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# Does parasitism influence sediment stability? Evaluation of trait-mediated effects of the trematode *Bucephalus minimus* on the key role of cockles *Cerastoderma edule* in sediment erosion dynamics

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# Does parasitism influence sediment stability? Evaluation of trait-mediated effects of the trematode *Bucephalus minimus* on the key role of cockles *Cerastoderma edule* in sediment dynamics

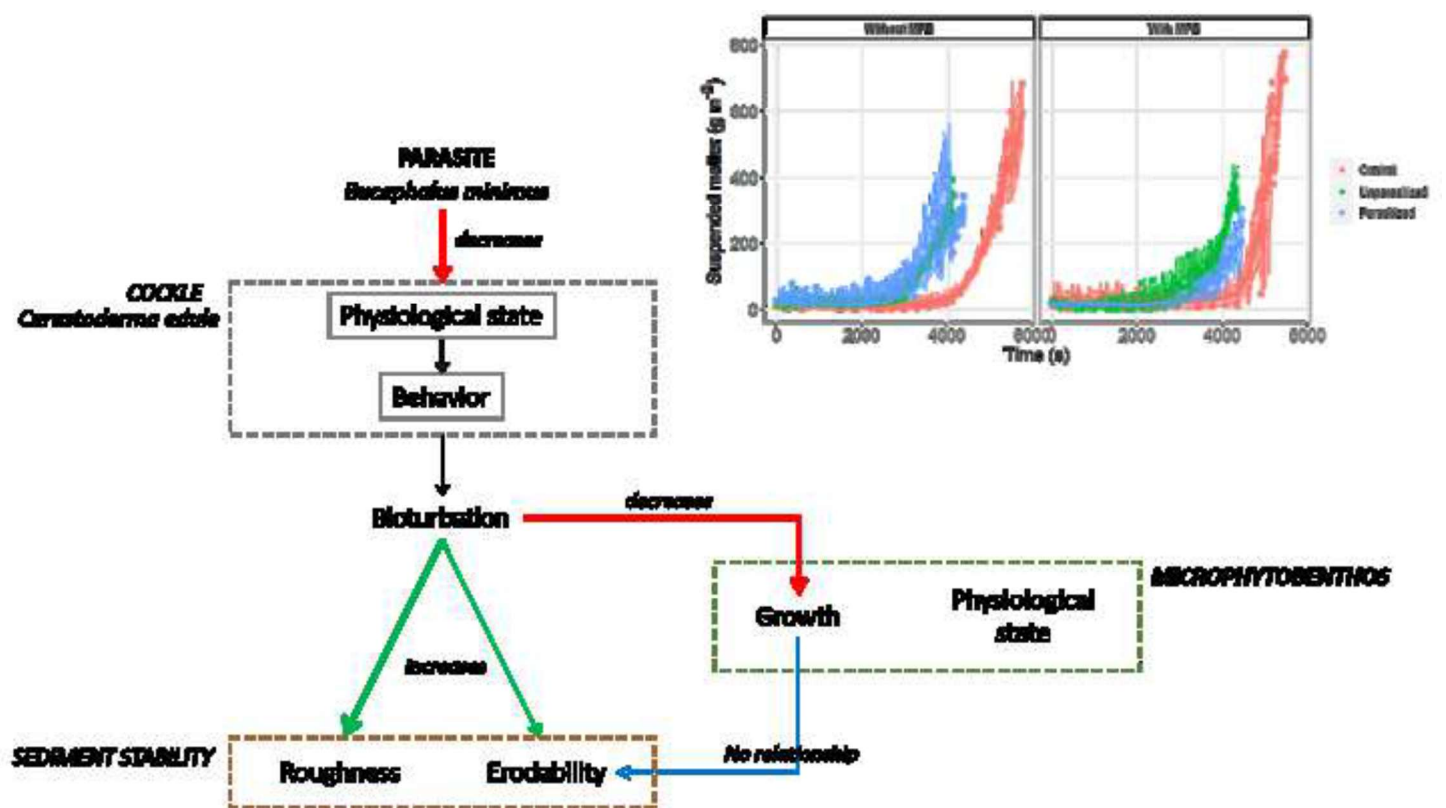
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\*Graphical Abstract



## Highlights

- The role of unparasitized and parasitized cockles in sediment dynamics was tested
- The influence of cockles on sediment erodability and hydrodynamics was disentangled
- Unparasitized cockles increased sediment erodability and roughness
- Parasitism slightly reduced the destabilising effect of its host
- Parasitized cockles with lowered metabolic rate and likely reduced bioturbation

1 **Does parasitism influence sediment stability? Evaluation of trait-**  
2 **mediated effects of the trematode *Bucephalus minimus* on the key**  
3 **role of cockles *Cerastoderma edule* in sediment dynamics**

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## 10 **Abstract**

11 In coastal environments, bioturbating organisms greatly influence physical and biogeochemical  
12 properties of sediments with consequences on central ecological processes as erosion dynamics. In  
13 addition to their direct impact on sediment stability, bioturbators can also influence sediment erosion  
14 processes while regulating the growth of microphytobenthic organisms that stabilize the surface layer  
15 of sediments. The direct and indirect influences of bioturbators on sediment dynamics depends on the  
16 magnitude of their activity and inherently on their physiological state. Bioturbating organisms are  
17 infected with various parasites that can have a substantial impact on the physiology and behaviour of  
18 their host. However, the knock-on effects of parasites on key ecosystem functions, such as sediment  
19 dynamics, remain poorly studied. Flume experiments were conducted to investigate the indirect  
20 influence of the trematode *Bucephalus minimus* parasitizing the common cockle *Cerastoderma edule*  
21 on the dynamics of sandy sediments enriched and unenriched with microphytobenthos (MPB). By  
22 impacting bed roughness and modulating sediment surface erodability, cockles destabilize sandy  
23 sediments. In sediments unenriched with MPB, there was no influence of parasitism on erosion  
24 process. Indeed, both unparasitized and parasitized organisms interfere with sediment stability in a  
25 similar way. Conversely, parasitism appears to slightly reduce the destabilisation effect of cockles in  
26 MPB-enriched sediments. In the latter, parasitized cockles do not interfere with MPB growth, while  
27 unparasitized organisms constrain the microalgae development. Sandy sediments without cockles  
28 show similar erosion dynamics irrespectively of the presence of MPB. Thus, the lower destabilisation  
29 effect of parasitized cockles is not related to an enhanced stabilisation effect of MPB. Parasitism  
30 reduces the metabolic rate of cockles, suggesting that parasitized cockles may have a lower  
31 bioturbation potential than unparasitized conspecifics. If so, the influence parasitized cockles have on  
32 sediment erodability and sediment roughness may be reduced. The lack of parasitism effect on the  
33 dynamics of MPB-unenriched sediments remains, nonetheless, unclear.

34 **Key words:** Cockle, Parasitism, Bioturbation, Microphytobenthos, Erosion, Roughness, Sediment  
35 erodability

## 36 **1. Introduction**

37 Since the early 1970s, the importance of biotic processes on sediment stability has been widely  
38 acknowledged (see Grabowski et al., 2011; Paterson and Black, 1999; Widdows and Brinsley, 2002  
39 for reviews). In particular, bioturbating species, i.e. macro- and meiofaunal organisms living onto or  
40 within the sediment matrix, greatly impact sediment cohesiveness and thus erodability. Through their  
41 locomotor, feeding, burrowing and ventilating activities, bioturbators induce particles and porewater  
42 transports (Kristensen et al., 2012), with cascading effects on the physical, geomorphological and  
43 biogeochemical properties of sediments (Aller, 1988, 1982; Jones and Jago, 1993; Rhoads and Young,  
44 1970). The activities of bioturbators therefore directly impacts sediments' properties that dictate their  
45 erodability, including sediments' particle size distribution, bulk density or moisture content (Graf and  
46 Rosenberg, 1997; Le Hir et al., 2007; Nowell et al., 1981). By their mere presence, bioturbators can  
47 also affect the sediment bed roughness. Indeed, the protruding of polychaete tubes in the water column  
48 or the presence of bivalve shells at the surface of the sediment bed alters the sediment-water interface  
49 topography, modulating the susceptibility of the bed to hydrodynamic erosive forces (Friedrichs et al.,  
50 2000; Moulin et al., 2007).

51 Along with their direct impact on sediment stability, bioturbators also indirectly influence its  
52 erodability while modulating the growth of microphytobenthic organisms. Microphytobenthos (MPB)  
53 is dominated by diatoms forming biofilms. The framework of these biofilms is created by extracellular  
54 polymeric substances (EPS) that are synthesized and exuded by diatoms. EPS increase the adhesion  
55 between sediment grains (see Stal, 2010 for a review), consequently stabilizing the surficial sediment  
56 layers (Holland et al., 1974; Miller et al., 1996; Paterson, 1989; Sutherland et al., 1998; Yallop et al.,  
57 1994). However, while grazing on MPB, deposit-feeders interfere with the stabilizing role of  
58 microphytobenthic biofilms (Kristensen et al., 2013; Orvain et al., 2004). Bioturbators also exert  
59 intense sediment reworking that negatively affect MPB, biofilms being disrupted and the abundance of  
60 microphytobenthic organisms reduced (Brustolin et al., 2016). Nonetheless, bioturbators can also  
61 stimulate nutrient fluxes on which MPB relies, thereby enhancing its growth and stabilizing effect  
62 (Eriksson et al., 2017; Needham et al., 2011; Swanberg, 1991). Finally, bioturbators can facilitate the  
63 growth of benthic unicellular algae by stabilizing sediments and reducing hydrodynamic stress

64 (Donadi et al., 2013). Complex interactions thus occur between bioturbators and microphytobenthic  
65 organisms, modulating their respective and combine influence on sediment stability (e.g., Brustolin et  
66 al., 2016; Orvain et al., 2014; Swanberg, 1991) and questioning the general view of bioturbators as  
67 bio-destabilisers and microphytobenthic organisms as bio-stabilisers.

68 Various environmental parameters moderate the activity of bioturbators (e.g., Maire et al., 2007;  
69 Ouellette et al., 2004; Pascal et al., 2019) and microphytobenthic organisms (MacIntyre et al., 1996)  
70 that probably modulate the balance between the respective influence of these two groups on sediment  
71 stability. Indeed, wild organisms naturally experience a wide variety of biotic and abiotic stressors that  
72 have interactive effects on their health. Regarding bioturbators, such stressors can affect their  
73 physiology and modulate the magnitude of their activity with consequences on ecosystem functioning  
74 (Dairain et al., 2018; Premo and Tyler, 2013; Przeslawski et al., 2009; Sturdivant et al., 2012).

75 Behavioural modifications could also modulate the effects that bioturbating organisms have on erosion  
76 processes. However, studies assessing the far-reaching consequences of environmental stressors on  
77 sediment stability remain scarce. To our knowledge, only the influence of intra-specific competition  
78 has been quantified by manipulating the density of targeted bioturbating species (e.g., Ciutat et al.,  
79 2007; Harris et al., 2015; Kristensen et al., 2013; Li et al., 2017). For example, through a set of annular  
80 flume experiments Ciutat et al. (2006) highlighted a non-linear density dependent effect of the  
81 common cockle *Cerastoderma edule* on the stability of a muddy sediment. At an intermediate density  
82 (i.e. 141 ind m<sup>-2</sup>) cockles have a higher effect on sediment resuspension than cockles at high density  
83 (i.e. 312 ind m<sup>-2</sup>). Similarly, the critical erosion velocity ( $U_{crit}^*$ , cm s<sup>-1</sup>) was lower for the intermediate  
84 density of cockles than for the highest tested density (Ciutat et al., 2006). This pattern may be related  
85 to an higher mucus production by the highest density of cockles that enhance sediment cohesion  
86 (Ciutat et al., 2006). However, it may also be suggested that intra-specific competition reduces the  
87 individual bioturbation rate of cockles (Duport et al., 2006), modulating the global effect of the  
88 population of cockles on sediment dynamics.

89 Among potential stressors, the influence of parasitism on bioturbators and their activity has been  
90 widely overlooked (Dairain et al., 2019). Parasites are widespread in natural environments (Dobson et  
91 al., 2008), where they greatly contribute to total biomass (Kuris et al., 2008). Parasites also have a



92 wide range of debilitating effects on their bioturbating hosts, including altered growth, behaviour,  
93 fecundity or survival (see Dairain et al., 2019 for a review). The direct effects exerted by parasites on  
94 bioturbators certainly have knock-on effects on their population, thus influencing their role as  
95 ecosystem engineers (Dairain et al., 2019; Thomas et al., 1999). First, through their impact on  
96 fecundity and survival, parasites are key drivers of host abundance and population size structure (de  
97 Montaudouin et al., 2003; Jensen and Mouritsen, 1992). Secondly, parasites likely modify phenotypic  
98 traits of bioturbators involved in their functional role, the so-called trait-mediated effects (Mouritsen  
99 and Poulin, 2002; Preston et al., 2016). For instance, trematode parasites commonly infect the mud  
100 snail *Peringia ulvae* (e.g., de Montaudouin et al., 2003; Thieltges et al., 2006). Trematodes have a  
101 wide range of adverse effects on their gastropod host, of which they significantly reduce the mud  
102 snail's mobility (Mouritsen and Jensen, 1994). The mud snail *P. ulvae* greatly affects sediment  
103 stability. By crawling at the sediment surface and producing faecal pellets and pseudofaeces, mud  
104 snails produce a biogenic "fluff layer" that is easily erodible (Andersen, 2001; Austen et al., 1999;  
105 Orvain et al., 2006, 2003). As a deposit-feeder, *P. ulvae* also grazes on MPB, which could interfere  
106 with the stabilizing effect of microalgae (Austen et al., 1999; Orvain et al., 2004). Over a large field  
107 study, Mouritsen and Haun (2008) investigated the impact of trematode-uninfected and infected  
108 populations of *P. ulvae* on sediment characteristics, MPB community structure and macrozoobenthic  
109 assemblage. While they did not report any significant impact of parasitism on sediment characteristics  
110 (e.g., organic content, median particle size), they highlighted that parasitized mud snails were  
111 associated with a significant decrease of the chlorophyll *a* content in the sediment and changes in the  
112 diatom community structure. The authors suggested that parasites decrease the sediment disturbance  
113 exerted by mud snails while reducing their mobility. Therefore, parasites may indirectly interfere with  
114 the release of nutrients mediated by bioturbation processes, leading to a decline in the MPB biomass.  
115 Considering the intricate link between MPB and sediment stability (see above), parasites may  
116 ultimately affect erosion processes.

117 To date, trait-mediated effects of parasites on their bioturbating host have been poorly studied (see  
118 Dairain et al., 2019 for a review) and their consequences on sediment stability have never been  
119 quantified. Considering the ubiquity of parasites in natural environment, their deleterious effect on the

120 physiology of their bioturbating hosts and their potential impacts on the behaviour of bioturbators, a  
121 better understanding of the role of parasites in sediment stability processes is crucial. Such studies may  
122 also allow to improve the modelling of sediment transport. This study therefore aims at evaluating the  
123 indirect influence of parasitism on sediment stability processes, focusing on a widespread bioturbator  
124 in intertidal areas of the Northern hemisphere, the common edible cockle *Cerastoderma edule*.

## 125 **2. Materials and methods**

### 126 **2.1. The host-parasite association**

127 This study focuses on the *Cerastoderma edule* (Bivalvia: Cardiidae) – *Bucephalus minimus*  
128 (Trematoda: Bucephalidae) host-parasite system.

129 The common edible cockle *C. edule* is a suspension-feeding bivalve widespread in semi-sheltered  
130 areas from the Barents Sea to West African lagoons (Bazaïri et al., 2003; Hayward and Ryland, 1995;  
131 Honkoop et al., 2008) where it can be dominant with respect to abundance and biomass (Beukema  
132 1976, Rakotomalala et al. 2015). In addition to its high economic value, *C. edule* plays a key role in  
133 ecosystem functioning, first as an important food resource for birds and benthic invertebrates (see  
134 Malham et al., 2012 for a review), and secondly as an ecosystem engineer species, mainly through its  
135 bioturbation activity. Indeed, while burrowing, migrating in the sediment column and crawling at the  
136 sediment surface *C. edule* generates particles transport (Flach, 1996; Mermillod-Blondin et al., 2004)  
137 and modifies the sediment matrix (Montserrat et al., 2009). The bioturbation generated by cockles  
138 greatly affects the sediment surface stability, with cockles mainly enhancing the erodability of the  
139 surface of cohesive sediments (Ciutat et al., 2007, 2006; Li et al., 2017; Neumeier et al., 2006). Some  
140 studies also showed that cockles could also enhance the stabilisation of sandy substrates by promoting  
141 biodeposition and increasing the sediment silt content (Soissons et al., 2019).

142 Cockles *C. edule* harbour a wide variety of pathogens and diseases (see de Montaudouin et al. 2009  
143 and Longshaw & Malham 2013 for reviews). Among them, digenean trematodes constitute the  
144 dominant group with at least 16 species parasitizing *C. edule* (de Montaudouin et al., 2009). Digenean  
145 trematodes display a complex life cycle, i.e. involving multiple hosts. Vertebrates serve as definitive  
146 hosts in which the parasites sexually reproduce. Trematode eggs are then released with faeces, hatch,  
147 and develop into a miracidium larvae which usually infects gastropods and, to a lesser extent, bivalves  
148 as first intermediate hosts. In these hosts, parasites multiply asexually in sporocysts/rediae, which  
149 produce a large number of parasitic clones, the so-called cercariae. The latter are shed into the  
150 environment and disperse through the water column before infecting a second intermediate host, either  
151 fish or invertebrates like bivalves or crustaceans, depending on the species. In these hosts the

152 trematodes develop into metacercariae and await ingestion by their definitive hosts (see Ginetsinskaya  
153 1988 for details on trematode life cycle). Cockles generally act as second intermediate host for  
154 digeneans. Nonetheless, three species of digeneans use cockles as first intermediate host, of which is  
155 *B. minimus* (de Montaudouin et al., 2009). The trematode *B. minimus* primarily infects the digestive  
156 gland and gonads of cockles where it gradually replaces the host's tissues. While asexually  
157 multiplying in cockles, *B. minimus* progressively invades the whole organisms (Magalhães et al., 2015  
158 and references therein). *B. minimus* has various adverse effects on cockles. The trematode is  
159 fundamentally damaging for the fecundity of cockles. It also causes histological lesions in the  
160 digestive gland of cockles, disturbing the functioning of this organs and altering the physiological state  
161 of cockles (Longshaw and Malham, 2013; Magalhães et al., 2015 and references therein). Finally, *B.*  
162 *minimus* could also alter the behaviour of cockles, that tend to migrate towards the sediment surface  
163 (Desclaux et al., 2002). Prevalences of *B. minimus* (i.e. percentage of infected host) in wild  
164 populations of *C. edule* are generally low. Nonetheless, the parasite prevalences can locally (and at  
165 certain time) reach high values (de Montaudouin et al., 2009; Magalhães et al., 2015) that are  
166 correlated with massive mortality events (Jonsson and Andé, 1992).

## 167 **2.2. Sampling of *Cerastoderma edule* and identification of cockles infected by *Bucephalus*** 168 ***minimus***

169 Cockles were collected by hand in March 2019 in Banc d'Arguin and in La Hume, two sandy areas  
170 in Arcachon Bay (44°42'N, 1°09'W), France, where prevalences of *Bucephalus minimus* are relatively  
171 high (ca. 10 %). Back in the laboratory, cockles were individually placed in plastic containers filled  
172 with seawater from Arcachon Bay in order to identified cockles uninfected and infected by *B. minimus*  
173 *via* cercariae emission. The seawater of containers was maintained at ca. 15–16°C for 24h. After this  
174 time, each container was placed under a stereomicroscope to detect the emission of cercariae of *B.*  
175 *minimus*. Once identified as uninfected or infected with *B. minimus*, cockles were maintained in a  
176 seawater open-circuit pending the experimentations.

## 177 **2.3. Sampling of sediment**

178 Cohesive and non-cohesive sediments were collected in Baie des Veys, (49°21'N, 1°08'W), and in  
179 Banc d'Arguin, (49°35'N, 1°14'W), France, respectively. The sediments were firstly dry-sieved  
180 through a 2 mm mesh to retain macrofauna and debris. Then a mixture of cohesive and non-cohesive  
181 sediment was prepared and kept several days in the dark before being introduced in experimental plots  
182 (see below). The sediment mixture finally consisted of slightly muddy-sand (sand = 95.4 %, mud = 4.4  
183 %, gravel = 0.2 % and  $D_{50} = 287.5 \mu\text{m}$ ).

#### 184 **2.4. Microphytobenthos culture**

185 Microphytobenthos biofilms (MPB) were collected on a mudflat in Baie des Veys by scratching the  
186 sediment surface. A MPB inoculum was then prepared by mixing biofilms collected in the field with  
187 the muddy-sand mixture (see above). The inoculum was placed under an 18:6 h dark-light cycle (light  
188 intensity =  $114 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) for at least 3 days in order to stimulate the growth of MPB  
189 before adding the inoculum to the sediment surface of experimental plots (see below).

#### 190 **2.5. Experimental design and setup**

191 Erosion experiments were conducted in March–April 2019. We tested for the separate and combined  
192 influence of cockles parasitized and unparasitized with *B. minimus* (“Cockle” factor) and MPB  
193 enrichment (“MPB” factor) on sediment stability. The “Cockle” factor encompassed three levels: no  
194 cockles (“Control”), presence of unparasitized cockles (“Unparasitized”) and presence of parasitized  
195 cockles (“Parasitized”) in experimental plots. There were two levels for the “MPB” factor:  
196 experimental plots were enriched with MPB or not enriched with MPB (“With MPB” and “Without  
197 MPB”, respectively). By combining these two factors, the experiment consisted of six treatments: (1)  
198 no cockles in sediment plots unenriched with MPB (“Control” - “Without MPB”), (2) no cockles in  
199 sediment plots enriched with MPB (“Control” - “With MPB”), (3) presence of unparasitized cockles in  
200 sediment plots unenriched with MPB (“Unparasitized” - “Without MPB”), (4) presence of  
201 unparasitized cockles in sediment plots enriched with MPB (“Unparasitized” - “With MPB”), (5)  
202 presence of parasitized cockles in sediment plots unenriched with MPB (“Parasitized” - “Without

203 MPB”), and (6) presence of parasitized cockles in sediment plots enriched with MPB (“Parasitized” -  
204 “With MPB”). Each treatment was replicated three times.

205 Experimental plots consisted of PVC tubes (internal diameter = 9.4 cm, height = 22 cm). Each  
206 experiment lasted 9 days (8 days for the “Control” experimental treatment, see below). On day 1  
207 experimental plots were filled with the slightly muddy-sand sediment mixture (sediment column of 21  
208 cm). On day 2, two unparasitized or parasitized cockles of similar size (total length = 22.6–27.8 mm)  
209 were added in each experimental plot (density of cockles = 288 ind. m<sup>-2</sup>). Then, experimental plots  
210 were placed in a semi-diurnal mesocosm with one diurnal emersion phase. On day 3, a 1-cm layer of  
211 sediment unenriched or enriched with MPB was added to the surface of sediment cores. From day 2 to  
212 day 9, an 18:6 h night-day alternation regime was applied using cool white lamps (light intensity = 114  
213  $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ ). The day phase corresponded to the diurnal emersion phase. Erosion experiments  
214 were conducted on day 9, corresponding to a MPB growth period of 6 days. The experiments lasted 8  
215 days for treatments without cockles (“Control”), the 1-cm layer of sediment unenriched or enriched  
216 with MPB being added on day 2 and the erosion experiment performed on day 8. Air-bubbling  
217 systems were added in the semi-diurnal mesocosm to maintain a fully oxygenated water. Daily, ca. 10  
218 % of the mesocosm total seawater volume was renewed. Over the incubation period, the seawater  
219 temperature averaged  $12.0 \pm 0.4$  °C and the salinity  $31.7 \pm 0.7$  (mean  $\pm$  SD).

## 220 **2.6. Microphytobenthos photosynthetic parameters**

221 At the end of the 6-day incubation period, and before erosion experiment, the superficial MPB  
222 chlorophyll *a* fluorescence in each experimental plot was measured using a Pulse Amplitude  
223 Modulated (PAM) fluorimeter (IMAGING-PAM *M-series*, Walz). Experimental plots were placed in  
224 the dark for ca. 5 min before a low frequency light was applied, allowing to determine the minimal  
225 level of fluorescence  $F_0$ . A saturating light pulse was then applied to determine the maximum  
226 fluorescence  $F_m$ . Finally, increasing actinic light pulses (nine 30-second steps from 0 to 701  $\mu\text{mol}$   
227  $\text{photons m}^{-2} \text{ s}^{-1}$ ) were applied. Steady state fluorescence ( $F_s$ ), maximal fluorescence ( $F_m'$ ) and effective  
228 quantum yield of the photosystem II (“yield”) were determined at each step:

$$yield = \frac{(F_m' - F_m)}{F_m'}$$

229  $F_0$  was used to estimate the photosynthetically active chlorophyll *a* biomass (referred later as  
 230 “Chlorophyll *a* biomass”; mg Chl *a* m<sup>-2</sup>) within the sediment photic layer using the standard curve:  
 231 *Chlorophyll a biomass* = 12.142  $F_0$  - 0.2012. The thickness of the sediment photic layer was ca. 200  
 232  $\mu$ m (Morelle et al., 2018). Thus we quantified chlorophyll *a* biomasses at the microscale and the  
 233 values obtained remain low as compared to MPB biomasses usually determined in the first cm of the  
 234 sediment column (i.e. usually > 100 mg m<sup>-2</sup>). Nonetheless, the relative comparisons of chlorophyll *a*  
 235 biomasses based on  $F_0$  are a good proxy to evaluate the potential productive chlorophyll *a* stock and  
 236 MPB growth performances in the sediment photic layer.

## 237 **2.7. Erosion procedure**

238 Erosion experiments were performed using the “Erodimetre” erosion flume described by Guizien et  
 239 al. (2012). The Erodimetre is a recirculating straight flume (length= 1.2 m long, width = 0.08 m,  
 240 height = 0.02 m) in which a unidirectional flow is generated by a pump. One sediment core was  
 241 sampled in each experimental plot using a sample carrier and then inserted into the flume with the  
 242 sediment surface flushing at the bottom of the Erodimetre. The flume was then carefully filled with  
 243 seawater before a current flow was applied. A frequency device associated to the recirculating water  
 244 pump was used to gradually increase the current speed from 0 to 20–30 Hz (i.e., current flow from 0  
 245 up to ca. 72.5 cm s<sup>-1</sup>) in 15 to 20 steps (increment of 1 Hz from 0 to 10 Hz and of 2 Hz from 10 to  
 246 maximum 30 Hz). Each step lasted 5 min.

247 The flow discharge was monitored using an electromagnetic flowmeter (Promag 10P,  
 248 Endress+Hauser). A multiprobe (DS5, Hydrolab) with turbidity and fluorescence sensors allowed to  
 249 continuously record the turbidity and to estimate the quantity of chlorophyll *a* in the water. Calibration  
 250 curves allowed for the calculation of the concentrations of suspended particulate matter (“suspended  
 251 matter”; g L<sup>-1</sup>) and chlorophyll *a* ( $\mu$ g L<sup>-1</sup>) in the water column ( $y = 0.026 x$ ,  $R^2 = 0.998$  and  $y = 0.0128$   
 252  $x^2 + 0.749 x$ ;  $R^2 = 0.998$  for suspended matter and chlorophyll *a*, respectively). A trap downstream the  
 253 sediment sample also allowed to measure the erosion of sandy particles. The total volume of the sand

254 trap is 17.7 cm<sup>3</sup>; erosion experiments were shortening if the sand trap was fulfilled before 30 Hz (i.e.  
255 current speed = ca. 72.5 cm s<sup>-1</sup>). The pressure upstream and downstream the sediment sample was  
256 finally recorded using a pressure sensor (deltabar P70, Endress+Hauser).

257 Bed shear stress ( $\tau$ , Pa) were determined for each sample following Guizien et al. (2012). Briefly, the  
258 head loss between the upstream and downstream parts of a smooth section in the flume tunnel was  
259 used to derive the averaged bed shear stress over rough sediment samples ( $\tau_0$ , Pa). Thus, bed shear  
260 stresses determined in this study take into account the bed deformation and the presence of physical  
261 objects that could protrude at the sediment-water interface, such as shell of cockles. Accordingly,  
262 shear velocities  $U^*$  (m s<sup>-1</sup>) were calculated as follows:

$$U^* = \sqrt{\tau_0/\rho}$$

263 with  $\tau_0$  the bed shear stress (Pa) and  $\rho$  the seawater volumetric mass density (1033 kg m<sup>-3</sup>).

264 The “law of the wall” was used to estimate the roughness length  $z_0$ (cm) for each sample:

$$U(z) = \frac{U^*}{k} \ln\left(\frac{z}{z_0}\right)$$

265 with  $k$  the von Karman’s constant ( $k = 0.41$ ). To this end, the relationship between the depth-averaged  
266 current velocity and the shear velocity was estimated using a simple linear regression. The relationship  
267 between these two variables can deviate from linearity because of the deformation of the sediment  
268 surface at high current flows and/or movements of cockles. Therefore, linear regressions were used on  
269 reduced ranges of current flows, only encompassing the linear part of the curve, i.e. when the bed  
270 topography was not yet deformed by ongoing erosion processes. The linear regression slope  
271 determined for each sample allowed to integrate the ‘law of the wall’ as follows:

$$\bar{U} = \frac{U^*}{k} \ln\left(\frac{h}{e(1) z_0}\right)$$

272

273 with  $h$  the height of the Erodimetre tunnel ( $h = 2$  cm).

274 Critical erosion thresholds for the chlorophyll  $a$  of biofilms of MPB and the sandy fraction of the  
275 sediment column were determined as the intercept of the best linear regression of chlorophyll  $a$   
276 concentration in the water column and sand volume, respectively, against  $\log(U^*+1)$ :



$$y = a \log(U^* + 1) + b$$

$$U_{crit}^* = 10^{(y-b)/a} - 1$$

277 with  $U_{crit}^*$  the critical shear velocity for erosion ( $\text{m s}^{-1}$ ),  $y$  the chlorophyll  $a$  concentration in the water  
278 column ( $\mu\text{g L}^{-1}$ ) or the volume of sand eroded ( $\text{m}^3$ ). Then, the critical bed shear stress for the  
279 chlorophyll  $a$  of the MPB biofilm and the sandy fraction of the sediment column were calculated as  
280 follows:

$$\tau_{crit} = \rho U_{crit}^{*2}$$

281 Regarding the muddy fraction of the sediment column, it was possible to discriminate the erosion of  
282 the biogenic fluff layer from the erosion of the sediment bed. Therefore, both critical erosion  
283 thresholds of the biogenic fluff layer and of the sediment bed were determined, following the  
284 procedure described above.

285 Finally, mean erosion rates of the MPB biofilm, muddy fraction and sandy fraction at the sediment-  
286 water interface were calculated over the three steps following the critical erosion incipient point taking  
287 into account the volume of the Erodimetre and the surface of the sediment sample. Regarding the  
288 muddy fraction, only fluxes following the erosion of the biogenic fluff layer were calculated. The  
289 software Matlab (v. 2019a, MathWorks) was used.

## 290 **2.8. Dissection of cockles**

291 Following the erosion experiment, cockles were placed in a seawater open-circuit for 24 h before  
292 being dissected to check for their parasitic status. First, the shell length of cockles was measured using  
293 a digital calliper. The shell was then opened by cutting the posterior adductor muscle, all soft tissues  
294 were extracted and squeezed between two transparent glass plates under stereomicroscope to check for  
295 infection with *B. minimus*. Then, soft tissues were dried (at least 48 h at 60 °C) and weight (dry  
296 weight, DW). DW were used to calculate individual metabolic rate following Brey (2010). Finally,  
297 population metabolic rates were estimated taking into account the density of cockles in experimental  
298 plots (density = 288 ind.  $\text{m}^{-2}$ ) (Cozzoli et al., 2018).

## 299 2.9. Statistical analyses

300 A Student t-test was used to assess the difference in individual metabolic rates standardized for shell  
301 length between unparasitized and parasitized cockles.

302 The influences of cockles (“Control”, i.e. no cockles, “Unparasitized”, i.e. presence of unparasitized  
303 cockles and “Parasitized”, i.e. presence of parasitized cockles) and MPB enrichment (“Without MPB”,  
304 i.e. unenriched with MPB or “With MPB”, i.e. enriched with MPB) on (1) growth of the MPB at the  
305 sediment surface of experimental plots following the 6-day incubation period, (2) critical bed shear  
306 stresses ( $\tau_{crit}$ ) of the different sediment fraction (chlorophyll *a*, muddy fraction and sandy fraction) and  
307 (3) fluxes of chlorophyll *a*, muddy particles (suspended matter) and sand at the sediment-water  
308 interface during erosion experiments were assessed using a PERmutational Multivariate ANalyses Of  
309 VARIANCES (PERMANOVA) (Anderson, 2001; McArdle and Anderson, 2001) without data  
310 transformation. The design consisted of two factors, namely “Cockles” (3 levels: “Control”,  
311 “Unparasitized”, “Parasitized”) and “MPB” (2 levels: “Without MPB” and “With MPB”). The  
312 PERMDISP procedure was used to test for the separate and combined effects of the two factors on  
313 dispersion (i.e. among-replicate variability) (Anderson, 2006).

314 Analyses of covariance (ANCOVA) were also used to investigate potential differences in the  
315 relationships between the metabolic rate of cockle populations and (1) the growth of MPB at the  
316 sediment-water interface, (2) the critical bed shear stresses ( $\tau_{crit}$ ) of the different sediment fraction  
317 (chlorophyll *a*, muddy and sandy fractions) and (3) the fluxes of chlorophyll *a*, muddy particles  
318 (suspended matter) and sand at the sediment-water interface during erosion experiments with MPB  
319 occurrence.

320 Shapiro and Levene tests were used to check for the normality of the data and homogeneity of the  
321 variances, respectively. Differences were considered significant with  $p < 0.05$ . All statistics were  
322 performed using the statistical software R (R Core Team, 2019).

### 323 **3. Results**

324 Dissections showed that one of the two cockles in one of the “Unparasitized” - “Without MPB”  
325 treatment was infected with the parasite *Bucephalus minimus*. Even though the infection was not  
326 widespread in the cockle tissues and of very low severity (only a very few sporocysts were observed,  
327 A.D. personal obs.), this replicate was excluded from our analyses. Therefore, there were only two  
328 replicates for the “Unparasitized” - “Without MPB” treatment while there were three replicates for the  
329 others.

#### 330 **3.1. Metabolic rates of cockles**

331 Individual metabolic rates of unparasitized and parasitized of cockles were  $0.22 \pm 0.01$  and  $0.16 \pm$   
332  $0.02$  mW (mean  $\pm$  SE), respectively. Parasitized cockles showed significantly lower individual  
333 metabolic rates as compared with unparasitized individuals when standardized for shell length (t-test,  $t$   
334  $= 2.40$ ,  $p < 0.05$ ). In averaged, parasitized cockles were 29.2 % lighter than unparasitized organisms  
335 when standardized for shell length.

#### 336 **3.2. Microphytobenthos growth**

##### 337 *3.2.1. Biomass of chlorophyll a*

338 Following the 6-day incubation period, chlorophyll *a* biomasses ranged between 0.17–0.42 and  
339 0.79–1.17 mg m<sup>-2</sup> in the sediment photic layers of experimental plots unenriched and enriched with  
340 MPB, respectively (Fig 1A). Biomasses of chlorophyll *a* at the sediment-water interface of  
341 experimental plots enriched with MPB were significantly higher than in experimental plots unenriched  
342 with MPB (Fig 1A, Table 1). Unparasitized cockles significantly reduced the chlorophyll *a* biomass as  
343 compared to biomasses in experimental plots without cockles. Conversely, there was no significant  
344 difference in chlorophyll *a* biomasses between “Control” and “Parasitized” (Fig. 1A, Table 1). Finally,  
345 there was no significant interaction between the “Cockle” and “MPB” factors on the chlorophyll *a*  
346 biomass (Table 1).

347 The chlorophyll *a* biomass at the sediment surface of experimental plots significantly decreased with  
348 the increase of the metabolic rate of cockle populations (Fig. 1A; ANCOVA,  $F = -4.4$ ,  $p < 0.01$ ). The  
349 slope of the relationship between both variables did not vary with MPB enrichment (“Without MBP”  
350 vs “With MPB”; ANCOVA,  $p = 0.91$ ).

### 351 3.2.2. *Effective quantum yield of the photosystem II*

352 Effective quantum yields of the photosystem II (PSII) ranged between 0.31–0.45 and 0.46–0.51 at  
353 the sediment-water interface of experimental plots unenriched and enriched with MPB, respectively  
354 (Fig 1B). Effective quantum yields of the PSII were significantly lower in experimental plots  
355 unenriched with MPB as compared to experimental plots enriched with MPB (Table 1). On the  
356 opposite, there was no significant influence of the “Cockle” factor on the effective quantum yield of  
357 the PSII and no interactive effects between both “Cockle” and “MPB” factors (Fig. 1B, Table 1).

358 The effective quantum yield of the PSII significantly decreased with the increase of the metabolic rate  
359 of cockle populations (Fig. 1B; ANCOVA,  $F = -4.4$ ,  $p < 0.01$ ). The slope of the relationship between  
360 these two variables did not significantly varied with MPB enrichment (“Without MBP” vs “With  
361 MPB”) (ANCOVA,  $p = 0.08$ ).

### 362 3.3. Shear velocity dynamics

363 The influence of cockles *C. edule* on the dynamics of shear velocity ( $U^*$ ,  $\text{cm s}^{-1}$ ) at the sediment-  
364 water interface of experimental plots as a function of the current flow is shown in Fig. 2.  $U^*$  ranged  
365 between 0.3–16.0 and 0–14.8  $\text{cm s}^{-1}$  at the sediment surface of experimental plots unenriched and  
366 enriched with MPB, respectively (Fig. 2). Overall,  $U^*$  increased with the current flow. For some  
367 samples, we observed a decrease of  $U^*$  at high current flows that evidenced modifications of the bed  
368 topography (and thus roughness) with the ongoing erosion.

369 In more details, without MPB and without cockles (“Without MPB” - “Control”),  $U^*$  slightly  
370 decreased from ca. 3.3  $\text{cm s}^{-1}$  to ca 2.0  $\text{cm s}^{-1}$  with the current flow increasing up 17.5  $\text{cm s}^{-1}$ . Then, it  
371 linearly increased up to ca. 5.1  $\text{cm s}^{-1}$ . This maximal  $U^*$  was attained for a current flow of ca. 50  $\text{cm s}^{-1}$ .  
372 Finally,  $U^*$  decreased and attained ca. 4.5  $\text{cm s}^{-1}$  at the end of the erosion experiment (maximal

373 current flow = 62 cm s<sup>-1</sup>) (Fig. 2). U\* dynamics at the surface of experimental plots with MPB and  
374 without cockles (“With MPB” - “Control”) was very similar to this latter pattern. However, there was  
375 no decrease of U\* at the highest current flows, that reached a stable value from a current flow of ca. 50  
376 cm s<sup>-1</sup> (Fig. 2). For the two “Control” treatments (i.e., without and with MPB), there was a low  
377 variability between the replicates.

378 Without MPB and with unparasitized cockles (“Without MPB” - “Unparasitized”), U\* slightly  
379 decreased from ca. 1.2 to 0.66 cm s<sup>-1</sup> with the current flow increasing from ca. 0.6 to 8.1 cm s<sup>-1</sup>. Then,  
380 U\* increased up to ca. 5.1 cm s<sup>-1</sup> (current flow = ca. 44.7 cm s<sup>-1</sup>). Overall, a similar pattern was  
381 observed at the surface of experimental plots with MPB and unparasitized cockles (“With MPB” -  
382 “Unparasitized”). Nonetheless, there was a high variability between the replicates. In particular, for  
383 one of them much higher values of U\* were recorded above a current flow of ca. 20.6 cm s<sup>-1</sup> as  
384 compared to those observed for the two other replicates (Fig. 2). For this replicate, U\* attained 14.1  
385 cm s<sup>-1</sup> (current flow = 48.1 cm s<sup>-1</sup>) at the end of the erosion experiment, while it attained 6.4 cm s<sup>-1</sup> for  
386 the two other ones.

387 Without MPB and with parasitized cockles (“Without MPB” - “Parasitized”), U\* slightly decreased  
388 from ca. 1.2 to 0.31 cm s<sup>-1</sup> with the current flow increasing from ca. 0.6 to 3.1 cm s<sup>-1</sup>. Then, U\*  
389 increased up to ca. 6.2 cm s<sup>-1</sup> (current flow = ca. 44.7 cm s<sup>-1</sup>). There was great variability between  
390 replicates. For one of the replicates, much higher values of U\* were recorded above a current flow of  
391 ca. 20.6 cm s<sup>-1</sup> as compared with the two other replicates (Fig. 2). For this replicate, U\* attained 16.0  
392 cm s<sup>-1</sup> (current flow = 42.5 cm s<sup>-1</sup>) at the end of the erosion experiment, while it attained ca. 5.8 cm s<sup>-1</sup>  
393 for the two others. On the other hand, there was a low variability in the dynamics of the U\* at the  
394 sediment surface of experimental plots with MPB and parasitized cockles (“With MPB” -  
395 “Parasitized”). In the latter case, U\* decreased from ca. 0.99 to 0.62 cm s<sup>-1</sup> with the current flow  
396 increasing from ca. 0.6 to 8.4 cm s<sup>-1</sup>. Then, it increased up to ca. 5.5 cm s<sup>-1</sup> (current flow = ca. 44.4 cm  
397 s<sup>-1</sup>).

398 Therefore, there was no influence of MPB enrichment or cockles on the U\* dynamics. The presence of  
399 the bivalve increased U\* (higher values of U\* as compared with “Control” experimental treatments).  
400 There was no influence of parasitism on U\* dynamics independently of the MPB enrichment.

401 However, there was an interactive effect between parasitism and MPB enrichment on  $U^*$ . In  
402 experimental plots unenriched MPB,  $U^*$  were higher for “Parasitized” than for “Unparasitized”. The  
403 opposite trend was noticed in experimental plots enriched with MPB.

404 The roughness length  $z_0$  was determined for each sample by focusing on the linear part of the  
405 relationship between the shear velocity  $U^*$  and the current flow (Fig. 2). Roughness lengths  $z_0$  ranged  
406 between 0.064–0.31 and 0.020–0.19 cm for experimental plots unenriched and enriched with MPB,  
407 respectively (Fig. 3). There was no significant effect of “Cockle” and “MPB” factors alone on  $z_0$  and  
408 no interactive effect (Fig. 3, Table 1). The roughness length  $z_0$  significantly increased with the increase  
409 of the metabolic rate of cockle populations (Fig. 3; ANCOVA,  $F = 3.1$ ,  $p < 0.01$ ). The slope of the  
410 relationship between both variables did not vary with the MPB enrichment (“Without MPB” vs “With  
411 MPB”) (ANCOVA,  $p = 0.20$ ).

### 412 **3.4. Sediment resuspension dynamics and erodability**

413 The erosion potential of unparasitized and parasitized cockles and the influence of MPB on sediment  
414 stability was measured in terms of suspended sediment concentration (chlorophyll *a* of MPB biofilms,  
415 muddy fraction and sandy fraction were differentiated) and critical bed shear stress for erosion ( $\tau_{crit}$ ,  
416 Pa). Fig. 4 illustrates the dynamics of sediment resuspension for the different fractions of the surface  
417 layers of the sediment column with the increasing current flow.

#### 418 *3.4.1. Mud fraction*

419 The concentration of suspended matter in the water column was recorded as a proxy of the erosion  
420 of the muddy fraction of the surface layers of the sediment column. Overall, the concentration of  
421 suspended matter exponentially increased as a function of the increasing current flow (Fig. 4A). We  
422 firstly observed the erosion of a biogenic fluff layer at low current velocity. It was followed by bed  
423 erosion (i.e., mass erosion) at the highest current velocities. Biofilms of MPB did not influence the  
424 kinetics of the erosion of the muddy fraction (Fig. 4A). Cockles destabilized sediment plots, that is the  
425 muddy fraction of the sediment column was eroded at lower current velocity (ca. 13 to 28  $\text{cm s}^{-1}$ ) as  
426 compared to the “Control” treatment (ca. 32 to 47  $\text{cm s}^{-1}$ ) (Fig. 4A). Without MPB, the parasite *B.*

427 *minimus* did not influence the erosion kinetics of fine particles. Conversely, with MPB, parasitism  
428 seemed to delay the erosion of these particles, erosion occurring at slightly higher current flow as  
429 compared with the “Unparasitized” treatment (Fig. 4A).

#### 430 3.4.2. Chlorophyll *a* fraction

431 The concentration of chlorophyll *a* in the water column over time was monitored as a proxy of the  
432 erosion of the biofilms of MPB.

433 Chlorophyll *a* concentrations in the water column of experimental plots unenriched and enriched with  
434 MPB ranged 5.7–9.7 and 6.1–15.1 mg m<sup>-2</sup>, respectively (Fig. 4B). The different experimental  
435 treatments showed similar erosion kinetics for chlorophyll *a*, that is the chlorophyll *a* concentration  
436 firstly decreased with the current flow. Above a flow ranging 25–45 cm s<sup>-1</sup>, there was an increase of  
437 the concentration of chlorophyll *a* with the increase of the current flow (Fig. 4B). The current flow  
438 from which there was an increase in the chlorophyll *a* concentration varied between experimental  
439 treatments. In particular, erosion of chlorophyll *a* was initiated for a lower current flow when cockles  
440 inhabited sediment plots. There were no effect of parasitism and MPB on the erosion kinetics of  
441 chlorophyll *a* (Fig. 4B).

#### 442 3.4.3. Sand fraction

443 Fig. 4C illustrates the thickness of sand eroded during erosion experiments. The thickness of sand  
444 eroded exponentially increased as a function of the increasing current flow for the different  
445 experimental treatments. Sandy particles were eroded at lower current flow when sediments were  
446 inhabited by cockles. In contrasts, there was no influence of MPB on the erosion kinetics of sandy  
447 particles. Without MPB, the parasite *B. minimus* did not influence the resuspension dynamics of the  
448 sandy fraction whereas parasitism delayed its erosion in MPB-enriched sediment plots. Indeed, erosion  
449 of sand occurred at higher current flow for the “Parasitized” treatment as compared with the  
450 “Unparasitized” one.

### 451 3.5. Critical bed shear stress

#### 452 3.5.1. Mud fraction

453 Regarding the muddy fraction, we discriminated the erosion of the biogenic fluff layer from the  
454 sediment bed erosion and therefore determined the critical erosion threshold for both of them (Fig. 5).  
455 Critical bed shear stresses ( $\tau_{crit}$ ) for the biogenic fluff layer ranged between 0.46–2.83 and 0.31–2.41  
456 Pa in experimental plots unenriched and enriched with MPB, respectively (Fig. 5). There was no  
457 significant influence of “Cockle” and “MPB” factors, and no interactive effect between them on  $\tau_{crit}$   
458 for the biogenic fluff layer (Table 1).  $\tau_{crit}$  significantly decreased with the increase of the metabolic rate  
459 of cockle populations (ANCOVA,  $F = -2.3$ ,  $p < 0.05$ ). This relationship was not influenced by the  
460 MPB enrichment (ANCOVA,  $p = 0.86$ ).  
461  $\tau_{crit}$  for the sediment bed ranged between 1.51–3.00 and 1.46–3.58 Pa for experimental plots  
462 unenriched and enriched with MPB, respectively (Fig. 5). Cockles significantly lowered  $\tau_{crit}$  for the  
463 sediment bed as compared to those determined for experimental plots without cockles (Table 1). There  
464 was no significant influence of “MPB” and no interactive effect between “Cockle” and “MPB” factors  
465 on  $\tau_{crit}$  for the sediment bed (Table 1).  $\tau_{crit}$  for the sediment bed significantly decreased with the  
466 increase of the metabolic rate of cockle populations (Fig. 5; ANCOVA,  $F = -5.49$ ,  $p < 0.01$ ). The  
467 enrichment with MPB did not significantly modify this relationship (Fig. 5; ANCOVA,  $p = 0.33$ ).

#### 468 3.5.2. *Chlorophyll a fraction*

469 Critical bed shear stresses ( $\tau_{crit}$ ) for the chlorophyll *a* of MPB biofilms ranged between 0.69–14.8  
470 and 0.77–2.66 Pa in experimental plots unenriched and enriched with MPB, respectively (Fig. 6).  
471 There were no significant effects of “Cockle” and “MPB” factors on  $\tau_{crit}$ , and no interactive effect  
472 between both of them (Table 1). There was no significant relationship between  $\tau_{crit}$  and the metabolic  
473 rate of cockle populations (Fig. 6; ANCOVA,  $p = 0.23$ ).

#### 474 3.5.3. *Sand fraction*

475 Critical bed shear stresses ( $\tau_{crit}$ ) for the sandy fraction of the sediment ranged between 0.46–2.33 and  
476 0.78–2.45 Pa in experimental plots unenriched and enriched with MPB, respectively (Fig. 6).  
477 Unparasitized and parasitized cockles significantly decreased  $\tau_{crit}$  as compared with experimental plots  
478 without cockles (Fig. 6, Table 1). Conversely, MPB enrichment did not influence  $\tau_{crit}$  (Table 1). There



479 was an interactive effect between “Cockle” and “MPB” factors on  $\tau_{\text{crit}}$  (Table 1). However pairwise  
480 comparisons did not evidence significant differences between entities.  $\tau_{\text{crit}}$  also significantly decreased  
481 with the increase in the metabolic rate of cockle populations (Fig.6; ANCOVA,  $F = -3.0$ ,  $p < 0.01$ ).  
482 This relationship was not affected by the enrichment with MPB (Fig. 6; ANCOVA,  $p = 0.053$ ).

### 483 3.6. Sediment erosion fluxes

#### 484 3.6.1. *Mud fraction*

485 Erosion fluxes of fine particles (mud fraction, “suspended matter”) at the sediment-water interface  
486 of experimental plots unenriched and enriched with MPB ranged between 0–0.26 and 0–0.23  $\text{g m}^{-2} \text{s}^{-1}$ ,  
487 respectively (Fig. 7). There were no significant effects of “Cockle” and “MPB” factors, and no  
488 interactive effect between them on fluxes of fine particles (Table 3). Erosion fluxes of fines particles at  
489 the sediment-water interface did not vary with the metabolic rate of cockle populations, independently  
490 of the enrichment with MPB (Fig 8; ANCOVA,  $p = 0.60$ ).

#### 491 3.6.2. *Chlorophyll a fraction*

492 Fluxes of chlorophyll *a* at the sediment-water interface of experimental plots unenriched and  
493 enriched with MPB ranged between 0.57–2.42 and 0.22–6.55  $\text{mg m}^{-2} \text{s}^{-1}$ , respectively (Fig. 7). There  
494 was no significant effect of the “MPB” factor (Table 1). Conversely, fluxes of chlorophyll *a* were  
495 enhanced in the presence of parasitized cockles as compared to what was observed with unparasitized  
496 cockles and without cockles (Fig. 7, Table 1). There was also an interactive effect between “Cockle”  
497 and “MPB” factors on fluxes of chlorophyll *a*, although pairwise comparisons did not evidence  
498 significant differences between entities.

499 A significant decrease of the flux of the chlorophyll *a* with the increase of the metabolic rate of cockle  
500 populations was observed in experimental plots enriched with MPB (Fig.8; ANCOVA,  $F = -3.6$ ,  $p <$   
501  $0.01$ ).

#### 502 3.6.3. *Sand fraction*

503 Erosion fluxes of sand at the sediment-water interface of experimental plots unenriched and enriched  
504 with MPB ranged between  $1.04\text{--}5.16 \cdot 10^{-6}$  and  $1.18\text{--}12.80 \cdot 10^{-6} \text{ dm s}^{-1}$ , respectively (Fig. 7). There was  
505 no significant effect of “Cockles” and “MPB” factors, and no interactive effect between them (Table  
506 1). Additionally, erosion fluxes of sand did not vary with metabolic rates of cockle populations,  
507 independently of the MPB enrichment (Figure 8; ANCOVA,  $p = 0.81$ ).

## 508 **4. Discussion**

509 In this study, we evaluated the separate and combined effects of the cockle *Cerastoderma edule* and  
510 microphytobenthos (MPB) on the stability of a sandy sediment with a very low proportion of fine  
511 particles (mud = 4.4 %). Furthermore, the indirect impact of the trematode parasite *Bucephalus*  
512 *minimus* infecting *C. edule* on sediment stability was assessed both in sediments enriched and  
513 unenriched with MPB. We hypothesized that parasites, through their deleterious effects on the host  
514 physiology, may lower their bioturbation rates, thereby influencing sediment dynamics. If so, MPB  
515 unenriched and enriched sediments should be less destabilized by parasitized cockles than by  
516 unparasitized ones. Indeed, sediments inhabited by parasitized cockles should be less rough as a result  
517 of the lower level of activity of parasitized organisms, especially with regards to their mobility.  
518 Moreover, parasitized cockles may have a lower physical destructing influence on MPB growth than  
519 unparasitized organisms. MPB should thus have a higher stabilisation effect in presence of parasitized  
520 cockles than with unparasitized organisms.

### 521 **4.1. Influence of parasitism on the metabolic rate of cockle**

522 The parasite *B. minimus* negatively affects the biomass of *C. edule*, with parasitized organisms 27 %  
523 lighter than unparasitized conspecific when standardized for shell length. However, biomasses  
524 determined during this study took into account both the cockle and parasite biomasses. The biomass of  
525 *B. minimus* can represent up to 34 % of the total flesh weight of the parasite-host system (Baudrimont  
526 and de Montaudouin, 2007). Therefore, the “real” biomasses of cockles alone were likely even lower  
527 than those presently determined.

528 The ecological metabolic theory speculates that there is an allometric relationship between the size  
529 of organisms and their physiological activity, especially respiration. Based on this postulate, Brey  
530 (2010) developed a method to determine the metabolic rates of organism from their biomass. More  
531 recently, Cozzoli et al., (2018) proposed to use the individual metabolic rate of bioturbating as an  
532 index of their bioturbation rates (mass of sediment eroded). In the present study, we calculated the  
533 metabolic rates of parasitized and unparasitized cockles and highlighted the negative influence of the

534 parasite *B. minimus* on its host. However, we suggest that caution should be taken when calculating  
535 the metabolic rate of organisms, from which their bioturbation potential is deduced (Cozzoli et al.,  
536 2018). In particular, the use of allometric relationships to estimate the biomass of organisms from their  
537 length should be avoid. Indeed, parasites can profoundly alter the growth rate of their host (Mouritsen  
538 and Jensen, 1994; Sousa, 1983), so that such allometric relationships between the length and weight of  
539 organisms greatly depend of their parasitic status (Pascal et al., 2016). The use of biomass-length  
540 correlation that do not take into account parasitism as a forcing variable may consequently lead to  
541 over- or underestimation of the real biomass of organisms (and excluding the parasite biomass) and,  
542 ultimately, metabolic rate and bioturbation potential.

#### 543 **4.2. Influence of parasitized cockles on hydrodynamics and sediment roughness**

544 Sediment dynamics depends on sediment erodability, that is the resistance of sediment to erosion,  
545 and bed shear stress induced by hydrodynamics forcing. Though their bioturbation, benthic organisms  
546 can greatly impact sediment cohesiveness and thus modulate sediment erodability as observed for  
547 gastropod snails (Orvain et al., 2003) and cockles (Soissons et al., 2019). In addition to their activity,  
548 the mere presence of bioturbators at the sediment surface can also alter the sediment bed roughness  
549 and therefore the relationship between the current velocity (hydrodynamic) and the bed shear stress  
550 (Le Hir et al. 2007 and references therein). Indeed, protruding benthic organisms can enhance erosion  
551 processes by increasing turbulences that cause a local increase in bed shear stress (Le Hir et al., 2007  
552 and references therein). In contrasts, at high density organisms can reduce flow velocity leading to the  
553 creation of skimming flow above them (Friedrichs et al., 2000). So far, critical erosion thresholds ( $\tau_{crit}$ )  
554 have been determined assuming a smooth sediment bed and thus led to underestimation of the  
555 influence of cockles and other bioturbating organisms on sediment roughness and their knock-on  
556 effects on sediment dynamics. Using the method of Guizien et al. (2012), we were able to strictly  
557 disentangle the influence of unparasitized and parasitized cockles *C. edule* on sediment erodability and  
558 sediment roughness.

559 Considering the presence of cockles as a categorical factor (i.e. without vs. with un- or parasitized  
560 cockles) we observed no significant effect of this bivalve on the roughness length  $z_0$ . In contrast, we

561 showed that cockles significantly increase bed roughness using a correlative approach. Indeed, there  
562 was a significant increase of the roughness length  $z_0$  with the increase of the metabolic rate of cockle  
563 populations. Thus, cockles enhanced the bottom shear stress for a given current velocity. Visual  
564 observations revealed that cockles were active during erosion experiments, migrating upside-down in  
565 the sediment column and regularly emerging at the sediment surface of experimental plots (G.M. and  
566 A.D., personal obs.). The migration behaviour of cockles caused the reworking of sediments with  
567 consequences on sediment topography. Additionally, the current flow at the sediment surface could  
568 have been modified by cockle shells that periodically emerged at the sediment-water interface.

569 Our study also highlights that the trematode parasite *B. minimus* modulates the influence of cockles on  
570 sediment topography and thus hydrodynamic. Indeed, this parasite negatively affects the metabolic  
571 rate of its host, that is expected to display a lower bioturbation rate (Cozzoli et al., 2018). This is in  
572 agreement with the positive correlation between the roughness length  $z_0$  and the metabolic rates of  
573 cockle populations. This correlation shows that parasitized cockles have a lower influence on sediment  
574 roughness, and thus sediment erosion, than their unparasitized conspecifics. The altered role of  
575 parasitized cockles on sediment roughness may be surprising. Indeed, *B. minimus* has been suggested  
576 to contribute to the emergence of its host at the sediment surface of tidal flats (Desclaux et al., 2002).

577 If so, we would expect that parasitized cockles enhance the roughness length by their mere presence at  
578 the sediment surface. On the opposite, parasitized cockles were burrowed during the incubation period  
579 of our experiment (A.D. personal observation). Therefore, the reduced effect of parasitized cockles on  
580 sediment roughness presently observed rather suggests that these organisms were less active (lower  
581 sediment reworking activity) than their unparasitized conspecifics once buried in the sediment. Indeed,  
582 several studies showed that parasitized bioturbators experience modifications of their locomotor  
583 activity (Mouritsen, 2002; Mouritsen and Jensen, 1994; Thomas and Poulin, 1998) that can be  
584 associated to reduced sediment reworking activity (Pascal, 2017). Regarding cockles, visual  
585 observations (A.D, personal obs.) suggested that parasitized organisms generated less marks and tracks  
586 at the sediment surface. Nonetheless, measurements of microtopographical roughness of the sediment  
587 surface remain to be conducted to accurately compare the effect of parasitized and unparasitized  
588 organisms on sediment roughness.

### 589 **4.3. Influence of parasitized cockles on sediment erodability**

590 The role of cockles *C. edule* on sediment stability has been largely investigated, both in the lab  
591 (Ciutat et al., 2007, 2006; Li et al., 2017; Neumeier et al., 2006; Rakotomalala et al., 2015) and in the  
592 field (Andersen et al., 2010; Montserrat et al., 2008; Rakotomalala et al., 2015). Even though there are  
593 some discrepancies between studies, cockles have been observed to mainly enhance the erosion of  
594 cohesive sediment (Ciutat et al. 2006, 2007, Rakotomalala et al. 2015). Indeed, cockles increase the  
595 resuspension and erosion rates of fine sediment particles and decrease critical erosion velocities  
596 (Ciutat et al. 2007). Although cockle *C. edule* inhabits both cohesive and non-cohesive sediments  
597 (Hayward and Ryland, 1995), the influence of this bivalve in the dynamics of non-cohesive sediments  
598 has been comparatively poorly investigated (Li et al., 2017; Soissons et al., 2019). Besides, previous  
599 studies conducted in both cohesive and non-cohesive sediments did not clearly distinguish between the  
600 role of cockles on sediment erodability and their impact on sediment roughness. Finally, annular  
601 flumes used so far only allow to quantify the effect of bioturbating organisms on the resuspension of  
602 muddy particles. In contrasts, the Erodometre allows us to follow the erosion kinetics of  
603 microphytobenthic, muddy and sandy particles. Our study thus brings new insights on the effect of  
604 cockles on the erodability of sandy sediments.

605 Although not discriminating between the role of cockles on sediment roughness and erodability, Li et  
606 al. (2017) recently showed that this bivalve does not significantly affect the critical erosion thresholds  
607 and sediment fluxes of a sandy sediment. Considering the presence of cockles as a categorical factor  
608 (i.e. without vs. with un- or parasitized cockles), and irrespectively of the presence of the parasite *B.*  
609 *minimus*, we highlight a more equivocal impact of this bivalve on sandy sediments. Indeed, cockles  
610 reduced the critical erosion thresholds for mass erosion of fine particles and erosion of sandy particles.  
611 The influence of cockles on sediment erodability was even more pronounced when we used the  
612 metabolic rate of cockle populations as a continuous explaining variable (Brey, 2010; Cozzoli et al.,  
613 2018). The critical erosion thresholds of the biogenic fluff layer, the bed and the sandy fraction  
614 significantly decreased with the increase of the metabolic rate of cockle populations. In addition to  
615 their impact on sediment roughness, cockles thus also modulate the erodability of sandy sediment and

616 overall enhance their erosion. Nonetheless, the relative importance of cockles on these two processes  
617 (roughness vs. erodability) remains to be investigated.

618 Critical erosion thresholds for the biogenic fluffy layer, sediment bed, and sandy particles also  
619 significantly decreased with the increase of the metabolic rate of cockle populations, confirming the  
620 reduced deleterious effect of parasitized cockles on sediment erodability as compared to unparasitized  
621 organisms. Such as for sediment roughness, the lower impact of parasitized cockles on sediment  
622 erodability could be related to a reduced bioturbation rate, especially a lower sediment reworking  
623 activity. Parasitized cockles therefore negatively interfere with the sediment cohesiveness to a lower  
624 extent than unparasitized organisms.

#### 625 **4.4. Interactive effect of parasitized cockles and microphytobenthos**

##### 626 *4.4.1. Influence of parasitized cockles on microphytobenthos growth*

627 We quantified the effective photosynthetic quantum yield of the photosystem II of benthic algae as a  
628 proxy of their physiological status. The value obtained for experimental plots enriched with MPB  
629 highlights the good physiological status of MPB biofilms. There was no significant effect of cockles,  
630 irrespectively of their parasitic status, on the physiological status of microphytobenthic organisms at  
631 the sediment surface. In contrast, we observed a decrease of the chlorophyll *a* biomass in the photic  
632 layer with the increase of the metabolic rate of cockle populations. Therefore, both unparasitized and  
633 parasitized cockles have a deleterious impact of the growth of benthic microalgae, but this effect  
634 depends on the presence of the parasite *B. minimus*. Indeed, this parasite restrains the deleterious effect  
635 of its host on the growth of benthic microalgae. As previously mentioned, the bioturbation activity of  
636 cockles is probably lowered by *B. minimus*. Thus, parasitized cockles could disrupt MPB biofilms to a  
637 lesser extent than unparasitized organisms. Indeed, through their sediment reworking activity, cockles  
638 mechanically disrupt MPB biofilms that leads to enhanced chlorophyll *a* erosion rates (Rakotomalala  
639 et al., 2015). By doing so, this bivalve could facilitate the resuspension of MPB in the water column,  
640 which then becomes available for filter-feeding organisms, including cockles (Ubertini et al., 2012).  
641 While our study clearly emphasises a deleterious effect of cockles on the growth of MPB, some  
642 previous ones have been highlighted that cockles promote their growth. The bioturbation generated by

643 this bivalve can, indeed, stimulate the organic matter remineralisation and fluxes of inorganic nutrients  
644 at the sediment-water interface (Mermillod-Blondin and Rosenberg, 2006; Swanberg, 1991). By doing  
645 so, cockles fuel the growth of benthic microalgae (Eriksson et al., 2017; Swanberg, 1991). Although  
646 we presently show that cockles interfere with the growth of MPB, we nonetheless suggest that these  
647 results are not inconsistent with previous studies showing a stimulating effect of *C. edule* on MPB.  
648 Indeed, we placed cockles in a sandy sediment with a low quantity of fine particles that thus might  
649 contain a very low proportion of organic matter available for remineralisation and the recycled  
650 nutrients on which benthic microalgae rely as compared to a cohesive sediment. Therefore, the  
651 influence of cockles on MPB growth might be environment-dependent. In this context, parasitized and  
652 unparasitized cockles might have contrasting effect depending on the sedimentary environment. In  
653 organic-enriched sediments unparasitized cockles would stimulate the growth of benthic microalgae to  
654 a higher extent than parasitized organisms, with potential effect on sediment stability. However, this  
655 remains to be investigated in future studies. Finally, it should be pointed out that cockles, as ecosystem  
656 engineers can modify their environment. In particular, in turbid waters cockles can promote the  
657 deposition of fine particles at the sediment surface, consequently leading to a muddification of sandy  
658 environments (Soissons et al., 2019). In this case, cockles might promote the growth of MPB, with  
659 consequences on sediment stability. In our experimental context, water turbidity was very low and  
660 such cascade effect was thus unlikely.

#### 661 *4.4.2. Indirect effects of parasitized cockles on sediment stability*

662 In MPB enriched plots, parasitized and unparasitized cockles have differential impact on the  
663 resuspension dynamics of fine particles, MPB biofilms and sandy particles. The erosion of the  
664 different sediment fractions was delayed when experimental plots were inhabited by parasitized  
665 cockles as compared to plots with unparasitized bivalves. Parasitized cockles have a lower detrimental  
666 effect on the growth of MPB biofilms than their unparasitized conspecifics. Moreover, the MPB  
667 growth was similar between plots without cockles and inhabited by parasitized cockles. Thus, it may  
668 be suggested that the lower destabilizing effect of cockles on sandy sediments as compared to  
669 unparasitized organism is due to a stabilisation effect by MPB biofilms. However, the resuspension



670 kinetics of fine particles, MPB biofilms and sandy particles were similar between experimental plots  
671 unenriched and enriched MPB. The enrichment of the sediment surface with MPB did not influence  
672 the critical erosion thresholds and sediment fluxes for the different sediment fractions neither. Thus,  
673 we presently did not observe any stabilising effect of MPB on a sandy sediment. This result may be  
674 surprising since several studies showed that biofilms of MPB can enhance sediment stability  
675 (Grabowski et al., 2011; Miller et al., 1996), mainly while increasing the critical erosion threshold (Le  
676 Hir et al. 2007 and references therein). However, these studies mostly focused on cohesive sediments.  
677 Comparatively, the role of MPB on the dynamics of sandy sediments has been less investigated and a  
678 weak influence of benthic microalgae on sediment stability is generally highlighted (Harris et al.,  
679 2015; Joensuu et al., 2018; Riethmueller et al., 1998). Non-cohesive sediments have larger sediment  
680 particles that might be more difficult to stick together than fine particles of cohesive sediments.  
681 Moreover, these sediments are mainly colonized by epipellic diatoms whereas epipsamic ones are  
682 dominant in non-cohesive environments. These latter do not actively migrate in the sediment column  
683 and are regarded as less efficient in stabilizing sediments than epipellic diatoms that colonize cohesive  
684 sediments (Holland et al., 1974; Paterson and Hagerthey, 2001; Vos et al., 1988). Therefore, a  
685 stabilisation effect of MPB in sandy sediments has only been evidenced when a thick MPB mat has  
686 developed (Yallop et al., 1994). In this study, biomasses of chlorophyll *a* in experimental plots  
687 enriched with MPB were low as compared to those reported in experimentally enriched cohesive  
688 sediments (Ubertini et al., 2015) and even in natural sandy sediments (Harris et al., 2015). Even  
689 though the total biomass of MPB biofilms could have been underestimated (the PAM fluorimeter  
690 measures the chlorophyll *a* fluorescence in the sediment photic zone and thus does not take into  
691 account benthic algae that migrate downward in the sediment column), we suggest that the quantity of  
692 MPB that had developed at the sediment-water interface of experimental plots enriched with MPB was  
693 insufficiently high to stabilize the sediment. Indeed, the high proportion of sand might have prevented  
694 the development of a protective biofilm by epipellic diatoms. Consequently, the lower destabilising  
695 effect of parasitized cockles *C. edule* on sandy sediment cannot be explained by a stabilisation effect  
696 due to the MPB biofilm.

697 The reasons behind the differential effect of parasitized cockles on the erosion kinetics of sandy  
698 sediment depending on the presence of a MPB biofilm remain unclear. Nonetheless, it should be  
699 mentioned that metabolic rate of parasitized cockles placed in experimental plots unenriched with  
700 MPB were more variable than those of conspecifics in plots enriched with MPB. Accordingly, some  
701 parasitized cockles in MPB-unenriched plots had similar metabolic rates, and bioturbation rates  
702 (Cozzoli et al., 2018), to those of unparasitized organisms. Organisms can vary in their response to  
703 parasitism, with some specimens more sensitive to this stress factors than others (Minchella, 1985).  
704 Due to the low number of replicates, this large inter-variability in metabolic rate between parasitized  
705 cockles in MPB-unenriched plots may have overridden a slight indirect influence of parasitism on  
706 sediment dynamics.

## 707 **5. Conclusion**

708 This study is the first to evaluate the indirect influence of parasitism on sediment dynamics  
709 processes. By comparing the impacts of parasitized and unparasitized bioturbating organisms on the  
710 erosion dynamics of a sandy sediment we put in evidence a slight impact of the trematode parasite  
711 *Bucephalus minimus* on the destabilisation potential of its host, the common cockle *Cerastoderma*  
712 *edule*, especially in MPB-enriched sediments. Indeed, the influence of parasitized cockles on sediment  
713 erodability and hydrodynamics appears reduced as compared to unparasitized organisms. This pattern  
714 may be attributed to the parasite lowering the bioturbation potential of its host as a result of an altered  
715 physiological state. As a consequence, parasitism also modulates the interaction between cockles and  
716 microphytobenthic organisms. Indeed, parasitized organisms have a less negative effect on MPB  
717 growth than unparasitized ones. Nonetheless, the biomasses of MPB biofilms that developed at the  
718 water-interface of sediment columns remained too low to efficiently stabilize this sandy sediment,  
719 irrespectively of the presence of parasitized and unparasitized cockles. The stabilisation effect of  
720 microphytobenthic organisms have been essentially reported in cohesive sediments. Indeed, cohesive  
721 sediments are characterised by a smaller grain size than sandy sediments. Through EPS production,  
722 microphytobenthic organisms can thus more efficiently bind sediment grains together and increase the  
723 stability of cohesive sediments (Grabowski et al., 2011; Yallop et al., 1994). In sandy environments, a

724 high turbidity of the water column and high deposition rate by cockles could nonetheless increase the  
725 mud content of the sediment surface (Soissons et al., 2019) and thus enhance the colonisation by  
726 epipellic diatoms. Therefore, the feedback loop between parasitism, cockles and MPB may thus  
727 modulate the stability of cohesive or muddified sandy sediments to a larger extent to what was  
728 observed in this study, but it remains to be investigated in future studies.

729

730 **Compliance with ethical standards**

731 **Declarations of interest**

732 None.

733 **Animal rights**

734 All applicable international, national and/or institutional guidelines for the care and use of  
735 animals were followed.

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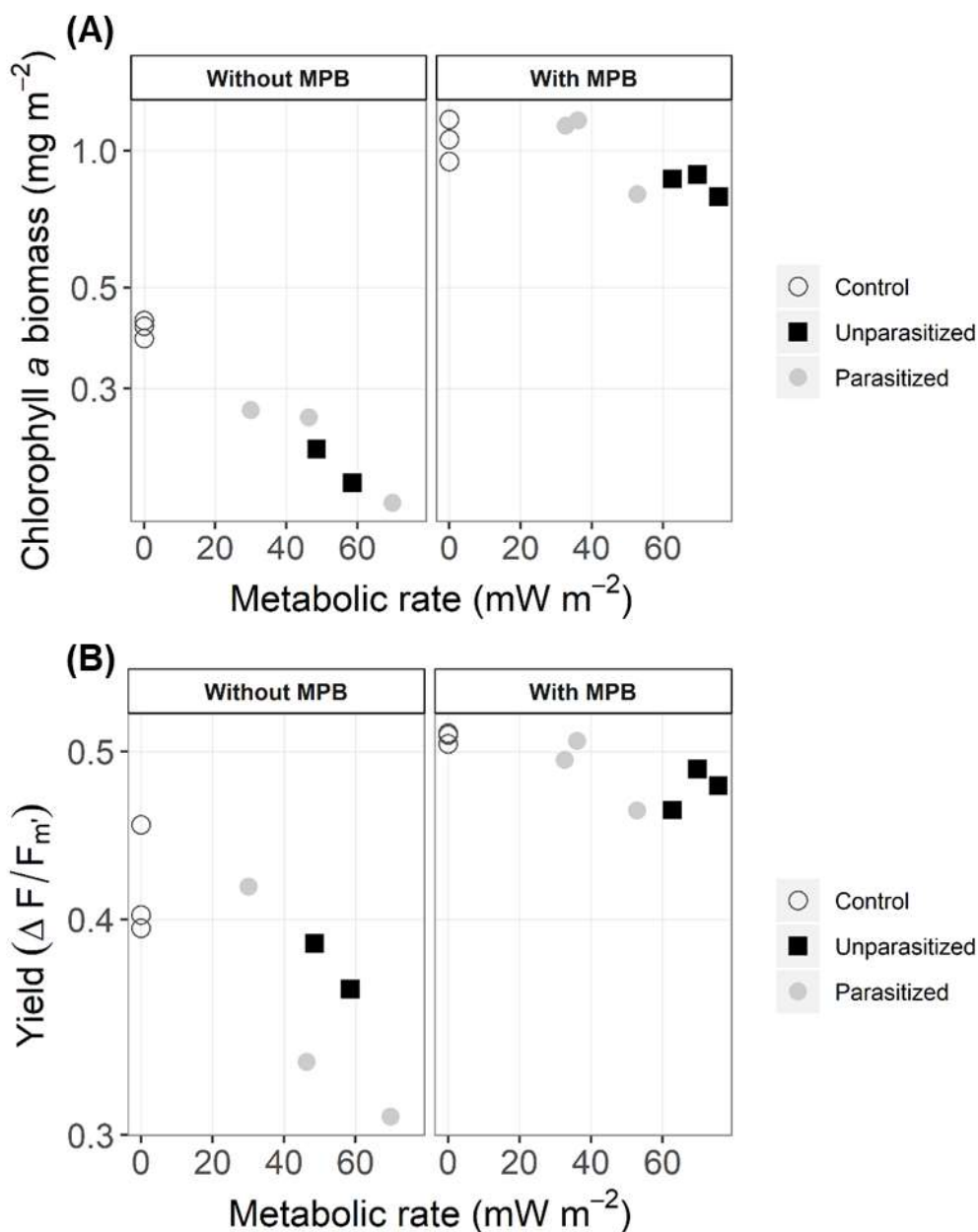


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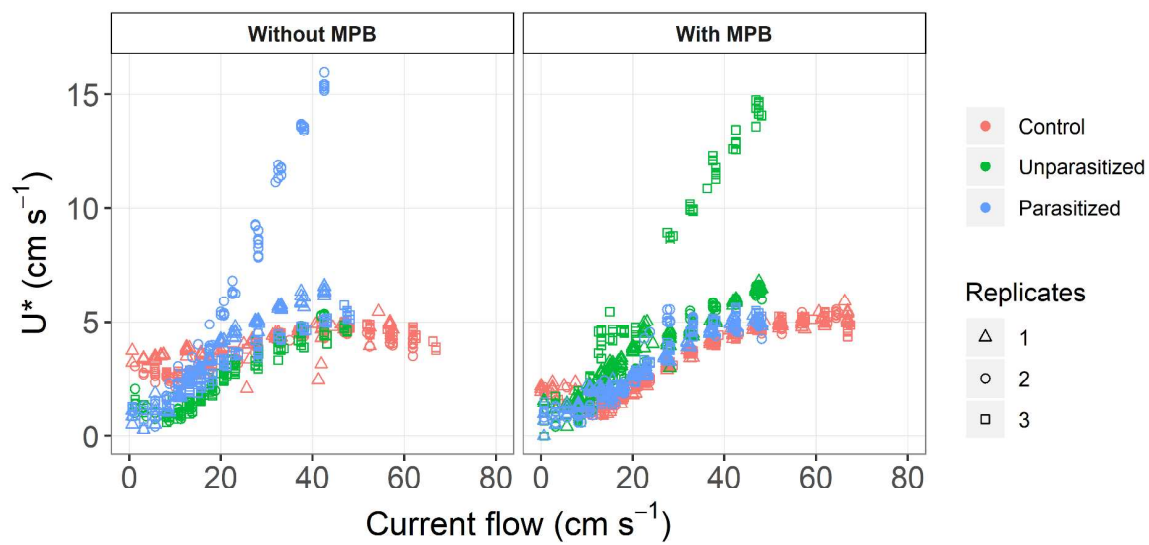
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**Table 1** Results of PERMANOVAs analyses evaluating the influence of “Cockle” (“Control”, i.e. no cockles, “Unparasitized”, i.e. presence of unparasitized cockles and “Parasitized”, i.e. presence of parasitized cockles) and “MPB” (“Without MPB”, i.e. no enrichment with MPB, “With MPB”, i.e. enrichment with MPB) factors on different variables determined over erosion experiments. P-values in bold indicate significant effect ( $p < 0.05$ ). \* denotes significant differences of dispersion (PERMDISP analysis,  $p < 0.05$ ).

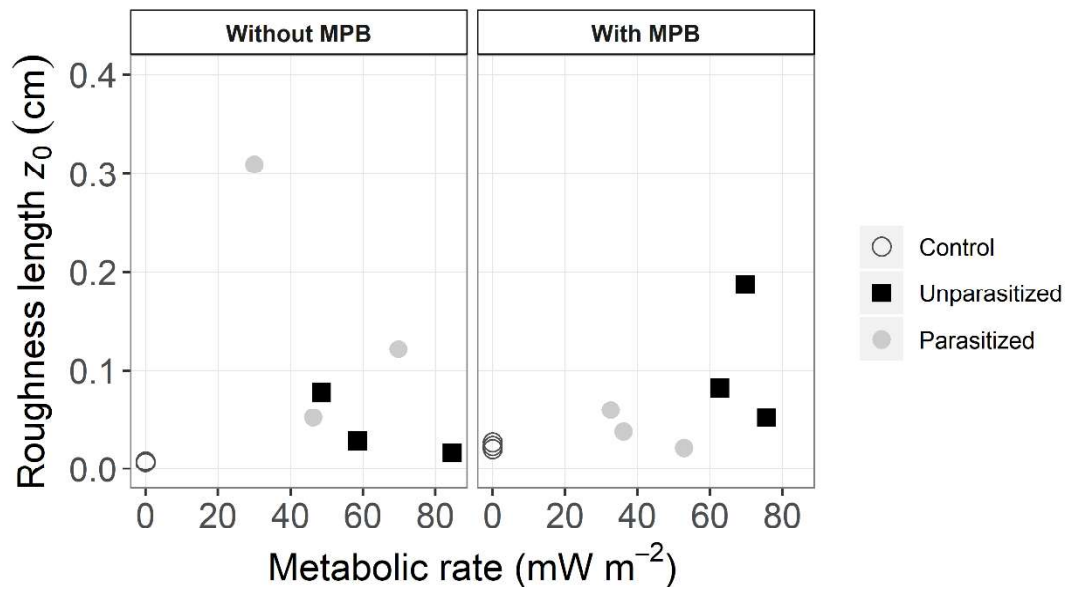
	df	Pseudo-F	P(perm)
<b><i>Chlorophyll a biomass</i></b>			
Cockle (1)	2	5.7	< <b>0.05</b>
MPB (2)	1	187.4	< <b>0.01</b>
(1) x (2)	2	1.1	0.38*
<b><i>Effective quantum yield of photosystem II</i></b>			
Cockle (1)	2	3.0	0.09
MPB (2)	1	53.7	< <b>0.01</b>
(1) x (2)	2	0.8	0.45*
<b><i>Roughness length <math>z_0</math></i></b>			
Cockle (1)	2	2.8	0.07*
MPB (2)	1	0.5	0.55
(1) x (2)	2	2.8	0.08*
<b><i>Critical bed shear stress (<math>\tau_{crit}</math>)</i></b>			
<b>Biogenic fluff layer – muddy fraction</b>			
Cockle (1)	2	2.8	0.12
MPB (2)	1	0.03	0.86
(1) x (2)	2	1.6	0.26*
<b>Mass erosion – muddy fraction</b>			
Cockle (1)	2	33.2	< <b>0.01</b>
MPB (2)	1	5.0	0.059
(1) x (2)	2	0.3	0.74
<b>Chlorophyll a</b>			
Cockle (1)	2	0.8	0.54*
MPB (2)	1	0.9	0.75*
(1) x (2)	2	1.3	0.17*
<b>Sandy fraction</b>			
Cockle (1)	2	11.7	< <b>0.01</b>
MPB (2)	1	0.004	0.96
(1) x (2)	2	6.7	< <b>0.05*</b>
<b><i>Fluxes of sediment</i></b>			
<b>Muddy fraction</b>			
Cockle (1)	2	0.2	0.80
MPB (2)	1	0.3	0.61
(1) x (2)	2	1.0	0.40
<b>Chlorophyll a of MPB biofilms</b>			
Cockle (1)	2	6.7	< <b>0.01*</b>
MPB (2)	1	1.9	0.20*
(1) x (2)	2	12.0	< <b>0.01*</b>
<b>Sandy fraction</b>			
Cockle (1)	2	0.8	0.51
MPB (2)	1	0.2	0.73*
(1) x (2)	2	1.2	0.34*



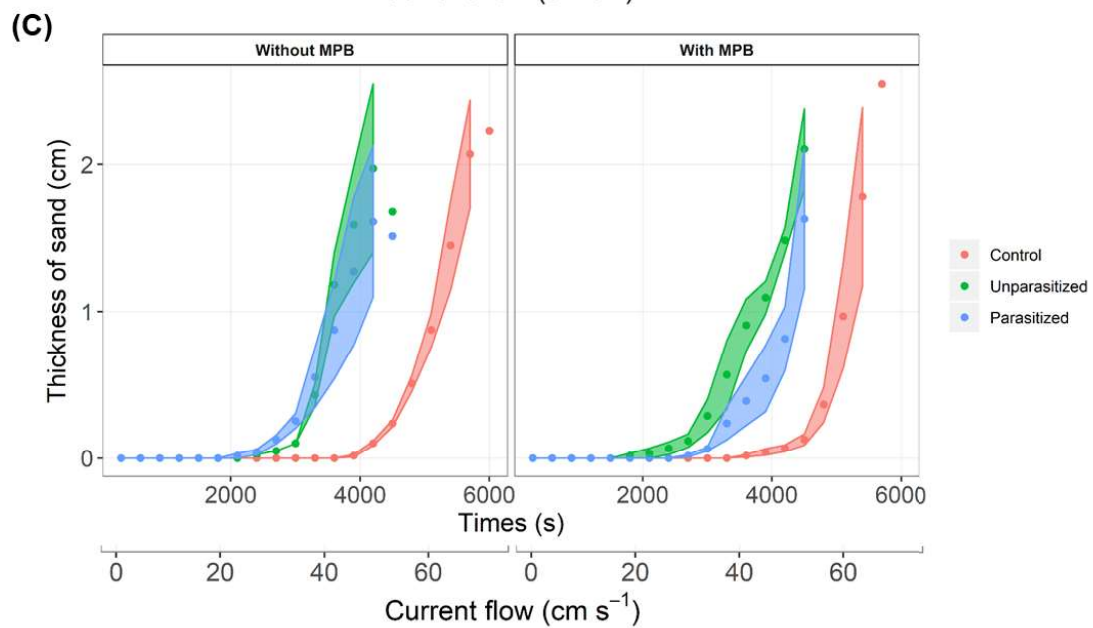
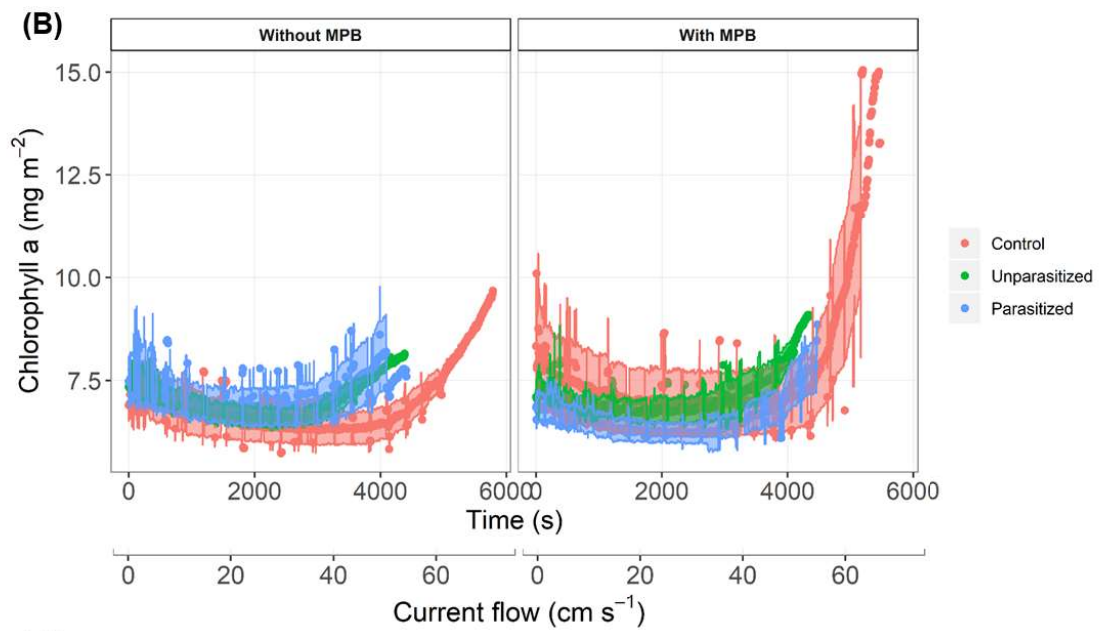
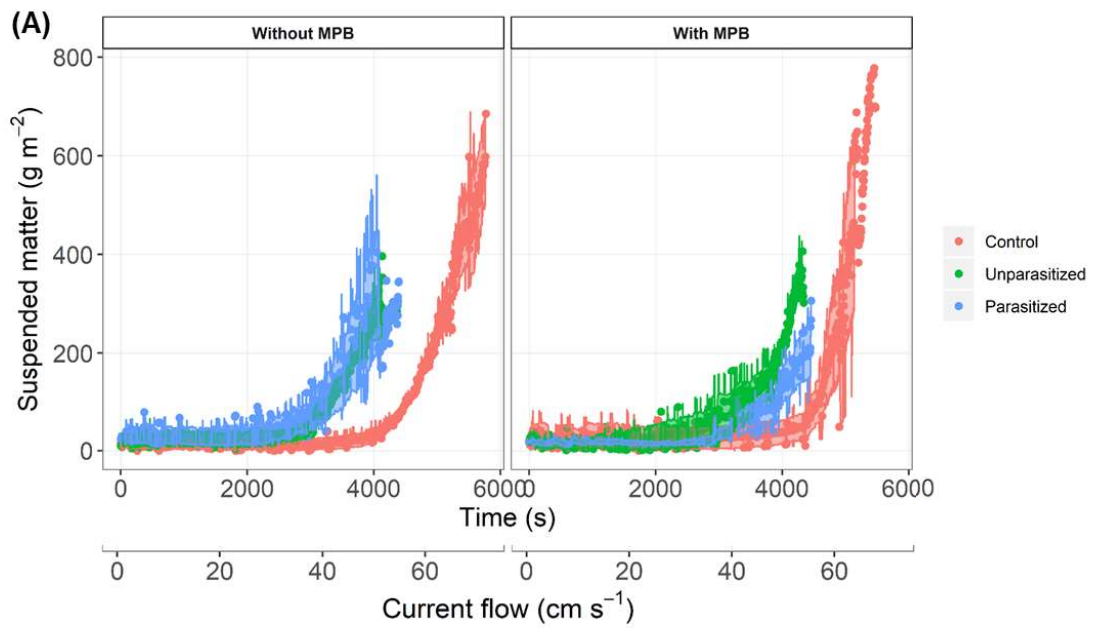
**Fig. 1** Relationships between (A) the biomass of chlorophyll a ( $\text{mg m}^{-2}$ ) and (B) associated mean effective quantum yield of photosystem II (“Yield”,  $\frac{\Delta F}{F_m'} = \frac{(F_m' - F_m)}{F_m'}$ ) determined in the photic layer at the sediment-water interface of experimental plots unenriched and enriched with microphytobenthos (MPB; “Without MPB” and “With MPB”, respectively) and the metabolic rate of cockles *Cerastoderma edule* unparasitized and parasitized with the trematode *Bucephalus minimus* ( $\text{mW m}^{-2}$ ). The “Control” treatment corresponds to experimental plots without cockles.  $N = 3$  for each treatment, except for the treatment “Unparasitized” – “Without MPB” for which  $N = 2$ .



**Fig. 2** Dynamics of the shear velocity  $U^*$  across a gradient of current flows ( $\text{cm s}^{-1}$ ) for sediment plots unenriched or enriched with microphytobenthos (MPB; “Without MPB” and “With MPB”, respectively) and influence of the cockle *Cerastoderma edule* unparasitized (“Unparasitized”) and parasitized (“Parasitized”) with the trematode *Bucephalus minimus*. The “Control” condition corresponds to experimental plots without cockles. Replicates are individualized.  $N = 3$  for each treatment, except for the treatment “Unparasitized” – “Without MPB” for which  $N = 2$ .

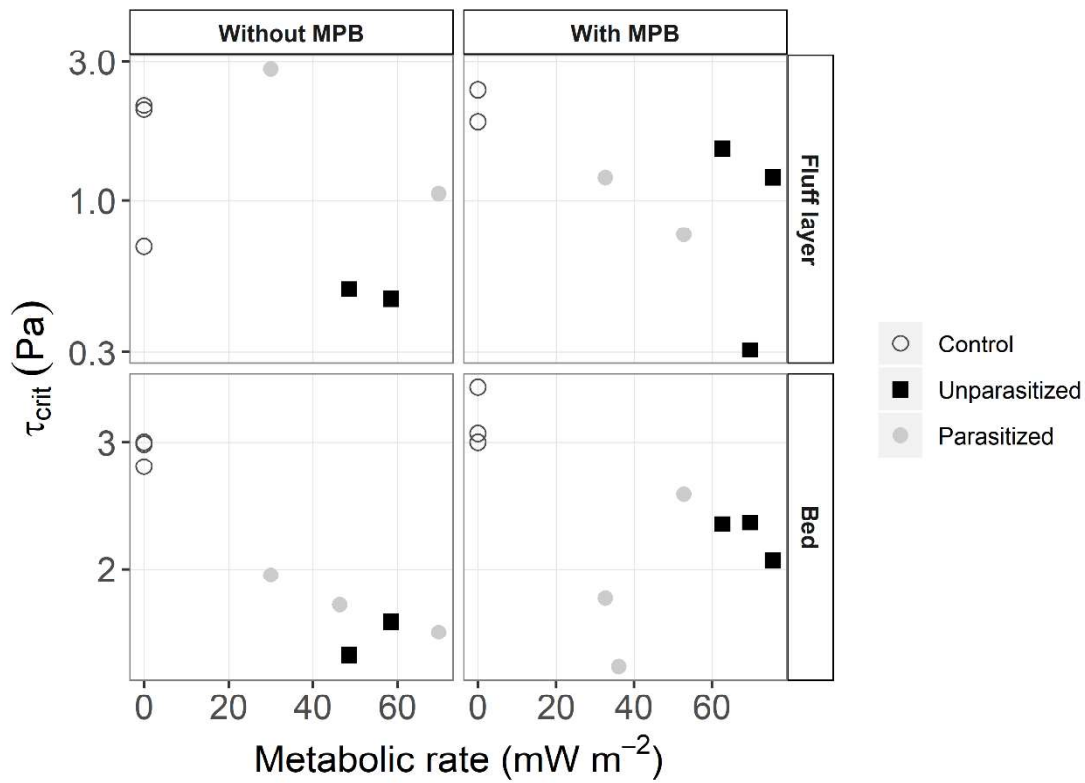


**Fig. 3** Relationship between the roughness length  $z_0$  determined at the surface of sediments unenriched or enriched with microphytobenthos (MPB; “Without MPB” and “With MPB”, respectively) and the metabolic rate of cockles *Cerastoderma edule* unparasitized and parasitized with the trematode *Bucephalus minimus* ( $\text{mW m}^{-2}$ ). The “Control” condition corresponds to experimental plots without cockles.  $N = 3$  for each treatment, except for the treatment “Unparasitized” – “Without MPB” for which  $N = 2$ .

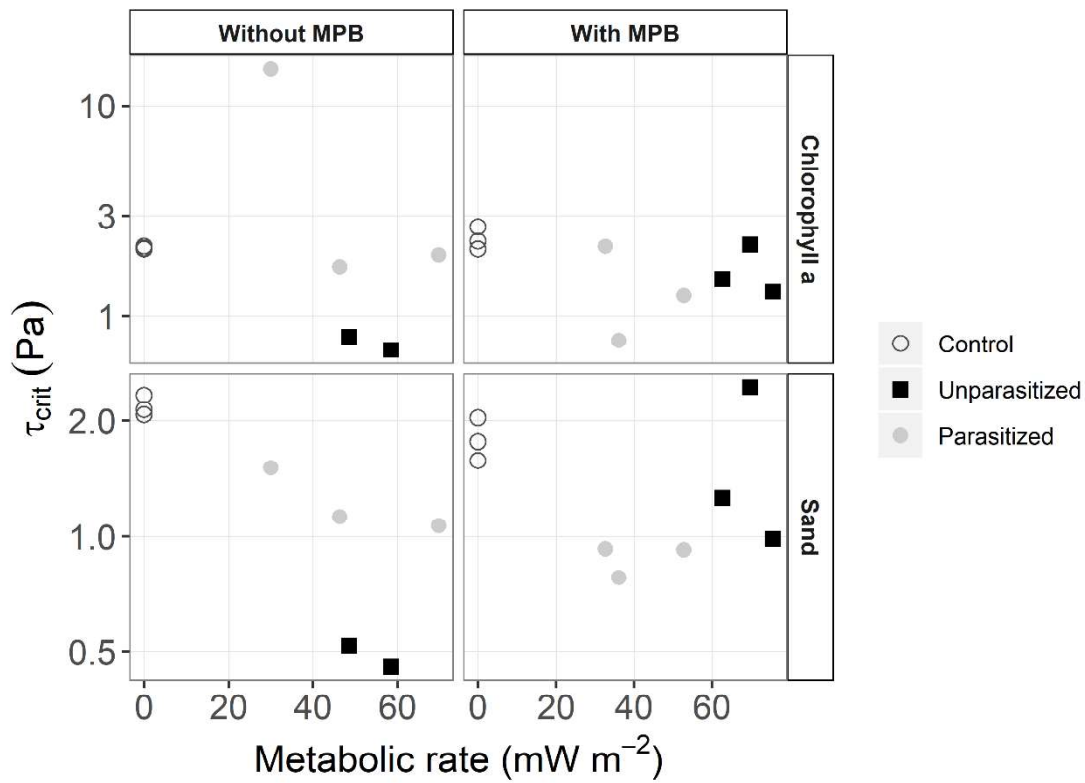


**Fig. 4** Temporal dynamics of the resuspension of (A) the muddy fraction (“Suspended matter”), (B) chlorophyll *a* of microphytobenthos (MPB) biofilms and (C) the sandy fraction of sediment columns unenriched or enriched with microphytobenthos (“Without MPB” and “With MPB”, respectively) and influence of the cockle *Cerastoderma edule* unparasitized (“Unparasitized”) and parasitized (Parasitized”) with the trematode *Bucephalus minimus* on sediment resuspension. The “Control” condition corresponds to experimental plots without cockles. Mean masses eroded are plotted, the coloured areas representing the standard error intervals around the mean. Regarding the muddy fraction, a sequential erosion was observed, the fluff layer was firstly eroded, followed by the sediment bed (mass erosion).  $N = 3$  for each experimental treatment, except for the treatment “Unparasitized” – “Without MPB” for which  $N = 2$ .

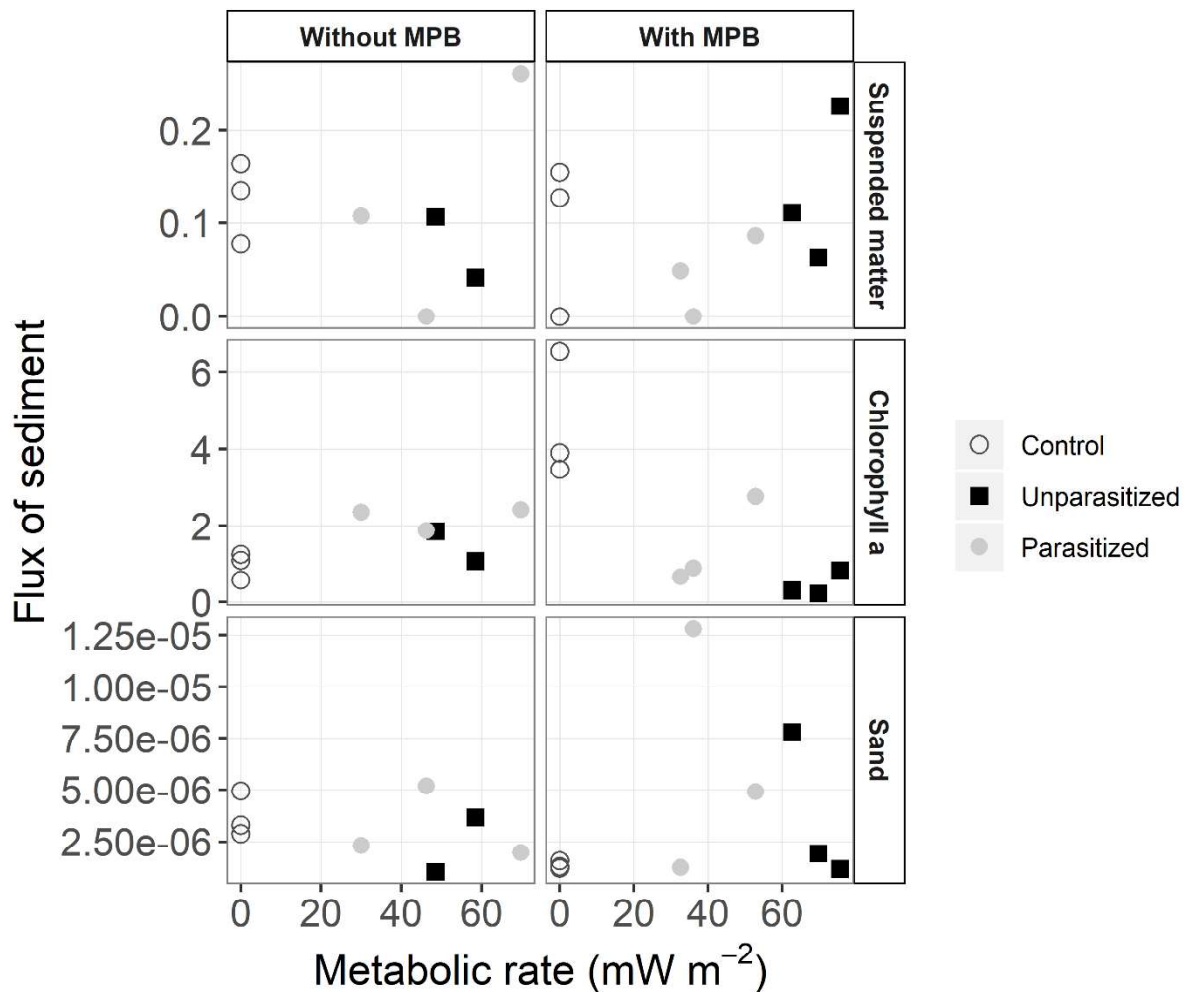




**Fig. 5** Critical bed shear stresses  $\tau_{crit}$  (Pa) for the muddy fraction of sediment columns unenriched and enriched with microphytobenthos (MPB; “Without MPB” and “With MPB”, respectively) as a function of the metabolic rate of cockles *Cerastoderma edule* unparasitized and parasitized with the trematode *Bucephalus minimus* ( $mW m^{-2}$ ). Critical bed shear stresses of the biogenic fluff layer and of the sediment bed have been discriminated. The “Control” condition corresponds to experimental units without cockles.  $N = 3$  for each treatment, except for the treatment “Unparasitized” – “Without MPB” for which  $N = 2$ .



**Fig. 6** Critical bed shear stresses  $\tau_{crit}$  (Pa) for the chlorophyll *a* of microphytobenthos biofilms and sandy fraction of sediment columns unenriched and enriched with microphytobenthos (MPB; “Without MPB” and “With MPB”, respectively) as a function of the metabolic rate of cockles *Cerastoderma edule* unparasitized and parasitized with the trematode *Bucephalus minimus* ( $\text{mW m}^{-2}$ ). The “Control” condition corresponds to experimental units without cockles.  $N = 3$  for each treatment, except for the treatment “Unparasitized” – “Without MPB” for which  $N = 2$ .



**Fig. 7** Fluxes of fine particles (“Suspended matter”,  $\text{g m}^{-2} \text{s}^{-1}$ ), chlorophyll *a* of microphytobenthic biofilms ( $\text{mg m}^{-2} \text{s}^{-1}$ ) and sand ( $\text{dm s}^{-1}$ ) at the sediment-water interface of experimental plots unenriched and enriched with microphytobenthic organisms (“Without MPB” and “With MPB”, respectively) as a function of the metabolic rate of cockles *Cerastoderma edule* unparasitized and parasitized with the trematode *Bucephalus minimus* ( $\text{mW m}^{-2}$ ). Fluxes were determined over the three erosion steps that followed critical erosion incipient point for each of the different fraction of the sediment column. Regarding the fine particles, fluxes were calculated following the initiation of the biogenic fluff layer. The “Control” condition corresponds to experimental units without cockles.  $N = 3$  for each experimental condition, except for the treatment “Unparasitized” – “Without MPB” for which  $N = 2$ .

**\*conflict of Interest Statement**

**Declaration of interests**

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: