



# **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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## **► To cite this version:**

Annabelle Dairain, Olivier Maire, Guillaume Meynard, Francis Orvain. 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. *Science of the Total Environment*, 2020, 733, pp.139307. <10.1016/j.scitotenv.2020.139307>. <hal-03793607>

**HAL Id: hal-03793607**

**<https://hal.science/hal-03793607v1>**

Submitted on 1 Oct 2022

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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

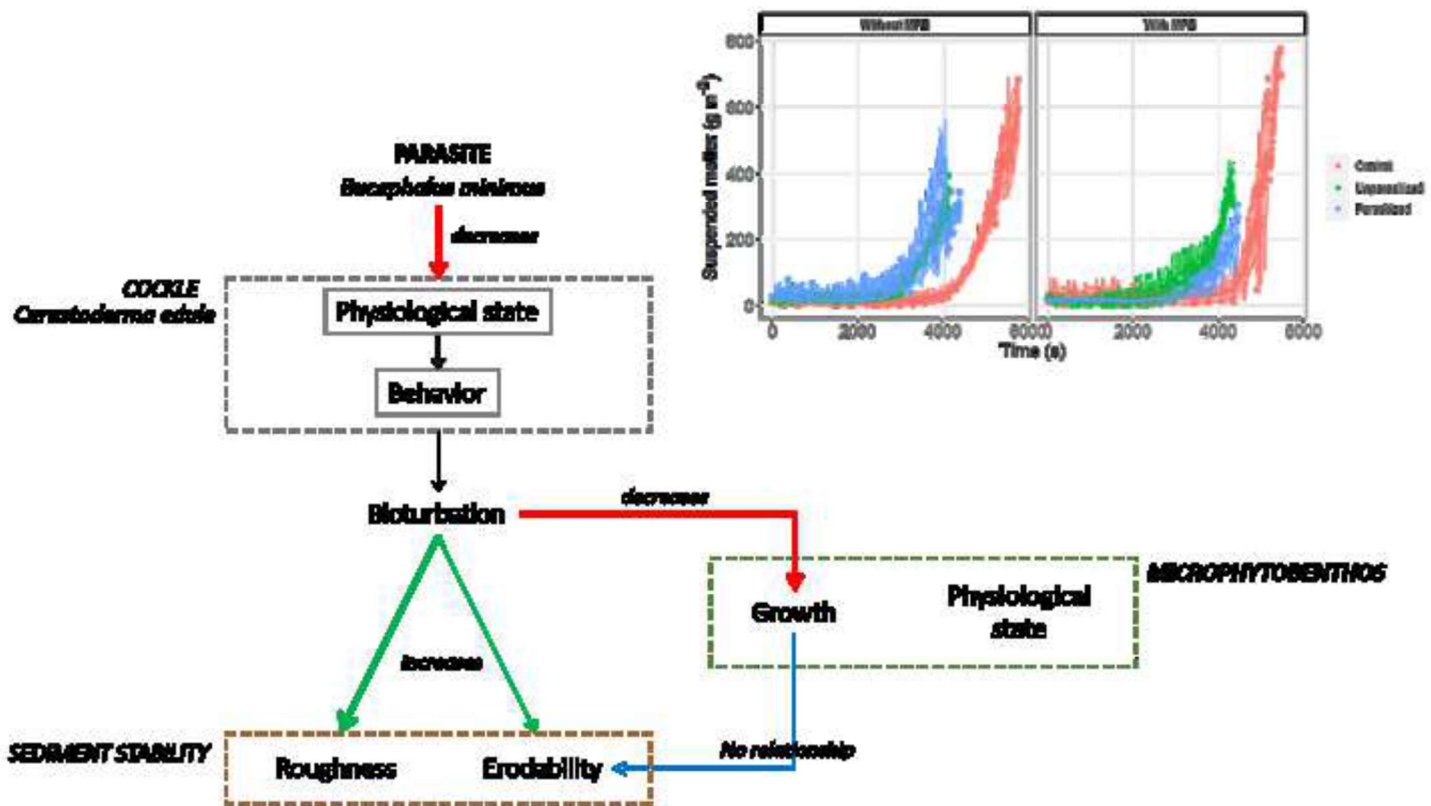
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\*Graphical Abstract



## 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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## Abstract

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

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

## 1. Introduction

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

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

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

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

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

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



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

To date, trait-mediated effects of parasites on their bioturbating host have been poorly studied (see Dairain et al., 2019 for a review) and their consequences on sediment stability have never been 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*.

## 2. Materials and methods

### 2.1. The host-parasite association

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

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

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

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

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

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

## **2.3. Sampling of sediment**

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

## **2.4. Microphytobenthos culture**

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

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

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

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

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

## 2.6. Microphytobenthos photosynthetic parameters

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

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

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

## 2.7. Erosion procedure

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

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

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

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

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

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

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

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

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

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

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

Critical erosion thresholds for the chlorophyll *a* of biofilms of MPB and the sandy fraction of the sediment column were determined as the intercept of the best linear regression of chlorophyll *a* 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 Erodometre 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).

## 2.9. Statistical analyses

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

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

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

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

### 3. Results

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

#### 3.1. Metabolic rates of cockles

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

#### 3.2. Microphytobenthos growth

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

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

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

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

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

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

### 3.3. Shear velocity dynamics

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

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

373 current flow =  $62 \text{ cm s}^{-1}$ ) (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  $\text{cm s}^{-1}$  (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  $0.66 \text{ cm s}^{-1}$  with the current flow increasing from ca.  $0.6$  to  $8.1 \text{ cm s}^{-1}$ . Then,  
 380  $U^*$  increased up to ca.  $5.1 \text{ cm s}^{-1}$  (current flow = ca.  $44.7 \text{ cm s}^{-1}$ ). 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.  $20.6 \text{ cm s}^{-1}$  as  
 384 compared to those observed for the two other replicates (Fig. 2). For this replicate,  $U^*$  attained  $14.1$   
 385  $\text{cm s}^{-1}$  (current flow =  $48.1 \text{ cm s}^{-1}$ ) at the end of the erosion experiment, while it attained  $6.4 \text{ cm s}^{-1}$  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  $0.31 \text{ cm s}^{-1}$  with the current flow increasing from ca.  $0.6$  to  $3.1 \text{ cm s}^{-1}$ . Then,  $U^*$   
 389 increased up to ca.  $6.2 \text{ cm s}^{-1}$  (current flow = ca.  $44.7 \text{ cm s}^{-1}$ ). 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.  $20.6 \text{ cm s}^{-1}$  as compared with the two other replicates (Fig. 2). For this replicate,  $U^*$  attained  $16.0$   
 392  $\text{cm s}^{-1}$  (current flow =  $42.5 \text{ cm s}^{-1}$ ) at the end of the erosion experiment, while it attained ca.  $5.8 \text{ cm s}^{-1}$   
 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  $0.62 \text{ cm s}^{-1}$  with the current flow  
 396 increasing from ca.  $0.6$  to  $8.4 \text{ cm s}^{-1}$ . Then, it increased up to ca.  $5.5 \text{ cm s}^{-1}$  (current flow = ca.  $44.4 \text{ cm}$   
 397  $\text{s}^{-1}$ ).

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.

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

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

### 3.4. Sediment resuspension dynamics and erodability

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

#### 3.4.1. Mud fraction

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

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

#### 3.4.2. Chlorophyll *a* fraction

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

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

#### 3.4.3. Sand fraction

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

### 3.5. Critical bed shear stress

#### 3.5.1. Mud fraction

Regarding the muddy fraction, we discriminated the erosion of the biogenic fluff layer from the sediment bed erosion and therefore determined the critical erosion threshold for both of them (Fig. 5). Critical bed shear stresses ( $\tau_{crit}$ ) for the biogenic fluff layer ranged between 0.46–2.83 and 0.31–2.41 Pa in experimental plots unenriched and enriched with MPB, respectively (Fig. 5). There was no significant influence of “Cockle” and “MPB” factors, and no interactive effect between them on  $\tau_{crit}$  for the biogenic fluff layer (Table 1).  $\tau_{crit}$  significantly decreased with the increase of the metabolic rate of cockle populations (ANCOVA,  $F = -2.3$ ,  $p < 0.05$ ). This relationship was not influenced by the MPB enrichment (ANCOVA,  $p = 0.86$ ).

$\tau_{crit}$  for the sediment bed ranged between 1.51–3.00 and 1.46–3.58 Pa for experimental plots unenriched and enriched with MPB, respectively (Fig. 5). Cockles significantly lowered  $\tau_{crit}$  for the sediment bed as compared to those determined for experimental plots without cockles (Table 1). There was no significant influence of “MPB” and no interactive effect between “Cockle” and “MPB” factors on  $\tau_{crit}$  for the sediment bed (Table 1).  $\tau_{crit}$  for the sediment bed significantly decreased with the increase of the metabolic rate of cockle populations (Fig. 5; ANCOVA,  $F = -5.49$ ,  $p < 0.01$ ). The enrichment with MPB did not significantly modify this relationship (Fig. 5; ANCOVA,  $p = 0.33$ ).

### 3.5.2. *Chlorophyll a fraction*

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

### 3.5.3. *Sand fraction*

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



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

### 3.6. Sediment erosion fluxes

#### 3.6.1. Mud fraction

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

#### 3.6.2. Chlorophyll *a* fraction

Fluxes of chlorophyll *a* at the sediment-water interface of experimental plots unenriched and 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 was no significant effect of the “MPB” factor (Table 1). Conversely, fluxes of chlorophyll *a* were enhanced in the presence of parasitized cockles as compared to what was observed with unparasitized cockles and without cockles (Fig. 7, Table 1). There was also an interactive effect between “Cockle” and “MPB” factors on fluxes of chlorophyll *a*, although pairwise comparisons did not evidence significant differences between entities.

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

#### 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  $1.04\text{--}5.16 \times 10^{-6}$  and  $1.18\text{--}12.80 \times 10^{-6} \text{ dm s}^{-1}$ , 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,  $p = 0.81$ ).

## 4. Discussion

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

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

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

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

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

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

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

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

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

Our study also highlights that the trematode parasite *B. minimus* modulates the influence of cockles on sediment topography and thus hydrodynamic. Indeed, this parasite negatively affects the metabolic rate of its host, that is expected to display a lower bioturbation rate (Cozzoli et al., 2018). This is in agreement with the positive correlation between the roughness length  $z_0$  and the metabolic rates of cockle populations. This correlation shows that parasitized cockles have a lower influence on sediment roughness, and thus sediment erosion, than their unparasitized conspecifics. The altered role of parasitized cockles on sediment roughness may be surprising. Indeed, *B. minimus* has been suggested to contribute to the emergence of its host at the sediment surface of tidal flats (Desclaux et al., 2002). If so, we would expect that parasitized cockles enhance the roughness length by their mere presence at the sediment surface. On the opposite, parasitized cockles were burrowed during the incubation period of our experiment (A.D. personal observation). Therefore, the reduced effect of parasitized cockles on sediment roughness presently observed rather suggests that these organisms were less active (lower sediment reworking activity) than their unparasitized conspecifics once buried in the sediment. Indeed, several studies showed that parasitized bioturbators experience modifications of their locomotor activity (Mouritsen, 2002; Mouritsen and Jensen, 1994; Thomas and Poulin, 1998) that can be associated to reduced sediment reworking activity (Pascal, 2017). Regarding cockles, visual observations (A.D, personal obs.) suggested that parasitized organisms generated less marks and tracks at the sediment surface. Nonetheless, measurements of microtopographical roughness of the sediment surface remain to be conducted to accurately compare the effect of parasitized and unparasitized organisms on sediment roughness.

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

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

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

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

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

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

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

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

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

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

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



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

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

## 5. Conclusion

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

736    **Acknowledgements**

737    The authors are grateful to H. Blanchet, A. Ciutat, A. Goedknecht, X. de Montaudouin, H.  
738    Moussard, A. Richard and T. Rodolfo-Damiano for their significant help with field work and  
739    assistance during lab experiments.

740    **Fundings**

741    The research leading to these results has received funding from the Interreg Atlantic Area  
742    Programme through the European Regional Development Fund for the project Co-Operation  
743    for Restoring Cockle Shellfisheries and its Ecosystem Services in the Atlantic Area  
744    (COCKLES, EAPA\_458/2016), [www.cockles-project.eu](http://www.cockles-project.eu).

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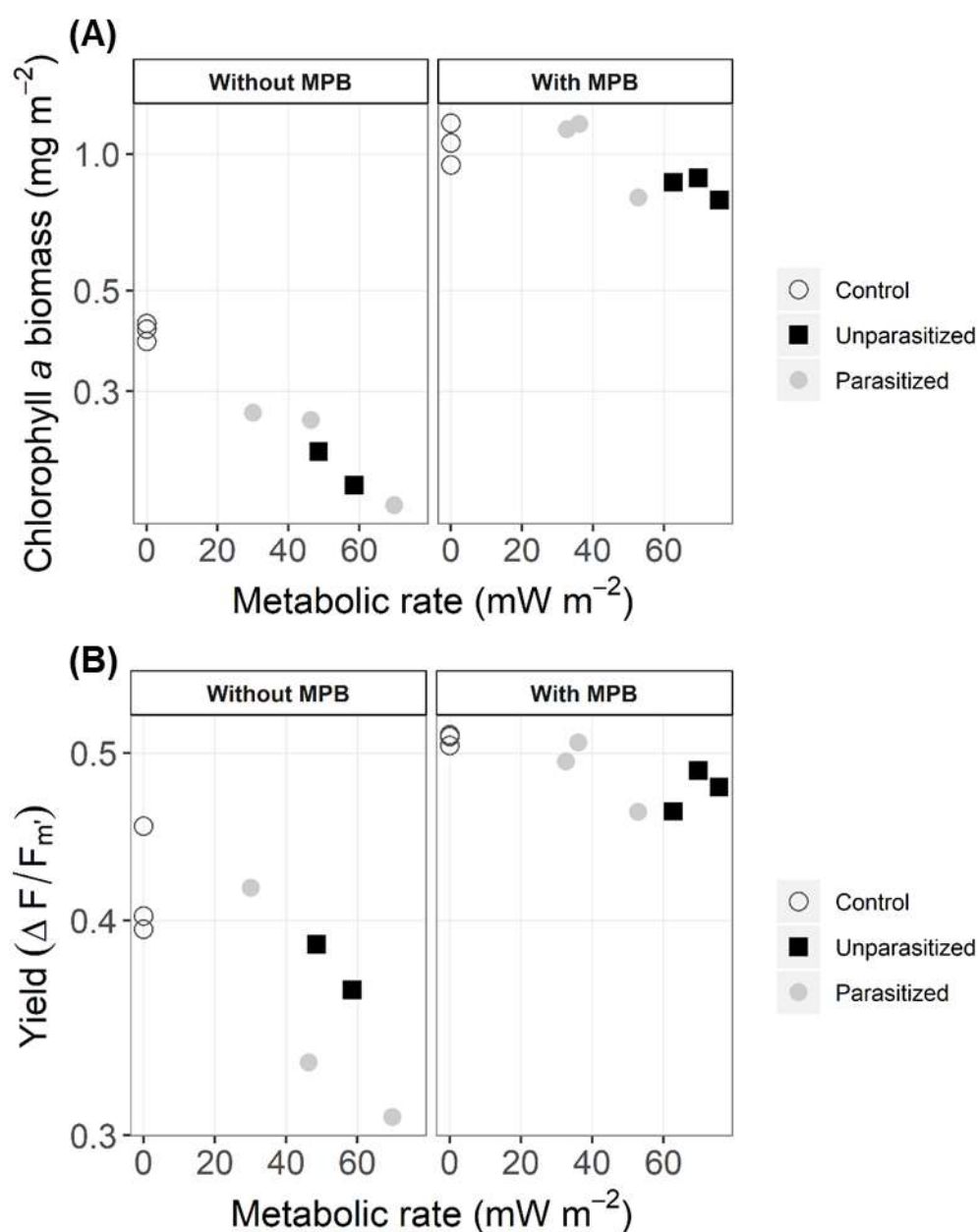


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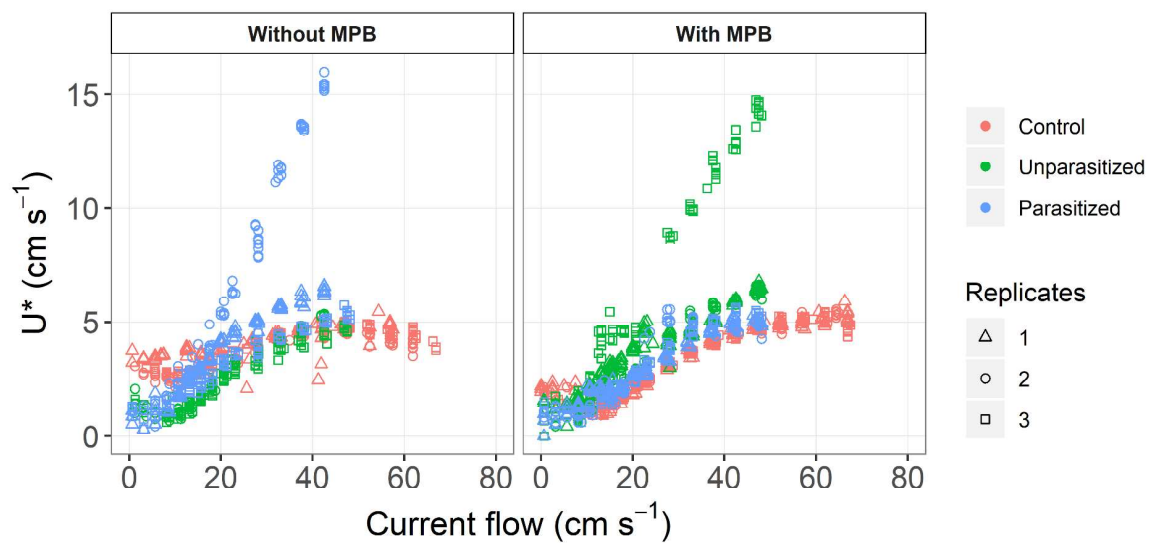
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**Table 1** Results of PERMANOVAs analyses evaluating the influence of “Cockle” (“Control”, i.e. no cockles, “Unparasitized”, i.e. presence of unparasitized cockles and “Parasitized”, i.e. presence of parasitized cockles) and “MPB” (“Without MPB”, 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,  $p < 0.05$ ).

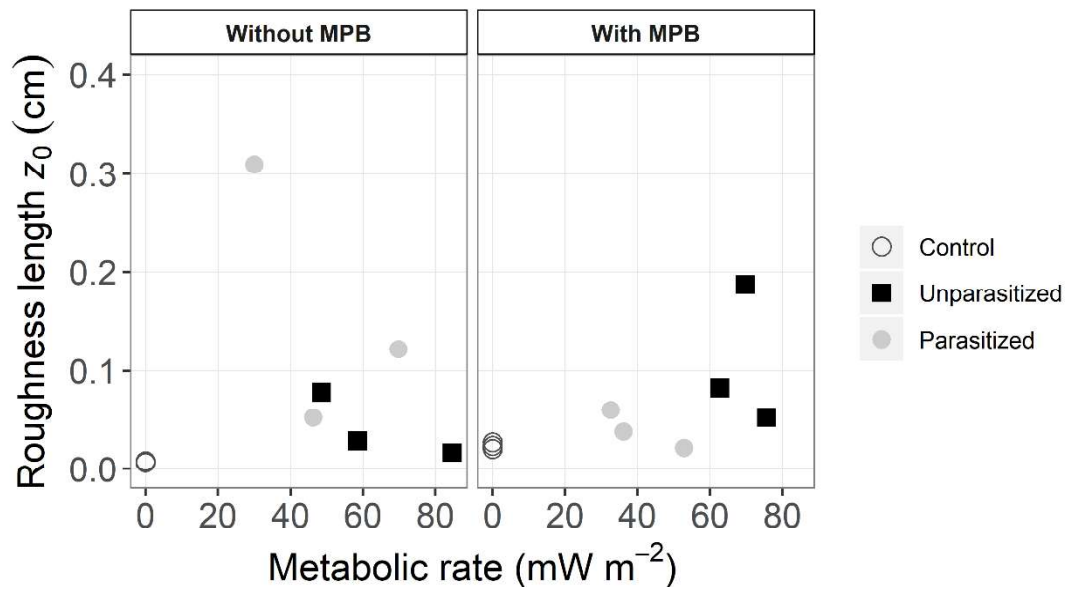
	df	Pseudo-F	P(perm)
<b><i>Chlorophyll a biomass</i></b>			
Cockle (1)	2	5.7	< <b>0.05</b>
MPB (2)	1	187.4	< <b>0.01</b>
(1) x (2)	2	1.1	0.38*
<b><i>Effective quantum yield of photosystem II</i></b>			
Cockle (1)	2	3.0	0.09
MPB (2)	1	53.7	< <b>0.01</b>
(1) x (2)	2	0.8	0.45*
<b><i>Roughness length <math>z_0</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*



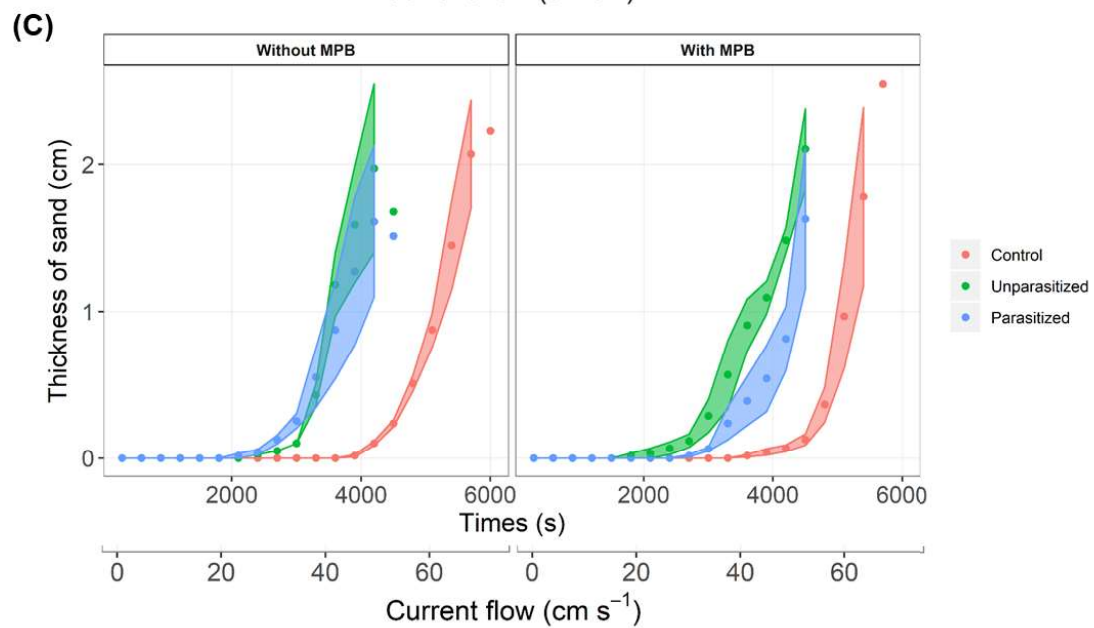
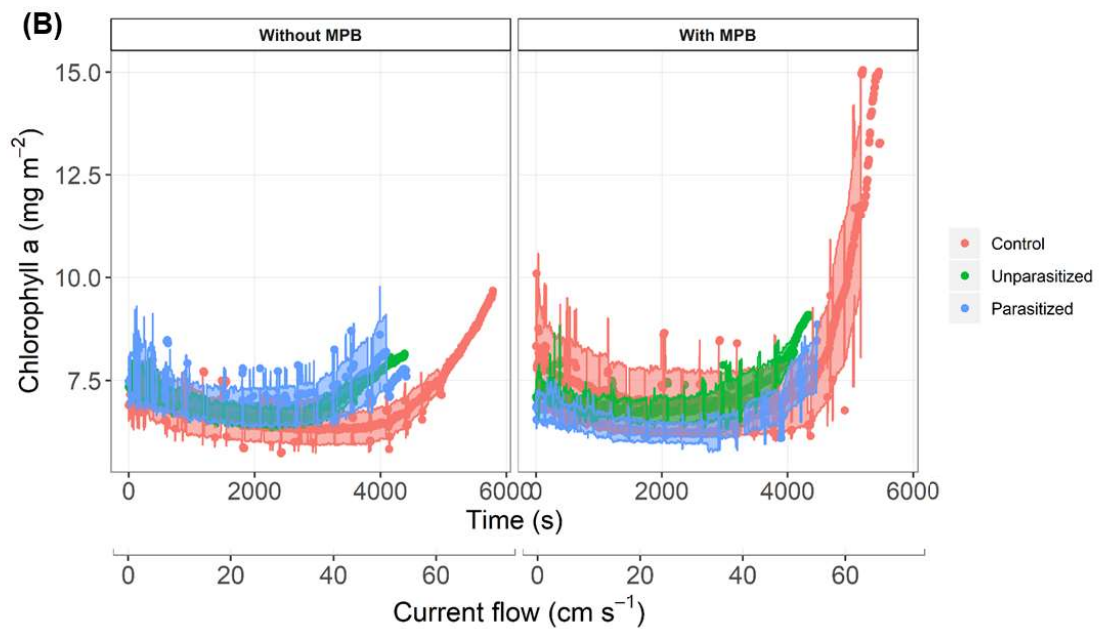
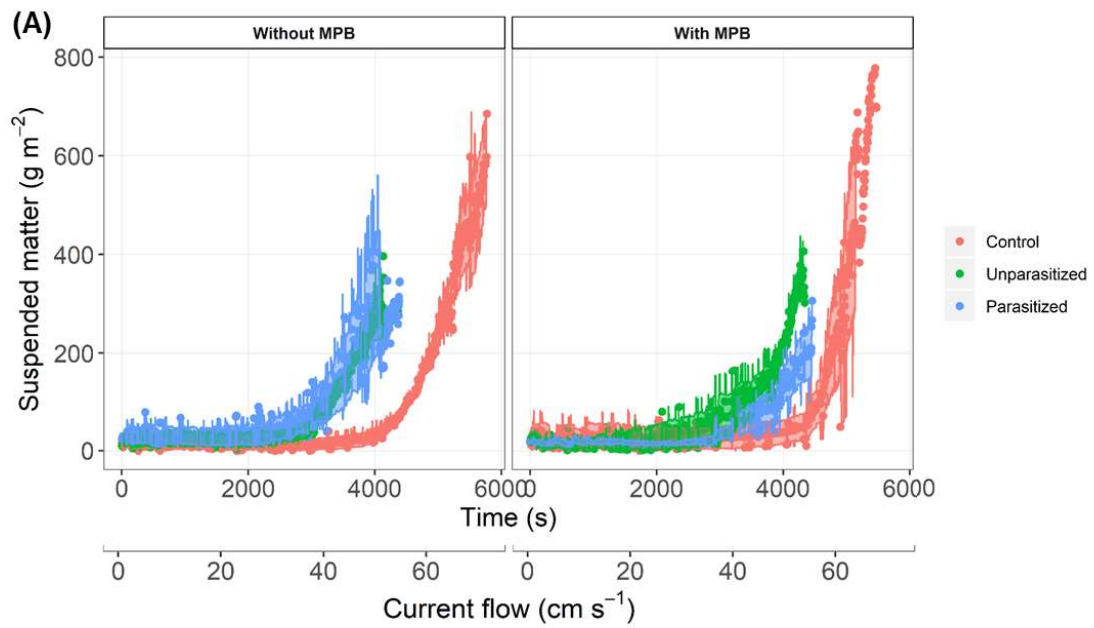
**Fig. 1** Relationships between (A) the biomass of chlorophyll a (mg m<sup>-2</sup>) and (B) associated mean effective quantum yield of photosystem II (“Yield”,  $\frac{\Delta F}{F_m'} = \frac{(F_{m'} - F_m)}{F_m'}$ ) determined in the photic layer at the sediment-water interface of experimental plots 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* (mW m<sup>-2</sup>). 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  $N = 2$ .

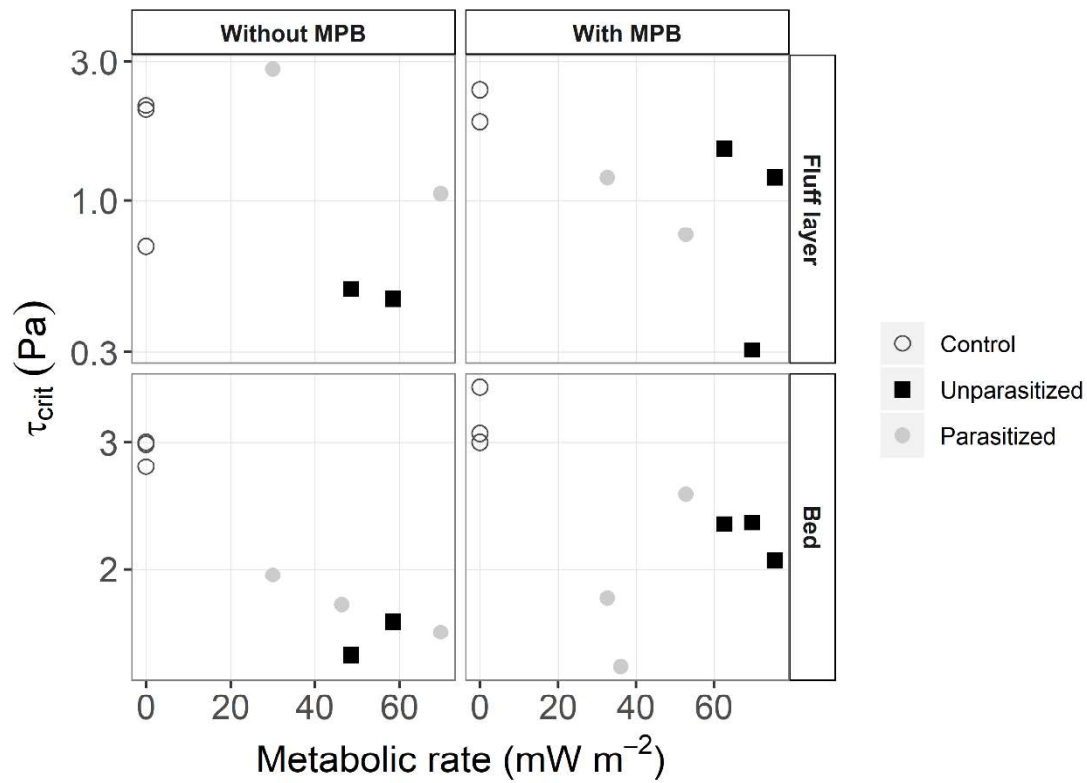


**Fig. 3** Relationship between the roughness length  $z_0$  determined at the surface of sediments unenriched or enriched with microphytobenthos (MPB; “Without MPB” and “With MPB”, respectively) and the metabolic rate of cockles *Cerastoderma edule* unparasitized and parasitized with the trematode *Bucephalus 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  $N = 2$ .

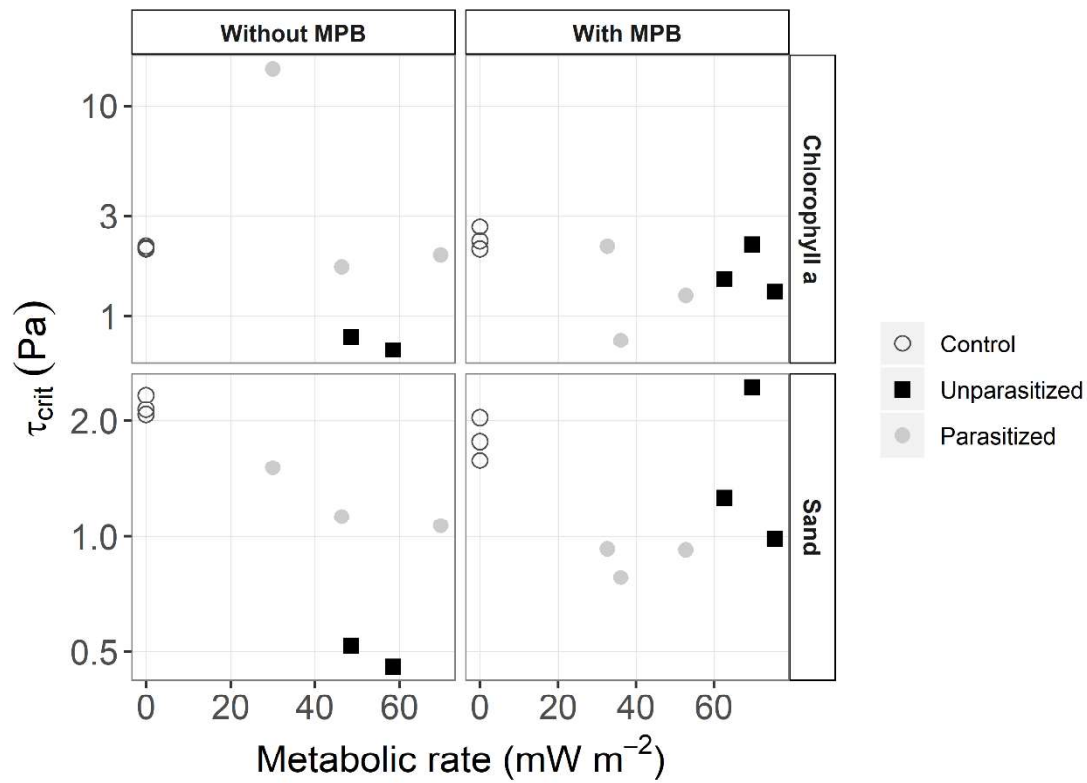


**Fig. 4** Temporal dynamics of the resuspension of (A) the muddy fraction (“Suspended matter”), (B) chlorophyll *a* of microphytobenthos (MPB) biofilms and (C) the sandy fraction of sediment columns unenriched or enriched with microphytobenthos (“Without MPB” and “With MPB”, respectively) and influence 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  $N = 2$ .

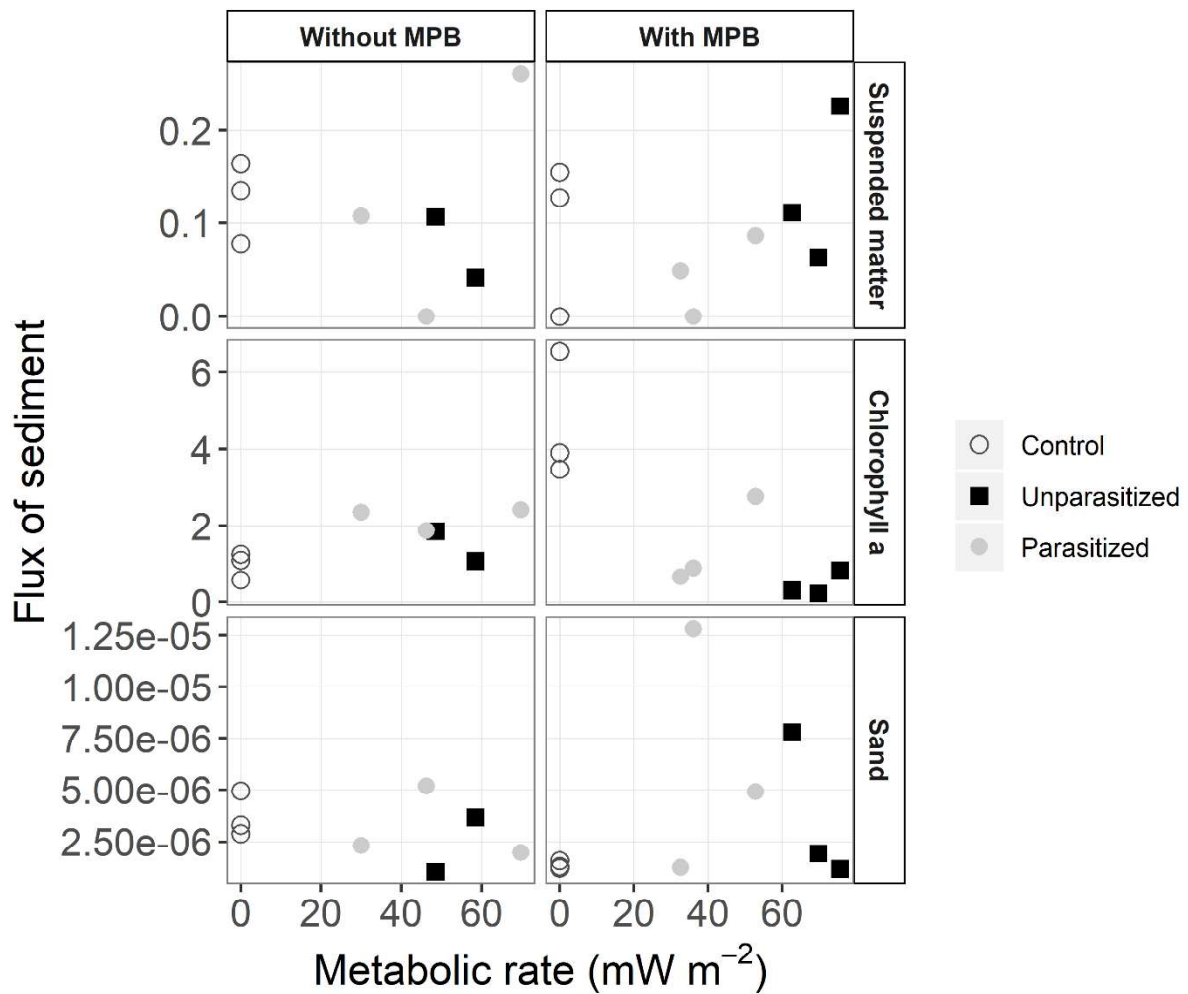




**Fig. 5** Critical bed shear stresses  $\tau_{crit}$  (Pa) for the muddy fraction of sediment columns unenriched and enriched with microphytobenthos (MPB; “Without MPB” and “With MPB”, respectively) as a function of the metabolic rate of cockles *Cerastoderma edule* unparasitized and parasitized with 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* ( $mW m^{-2}$ ). 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”, g m<sup>-2</sup> s<sup>-1</sup>), chlorophyll *a* of microphytobenthic biofilms (mg m<sup>-2</sup> s<sup>-1</sup>) and sand (dm s<sup>-1</sup>) 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* (mW m<sup>-2</sup>). 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: