding author:** Dipartimento di Scienze e Tecnologie Biologiche ed Ambientali.  
22 Centro Ecotekne Pal. B S.P. 6 Lecce – Monteroni, 73100 Lecce, Italy;  
23 francesco.cozzoli@unisalento.it

24 <sup>§</sup>**Corresponding author:** School of Marine Science, Sun Yat-sen University, 510275  
25 Guangzhou, China; huzh9@mail.sysu.edu.cn.

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27 **Abstract**

28 Predictive models accounting for the effect of bioturbation on sediment resuspension must be  
29 based on ecological theory as well as on empirical parametrizations. The scaling trend of  
30 individual metabolic and activity rates with body mass may be a key to the mechanistic  
31 understanding of the observed patterns. With this study we tested if general size scaling rules  
32 in bio-mediated sediment resuspension may apply to a broad range of physical contexts for  
33 the endobenthic bivalve *Cerastoderma edule*. The effect on sediment resuspension of  
34 populations of *C. edule* differing by individual size was measured across physical gradients of  
35 current velocity and sediment composition in terms of fraction of fine particles. *C. edule* were  
36 able to enhance the resuspension of sediment containing silt, while they had scarce effect on  
37 the resuspension of coarse sediment. The effect of bioturbation was maximal at intermediate  
38 current velocity, when the hydrodynamic forcing is not strong enough to overcome the abiotic  
39 sediment resistance but it is able to suspend the bioturbated sediment. Although differences in  
40 sediment silt content and intensities of hydrodynamic stress have a relevant influence in  
41 determining the bioturbators individual contribution to sediment resuspension, the observed  
42 mass scaling trend is consistent across all treatments and close to theoretical expectation for  
43 size scaling of individual metabolic rates. This observation supports the hypothesis that the  
44 contribution of individual bioturbators to sediment resuspension is directly related to their  
45 energy use. Therefore, the proposed approach allows the formulation of expectations of biotic  
46 contribution to sediment resuspension based on the general size scaling laws of individual  
47 energy use.

48 *Keywords:* bioturbation; cohesiveness; body size; allometry; sediment resuspension;  
49 *Cerastoderma edule*

50

## 51 **1 Introduction**

52 Sediment resuspension is mainly driven by the interaction between hydrodynamic forcing  
53 and sediment particles (Le Hir, et al., 2000; Winterwerp & van Kesteren, 2004; Fagherazzi &  
54 Wiberg, 2009; Zhou, et al., 2015), the outcome of which may be heavily modulated by biotic  
55 agents (Le Hir, et al., 2007; Grabowski, et al., 2011; Friedrichs, 2011; Wilkes, et al., 2019).  
56 In particular, the macrozoobenthic organisms disrupt and remix the sediment with their  
57 moving, feeding and respiration activities in a process called bioturbation (Meysman, et al.,  
58 2006; Kristensen, et al., 2012). Bioturbation alters the bottom sediment composition,  
59 geochemistry and erodibility (Le Hir, et al., 2007; Sandford, 2008; Gogina, et al., 2018; Li, et  
60 al., 2019). It happens at a local scale, but the effects may be important for broader landscape  
61 processes (Widdows & Brinsley, 2002; Bentley Sr, et al., 2014; Walles, et al., 2015). The  
62 bioturbators' ecosystem engineering [*sensu* (Jones, et al., 1994; Jones, et al., 1997)] of wet  
63 sediment dynamics impacts the short- and long-term development of coastal geomorphology  
64 (Winterwerp, et al., 2018; Gao, 2019), ecology (Zhu, et al., 2016; Lukwambe, et al., 2018;  
65 Mermillod-Blondin, et al., 2018; Savelli, et al., 2019) and services provided to the human  
66 society (Barbier, 2013; Bouma, et al., 2014; Lin, et al., 2018; Silva, et al., 2019). The role of  
67 bioturbation should hence be taken into account in order to implement Ecosystem-Based  
68 management of coastal areas (Braeckman, et al., 2014; Van der Biest, et al., 2020).  
69 The large majority of flume experiments [*e.g.* (Widdows, et al., 1998; Willows, et al., 1998;  
70 Orvain, et al., 2003; Kristensen, et al., 2013; Rakotomalala, et al., 2015; Cozzoli, et al.,  
71 2019)], field observations [*e.g.* (Neumeier, et al., 2006; Montserrat, et al., 2008; Harris, et al.,  
72 2015; Joensuu, et al., 2018; Hillman, et al., 2019)] and simulation studies [*e.g.* (Sandford,  
73 2008; Orvain, et al., 2012; Nasermoaddeli, et al., 2018; Angeletti, et al., 2019)] agree that the  
74 presence of bioturbators generally enhance sediment resuspension. However, bio-mediated  
75 sediment dynamics often have complex non-linear behaviour (Balke, et al., 2012; Salvador

76 de Paiva, et al., 2018; Fang, et al., 2019; Xie, et al., 2019). For instance, some field  
77 transplantation studies report tidal flat accretion in presence of high densities of the  
78 bioturbator *Cerastoderma edule* (Andersen, et al., 2010; Donadi, et al., 2013), whereas flume  
79 studies often show an increase in sediment resuspension.

80 Predictive models of bio-mediated physical dynamics should be based on generally valid  
81 physicochemical and biological laws (van Prooijen, et al., 2011), able to encompass the broad  
82 span of functional (Queirós, et al., 2013) and spatial (Gogina, et al., 2020) diversity observed  
83 in nature. The individual size is a generally valid descriptor of the intensity of individual  
84 bioturbation activity, with larger bioturbators having a higher bioturbation potential (Solan, et  
85 al., 2004b; Gilbert, et al., 2007) and generating a greater increase in resuspension of bottom  
86 sediment (Cozzoli, et al., 2018; Cozzoli, et al., 2019) and chlorophyll-a (Rakotomalala, et al.,  
87 2015). This is because individual metabolic and activity rates increase with the individual  
88 body mass following a power law with a scaling exponent of 0.66 or 0.75 (West, et al., 1997;  
89 Kooijman, 2000; Vladimirova, et al., 2003; van der Meer, 2006; Hou, et al., 2008; Brey,  
90 2010). A scaling exponent positive but lower than unity implies that, although the overall  
91 individual metabolic rate increase with body mass, the metabolic rate per unit of mass  
92 decrease with body mass with a scaling exponent of -0.33 or -0.25. The mass scaling of  
93 metabolic rates is considered one of the most "universal" trends in ecology and it has  
94 implications at any level of organization. Models based on the mass scaling of metabolic rates  
95 can be used to predict general trends from individuals to ecosystems (Brown, et al., 2004;  
96 Harris, et al., 2006; Martin, et al., 2013). In the case of bioturbation, the allometric scaling of  
97 metabolic rates implies that larger individuals, having stronger respiration, feeding, burrowing  
98 and moving activity, generate larger mechanical disturbance and hence weaken a larger  
99 volume of the surrounding sediment. However, smaller individuals should have a larger effect  
100 per unit of body mass because of their higher mass specific metabolic rate. Metabolic scaling



101 of bioturbation potential highlights the importance of the size structure of bioturbator  
102 communities in determining the bioturbator influence on sediment characteristics (Cozzoli, et  
103 al., 2018; Wrede, et al., 2019). The relationship between bioturbators metabolic rates at  
104 population level and bio-mediated effects on sediment resuspension are generally valid for a  
105 range of hydrodynamics stress conditions and a range of taxonomic and functional diversity  
106 of the bioturbators (Cozzoli, et al., 2019).

107 Not only the intrinsic characteristics of the bioturbators, but also the extrinsic environmental  
108 context can generate variations in bio-mediated sediment resuspension. In particular, the  
109 sediment composition in terms of particle size distribution strongly affects resistance to  
110 erosion. Silty (particles diameters  $< 63 \mu\text{m}$ ) and sandy (particles diameters between  $63 \mu\text{m}$   
111 and  $2 \text{ mm}$ ) sediments have different physical - chemical properties: as opposed to sand, silt  
112 particles develop an asymmetric electrical charge distribution on their surfaces. This exerts a  
113 net attractive force between particles, called cohesion. Once the amount of fine particles  
114 reaches a certain threshold (*ca.* 10%), cohesion forces confer plasticity and “stickiness” to the  
115 whole sediment mass, making it less erodible (van Ledden, et al., 2004; Winterwerp & van  
116 Kesteren, 2004). Erosion and resuspension of non-cohesive sediment occurs once the  
117 hydrodynamic stress exceeds the threshold for particle motion. The drivers of cohesive  
118 sediment resuspension are more complex and relate not only to particle size and  
119 hydrodynamic stress but also to the sediment compaction and mineral composition (Hayter &  
120 Mehta, 1986; Winterwerp & van Kesteren, 2004; van Prooijen & Winterwerp, 2010) and to  
121 the presence of microphytobenthos, which glues together sediment grains by producing  
122 extracellular polymeric substance and hence increases sediment resistance to erosion  
123 (Sutherland & Grant, 1998). The resuspension of sediments with different levels of  
124 cohesiveness may be differently influenced by the effect of bioturbation activity. For instance,  
125 recent field observations (Harris, et al., 2015; Joensuu, et al., 2018; Bernard, et al., 2019;

126 Hillman, et al., 2019), flume studies (Li, et al., 2017; Soissons, et al., 2019) and sediment  
127 transport models (Nasermoaddeh, et al., 2018) showed that bioturbators enhance the  
128 resuspension of fine sediment but have limited influence on coarse sediment.

129 Physical and biological drivers of sediment resuspension may establish complex interactions,  
130 the effect of which has not yet been fully understood. In particular, the relationship between  
131 bioturbators individual mass and bio-mediated sediment resuspension has not yet been  
132 investigated across a range of extrinsic environmental conditions such as the composition and  
133 degree of cohesiveness of the bioturbated sediment. Whereas field observations can be used to  
134 investigate the effect of benthic organisms on sediment resuspension [*e.g.* (Orvain, et al.,  
135 2007; Andersen, et al., 2010; Ubertini, et al., 2012; Savelli, et al., 2019)], stochasticity and  
136 covariance between explanatory variables in the natural environment hamper the mechanistic  
137 understanding of the processes involved. Studies conducted over fully factorial experimental  
138 designs (*i.e.* crossing all combinations of target sources of variation) under controlled  
139 (mesocosm) conditions are needed to disentangle the role of the different intrinsic and  
140 extrinsic drivers of bio-mediated sediment dynamics (Orvain, et al., 2006; van Prooijen, et al.,  
141 2011). Therefore, we used recirculating annular flumes in controlled mesocosm conditions to  
142 test the hypotheses that the effect of the bioturbators on sediment resuspension should reflect  
143 the intrinsic scaling trends of individual metabolic and activity rates over a range of extrinsic  
144 conditions in terms of hydrodynamic stress and sediment silt fraction.

## 145 2 Material and Methods

### 146 2.1 Experimental design

147 The principal idea of this experiment is to explore how sediment resuspension is influenced  
148 by physical and biological drivers (Figure 1). Therefore, we used a mesocosm approach to  
149 quantify the importance of these drivers under controlled conditions, excluding bioturbator  
150 behavioural changes in response to other environmental cues [*e.g.* acidification (Yvon-  
151 Durocher, et al., 2012; Ong, et al., 2017); temperature (Verdelhos, et al., 2015a); salinity  
152 (Verdelhos, et al., 2015b); food availability (Maire, et al., 2006)]. By mixing different types  
153 of natural sediments, we were able to obtain 4 different levels of sediment silt volume content  
154 (0 %, 4 %, 10 % and 28 %, Table 1) ranging from sand to sandy mud (van Rijn, 2007).  
155 Recirculating annular flumes were used to simulate the natural dynamic changes in current  
156 velocity during the tidal flooding of a mudflat (from 5 to 30 cm sec<sup>-1</sup> by steps of 5 cm sec<sup>-1</sup>,  
157 each step lasting 20 minutes). Variations in sediment resuspension were approximated from  
158 water turbidity. To better focus on the contribution of the individual bioturbation activity, we  
159 kept the overall bioturbators biomass constant (19 g Ash Free Dry Weight m<sup>-2</sup>) as we  
160 simultaneously varied the body size and the density of the tested specimens. Four different  
161 size classes of individuals were used (36, 93, 247 and 576 mg AFDW of individual body  
162 mass, Table 2). We chose to use an intermediate overall biomass of *C. edule* to avoid  
163 overlapping between individuals' areas of influence (Zwarts, et al., 1994; Willows, et al.,  
164 1998; van Prooijen, et al., 2011; Cozzoli, et al., 2018) while still having a clear and detectable  
165 effect on sediment resuspension. Following a factorial design, each experimental treatment (2  
166 replicates) was representative of a unique combination of bioturbators' individual size and  
167 sediment composition in terms of silt content, for a total of 32 experimental runs with  
168 bioturbators, each of which always used homogeneously sized individuals. Each of the  
169 experimental runs with bioturbators was associated to a control run using the same sediment

170 type and current velocity gradient but without bioturbators. Considering that 6 repeated  
171 measurements were taken at different current velocity levels for each run, we collected a total  
172 of 384 data points (192 observations from bioturbated runs + 192 observations from control  
173 runs, Figure 1). A numbers of replicates per treatment higher than the 2 we used would have  
174 possibly given greater reliability and reproducibility to our analysis. However, the logistic  
175 efforts necessary for empirical testing did not make it possible to collect other measures.  
176 While the dataset we collected may be regarded as not being "optimal", it is one of the most  
177 complete experimental datasets (to our knowledge) on biota-mediated sediment resuspension  
178 that has been measured according to gradients of individual size, individuals' density,  
179 hydrodynamic energy and sediment composition. The obtained dataset is available as  
180 appendix of this study (Appendix A) and in the OSF repository at DOI  
181 10.17605/OSF.IO/BCWFH.

## 182 2.2 Model organisms

183 In this experiment, we used as model organism the bivalve *Cerastoderma edule* (Linnaeus,  
184 1758). *C. edule* (common cockle) is a species of saltwater clam in the family of Cardiidae  
185 which is widely distributed in waters off northern Europe as far north as Iceland and into  
186 waters of western Africa as far south as Senegal (Boyden, 1971). The ribbed oval shells can  
187 reach 6 cm across and are white, yellowish or brown in colour. *C. edule* is a key element of  
188 estuarine food webs, consuming suspended organic matter and being a main source of food  
189 for birds (Bijleveld, et al., 2016). It is harvested commercially and eaten in much of its range  
190 (Boyden, 1971). According to the Oosterschelde (NL) observations presented in (Cozzoli, et  
191 al., 2014), this species can reach a relatively large individual body mass (up to 600 mg Ash  
192 Free Dry Weight; on average 177 mg AFDW  $\pm$  202 s.d.), high density (up to 457 Ind. m<sup>-2</sup>; on  
193 average 94 Ind. m<sup>-2</sup>  $\pm$  55 s.d.) and biomass (up to 84 g AFDW m<sup>-2</sup>; on average 16 g AFDW  
194 m<sup>-2</sup>  $\pm$  20 s.d.). *C. edule* is commonly found in a large variety of sediments ranging from fine

195 mud to sand, with a preference for cohesive sediments (Cozzoli, et al., 2013). The thermal  
196 optimum for *C. edule* activity is 20 - 23 °C, above which the activity of the animal decreases  
197 due to thermal stress, until a 100% of mortality when exposed for 120 hours to 32 °C  
198 (Verdelhos, et al., 2015a). The salinity optimum is around 20-25, with a tolerance range from  
199 fully marine (35) to brackish (10-15) (Verdelhos, et al., 2015b). Ocean acidification,  
200 especially if associated to warming, may have a detrimental effect on physiological  
201 performances and fitness of *C. edule* (Ong, et al., 2017).

202 *C. edule* is a filter feeder and shallow endobenthic burrower. Its short siphons usually emerge  
203 from the sediment surface (Flach, 1996). Field and laboratory observations showed that its  
204 reworking of the sediment is mostly related to bio-deposition, vertical and horizontal  
205 movements and valve adduction that destabilize the cohesive sediment, making it more  
206 erodible [e.g. (Flach, 1996; Ciutat, et al., 2007; Montserrat, et al., 2009; Li, et al., 2017)]. By  
207 doing so, bioturbation by *C. edule* also enhances the resuspension of organic material and  
208 microphytobenthos (Ubertini, et al., 2012; Rakotomalala, et al., 2015). The feeding rate of *C.*  
209 *edule* is not significantly affected by changes in current speed, at least between 5 and 35 cm  
210  $\text{sec}^{-1}$  (Widdows & Navarro, 2007). The material filtered out from the water column is  
211 deposited in the form of faeces (digested organic material) and pseudofaeces (discarded  
212 sediment). Loose mucus bound pseudofaeces have a lower erosion threshold (current velocity  
213 of 15  $\text{cm sec}^{-1}$ ) compared to faecal pellets (25  $\text{cm sec}^{-1}$ ). At flows below these thresholds,  
214 biodeposits generated from *C. edule* tend to sediment and accumulate on the bed (Widdows  
215 & Navarro, 2007).

216 *C. edule* is an excellent model organism to study bioturbation effects with high potential for  
217 generalization because: *i*) it adapts well to laboratory conditions; *ii*) it constitutes a  
218 predominant portion of the bioturbators intertidal biomass (Kater, et al., 2006) on a broad  
219 geographical scale (Boyden, 1971); *iii*) recent evidence showed that the effect of this species

220 on sediment resuspension is common to a broad range of bioturbators functional types  
221 (Cozzoli, et al., 2018; Cozzoli, et al., 2019); *iv*) the physiology and energetic of *C. edule* has  
222 been carefully investigated due to the relevance of this species as ecological indicator and bio-  
223 accumulator of pollutants (Fernández-Tajes, et al., 2011) *v*) its commercial importance for  
224 shell fisheries and clam digging (Boyden, 1971).

### 225 *2.3 Experimental devices*

226 The recirculating annular flumes we used are a variation of the design described by  
227 (Widdows, et al., 1998). The annular channel has a surface of 157 cm<sup>2</sup> and an overall height  
228 of 40 cm, of which the bottom 5 cm are filled with a pebbled bed to allow water drainage,  
229 followed by 10 cm of consolidated sediment and 20 cm of filtered marine seawater (31.4 L).  
230 The water motion is generated by a smooth disk rotating 3 cm below the water surface, which  
231 is driven by a microprocessor-controlled engine. Technical drawings and pictures of the  
232 annular flume can be found in Appendix B. An acoustic Doppler velocimetry probe was used  
233 to calibrate water velocity as a function of engine rotation speed. Water turbidity is measured  
234 using an optical backscatter sensor (OBS 3+, Campbell scientific) facing the water  
235 perpendicularly to the current direction at a height of 10 cm from the sediment surface. The  
236 effect of suspended sediment on light absorption was measured by the OBS sensors in  
237 nephelometric turbidity units every 30 seconds and converted into suspended sediment  
238 concentration (g L<sup>-1</sup>) based on calibration by gravimetric analysis (Appendix B).

### 239 *2.4 Experimental procedures*

240 *Sediment preparation:* The sediment was collected in late winter 2015 at location Oesterdam  
241 (51° 30' N 4° 10' E, sandy sediment) and Zandkreek Dam (51°32'N 3°52'E, silty sediment)  
242 in the Oosterschelde and carefully sieved over a 1 mm sieve to avoid the presence of large  
243 particles (stones, shells, wooden pieces) and remove larger animals. Successively, the

244 sediment was covered with a thick black plastic film for at least two weeks and sieved again  
245 to remove remaining residual fauna. For each type of sediment composition, a homogeneous  
246 matrix was obtained by adding silty sediment to a sandy matrix until reaching the desired  
247 level of silt. The sediment was mixed manually. During mixing and sequential silt addition,  
248 the percentage of silt in the sediment mass was measured by using a Malvern Mastersizer  
249 2000® particle size analyser. Following this procedure, we obtained 4 different types of  
250 sediment compositions, with no (0%), low (4%), intermediate (10%) and high (28%) silt  
251 volume fraction (Table 1). The so prepared wet sediment was put in the flumes, mixed to a  
252 smooth mass and allowed to consolidate until creating a layer of 10 cm height with a smooth  
253 surface. Excess water in the sediment was drained through the pebbled bed placed at the  
254 bottom. After 96 h, the flumes were filled with 31.4 L of filtered seawater (height of the  
255 water column 20 cm). To prevent damage to the freshly-consolidated sediment surface, a  
256 sheet of bubble plastic was placed on top of it before gently spraying water into the flume.  
257 Although the sediment bottoms we obtained by this procedure may slightly differ from the  
258 natural ones in term of grain size distribution, compaction and porewater gradient (Porter, et  
259 al., 2006), they offer a representation of the sediment cohesiveness gradient that may be  
260 observed along a mudflat tidal transect (Cozzoli, et al., 2013).

261 Collection and measurement of specimens: *C. edule* specimens were collected at the  
262 Oesterdam during spring 2015. The authorization for specimen collection was issued by the  
263 competent authority Rijkswaterstaat. After collection, the specimens were allowed to  
264 acclimate for two weeks in a mesocosm at 18 °C. During the acclimation period, the  
265 specimens were kept in the same sediment used for the experiment. Four different shell  
266 length classes (15, 20, 27 and 35 mm of shell diameter [ $\pm 0.5$  mm measurement error]) were  
267 selected to cover the *C. edule* size gradient commonly observed in nature (Table 2).  
268 Individual sizes were expressed as individual body masses ( $M$ , mg Ash Free Dry Weight) and

269 were estimated from the length of the cockles' shells according to the length-mass  
270 relationships provided from the Monitor Taskforce of the Royal Netherlands Institute for Sea  
271 Research (NIOZ), Yerseke. The mortality during the experiment was low and the specimens  
272 were released at the collection site at the end of the experiments.

273 Specimens addition: A total biomass of 3 g AFDW (corresponding to 19 g AFDW m<sup>-2</sup>) of *C.*  
274 *edule* specimens of four different size classes (Table 2) were evenly distributed over the  
275 sediment surface and allowed to settle for 48 h. The choice of a longer time interval (48 h)  
276 compared with the typical interval between erosion stress peaks (typically 12 or 24 h in a  
277 tidal system) was necessary to give the animals the time to properly settle in the new  
278 environment and recover from manipulation stress. Most of them were buried within a few  
279 minutes after being placed in the flume and non-burrowing individuals were replaced. During  
280 their presence in the flume, some specimens crawled on and below the sediment surface,  
281 leaving evident tracks.

282 Erosion runs: To simulate the natural dynamic changes in current velocity during flood tide,  
283 we increased the current velocity ( $V$ , cm sec<sup>-1</sup>) from 5 to 30 cm sec<sup>-1</sup> in steps of 5 cm sec<sup>-1</sup>,  
284 each step lasting 20 minutes. According to (Roberts, et al., 2000) and using a constant  
285 friction factor for the sediment surface of 0.002, the range of current velocity used should  
286 correspond to a range of bottom shear stresses between 0.05 and 0.25 Pa for a flat bottom.  
287 Biogenic bottom roughness may increase the friction factor in presence of bioturbators,  
288 implying a damping of bottom shear stress (Friedrichs, 2011; Anta, et al., 2013).

289 Bioturbator and control treatments have been prepared and run simultaneously. Each  
290 treatment (2 bioturbated runs + 2 control runs) was carried out on the same day. According to  
291 the availability of experimental flumes and considering the long preparation time to obtain a  
292 consolidated bottom, we took *ca.* 2 months to complete the experiment.

293 *2.5 Data Analysis*



294 In this study, we did not consider extremely high values of suspended sediment deriving by  
 295 general failures of the flume bed and consequent mass erosion (Mehta & Partheniades, 1982;  
 296 van Prooijen & Winterwerp, 2010), although such mass erosion happened in some  
 297 treatments. Therefore, the collected dataset was preliminary inspected and records of mass  
 298 erosion events were removed from the analysis. We also removed some records clearly  
 299 biased by optical disturbance to the OBS sensor.

300 To express sediment resuspension in spatial units, we converted the measured suspended  
 301 sediment concentration ( $SSC$ ,  $\text{g L}^{-1}$ ) to total mass of suspended sediment per unit of sediment  
 302 surface ( $R_{TOT}$ ,  $\text{g m}^{-2}$ ) as:

$$303 \quad R_{TOT} = \frac{SSC * Volume}{Area} \quad \text{Eq. 1}$$

304 where  $Area$  is the surface area of the experimental flumes ( $0.157 \text{ m}^2$ ) and  $Volume$  is the  
 305 amount of contained water ( $31.4 \text{ L}$ ). The development of sediment erosion at the increase of  
 306 current velocity in the experimental flumes was analysed by visual inspection of the erosion  
 307 curves. Following (Kristensen, et al., 2013), the erosion thresholds, expressed as critical flow  
 308 velocity for starting sediment resuspension ( $V$ ,  $\text{cm sec}^{-1}$ ) were estimated for each treatment as  
 309 the zero  $R_{TOT}$  intercept from a regression of  $R_{TOT}$  measured at the end of each velocity step  
 310 (*i.e.* average  $R_{TOT}$  recorded during of the last two minutes of each current velocity step)  
 311 against  $V$ . Only measurements above the erosion threshold were used for this calculation.

312 The amount of suspended sediment due to bioturbation  $R_{BIO}$  ( $\text{g m}^{-2}$ ) was calculated for each  
 313 replicate as:

$$314 \quad R_{BIO} = R_{TOT(Bioturbated)} - R_{TOT(Control)} \quad \text{Eq. 2}$$

315 where  $R_{TOT(Bioturbated)}$  ( $\text{g m}^{-2}$ ) is the amount of sediment suspended at the end of each  
 316 current velocity step in the bioturbated treatment and  $R_{TOT(Control)}$  ( $\text{g m}^{-2}$ ) is the amount of  
 317 sediment suspended in the corresponding control treatment.

318 The variation in  $R_{BIO}$  across experimental treatments and increasing current velocity ( $V$ ,  $\text{cm}$   
 319  $\text{sec}^{-1}$ ) steps was analysed by linear mixed ANCOVA. The different types of sediment  
 320 composition in terms of silt fraction (*Silt*) were used as categorical explanatory variable. The  
 321 current velocity ( $V$ ,  $\text{cm sec}^{-1}$ ) and the individual mass of the bioturbators ( $M$ ,  $\text{mg AFDW}$ )  
 322 were used as continuous explanatory variables. The response variable  $R_{BIO}$  and the  
 323 explanatory variable  $M$  were normalized *via* log transformation. A third degree polynomial  
 324 function of the explanatory variable  $V$  was used to account for asymmetric concavity in the  
 325 shape of relationship between current velocity and  $R_{BIO}$ :

$$326 \quad \log(R_{BIO}) \sim \log(M) * (V + V^2 + V^3) * Silt \quad \text{Eq. 3}$$

327 where the operator “\*” indicates use of the individual variables and their interaction terms.  
 328 We included the experimental runs as random term in the ANCOVA to account for non-  
 329 independence of the observations. This allows to treat properly the effect of  $V$ , which is  
 330 affected by repeated measurements during each erosion run. Selection of predictive variables  
 331 and interaction terms was assessed by bi-directional stepwise elimination procedure. All  
 332 analyses were performed within the free software environment R (R Core Team, 2019) using  
 333 the package lme4 (Bates, et al., 2015) and lmerTest (Kuznetsova, et al., 2017).

### 334 3 Results

#### 335 3.1 Erosion curves

336 General bottom failure and mass erosion occurred at some current velocities ( $V$ ,  $\text{cm sec}^{-1}$ ) (all  
337 the bioturbated treatments above  $V$  of  $20 \text{ cm sec}^{-1}$  for the sediment with 4 % silt content), for  
338 some replicates (one replicate each for the treatments with 10 % and 28% silt content and  
339 individual body mass  $M$  of 36 mg AFDW) and for one entire treatment (silt content 10 % and  
340  $M = 247 \text{ mg AFDW}$ ). These observations were probably related to lack of consolidation of  
341 the sediment in the experimental flumes and outranged the turbidity sensor detection range.  
342 Therefore, they were not considered in the following analyses (Figure 2).

343 In the absence of bioturbation, the critical flow velocity for erosion varied from  $13.6 \text{ cm sec}^{-1}$   
344 for sediment with 28% of silt to  $17.2 \text{ cm sec}^{-1}$  for sediment with 8% of silt (Figure 2, Table  
345 3). Sediments with 0 % and 4 % of silt content were the most erodible at the higher current  
346 velocity ( $> 20 \text{ cm sec}^{-1}$ ), reaching a  $R_{TOT}$  value of  $121 \pm 27.18$  (s. d.)  $\text{g m}^{-2}$  and  $187 \pm 115 \text{ g}$   
347  $\text{m}^{-2}$  at maximal  $V$  ( $30 \text{ cm sec}^{-1}$ ), respectively (Figure 2). As we realized during the  
348 experiment,  $R_{TOT}$  values for the sediment with 0% silt content may be slightly overestimated  
349 due to the presence of some unidentified kind of organic matter generating a small amount of  
350 foam and light hampering at high current velocity. Although we washed the sediment several  
351 times, we were not able to remove this effect. Mass erosion was observed in some not  
352 bioturbated controls for the sediment with 4 % of silt content at  $V$  of  $30 \text{ cm sec}^{-1}$ . Sediments  
353 with 10 % and 28 % of silt content had relatively low values of  $R_{TOT}$  ( $61 \pm 59 \text{ g m}^{-2}$  and  $36 \pm$   
354  $74 \text{ g m}^{-2}$ , respectively) even at water velocity of  $30 \text{ cm sec}^{-1}$  (Figure 2).

355 For bioturbated treatments with 0% of silt content, we observed a moderate increase in  $R_{TOT}$   
356 at intermediate  $V$  values only ( $15 - 25 \text{ cm sec}^{-1}$ ) for  $M = 36 \text{ mg AFDW}$  and  $M = 247 \text{ mg}$   
357 AFDW. In these two treatments we also observed a decrease in critical flow velocity for  
358 erosion from  $15.5$  to  $8.5 \text{ cm sec}^{-1}$ . A moderate decrease in  $R_{TOT}$  at maximal  $V$  was observed in

359 the two other bioturbated treatments ( $M = 93$  mg AFDW and  $M = 576$  mg AFDW) (Figure  
 360 2). The presence of *C. edule* had the strongest effect on  $R_{TOT}$  in the treatments with 4 % of silt  
 361 content. In this case, the bioturbators generated a decrease in the critical flow velocity for  
 362 erosion from 15.2 to *ca.* 5 cm sec<sup>-1</sup> (9 cm sec<sup>-1</sup> in the treatment with  $M = 576$  mg AFDW,  
 363 Table 3). This led to a moderate increase of  $R_{TOT}$  already at  $V = 10$  cm sec<sup>-1</sup> (especially the  
 364 two smaller size classes) and a very strong increase at  $V$  between 10 and 20 cm sec<sup>-1</sup>. The  
 365 presence of bioturbators triggered mass erosion at  $V = 25$  cm sec<sup>-1</sup> (Figure 2). *C. edule* had  
 366 also a strong effect on sediment resuspension at 10 % and 28 % of silt content, although  
 367 without triggering mass erosion. In the case of the bioturbated sediment with 10% of silt  
 368 content, the critical flow velocity for erosion decreased from 17.2 to 10-12 cm sec<sup>-1</sup> (Table 3).  
 369 A consistent increase in  $R_{TOT}$  due to bioturbation activity was observed starting from  $V = 15$   
 370 cm sec<sup>-1</sup> and continuously increasing with  $V$  until a value of  $+ 150 \pm 16$  g m<sup>-2</sup> for the  
 371 treatment with  $M = 93$  mg AFDW. Bioturbators did not affect the critical flow velocity for  
 372 erosion of the sediment with 28 % of silt content (*ca.* 12 cm sec<sup>-1</sup>, Table 3). Above this  
 373 threshold the bioturbators enhanced the erosion flux, leading to a maximal increment in  $R_{TOT}$   
 374 of  $+ 153 \pm 19$  g m<sup>-2</sup> for the treatment with  $M = 36$  mg AFDW (Figure 2).

### 375 3.2 Biotic contribution to sediment resuspension

376 Following the logarithmic transformation, the negative values of mass of suspended sediment  
 377 due to bioturbation activity ( $R_{BIO}$ , g m<sup>-2</sup>, Equation 2) were excluded from the analysis.  
 378 Negative values of  $R_{BIO}$  implies a decrease in sediment resuspension in presence of  
 379 bioturbators and were observed mostly in the sediment with 0% silt content. As a  
 380 consequence of this selection and of that one made previously to avoid observations biased  
 381 by optical disturbance to the sensor, the total number of  $R_{BIO}$  values included in the analysis  
 382 has dropped to 135 (Table 4). The full mixed ANCOVA model of the variation  $R_{BIO}$  using the  
 383 silt content of the sediment (*Silt*), the current velocity ( $V$ , cm sec<sup>-1</sup>) and the individual mass of

384 the bioturbators ( $M$ , mg AFDW) as explanatory variables (Equation 3) was simplified by bi-  
385 directional elimination stepwise procedure. Following this procedure, the square term of the  
386 polynomial of  $V$ , the third order interaction terms and some of the second order interaction  
387 terms were eliminated. The full model (i.e. prior to variables selection) is available as an  
388 appendix (Appendix C). The fixed terms in the simplified ANCOVA model explains 76% of  
389 the observed variance in  $R_{BIO}$ , while random variation among experimental runs was able to  
390 explain the 8% only (Table 5).

391 The model has good performances in predicting  $R_{BIO}$  for sediment with silt content higher  
392 than 0 %. Given the low influence of the bioturbators on the resuspension of the pure sandy  
393 sediment (Figure 2), the model fails in predicting  $R_{BIO}$  for these treatments (Figure 3, Figure  
394 4).  $R_{BIO}$  significantly ( $p < 0.001$ ) increases with the increase of  $V$  independently from the  
395 sediment silt content and the body mass of bioturbators (Table 5, Figure 3, Figure 4). The  
396 significant ( $p < 0.001$ ) and negative coefficient for  $V^3$  implies a concave shape in the  
397 relationship between  $R_{BIO}$  and  $V$  (Table 5, Figure 3). The concavity of the relationship varies  
398 significantly ( $p < 0.001$ ) across sediment silt contents, being maximal for the sandy sediment,  
399 intermediate for sediments with 10% and 28% silt content and minimal for the sediment with  
400 4 % of silt content (Table 5, Figure 3). However, the nearly linear relationship between  $V$  and  
401  $R_{BIO}$  estimated for the sediment with 4 % silt content is likely to be an experimental artefact  
402 related to the lack of observations for bioturbated treatments at  $V$  higher than  $20 \text{ cm sec}^{-1}$   
403 (Figure 2). Independently of the intensity of  $V$  and with only marginal variation across types  
404 of sediment composition ( $p > 0.05$ ),  $R_{BIO}$  scales significantly ( $p < 0.001$ ) and negatively  
405 (scaling exponent =  $-0.42 \pm 0.22$ ) with  $M$  (Table 5, Figure 4).

## 406 **4 Discussion**

407 In our experiments we used a full factorial combination of physical (sediment composition,  
408 hydrodynamic stress) and biological (bioturbator size/density ratio) drivers of bio-mediated  
409 sediment resuspension to disentangle the specific importance of each component and reveal  
410 the effect of their interactions (Figure 1). Although sediment resuspension patterns change  
411 across sediment types, the intrinsic scaling to the individual mass of the bioturbators was  
412 independent of the extrinsic physical context.

### 413 *4.1 Effect of hydrodynamic stress and sediment composition on bio-mediated sediment* 414 *resuspension*

415 In accordance with previous flumes (Li, et al., 2017; Soissons, et al., 2019) and field (Harris,  
416 et al., 2015; Joensuu, et al., 2018; Bernard, et al., 2019) observations, bioturbation had a  
417 limited influence on the resuspension of pure sandy sediment, whereas it had a strong  
418 influence on resuspension of silt-containing sediments, even if only a low amount of silt was  
419 present (4 % volume fraction). In the case of sandy sediment, increments in sediment  
420 resuspension can be related to the exposure of otherwise buried fine particles to the buoyant  
421 action of the water (Volkenborn, et al., 2009; van Prooijen, et al., 2011). In the case of  
422 cohesive sediment, the bioturbation disrupts the cohesiveness and compaction in the upper  
423 sediment layers, generating a fluff layer (Shimeta, et al., 2002; Orvain, et al., 2003; Orvain,  
424 2005). The fluff layer is less resistant to erosion than the not-bioturbated sediment, so that  
425 bioturbation decreases the critical flow velocity for erosion and enhances the erosion fluxes  
426 of cohesive sediment. Therefore, *C. edule* changed the sediment response to hydrodynamic  
427 stress by making the otherwise erosion-resistant cohesive sediments as erodible as the non-  
428 cohesive ones. Above the threshold for cohesiveness (10 % silt fraction), the effects of  
429 bioturbation on sediment resuspension no longer increases with sediment silt content. These  
430 observations support what was recently predicted by a landscape-scale model of biota-

431 mediated sediment resuspension on the basis of field observations of suspended sediment  
432 concentration: the resuspension of fine silt in the southern North Sea is very sensitive to the  
433 occurrence of bioturbators, whereas coarser sediment particles are less affected  
434 (Nasermoaddeli, et al., 2018).

435 Our results suggest that if the hydrodynamic forcing is limited, the contribution of  
436 bioturbation on sediment resuspension is relatively low. As well, if the hydrodynamics are  
437 strong enough (or the sediment resistance weak enough, as it is in the case of non-cohesive  
438 sediment) to erode the non-bioturbated sediment, the relative contribution of bioturbators to  
439 sediment resuspension decreases because the additional bioturbation is less relevant for  
440 particle motion. Bioturbation effects are maximal at intermediate current velocity, when the  
441 hydrodynamic forcing is not strong enough to overcome the abiotic sediment resistance (that  
442 is enhanced by cohesiveness) but are able to suspend the bioturbated sediment. This  
443 interpretation is in line with the observations of (Moore, 2006), who noted that ecosystem  
444 engineering in river morphodynamics can be more important with moderate hydrodynamic  
445 energy and high bioturbators activity. Tending to be zero at very high and very low current  
446 velocities for each type of sediment, the amount of suspended sediment due to bioturbation  
447 activity has *per se* only marginally significant changes across sediment types. Neither is  
448 changing its linear relationship with the current velocity. What actually changes across the  
449 types of sediment is the current velocity at which bioturbators peak their effect on  
450 resuspension. In sandy sediments, the bioturbators have a maximal effect at current velocity  
451 of  $20 \text{ cm sec}^{-1}$ , above which the hydrodynamic stress starts to be able to suspend the non-  
452 bioturbated sediment. Assuming a concave shape for the relationship between current velocity  
453 and bioturbators contribution to sediment resuspension (Equation 3, Table 5), the maximal  
454 effect on cohesive sediment resuspension should occur at a current velocity of *ca.*  $40 \text{ cm sec}^{-1}$ .  
455 It also follows that the current velocity at which the bioturbators no longer have an

456 appreciable effect on the resuspension (*i.e.*  $< 1 \text{ g m}^{-2}$ ) of the sediment is greater for the  
457 cohesive sediment (*ca.*  $60 \text{ cm sec}^{-1}$ ) than for the non-cohesive (*ca.*  $40 \text{ cm sec}^{-1}$ ). It must be  
458 however considered that our observations concern supply-limited erosion only (Mehta &  
459 Partheniades, 1982; van Prooijen & Winterwerp, 2010). At current velocity higher than the  
460 maximal we tested or in presence of waves, mass erosion (that may be triggered or anticipated  
461 by the presence of bioturbators, as we observed in the treatments with 4 % of silt content)  
462 may deviate from our expectations.

#### 463 *4.2 Allometric scaling of individual contribution to sediment resuspension*

464 Given a fixed biomass, the contribution of a population of bioturbators to sediment  
465 resuspension decrease with the bioturbators individual size. The estimated mass scaling  
466 exponent ( $-0.42 \pm 0.22$ ) is different from either 0 (*i.e.* bio-mediated sediment resuspension  
467 directly proportional to the population biomass) and -1 (*i.e.* bio-mediated sediment  
468 resuspension directly proportional to the individuals' density in the case of biomass  
469 equivalence across size classes). It is instead close to the theoretical expectations of -0.33 or -  
470 0.25 for size scaling of individual metabolic rates per unit of biomass. In this respect, our  
471 observations support the hypothesis that the contribution of bioturbators to sediment  
472 resuspension is related to their metabolic and activity rate, rather than to their mere presence,  
473 biovolume or spatial density (Cozzoli, et al., 2018; Cozzoli, et al., 2019). Therefore, a certain  
474 biomass of smaller organism would generate a stronger disturbance of the sediment than the  
475 same biomass of larger organisms because smaller organisms have higher metabolic rates per  
476 unit of body mass. It follows that information on the size structure of the bioturbating  
477 communities [*e.g.* (Gjoni, et al., 2017; Gjoni & Basset, 2018)] and on the individual  
478 metabolic responses to internal and external conditions [*e.g.* (Rosenfeld, et al., 2015; Shokri,  
479 et al., 2019)] is needed to predict the bioturbation effects on sediment resuspension.

480 Extrapolations based on bioturbators' overall biomass or density should instead be treated



481 with caution, because they may estimate wrongly the contribution of individuals differing by  
482 body mass and activity level.

483 Although differences in sediment silt content and intensities of hydrodynamic stress have a  
484 relevant influence in determining the bioturbators' individual contribution to sediment  
485 resuspension, the observed mass scaling trend is constant across all treatments. Therefore,  
486 size allometries in bio-mediated sediment resuspension can be generally applied to different  
487 sediment compositions as well as to different functional types of bioturbators (Cozzoli, et al.,  
488 2018; Cozzoli, et al., 2019). This finding expands the possibility to simplify and generalize  
489 the process-based modelling of bioturbators-sediment interactions [*sensu* (van Prooijen, et  
490 al., 2011)] by establishing a link between the energetic of the organisms and their effect on  
491 the surrounding environment (Humphries & McCann, 2014). As an example referred to field  
492 conditions, the bioturbators size, overall biomass and community bioturbation activity  
493 generally peak in the intermediate-high part of the mudflat, where the hydrodynamic energy  
494 is moderate and the sediment has an intermediate to high silt fraction (Pearson & Rosenberg,  
495 1978; Nilsson & Rosenberg, 2002), *i.e.* where bioturbators are also more effective in  
496 enhancing sediment resuspension. Thus, our results confirm and strengthen the hypothesis  
497 that bioturbators mostly enhance the erosion of the upper shore, potentially inducing a  
498 downward shift of the tidal flat (Wood & Widdows, 2002; Orvain, et al., 2012). More  
499 generally, distribution models of benthic populations in relation to hydrodynamic and  
500 sediment characteristics can be used to produce spatially explicit estimates of the individual  
501 mass, abundance and therefore the potential effect on sediment resuspension of bioturbators  
502 in natural conditions.

#### 503 *4.3 Mechanisms to be further investigated*

504 In this study we attribute the changes in turbidity to changes in sediment erodibility.

505 However, some other mechanisms involved in bio-mediated sediment resuspension must be  
506 considered. *C. edule* filter particles that are suspended in the water column while feeding.  
507 The clearance activity may affect the amount of turbidity measured in the water in  
508 recirculating flumes, possibly leading to an underestimation of the effect of *C. edule*  
509 bioturbation on erosion rate, compared to field settings. This underestimation can reach a  
510 factor of 2 in the case of chlorophyll-a suspension (Rakotomalala, et al., 2015). Despite  
511 deserving to be examined more carefully, three main arguments suggests that suspended  
512 sediment filtration can generate only a minor bias on our observations. Firstly, the filtered  
513 sediment is not retained in the body of the bioturbators, but it is rather quickly expelled in the  
514 form of pseudofaeces, that are easily erodible and likable to be re-suspended immediately at  
515 current velocity  $> 15 \text{ cm sec}^{-1}$  (Widdows & Navarro, 2007), *i.e.* with a similar critical flow  
516 velocity for erosion to cohesive not-bioturbated sediment. Still, part of the decrease in  
517 suspended sediment at high current velocity that we observed in some treatments with non-  
518 cohesive sediment could be related to increased sediment strength by pelletization (Briggs, et  
519 al., 2015). Secondly, being both fuelled by the individual metabolic rate, the magnitude of the  
520 physiological activities involved in sediment destabilization and of the individual clearance  
521 rate increase with body mass (decrease per unit of mass) with a similar scaling exponent  
522 (Smaal, et al., 1997), leading to a substantial process balance across size classes. Thirdly,  
523 previous studies comparing multiple types of bioturbators in a similar experimental setup  
524 (Cozzoli, et al., 2018; Cozzoli, et al., 2019) did not show relevant differences in the  
525 resuspension of sediment in the presence of filter feeders (*e.g. C. edule*) or bottom-feeders  
526 (*e.g. Arenicola marina*).

527 Another mechanism to be further investigated is the effect of the structural modification of  
528 the bottom surface roughness by bioturbators, which can be generated both in autologous  
529 (emerging shells) and allogenic (disruption of the sediment surface) way. Bio-mediated

530 increases in bottom roughness could shelter the sediment surface from shear flow (Friedrichs,  
531 et al., 2009; Friedrichs, 2011; Anta, et al., 2013). In the case of cohesive sediment, increased  
532 bottom roughness may generate a reduction in sediment resuspension when the  
533 hydrodynamic forcing is low (shear stress  $< 10 \text{ cm sec}^{-1}$ ) and/or the bioturbators abundance  
534 (Ciutat, et al., 2007) or activity (Cozzoli, et al., 2019) is higher than what used in this  
535 experiment. The reduction in cohesive sediment resuspension is suppressed at higher  
536 hydrodynamic stress by the opposite destabilizing effect (Cozzoli, et al., 2019). With the  
537 current experiment we show that, in case on pure sandy sediment, the sheltering and  
538 pelletization effects could be the predominant influence of bioturbators, leading to a minor  
539 reduction in sand resuspension at high current stress ( $30 \text{ cm sec}^{-1}$ ), even at the relatively low  
540 number of organisms we used.

541 It must also be considered that in our experiment the individual body mass was calculated  
542 based on shell length. Given the approximately spherical shape of *C. edule*, the individual  
543 mass scales with the shell length with an exponent close to 3 (actually, 2.8). Therefore, our  
544 observation could be eventually interpreted as an inverse proportionality between shell length  
545 and effect on sediment resuspension ( $2.8 * -0.42 = -1.12$ ), which further leads to other  
546 influencing factors such as burial depth, destabilization sediments beyond the surface layer  
547 and autogenous modification of the bottom roughness. This interpretation should be rejected  
548 considering that: *i*) given the experimental design we used, an inverse proportionality to the  
549 individual length should exclude any effect of the individuals numerical density or total  
550 biomass, and this is contrasting with all previous knowledge *ii*) previous experiments  
551 comparing bioturbators with different physical shapes and therefore different scaling  
552 coefficient for the mass ~ length relationship and/or generating different morphological  
553 alterations of the bottom surface and/or with different burying depth related to their body  
554 length showed no significant change in bioturbation effect on sediment resuspension

555 (Cozzoli, et al., 2018; Cozzoli, et al., 2019).

556 Finally, factorial experiments accounting for the effect of temperature change on bio-  
557 mediated sediment resuspension could offer a definitive confirmation of the dependence on  
558 metabolism of bioturbator populations. Water temperature is indeed a key regulator of  
559 metabolic rates in ectotherms such as macrozoobenthic bioturbators (Brown, et al., 2007).  
560 Beyond the effect of variation in physical factors (Nguyen, et al., 2019) it is expected that the  
561 biotic contribution to sediment resuspension should increase positively with temperature  
562 similarly to the individual metabolic rates, *i.e.* according to a positive Boltzmann – Arrhenius  
563 relationship (Brown, et al., 2007). Therefore, metabolic-based approaches may help  
564 explaining global and seasonal variations in biotic influences on sediment dynamics (Cozzoli,  
565 et al., 2018; Wrede, et al., 2018).

566

## 567 **5 Conclusion**

568 With this study, we quantified the role of major sources of abiotic and biotic variability in  
569 enhancing sediment resuspension by highlighting the combined role of physical and  
570 biological factors in determining sediment resuspension. We observed that differences in  
571 sediment silt content and intensities of hydrodynamic stress have a major influence in  
572 determining the final amount of suspended sediment. However, the observed mass scaling  
573 trend of bioturbators' individual contribution to sediment resuspension is *i)* close to the size  
574 scaling trend of individual metabolic rates and *ii)* constant at the variation of the  
575 environmental conditions. In the light of these findings, the bioturbators can be seen as  
576 energy transfer units that convert the chemical energy contained in the food web into kinetic  
577 energy that is discharged onto the sediment. The observation of a mass scaling exponent  
578 similar to that of mass specific individual metabolic rates suggests that a somehow constant  
579 fraction of metabolic energy is discharged onto the sediment at individual level. While the  
580 intensity of the energy flow is determined by the body size and energy requirement of the  
581 bioturbators, its effect on sediment resuspension is mediated by the hydrodynamic stress and  
582 the mechanical characteristics of the sediment itself.

583 The metabolic dependency of bio-mediated sediment dynamics that we describe places our  
584 observations within the broader context of metabolic ecological theories [*e.g.* (Kooijman,  
585 2000; Brown, et al., 2004; Glazier, 2005; Hou, et al., 2008)]. It establishes a connection  
586 between ecosystem engineering and general models of organisms metabolic [*e.g.* (Yvon-  
587 Durocher, et al., 2012)] and demographic [*e.g.* (Dossena, et al., 2012; Lindmark, et al., 2018;  
588 Bryndum-Buchholz, et al., 2019; Jørgensen, et al., 2019)] responses to global environmental  
589 changes. Hence, our observations supports the parametrization of general, predictive models  
590 of bio-mediated sediment dynamics at local [*e.g.* (Aquino, et al., 2017; Winterwerp, et al.,  
591 2018)], tidal transect [*e.g.* (Wood & Widdows, 2002; Orvain, et al., 2012)] and landscape [*e.g.*

592 (Nasermoaddeli, et al., 2018; Angeletti, et al., 2019)] scale. By doing so, they open a venue to  
593 the formulation of general expectations about future scenarios of bio-mediated sediment  
594 resuspension.

Journal Pre-proof

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- 920

921 **TABLES**

922 **Table 1:** Types of sediment composition. Percentages in volume of the different sediment  
 923 size classes (silt < 63  $\mu\text{m}$ ; very fine sand 63-125  $\mu\text{m}$ ; fine sand 125-250  $\mu\text{m}$ ; medium sand  
 924 250-500  $\mu\text{m}$ ; coarse sand > 500  $\mu\text{m}$ ) and median (D50), tenth (D10) and ninetieth percentile  
 925 (D90) of the sediment grain size distribution ( $\mu\text{m}$ ).

926

<b>Silt</b>	<b>Very fine</b>	<b>Fine</b>	<b>Medium</b>	<b>Coarse</b>	<b>D10</b>	<b>D50</b>	<b>D90</b>
(%)	(%)	(%)	(%)	(%)	( $\mu\text{m}$ )	( $\mu\text{m}$ )	( $\mu\text{m}$ )
0	0	30	61	9	189	305	488
4	1	31	55	9	159	291	489
10	5	33	45	7	94	257	468
28	14	30	24	3	8	153	383

927

928 **Table 2:** Bioturbators size classes. Sediment resuspension was measured in the abiotic  
929 controls and in 4 treatments with biomass equivalents (overall biomass 19 g Ash Free Dry  
930 Weight  $\text{m}^{-2}$ ) of differently sized bioturbators ( $M$ , mg AFDW).

931

<b>Shell length</b>	<b>Body mass</b>	<b>Density of individuals</b>
(mm)	( $M$ , mg AFDW)	( $D$ , Ind. $\text{m}^{-2}$ )
15	36	530
20	93	247
27	247	77
35	576	33

932

933

934 **Table 3:** For each treatment with different sediment silt volume content (%) and bioturbators935 individual body mass ( $M$ , mg AFDW), the critical flow velocity for erosion ( $\text{cm sec}^{-1}$ ) were936 estimated as the zero  $R_{TOT}$  intercept from a regression of measured  $R_{TOT}$  against  $V$ 

937 (Kristensen, et al., 2013).

938

<i>Silt (%)</i>	<i>M</i>	<i>V-Intercept</i>	<i>V-Slope</i>	Critical flow velocity for erosion
0	0	-121.3	7.8	15.5
0	36	-48.6	5.7	8.5
0	93	-75.2	5.1	14.8
0	247	-53.6	6.2	8.58
0	576	-88.8	6.2	14.4
4	0	-167.8	11.1	15.2
4	36	-92.2	16.2	5.7
4	93	-70.1	14	5
4	247	-77.6	14.5	5.4
4	576	-106	11	9.6
10	0	-100.1	5.8	17.2
10	36	-108.5	9.6	11.3
10	93	-102.6	9.5	10.8
10	576	-102.2	8.1	12.6
28	0	-94.3	6.9	13.6
28	36	-103.1	9.3	11.1
28	93	-91.7	7.9	11.6
28	247	-76.3	6.4	12
28	576	-98.1	7.6	13

939

940

941 **Table 4:** Number of observations included in the ANCOVA model of the amount of  
 942 suspended sediment due to bioturbation ( $R_{BIO}$ , g m<sup>-2</sup>, Table 5). The initial number of 192  $R_{BIO}$   
 943 measures (4 silt levels X 4 size levels X 6 current velocity step X 2 replicates) was reduced to  
 944 135 in way to avoid observations biased by optical disturbance to the sensor, observations  
 945 related to mass erosion events and observations of decreased sediment resuspension in  
 946 presence of bioturbators.

947

Silt (%)	Body mass (mg AFDW)			
	36	93	247	576
0	9 <sup>b,c</sup>	9 <sup>b</sup>	10 <sup>b</sup>	7 <sup>b</sup>
4	8 <sup>d</sup>	6 <sup>c,d</sup>	8 <sup>d</sup>	8 <sup>d</sup>
10	6 <sup>d</sup>	12 <sup>a</sup>	0 <sup>e</sup>	12 <sup>a</sup>
28	6 <sup>d</sup>	12 <sup>a</sup>	12 <sup>a</sup>	11 <sup>c</sup>

948

949 *a: complete set of 12 measures for treatment (6 current velocity steps X 2 replicates)*

950 *b: observations missing due reduction in sediment resuspension with bioturbators*

951 *c: observations missing due to optical disturbance to the OBS sensor*

952 *d: observations missing due to mass erosion events (current velocity higher than 20 cm sec<sup>-1</sup>)*

953 *d: observations missing due to mass erosion events (one replicate)*

954 *e: observations missing due to mass erosion events (whole treatment)*

955

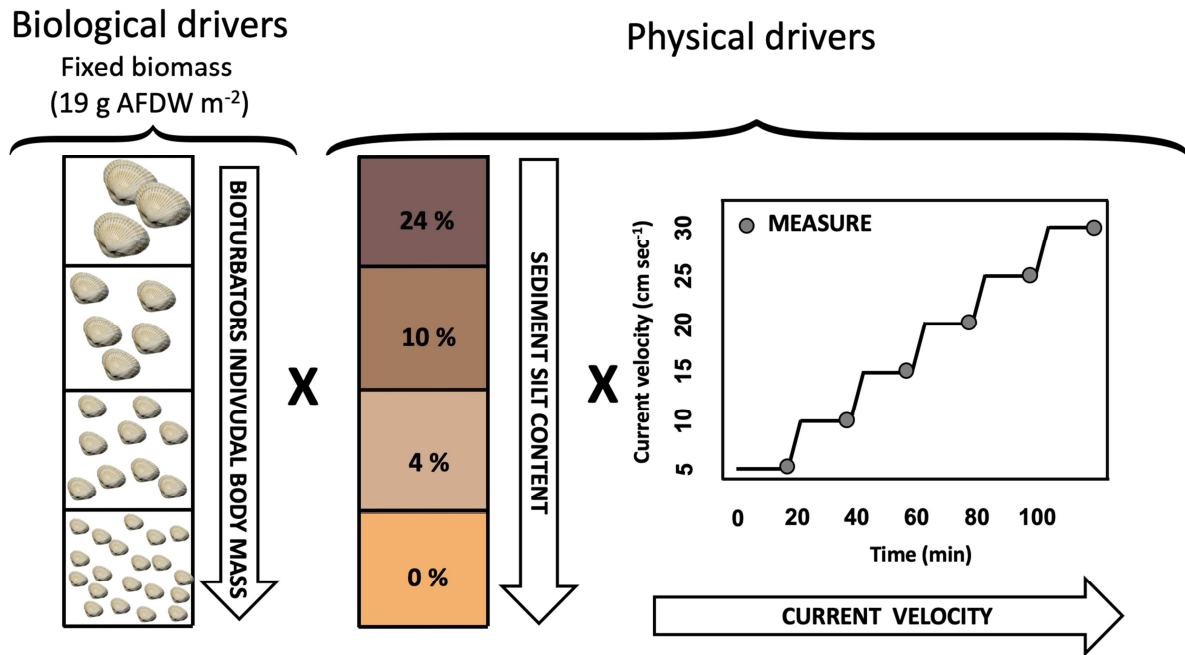


956 **Table 5:** Summary of the mixed ANCOVA model of the amount of suspended sediment due  
 957 to bioturbation ( $R_{BIO}$ ,  $\text{g m}^{-2}$ ) using the silt content of the sediment as categorical explanatory  
 958 variable and the current velocity ( $V$ ,  $\text{cm sec}^{-1}$ ) and the individual mass of the bioturbators ( $M$ ,  
 959  $\text{mg AFDW}$ ) as continuous explanatory variables. The response variable  $R_{BIO}$  and the  
 960 explanatory variable  $M$  were normalized *via* log transformation. A third degree polynomial  
 961 function of the variable  $V$  was used to account for non-linearity in the relationship between  
 962 current velocity and  $R_{BIO}$ . Since we took repeated measurements of the same experimental  
 963 units through a  $V$  gradient, we included the experimental runs as random term in the  
 964 ANCOVA to account for non-independence of the observations. Selection of predictive  
 965 variables and interaction terms was assessed by a bi-directional elimination stepwise  
 966 procedure. Only significant variables and interaction terms are reported in the summary table.  
 967 The full model (i.e. prior to variables selection) is available as an appendix (Appendix C).

Predictors	Estimates	$\log(R_{BIO})$	
		95% CI	$p$
(Intercept)	1.47	0.23 – 2.72	0.028
$\log(M)$	-0.42	-0.64 – -0.20	0.001
$V$	0.24	0.20 – 0.28	<0.001
$V^3$	-0.0002	-0.0002 – -0.0001	<0.001
Silt 4 %	1.01	0.34 – 1.69	0.006
Silt 10 %	0.46	-0.27 – 1.19	0.228
Silt 28 %	0.13	-0.54 – 0.80	0.702
$V^3$ :Silt 4 %	0.0003	0.0002 – 0.0003	<0.001
$V^3$ :Silt 10 %	0.0001	0.0001 – 0.0002	<0.001
$V^3$ :Silt 28 %	0.0001	0.0001 – 0.0002	<0.001
<b>Random Effects</b>			
$\sigma^2$	0.37		
$\tau_{00 \text{ Run}}$	0.29		
ICC	0.44		
$N_{\text{Run}}$	28		
Observations	135		
Marginal $R^2$ / Conditional $R^2$	0.77 / 0.87		

968

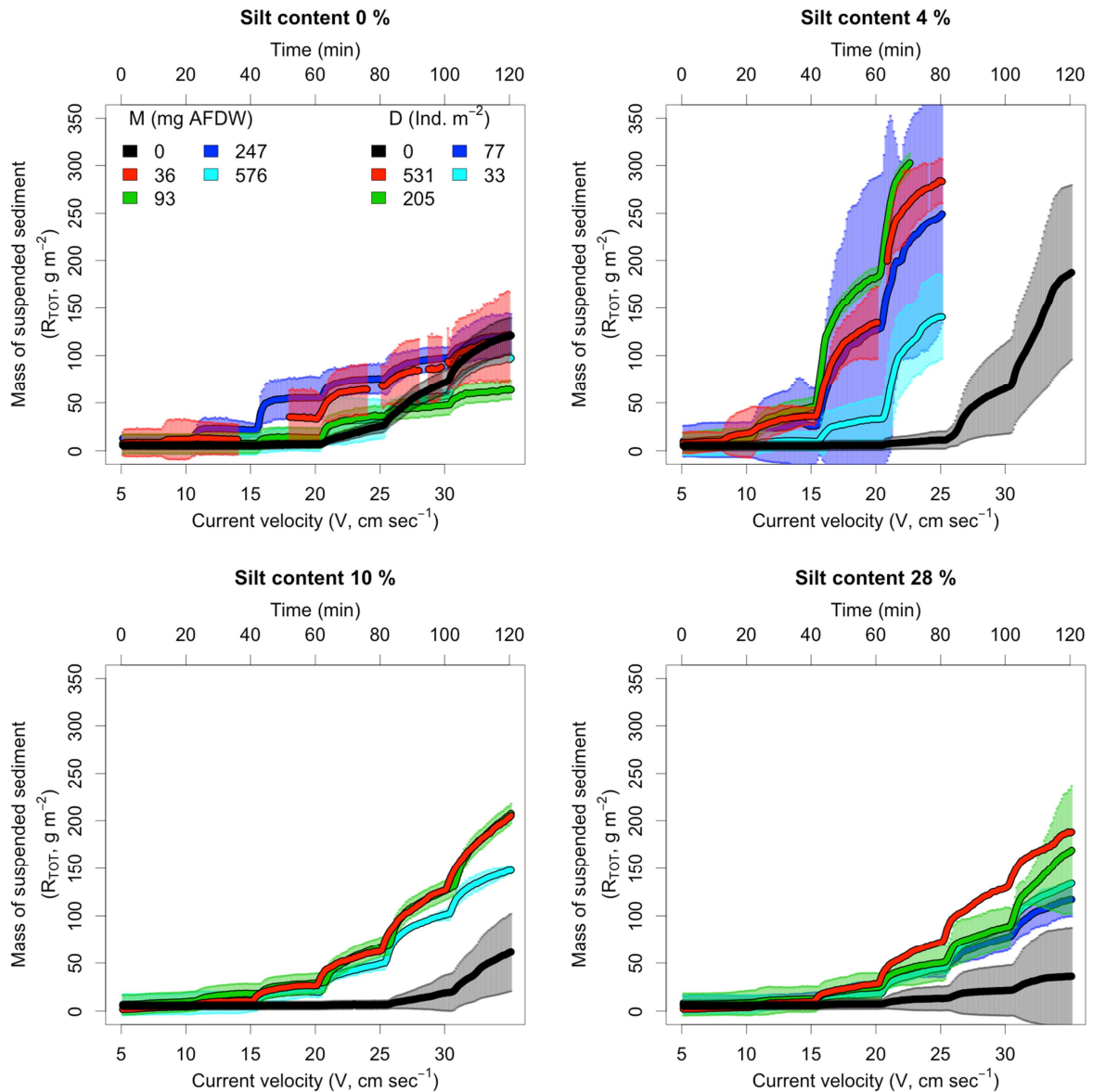
## 969 FIGURES



970

971 **Figure 1:** Experimental design. Keeping fixed an overall *C. edule* biomass of 19 g AFDW m<sup>-2</sup>, we crossed in a full factorial design 4 different size classes of individuals (36, 93, 247 and  
 972 576 mg AFDW of individual body mass), 4 levels of sediment silt volume content (0 %, 4 %,  
 973 10 % and 28 %) and 6 levels of current velocity (from 5 to 30 cm sec<sup>-1</sup> by steps of 5 cm sec<sup>-1</sup>,  
 974 each step lasting 20 minutes). Each of the experimental runs with bioturbators was associated  
 975 to a control run using the same sediment type and current velocity gradient but without  
 976 bioturbators. Each experimental treatment was replicated twice.

978



979

980

**Figure 2:** Overall mass of suspended sediment ( $R_{TOT}$ ,  $g\ m^{-2}$ ) for different sediment silt

981

volume content (%) across a gradient of current velocity ( $V$ ,  $cm\ sec^{-1}$ ) and bioturbators

982

individual body mass ( $M$ , mg AFDW, coloured lines), average of two replicates for each

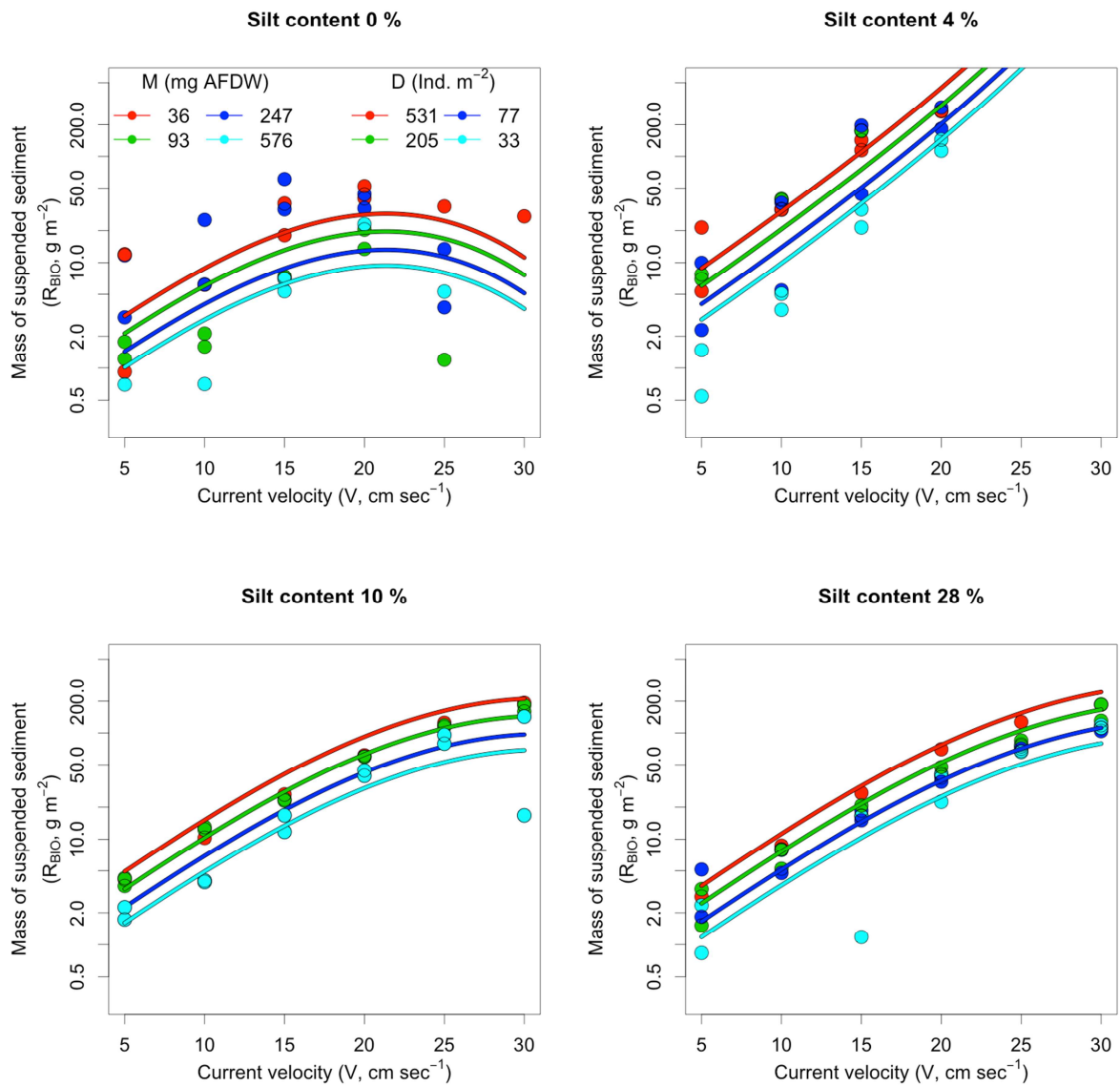
983

treatment (when available). The coloured areas represent the 95 % confidence intervals

984

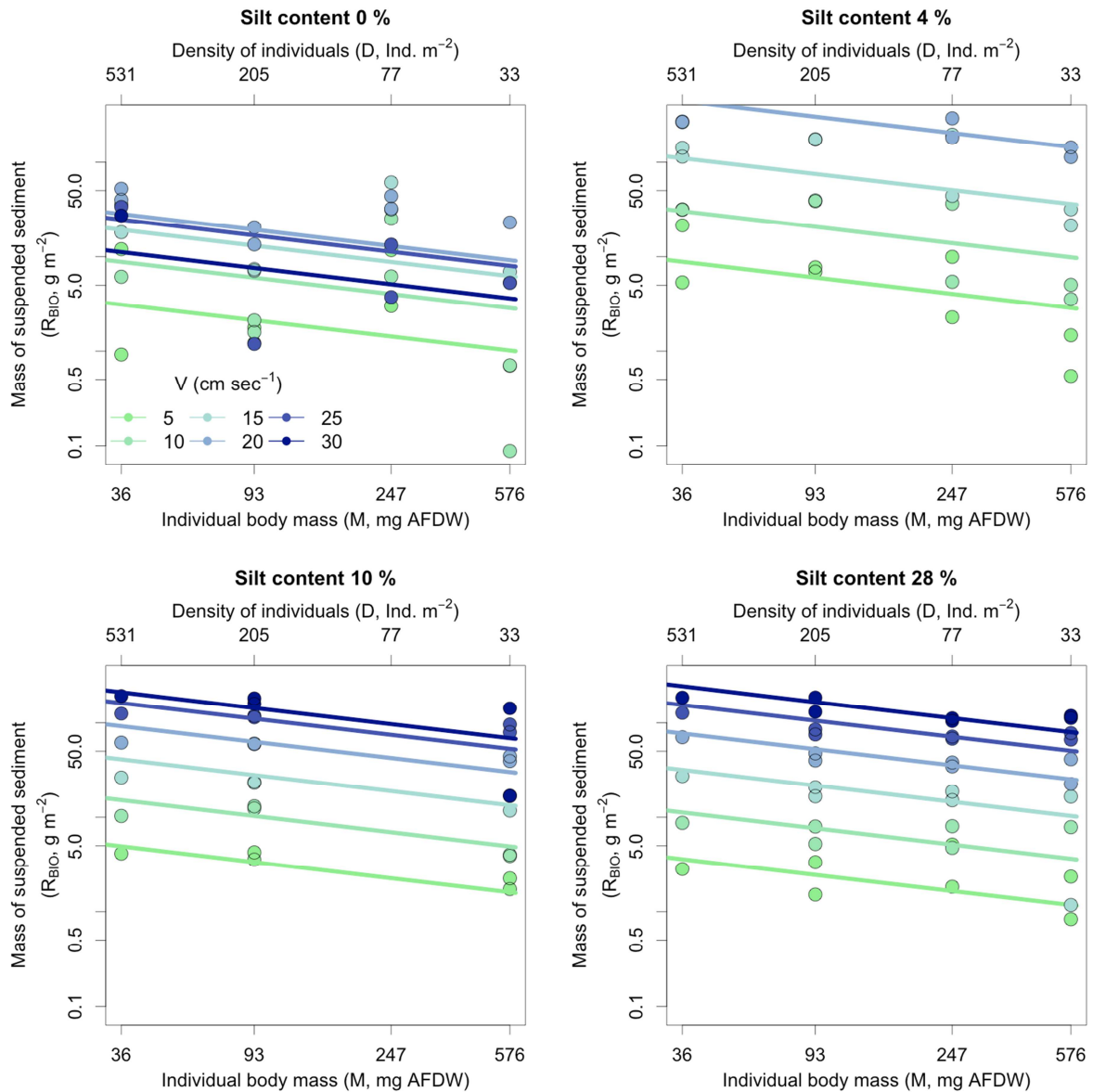
around the average trends.

985



986

987 **Figure 3:** Relationship between current velocity ( $V$ ,  $\text{cm sec}^{-1}$ ) and mass of suspended  
 988 sediment due to bioturbation ( $R_{BIO}$ ,  $\text{g m}^{-2}$ ) for different sediment silt volume content (%) and  
 989 bioturbators individual body mass ( $M$ , mg AFDW), as predicted from the ANCOVA model  
 990 in Table 5.



991

992 **Figure 4:** Individual body mass ( $M$ ,  $mg\ AFDW$ ) scaling of the mass of suspended sediment  
 993 due to bioturbation ( $R_{BIO}\ g\ m^{-2}$ ) for different sediment silt volume content (%) and current  
 994 velocities ( $V$ ,  $cm\ sec^{-1}$ ), as predicted from the ANCOVA model in Table 5.

**Highlights:**

- Bioturbators affect sediment resuspension.
- The effect of bioturbators was compared across different sediment types.
- Bioturbation effect was maximal at intermediate current and on cohesive sediment.
- The individual effect of bioturbators scales with size similarly to metabolic rate.
- The size scaling trend is independent of the sediment composition.

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**Declaration of interests**

**X** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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