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

Annabelle Dairain [a,*,1], Olivier Maire [b], Guillaume Meynard [a], Francis Orvain [a]

[a] *Unité Biologie des ORganismes et Ecosystèmes Aquatiques (FRE 2030 BOREA), Sorbonne Université, Muséum National d'Histoire Naturelle, CNRS, Université Pierre et Marie Curie, Université de Caen Normandie, IRD 207, Université des Antilles, Esplanade de la paix, F-14032, Caen, France*
[b] *Univ. Bordeaux, EPOC, UMR CNRS 5805, F-33400 Talence, France*

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 show lowered metabolic rate and likely reduced bioturbation.

GRAPHICAL ABSTRACT
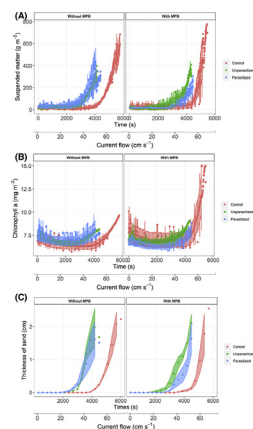
ARTICLE INFO

ABSTRACT

In coastal environments, bioturbators greatly influence the physical and biogeochemical properties of sediments with consequences for central ecological processes such as erosion dynamics. In addition to their direct impact on sediment stability, bioturbators can have an impact on sediment erosion processes by modulating the growth of microphytobenthic organisms that stabilise the surface layer of sediments. The direct and indirect influences of bioturbators on sediment dynamics depend on the magnitude of their activity and inherently on their physiological state. Bioturbators are infected by various parasites, which have a substantial impact on their physiology and behaviour. However, the knock-on effects of parasites on key ecosystem functions like sediment dynamics remain poorly studied. We conducted flume experiments to investigate the indirect influence of the trematode *Bucephalus minimus* parasitising the common cockle *Cerastoderma edule* on the dynamics of sandy sediments enriched or not with microphytobenthos (MPB). Cockles modified bed roughness, sediment surface erodibility and hence destabilised sandy sediments. In sediments not enriched with MPB, both unparasitised and parasitised organisms had a similar impact on the stability of sandy sediments. In contrast, parasitism slightly reduced the destabilisation effect of cockles in MPB-enriched sediments. In the latter, parasitised cockles did not interfere

* Corresponding author at: Marine Biology Research Group, Department of Biology, Ghent University, Krijgslaan 281/S8, Ghent 9000, Belgium.
  E-mail address: annabelle.dairain@ugent.be (A. Dairain).
[1] Present address: Marine Biology Research Group, Department of Biology, Ghent University, Krijgslaan 281/S8, Ghent 9000, Belgium.

Roughness
Sediment erodibility

with MPB growth whereas unparasitised organisms constrained the microalgae development. However, the enrichment of the surface layers of sandy sediments with MPB did not modulate the erosion dynamics of these environments. Thus, the lower destabilisation effect of parasitised cockles was not here linked to a stabilisation effect of MPB. When standardised for length, parasitised cockles were lighter than unparasitised organisms. Weakened cockles may have had a lower bioturbation potential than unparasitised conspecifics. If so, the influence parasitised cockles had on sediment erodibility and sediment roughness may have been reduced. The absence of a parasitism effect on the dynamics of MPB-unenriched sediments remains nonetheless unclear.

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 on the surface of or inside the sediment matrix, greatly impact sediment cohesiveness and thus erodibility. Through their locomotor, feeding, burrowing and ventilating activities, bioturbators induce particle 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 influence sediment properties that in turn, determine their erodibility, including sediment particle size distribution, bulk density and 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. For instance, the protrusion of polychaete tubes into the water column or the presence of bivalve shells on the surface of the sediment bed alters the sediment-water interface topography and modulates the susceptibility of the sediment 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 sediment erodibility by, for instance, modulating the growth of microphytobenthic organisms. Microphytobenthos (MPB) is dominated by diatoms that form biofilms. The framework of these biofilms is created by extracellular polymeric substances (EPS) that are synthetized and exuded by diatoms. EPS increase the adhesion between sediment grains (see Stal, 2010 for a review) thereby stabilising the surface layers of the sediment column (Holland et al., 1974; Miller et al., 1996; Paterson, 1989; Sutherland et al., 1998; Yallop et al., 1994). However, deposit feeders graze on MPB and, as a consequence, interfere with the stabilising role of microphytobenthic biofilms (Kristensen et al., 2013; Orvain et al., 2004). Bioturbators are also responsible for intense sediment reworking that disrupts MPB biofilms and reduces the abundance of microphytobenthic organisms (Brustolin et al., 2016; Montserrat et al., 2009). In sharp contrast, bioturbators can stimulate nutrient fluxes on which MPB relies, thereby enhancing MPB growth and its stabilising effects (Eriksson et al., 2017; Needham et al., 2011; Swanberg, 1991). Bioturbators can also stabilise sediments and reduce the hydrodynamic stress, thereby facilitating the growth of unicellular benthic algae (Donadi et al., 2013). The complex interactions between bioturbators and microphytobenthic organisms thus modulate their respective and combined influence on sediment stability (e.g., Brustolin et al., 2016; Orvain et al., 2014; Swanberg, 1991).

In natural environments, wild organisms are seldom in optimal environmental conditions, and different abiotic and biotic factors can modify their physiology and activity (e.g., MacIntyre et al., 1996; Maire et al., 2007; Ouellette et al., 2004; Pascal et al., 2019). In particular, various stressors can modulate the magnitude of the activity of bioturbators with consequences for ecosystem functioning (Dairain et al., 2018; Premo and Tyler, 2013; Przeslawski et al., 2009; Sturdivant et al., 2012). Behavioural modifications in

particular can regulate the roles played by bioturbating organisms in erosion processes (Orvain et al., 2003a). However, studies that assess the far-reaching consequences of environmental stressors on sediment stability are rare. 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 instance, Ciutat et al. (2006) highlighted a non-linear density dependent effect of the common cockle *Cerastoderma edule* on the stability of a muddy sediment assessed in terms of critical erosion shear stress (U^*_{crit}) and sediment resuspension dynamics through a set of annular flume experiments.

Among potential stressors, the influence of parasitism on bioturbators and their activity has been widely overlooked (Dairain et al., 2019). Yet, parasites are widespread in natural environments (Dobson et al., 2008), where they greatly contribute to total biomass (Kuris et al., 2008). They 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, parasites are key drivers of bioturbator abundance and population size structure (Xavier de Montaudouin et al., 2003; Jensen and Mouritsen, 1992). Secondly, parasites likely modify the phenotypic traits of the bioturbators involved in their functional role, the so-called trait-mediated effects (Mouritsen and Poulin, 2002; Preston et al., 2016). As an illustration, trematode parasites commonly infect the mud snail *Peringia ulvae* (e.g., Xavier de Montaudouin et al., 2003; X. de Montaudouin et al., 2003; Thieltges et al., 2006), thereby significantly reducing the mud snail's mobility (Mouritsen and Jensen, 1994). The mud snail *P. ulvae* greatly affects sediment stability by producing a biogenic "fluff layer" that is easily erodible (Andersen, 2001; Austen et al., 1999; Orvain et al., 2003a, 2006). As a deposit feeder, *P. ulvae* also grazes on MPB, which could interfere with the stabilising effect of microalgae (Austen et al., 1999; Orvain et al., 2004). In a large field study, Mouritsen and Haun (2008) investigated the impact of trematode-uninfected and infected populations of *P. ulvae* on sediment characteristics and MPB community structure. These authors showed that although the parasites did not modify the role of their mud snail host on sediment characteristics (e.g., organic content, granulometry), the parasitised mud snails were associated with a significant decrease in the sediment chlorophyll *a* content and with changes in the diatom community structure. By reducing the mobility of mud snails, parasites may have interfered with the sediment disturbing effect of *P. ulvae* and with the release of nutrients through bioturbation processes, leading to a decline in the MPB biomass. Given 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 (Dairain et al., 2019) and their consequences for sediment stability have never been quantified. Considering the ubiquity of parasites in natural environments, their deleterious effects on the physiology of their bioturbating hosts and their potential impacts on the

behaviour of the hosts, a better understanding of the role of parasites in sediment stability processes is essential. Such studies will also improve the modelling of sediment transport. Therefore, the aim of the present study was to evaluate the indirect influence of parasitism on sediment stability processes, using a widespread bioturbator in intertidal areas of the Northern Hemisphere, the common edible cockle *Cerastoderma edule*. The separate and combined effects of cockles (both parasitised and unparasitised) and MPB on the stability of a sandy sediment with a low proportion of mud were also assessed. Full factorial laboratory mesocosm experiments were performed. We preferred laboratory experiments to field investigations as confounding factors may make it more difficult to study and quantify the role of the selected factors on sediment dynamics.

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 in terms of 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 as an important food resource for birds and benthic invertebrates (see Malham et al., 2012 for a review), and also as an ecosystem engineer species, mainly because of its bioturbation activity. Indeed, while burrowing, migrating into the sediment column and crawling at the sediment surface *C. edule* causes particle movement (Flach, 1996; Mermillod-Blondin et al., 2004) and modifies the sediment matrix (Montserrat et al., 2009). The bioturbation generated by cockles greatly affects the stability of the sediment surface, mainly by increasing the erodibility of the surface of cohesive sediments (Ciutat et al., 2007, 2006; Li et al., 2017; Neumeier et al., 2006). Nonetheless, cockles could also enhance the stabilisation of sandy substrates by promoting biodeposition and increasing the sediment silt content (Soissons et al., 2019; Widdows and Navarro, 2007).

Cockles *C. edule* harbour a wide variety of pathogens and diseases (see de Montaudouin et al., 2009 and Longshaw and Malham, 2013 for reviews). Among them, digenean trematodes are the dominant group with at least 16 species parasitizing *C. edule* (de Montaudouin et al., 2009). Digenean trematodes have 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 infect 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, 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 the 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 organism (Magalhães et al., 2015 and references therein). *B. minimus* has various adverse effects on cockles. The trematode causes serious damages to cockle fecundity. It also causes histological lesions in the cockle's digestive gland, disturbing organ functioning and altering the physiological state of cockles (Longshaw and Malham, 2013; Magalhães et al., 2015 and references therein). Finally, *B. minimus* could alter the behaviour of cockles, which tend to migrate towards the sediment surface (Desclaux et al., 2002). Prevalences of *B. minimus* (i.e. percentae of infected hosts) in wild populations of *C. edule* are generally low. Nonetheless, parasite prevalences can locally (and at certain period) 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. Experimental design

A fully crossed factorial experiment in mesocosm conditions was conducted in March–April 2019, in which we tested the separate and combined influence of cockles parasitised and unparasitised by *B. minimus* ("Cockle" factor) and MPB enrichment ("MPB" factor) on sediment stability. The "Cockle" factor encompassed three levels: no cockles ("Control"), presence of unparasitised cockles ("Unparasitised") and presence of parasitised cockles ("Parasitised") in the experimental plots. The "MPB" factor also had two levels: 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 not enriched with MPB ("Control" - "Without MPB"), (2) no cockles in sediment plots enriched with MPB ("Control" - "With MPB"), (3) presence of unparasitised cockles in sediment plots not enriched with MPB ("Unparasitised" - "Without MPB"), (4) presence of unparasitised cockles in sediment plots enriched with MPB ("Unparasitised" - "With MPB"), (5) presence of parasitised cockles in sediment plots not enriched with MPB ("Parasitised" - "Without MPB"), and (6) presence of parasitised cockles in sediment plots enriched with MPB ("Parasitised" - "With MPB"). Each treatment was replicated three times.

2.3. Experimental setup

2.3.1. 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 *B. minimus* are relatively high (ca. 10%). Back in the laboratory, the cockles were placed in individual plastic containers filled with seawater from Arcachon Bay in order to identify cockles not infected and infected by *B. minimus* via cercariae emission. The seawater in the containers was maintained at ca. 15–16 °C for 24 h. After which each container was placed under a stereomicroscope to detect the emission of cercariae of *B. minimus*. Once identified as not infected or infected by *B. minimus*, the cockles were maintained in a seawater open circuit pending experimentation.

2.3.2. 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, where two relatively dense populations of cockles occur. The sediments were first sieved through a 2 mm mesh to retain macrofauna and debris. Then a mixture of cohesive and non-cohesive sediment was prepared and kept for approximatively a week in the dark before being introduced in the 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 μm). This particular type of sediment is preferentially colonised by *C. edule* (Cozzoli et al., 2013; X. de Montaudouin et al., 2003; Huxham and Richards, 2003).

2.3.3. Microphytobenthos culture

Microphytobenthos biofilms (MPB) were collected on a mudflat in *Baie des Veys* by scratching the sediment surface. An MPB inoculum was then prepared by mixing the biofilms collected in the field with

the muddy sand mixture (see above). The inoculum was kept under an 18:6 h dark-light cycle (light intensity = 46.5 μmol photons m^{-2} s^{-1}) for at least three days in order to stimulate the growth of MPB before adding the inoculum to the surface of the sediment in the experimental plots (see below) (Orvain et al., 2003b). The 6 h of exposure to light corresponds to the diurnal phase of a semi-diurnal tidal cycle.

2.3.4. Mesocosm incubation

The experimental plots consisted of PVC tubes (internal diameter = 9.4 cm, height = 22 cm). Each incubation period lasted nine days (eight days in the "Control" treatment, see below). On day 1 the experimental plots were filled with the slightly muddy sand sediment mixture (sediment column of 21 cm). On day 2, two unparasitised or parasitised cockles of similar size (total length = 22.6–27.8 mm) were added in each experimental plot (density of cockles = 288 ind. m^{-2}). The experimental plots were then placed in a mesocosm in a semi-diurnal tidal cycle (one diurnal emersion phase). On day 3, a 1-cm layer of sediment not enriched or enriched with MPB was added to the surface of the sediment cores. From day 2 to day 9, an 18:6 h night-day alternation regime was applied using cool white lamps (light intensity = 46.5 μmol photon m^{-2} s^{-1}). The day phase corresponded to the diurnal emersion phase. Erosion experiments were conducted on day 9, corresponding to an MPB growth period of six days. The incubations lasted eight days in the "Control" treatments: the 1-cm layer of sediment not enriched or enriched with MPB was added on day 2, and the erosion experiment was performed on day 8. Air-bubbling systems were added in the mesocosm to keep the water fully oxygenated. Approximately 10% of the total volume of mesocosm seawater volume was renewed each day. The seawater temperature over the incubation period averaged 12.0 ± 0.4 °C and the salinity 31.7 ± 0.7 (mean ± SD; daily measurement).

2.4. Microphytobenthos photosynthetic parameters

At the end of the 6-day incubation period, and before the 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). The experimental plots were placed in the dark for ca. 5 min before a low frequency light was applied to determine the minimum level of fluorescence F_0. A saturating light pulse was then applied to determine the maximum fluorescence F_m. The effective quantum yield of the photosystem II ("yield") was determined as follows:

$$yield = \frac{(F_m - F_0)}{F_m} \tag{1}$$

F_0 was used to estimate the photosynthetically active chlorophyll *a* biomass (hereafter referred to 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 μm (Morelle et al., 2018). In this way, we quantified chlorophyll *a* biomasses at the microscale and the values obtained remain low compared to the MPB biomasses usually measured in the top cm of the sediment column (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 superficial sediment photic layer (e.g., Honeywill et al., 2002; Kromkamp et al., 1998).

2.5. 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, 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. This coring procedure could have slightly deformed the surface of the sediment, in particular, a small domed sediment-water interface could have been observed. However, the same method was used for each sample and it is thus likely that each sample showed the same bias. The sample carrier was then inserted into the flume with the sediment surface flush with the bottom of the Erodimetre. The flume was carefully filled with seawater and a current flow was then applied. A frequency device connected to the recirculating water pump was used to gradually increase the current flow from 0 up to ca. 72.5 cm s^{-1} in up to 20 steps. 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 made it possible to continuously record turbidity and to estimate the quantity of chlorophyll *a* in the water. Calibration curves enabled calculation of the concentrations of suspended particulate matter ("suspended matter"; g L^{-1}) and chlorophyll *a* (μg 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 from the sediment sample enabled us to measure the erosion of sand particles. The total volume of the sand trap was 17.7 cm^3; erosion experiments were shortened if the sand trap was filled before the maximum current speed (ca. 72.5 cm s^{-1}) was reached. Finally, the pressure upstream and downstream from the sediment sample was recorded using a pressure sensor (deltabar P70, Endress+Hauser).

Bed shear stress (τ) was 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 (τ_0). Thus, bed shear stresses determined in this study account for bed deformation and for the presence of physical objects that could protrude at the sediment-water interface, such as cockle shells. Accordingly, shear velocities U* (m s^{-1}) were calculated as follows:

$$U^* = \sqrt{\tau_0 / \rho} \tag{2}$$

where τ_0 is the bed shear stress (Pa) and ρ is the seawater volumetric mass density (1024 kg m^{-3}) (Supplement S1).

The so-called von Karman-Prandtl "law of the wall" (Eq. (3)) relationship was used to estimate the roughness length z_0 (cm) for each sample (Orvain et al., 2003a):

$$U(z) = \frac{U^*}{k} \ln\left(\frac{z}{z_0}\right) \tag{3}$$

where k is the von Karman 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 due to movements of the cockles. Therefore, linear regressions were used on reduced ranges of current flows that only included the linear part of the curve, i.e. when the bed topography was not yet deformed by ongoing erosion processes (Supplement S2). The linear regression slope determined for each sample allowed us to integrate the "law of the wall" as follows:

$$\overline{U} = \frac{U^*}{k} \ln\left(\frac{h}{exp(1) z_0}\right) \tag{4}$$

where h is the height of the Erodimetre 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 $\log_{10}$ $(U^* + 1)$:

$$y = a \log_{10}(U^* + 1) + b \tag{5}$$

$$U^*_{crit} = 10^{\frac{(y-b)}{a}} - 1 \tag{6}$$

where U^*_{crit} is the critical shear velocity for erosion (m s^{-1}), y the chlorophyll a concentration in the water column (μg L^{-1}) or the thickness of eroded sand (cm). Then, the critical bed shear stress for the chlorophyll a of the MPB biofilm and the sand fraction of the sediment column were calculated as follows:

$$\tau_{crit} = \rho\, U^{*2}_{crit} \tag{7}$$

The concentration of suspended matter in the water column (turbidity) was recorded as a proxy of the erosion of the mud fraction of the sediment column. Regarding this fraction, it was possible to distinguish erosion of the biogenic fluff layer from erosion of the sediment bed ("mass erosion", Supplement S3 and Supplement S4). Therefore, both critical erosion thresholds of the biogenic fluff layer and of the sediment bed were determined following the procedure described above.

Finally, mean erosion rates of the MPB biofilm, mud fraction and sand fraction at the sediment-water interface were calculated over the three steps following the critical erosion incipient point taking into account the volume of the Erodimetre and the surface of the sediment sample. Regarding the mud fraction, only fluxes that occurred after the erosion of the biogenic fluff layer were calculated. The Matlab computing environment (v. 2019a, MathWorks) was used.

2.6. Dissection of cockles

Following the erosion experiment, the cockles were placed in a seawater open circuit for 24 h before being dissected to check their parasitic status. First, the length of the cockles shell was measured using a digital calliper. The shell was then opened by cutting the posterior adductor muscle, all soft tissues were extracted and squeezed between two transparent glass plates under a stereomicroscope to check for infection with *B. minimus*. The soft tissues were then dried for at least 48 h at 60 °C and weighted (dry weight, DW).

2.7. Statistical analyses

A Student's t-test was used to assess the difference in DW standardised for shell length between unparasitised and parasitised cockles. The influence of cockle and MPB enrichment on (1) growth of the MPB at the sediment surface of the experimental plots following the 6-day incubation period, (2) critical bed shear stresses (τ_{crit}) of the different sediment fractions (chlorophyll a, mud fraction and sand fraction) and (3) fluxes of chlorophyll a, mud particles (suspended matter) and sand at the sediment-water interface during the 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, "Cockles" (3 levels: "Control", "Unparasitised", "Parasitised") 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 biomass of cockles and (1) the growth of MPB at the sediment-water interface, (2) the critical bed shear stress (τ_{crit}) of the different sediment fractions (chlorophyll a, mud and sand fractions) and (3) the fluxes of chlorophyll a, mud 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 at $p < 0.05$. All statistical analyses were performed using the free computing environment R (R Core Team, 2019).

3. Results

Dissections showed that one of the two cockles in one of the "Unparasitised" - "Without MPB" treatment was infected by 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, personal obs.), this replicate was excluded from our analyses. Therefore, there were only two replicates for the "Unparasitised" - "Without MPB" treatment while there were three replicates for the others.

3.1. Biomass of cockles

The individual biomass of unparasitised and parasitised of cockles was respectively 152.7 ± 12.0 and 102.2 ± 14.6 mg DW (mean ± SE). On averaged, parasitised cockles were 27.3% lighter than unparasitised organisms when standardised for shell length (t-test, $t = 2.47$, $p < 0.05$).

3.2. Microphytobenthos growth

3.2.1. Biomass of chlorophyll a

Following the 6-day incubation period, chlorophyll a biomass ranged between 0.17–0.42 and 0.79–1.17 mg m^{-2} in the sediment photic layers of the experimental plots "Without MPB" and "With MPB", respectively (Fig. 1A). The biomasses of chlorophyll a at the sediment surface of the experimental plots "With MPB" were significantly higher than in the plots "Without MPB" (Fig. 1A, Table 1). The chlorophyll a biomass was significantly reduced in the experimental plots with unparasitised cockles compared to the biomass in the plots without cockles. Conversely, there was no significant difference in chlorophyll a biomass between "Control" and "Parasitised" (Fig. 1A, Table 1). Finally, there was no significant interaction between the "Cockle" and "MPB" factors on the chlorophyll a biomass (Table 1).

The biomass of chlorophyll a in the photic layer of the sediment column decreased significantly with an increase in the biomass of cockle populations (Fig. 1A; ANCOVA, $F = -4.6$, $p < 0.01$). The slope of the relationship between both variables did not vary with MPB enrichment (ANCOVA, $p = 0.96$).

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 surface of the experimental plots "Without MPB" and "With MPB", respectively (Fig. 1B). Effective quantum yields of the PSII were significantly lower in the experimental plots "Without MPB" compared to the plots "With MPB" (Table 1). In contrast, there was no significant influence of the "Cockle" factor on the effective quantum yield of the PSII and no interactive effects between the "Cockle" and "MPB" factors (Fig. 1B, Table 1).

The effective quantum yield of the PSII decreased significantly with an increase in the biomass of cockle populations (Fig. 1B; ANCOVA, $F = -4.6$, $p < 0.01$). The slope of the relationship between these two variables did not vary significantly with MPB enrichment (ANCOVA, $p = 0.054$).
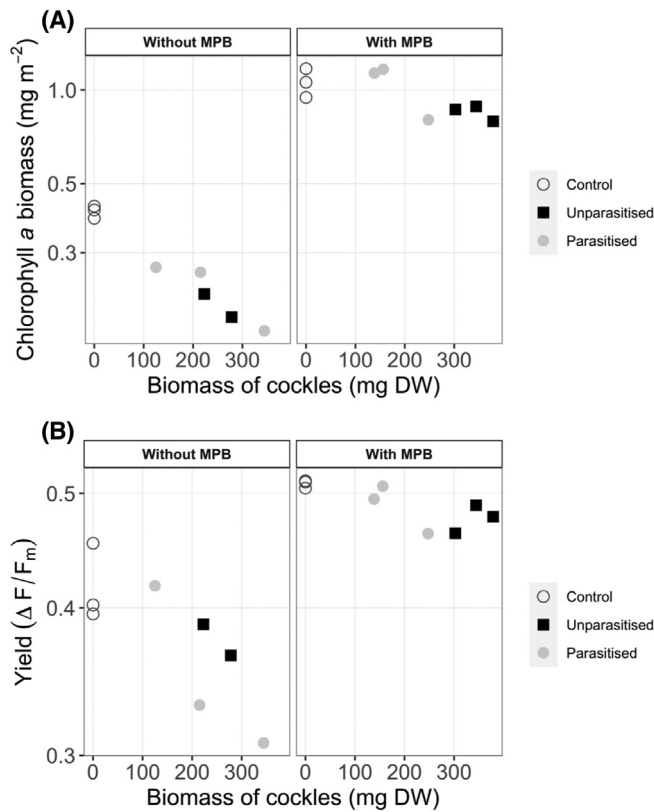
Fig. 1. Relationships between (A) the biomass of chlorophyll a (mg m^{-2}) and (B) associated mean effective quantum yield of photosystem II ("Yield") measured in the photic layer at the sediment-water interface of experimental plots not enriched and enriched with microphytobenthos (MPB; "Without MPB" and "With MPB", respectively) and the biomass of cockles *Cerastoderma edule* unparasitised and parasitised by the trematode *Bucephalus minimus* (mg dry weight). "Control" = experimental plots without cockles. $N = 3$ for each treatment, except for the treatment "Unparasitised" – "Without MPB" for which $N = 2$.

3.3. Shear velocity dynamics

The influence of cockles *C. edule* on the dynamics of shear velocity (U*, cm s^{-1}) at the sediment surface 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 cm s^{-1} at the sediment surface of the experimental plots "Without MPB" and "With MPB", respectively (Fig. 2). Overall, U* increased with the current flow. For the "Control" - "Without MPB" samples, we observed a decrease in U* at high current flows, evidence for modifications in bed topography (and hence roughness) with the ongoing erosion.

In more detail, for the "Without MPB" - "Control" plots, U* slightly decreased from ca. 3.3 cm s^{-1} to ca 2.0 cm s^{-1} with the current flow increasing up to 17.5 cm s^{-1}. This initial decrease in U* is an artefact. Air bubbles were initially present on the plexiglass sides of the Erodimeter. The initial increases in the water current in the Erodimeter drove out these bubbles and influenced the head loss between the upstream and downstream parts of the samples (current flow ca. 10–15 cm s^{-1}). As a result, we recorded a decrease in U*. After this initial decrease, U* linearly increased up to ca. 5.1 cm s^{-1}. This maximum U* was reached with a current flow of ca. 50 cm s^{-1}. Finally, U* decreased and reached ca. 4.5 cm s^{-1} at the end of the erosion experiment (maximum current flow = 62 cm s^{-1}) (Fig. 2). U* dynamics at the surface of the experimental plots "With MPB" - "Control" was very similar to the latter pattern. However, there was no decrease in U* at the highest current flows, which reached a stable value starting from a current flow of ca. 50 cm s^{-1} (Fig. 2). For the two "Control" treatments (i.e., without and with MPB), there was little variability between the replicates.

Table 1

Results of PERMANOVA analyses of the influence of the "Cockle" ("Control", i.e. no cockles, "Unparasitised", i.e. presence of unparasitised cockles and "Parasitised", i.e. presence of parasitised 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 effects ($p < 0.05$). * denotes significant differences in dispersion (PERMDISP analysis, p < 0.05).

	df	Pseudo-F	P(perm)
Chlorophyll *a* biomass			
Cockle (1)	2	5.7	**<0.05**
MPB (2)	1	187.4	**<0.01**
(1) × (2)	2	1.1	0.37*
Effective quantum yield of photosystem II			
Cockle (1)	2	3.0	0.09
MPB (2)	1	53.7	**<0.01**
(1) × (2)	2	0.8	0.45*
Roughness length *z*₀			
Cockle (1)	2	2.8	0.07*
MPB (2)	1	0.5	0.55
(1) × (2)	2	2.8	0.08*
Critical bed shear stress (τ_{crit})			
Biogenic fluff layer – muddy fraction			
Cockle (1)	2	5.5	**<0.05**
MPB (2)	1	0.33	0.59
(1) × (2)	2	1.32	0.31*
Mass erosion – muddy fraction			
Cockle (1)	2	0.3	0.93
MPB (2)	1	0.8	0.85
(1) × (2)	2	2.4	0.08
Chlorophyll a			
Cockle (1)	2	0.7	0.48*
MPB (2)	1	1.0	0.48*
(1) × (2)	2	1.2	0.19*
Sandy fraction			
Cockle (1)	2	3.9	0.06
MPB (2)	1	0.4	0.53
(1) × (2)	2	3.2	0.08*
Sediment fluxes			
Muddy fraction			
Cockle (1)	2	0.6	0.60
MPB (2)	1	5.1	0.05
(1) × (2)	2	1.5	0.28
Chlorophyll a of MPB biofilms			
Cockle (1)	2	1.4	0.28
MPB (2)	1	0.06	0.89
(1) × (2)	2	2.7	0.08*
Sandy fraction			
Cockle (1)	2	0.6	0.63
MPB (2)	1	0.1	0.79*
(1) × (2)	2	0.9	0.48*

At the sediment surface of the plots "Without MPB" - "Unparasitised", U* decreased slightly from ca. 1.2 to 0.66 cm s^{-1} with an increased in the current flow from ca. 0.6 to 8.1 cm s^{-1} (artefact due to air bubbles along the plexiglass walls that were driven out). Then, U* increased up to ca. 5.1 cm s^{-1} (current flow = ca. 44.7 cm s^{-1}). Overall, a similar pattern was observed at the surface of the experimental plots "With MPB" - "Unparasitised". Nonetheless, the variability between the replicates was high. In particular, in one replicate, U* reached 14.1 cm s^{-1} (current flow = 48.1 cm s^{-1}) at the end of the erosion experiment, while it reached 6.4 cm s^{-1} in the two other experiment.

At the surface of the experimental plots "Without MPB" - "Parasitised", U* decreased slightly from ca. 1.2 to 0.31 cm s^{-1} with an increase in the current flow from ca. 0.6 to 3.1 cm s^{-1}. Once again, this initial decrease of U* is an artefact related to air bubbles along the wall sides of the Erodimeter that were driven out. Then, U* increased up to ca. 6.2 cm s^{-1} (current flow = ca. 44.7 cm s^{-1}). In one of the replicates, U* reached 16.0 cm s^{-1} (current flow = 42.5 cm s^{-1}) at the end of the
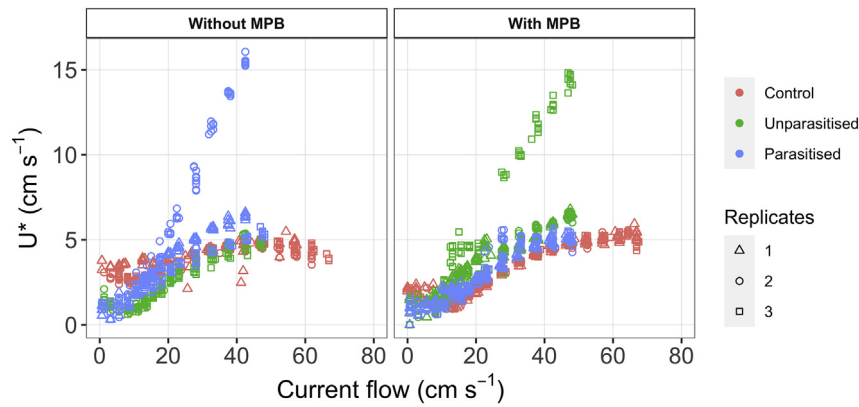
Fig. 2. Dynamics of the shear velocity U* across a gradient of current flow (cm s^{-1}) for sediment plots not enriched or enriched with microphytobenthos (MPB; "Without MPB" and "With MPB", respectively) and influence of the cockle *Cerastoderma edule* unparasitised ("Unparasitised") and parasitised ("Parasitised") by the trematode *Bucephalus minimus*. "Control" = experimental plots without cockles. Three individual replicates (N = 3) were made for each treatment, except for the treatment "Unparasitised" – "Without MPB" for which N = 2.

erosion experiment, whereas it was only ca. 5.8 cm s^{-1} in the two other experiments. In contrast, there was little variability in the dynamics of U* at the sediment surface of the plots "With MPB" - "Parasitised". In the latter case, U* decreased from ca. 0.99 to 0.62 cm s^{-1} with an increase in the current flow from ca. 0.6 to 8.4 cm s^{-1}. U* then increased up to ca. 5.5 cm s^{-1} (current flow = ca. 44.4 cm s^{-1}).

Therefore, MPB enrichment or cockles did not influence U* dynamics. The presence of the bivalve increased U* (higher values of U* compared with the "Control" treatments). Parasitism did not influence U* dynamics independently of MPB enrichment. However, there was an interactive effect between parasitism and MPB enrichment on U*. In the experimental plots "Without MPB", U* was higher in the "Parasitised" plots than in the "Unparasitised" plots. The opposite trend was observed in the experimental plots "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; Supplementary S2). z_0 ranged between 0.064–0.31 and 0.020–0.19 cm in the experimental plots "Without MPB" and "With MPB", respectively (Fig. 3). There was no significant effect of the "Cockle" and "MPB" factors alone on z_0 nor an interactive effect (Fig. 3, Table 1). z_0 significantly increased with an increase in the biomass of the cockle populations (Fig. 3; ANCOVA, F = 3.6, p < 0.01). The slope of the relationship between the two variables did not vary with MPB enrichment (ANCOVA, p = 0.20).
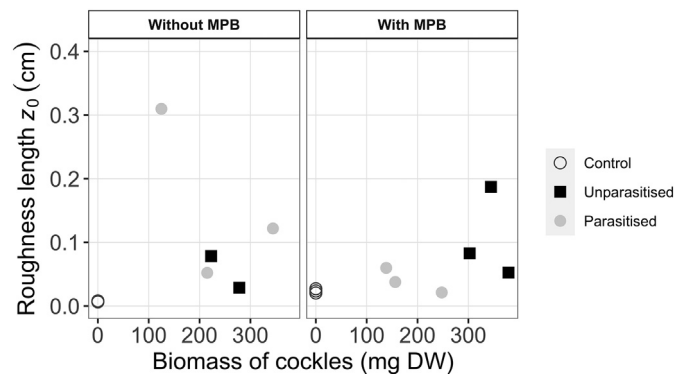

Fig. 3. Relationship between the roughness length z_0 measured at the surface of sediments not enriched or enriched with microphytobenthos (MPB; "Without MPB" and "With MPB", respectively) and the biomass of cockles *Cerastoderma edule* unparasitised and parasitised by the trematode *Bucephalus minimus* (mg dry weight). "Control" = experimental plots without cockles. N = 3 for each treatment, except for the treatment "Unparasitised" – "Without MPB" for which N = 2.

3.4. Sediment resuspension dynamics and erodibility

The erosion potential of unparasitised and parasitised cockles and the influence of MPB on sediment stability was measured in terms of suspended sediment concentration (chlorophyll *a* of MPB biofilms, mud fraction and sand fraction were differentiated) and critical bed shear stress for erosion (τ_{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

Overall, the concentration of suspended matter increased exponentially as a function of the increasing current flow (Fig. 4A). We first observed the erosion of a biogenic fluff layer at low current velocity (Supplement S4), followed by bed erosion (i.e., mass erosion) at the highest current velocities (Supplement S4). Biofilms of MPB did not influence the kinetics of the erosion of the mud fraction (Fig. 4A). Cockles destabilised the sediment plots, that is the mud fraction of the sediment column was eroded at lower current velocity (ca. 13 to 28 cm s^{-1}) compared to the "Control" treatment (ca. 32 to 47 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 that occurred at a slightly higher current flow, compared with the "Unparasitised" 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 the experimental plots "Without MPB" and "With MPB" ranged 5.7–9.7 and 6.1–15.1 mg m^{-2}, respectively (Fig. 4B). The different experimental treatments showed similar erosion kinetics for chlorophyll *a*, that is the chlorophyll *a* concentration first decreased with an increase in the current flow. Above a flow ranging 25–45 cm s^{-1}, there was then an increase in the concentration of chlorophyll *a* with an increase in the current flow (Fig. 4B). The erosion of chlorophyll *a* was initiated at a lower current flow when cockles inhabited the sediment plots. There was no effect of parasitism and MPB enrichment on the erosion kinetics of chlorophyll *a* (Fig. 4B).

3.4.3. Sand fraction

Fig. 4C illustrates the thickness of eroded sand during the erosion experiments. The thickness of eroded sand increased exponentially as a
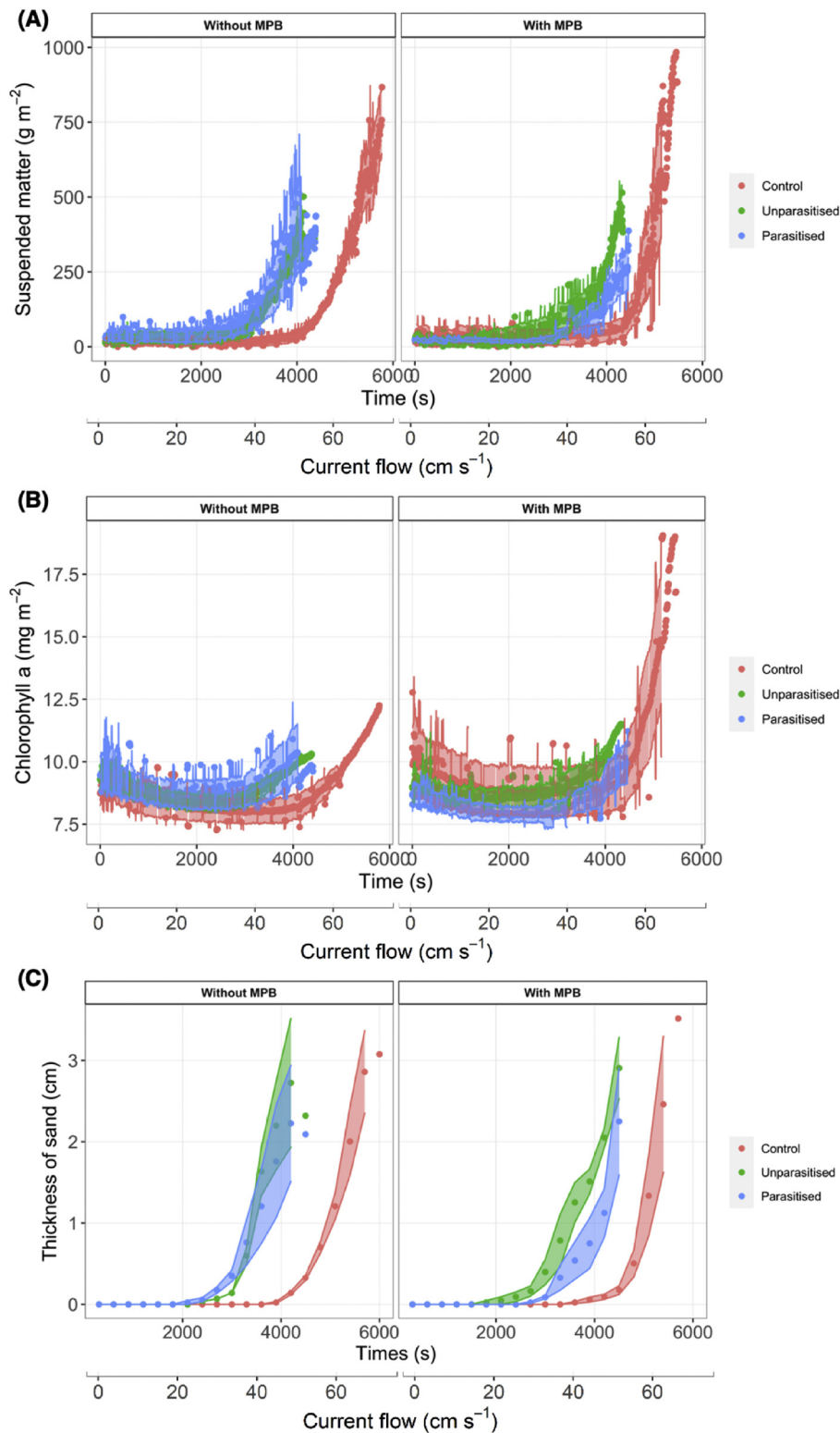
Fig. 4. Temporal changes in the resuspension dynamics of (A) the muddy fraction ("Suspended matter"), (B) chlorophyll *a* of microphytobenthos (MPB) biofilms and (C) the sandy fraction of sediment columns not enriched or enriched with microphytobenthos ("Without MPB" and "With MPB", respectively) and influence of the cockle *Cerastoderma edule* unparasitised ("Unparasitised") and parasitized ("Parasitised") by the trematode *Bucephalus minimus* on sediment resuspension. "Control" = experimental plots without cockles. Mean masses eroded are plotted. Coloured areas represent the standard error around the mean. *N* = 3 for each experimental treatment, except for the treatment "Unparasitised" – "Without MPB" for which *N* = 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

function of the increasing current flow for the different experimental treatments. Sand particles were eroded at a lower current flow when sediments were inhabited by cockles. In contrast, there was no

influence of the "MPB" factor on the erosion kinetics of sand particles. "Without MPB", the parasite *B. minimus* did not influence the resuspension dynamics of the sand fraction whereas parasitism delayed its

erosion in the plots "With MPB". Indeed, erosion of sand occurred at a higher current flow for the "Parasitised" treatment compared with the "Unparasitised" one.

3.5. Critical bed shear stress

3.5.1. Mud fraction

Regarding the mud 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, Supplement S4). Critical bed shear stresses (τ_{crit}) for the biogenic fluff layer ranged between 0.5–2.9 and 0.4–2.1 Pa in the experimental plots "Without MPB" and "With MPB", respectively (Fig. 5). There was no significant influence of "MPB" and no interactive effect between the "Cockle" and "MPB" factors on τ_{crit} for the biogenic fluff layer (Table 1). In contrast, the presence of cockles decreased significantly τ_{crit} (Fig. 5, Table 1). τ_{crit} for the biogenic fluff layer decreased significantly with an increase in the biomass of cockle populations (ANCOVA, $F = -3.8$, $p < 0.01$). This relationship was not influenced by the enrichment with MPB (ANCOVA, $p = 0.29$).

τ_{crit} for the sediment bed ranged between 0.84–11.7 and 0.80–5.62 Pa for the experimental plots "Without MPB" and "With MPB", respectively (Fig. 5). There was no significant influence of the "MPB" and "Cockle" factors, and no interactive effect between them on τ_{crit} for the sediment bed (Table 1). There was no significant relationship between τ_{crit} for the sediment bed and the biomass of cockle populations, irrespectively of the enrichment with MPB (Fig. 5; ANCOVA, $p = 0.98$).

3.5.2. Chlorophyll a fraction

Critical bed shear stresses (τ_{crit}) for the chlorophyll *a* of MPB biofilms ranged between 0.8–14.7 and 0.8–2.5 Pa in the experimental plots "Without MPB" and "With MPB", respectively (Fig. 6). There were no significant effects of the "Cockle" and "MPB" factors on τ_{crit}, and no interactive effect between them (Table 1). There was no significant relationship between τ_{crit} and the biomass of cockle populations, irrespectively of the enrichment with MPB (Fig. 6; ANCOVA, $p = 0.23$).
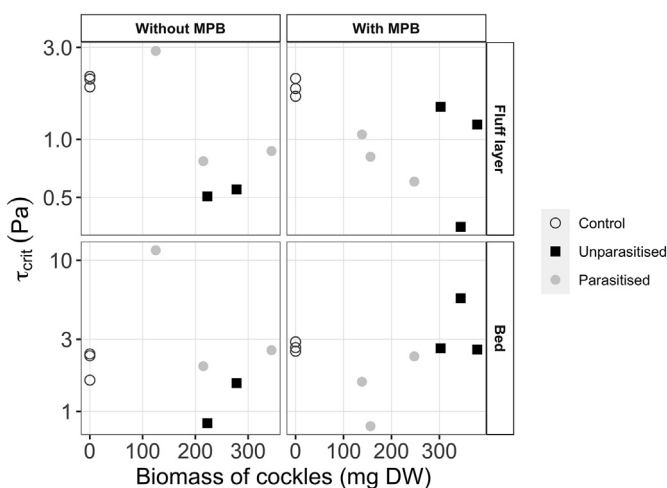
Fig. 5. Critical bed shear stresses τ_{crit} (Pa, logarithmic scale) for the mud fraction of sediment columns not enriched and enriched with microphytobenthos (MPB; "Without MPB" and "With MPB", respectively) as a function of the biomass of cockles *Cerastoderma edule* (mg dry weight) unparasitised and parasitised by the trematode *Bucephalus minimus*. Critical bed shear stresses of the biogenic fluff layer and of the sediment bed (mass erosion) are distinguished. "Control" = experimental units without cockles. $N = 3$ for each treatment, except for the treatment "Unparasitised" – "Without MPB" for which $N = 2$.
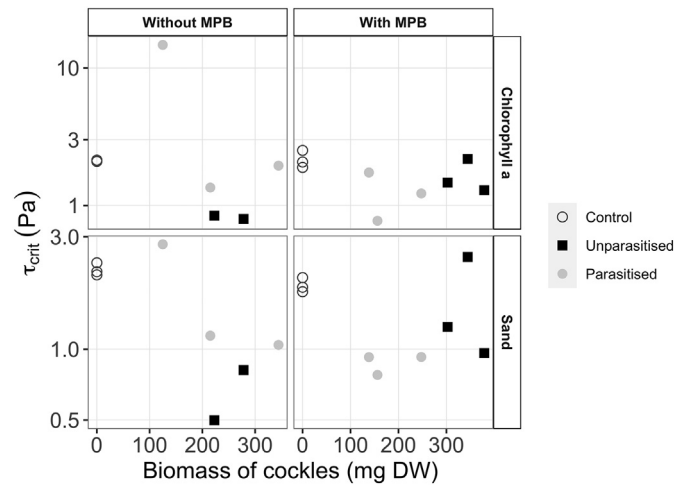
Fig. 6. Critical bed shear stresses τ_{crit} (Pa, logarithmic scale) for the chlorophyll *a* of microphytobenthos biofilms and sandy fraction of sediment columns not enriched and enriched with microphytobenthos (MPB; "Without MPB" and "With MPB", respectively) as a function of the biomass of cockles *Cerastoderma edule* (mg dry weight) unparasitised and parasitised by the trematode *Bucephalus minimus* (mW m^{-2}). "Control" = experimental units without cockles. $N = 3$ for each treatment, except for the treatment "Unparasitised" – "Without MPB" for which $N = 2$.

3.5.3. Sand fraction

Critical bed shear stresses (τ_{crit}) for the sand fraction of the sediment ranged between 0.8–2.8 and 0.8–2.5 Pa in the experimental plots "Without MPB" and "With MPB", respectively (Fig. 6). There were no significant effects of the "Cockle" and "MPB" factors on τ_{crit}, and no interactive effect between them (Table 1). τ_{crit} significantly decreased with an increase in the biomass of cockle populations (Fig. 6; ANCOVA, $F = -2.6$, $p < 0.05$). This relationship was not affected by the enrichment with MPB (Fig. 6; ANCOVA, $p = 0.12$).

3.6. Sediment erosion fluxes

3.6.1. Mud fraction

Erosion fluxes of fine particles of the biogenic fluff layer (mud fraction, "suspended matter") at the sediment-water interface of the experimental plots "Without MPB" and "With MPB" ranged between 0.07–0.33 and 0.007–0.16 g m^{-2} s^{-1}, respectively (Fig. 7). There were no significant effects of the "MPB" and "Cockle" factors, and no interactive effect between them on the fluxes of fine particles (Table 1). There was no significant relationship between the erosion flux of fines particles at the sediment-water interface and the biomass of the population of cockles, independently of the enrichment with MPB (Fig. 7; ANCOVA, $p = 0.73$).

3.6.2. Chlorophyll a fraction

Fluxes of chlorophyll *a* at the sediment-water interface of the experimental plots "Without MPB" and "With MPB" ranged between 0.87–3.07 and 0.28–8.29 µg m^{-2} s^{-1}, respectively (Fig. 7). There was no significant effect of the "MPB" and "Cockle" factors, and no interactive effect between them (Table 1).

A significant decrease of the flux of the chlorophyll *a* with an increase in the biomass of cockle populations was observed in the experimental plots enriched with MPB (Fig. 7; ANCOVA, $F = -2.3$, $p < 0.05$).

3.6.3. Sand fraction

Erosion fluxes of sand at the sediment-water interface of the experimental plots "Without MPB" and "With MPB" ranged between 13.1–65.3 and 14.9–162.0 µm s^{-1}, respectively (Fig. 7). There was no significant effect of the "Cockle" and "MPB" factors, and no interactive effect between them (Table 1). The erosion flux of sand did not vary
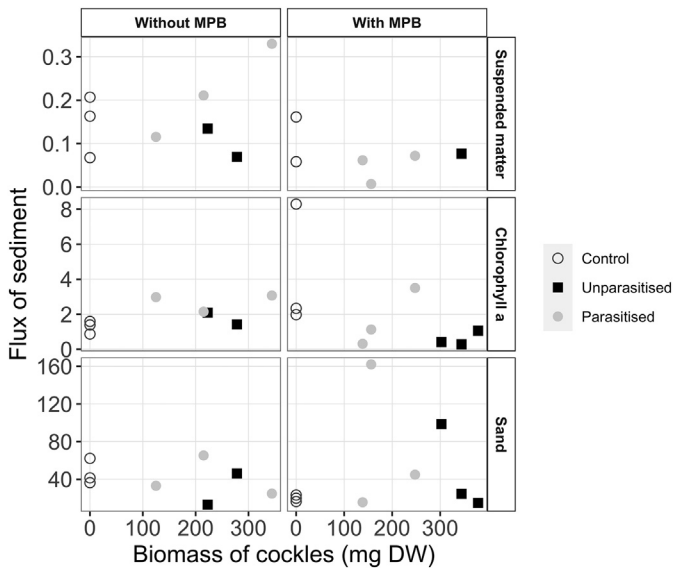
Fig. 7. Fluxes of fine particles ("Suspended matter", g m^{-2} s^{-1}), chlorophyll *a* of microphytobenthic biofilms (μg m^{-2} s^{-1}) and sand (μm s^{-1}) at the sediment-water interface of experimental plots not enriched and enriched with microphytobenthic organisms ("Without MPB" and "With MPB", respectively) as a function of the biomass of cockles *Cerastoderma edule* (mg dry weight) unparasitised and parasitised by the trematode *Bucephalus minimus*. Fluxes were determined over the three erosion steps which followed critical erosion incipient point for each of the different fraction of the sediment column. Regarding the fine particles, fluxes were calculated when erosion of the biogenic fluff layer began. "Control" = experimental units without cockles. *N* = 3 for each experimental condition, except for the treatment "Unparasitised" – "Without MPB" for which *N* = 2.

with the biomass of cockle populations, independently of the MPB enrichment (Fig. 7; ANCOVA, *p* = 0.95).

4. Discussion

In this study, we evaluated the indirect impact of the trematode parasite *Bucephalus minimus* infecting cockles *Cerastoderma edule* on the stability of a sandy sediment with a very low proportion of fine particles (mud = 4.4%). The combined effects of unparasitised and parasitised cockles and microphytobenthos (MPB) on sediment stability were also assessed. We hypothesised that parasites, through their deleterious effects on the host physiology, may lower their bioturbation rates, thereby influencing sediment dynamics. If so, MPB not enriched and enriched sediments should be less destabilised by parasitised cockles than by unparasitised ones. Indeed, sediments inhabited by parasitised cockles should be less rough as a result of the lower level of activity of parasitised organisms, especially with regards to their mobility. Moreover, parasitised cockles may have a lower physical destructing effect on MPB than unparasitised organisms. MPB should thus have a higher stabilisation effect in presence of parasitised cockles than with unparasitised organisms.

4.1. Influence of parasitism on cockles

The parasite *B. minimus* negatively affected the biomass of *C. edule*, with parasitised organisms 27% lighter than unparasitised conspecifics when standardised for shell length. However, the biomasses determined in this study took both the cockle and parasite biomasses into account. 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" biomass of cockles alone was likely even lower than determined here.

The ecological metabolic theory stipulates that the metabolic rate of organisms, especially respiration, is proportional to their size and

mass (Brown et al., 2004). Based on this theory, Brey (2010) developed a method to determine the metabolic rates of an organism from its biomass. More recently, Cozzoli et al. (2018, 2019) proposed a framework to upscale the influence of bioturbators on sediment dynamics from their metabolic rates. These authors indeed suggest that the individual metabolic rate of a bioturbator could be used as an index of its bioturbation rate (mass of sediment eroded). Since we provide evidence that parasitised cockles are lighter than unparasitised organisms when standardised for shell length, it is possible that the parasite *B. minimus* also negatively affects the metabolic rate of its host (Brey, 2010) which would thus exhibit a lower bioturbation activity (Cozzoli et al., 2018, 2019). Nonetheless, we refrained from calculating and using the metabolic rates of parasitised and unparasitised cockles in our analyses because the model developed by Brey (2010) to determine the metabolic rate of organisms from their weight does not take parasitism as a forcing variable into account. The trematode *B. minimus* could increase the metabolic demand of cockles (Magalhães et al., 2017) and estimating the metabolic rate of parasitised cockles using Brey's method may thus lead to an underestimation of the actual metabolic rate of these organisms. In contrast, we suggest that using the upscale theory developed by Cozzoli et al. (2018, 2019) will here lead to overestimate the bioturbation activity of cockles. Indeed, by stimulating the energetic metabolic demand of its host, parasites could reduce the energy available for other activities, especially those related to locomotion (Mouritsen and Jensen, 1994), and hence bioturbation. In other words, it is possible that the bioturbation activity of parasitised cockles would be reduced even though organisms would show a high metabolic rate. In the aim of accurately estimating organisms' metabolic rates from their weight and upscaling the influence of bioturbators on sediment dynamics from this estimate, it thus appears crucial to take parasitism influence in metabolic models into account.

4.2. Influence of parasitised cockles on hydrodynamics and sediment roughness

Sediment dynamics depends on sediment erodibility, 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 erodibility as observed for gastropod snails (Orvain et al., 2003a) 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 near-bed flow velocity leading to the creation of a skimming flow above them (Friedrichs et al., 2000). So far, critical erosion thresholds (τ_{crit}) have been determined assuming a smooth sediment bed, hence underestimating the influence of cockles and other bioturbators on sediment roughness and their knock-on effects on sediment dynamics. Using the method of Guizien et al. (2012), we were able to disentangle strictly the influence of unparasitised and parasitised cockles *C. edule* on sediment erodibility and sediment roughness.

Considering the presence of cockles as a categorical factor (i.e. without vs. with un- or parasitised cockles) we did not observe a significant effect of this bivalve on the roughness length z_0. Using a correlative approach, we conversely demonstrated that cockles significantly increase the bed roughness. Indeed, there was a significant increase of the roughness length z_0 with an increase in the biomass of cockle populations. Thus, cockles enhanced the bottom shear stress for a given current velocity. Visual observations revealed that the cockles were active during

erosion experiments: they migrated upside-down in the sediment column and emerged regularly at the sediment surface of the experimental plots (personal obs.). The migration behaviour of the cockles caused the reworking of sediments with consequences on sediment topography. Additionally, the current flow at the sediment surface could have been modified by the cockle shells that emerged periodically at the sediment surface.

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 biomass of its host when standardised for shell length. Parasitised cockles were thus weaker than unparasitised conspecifics and were expected to display a lower bioturbation rate (Cozzoli et al., 2018, 2019). We indeed evidenced that parasitised cockles have a lower influence on sediment roughness, and thus sediment erosion, than unparasitised conspecifics. The altered role of parasitised cockles on sediment roughness may be surprising since *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 parasitised cockles enhance the roughness length by their presence at the sediment surface. On the opposite, parasitised cockles remained burrowed during the incubation period of our experiment (personal obs.). Therefore, the reduced effect of parasitised cockles on sediment roughness observed here rather suggests that these organisms were less active (lower sediment reworking activity) than their unparasitised conspecifics once buried within the sediment. Indeed, several studies showed that parasitised 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 (personal obs.) suggested that parasitised organisms generated less marks and tracks at the sediment surface. Nonetheless, measurements of microtopographical roughness of the sediment surface still need to be conducted to accurately compare the effect of parasitised and unparasitised organisms on sediment roughness.

4.3. Influence of parasitised cockles on sediment erodability

Although *C. edule* inhabits both cohesive and non-cohesive sediments (Cozzoli et al., 2013; Hayward and Ryland, 1995), the influence of this bivalve in the dynamics of non-cohesive sediments has not been thoroughly investigated to date (Li et al., 2017; Soissons et al., 2019). What is more, previous studies conducted in both cohesive and non-cohesive sediments failed to clearly distinguish between the role of cockles on sediment erodibility and their impact on sediment roughness. Finally, the annular flumes used so far only enable quantification of the effect of bioturbating organisms on the resuspension of mud particles, whereas the Erodimetre allowed us to monitor the erosion kinetics of microphytobenthic, mud and sand particles. Our study thus provides new insights into the effect of cockles on the erodibility of sandy sediments.

Although they did not discriminate between the role of cockles on sediment roughness and erodibility, Li et al. (2017) recently showed that this bivalve does not significantly affect the critical erosion thresholds and sediment fluxes in a sandy sediment. Considering the presence of cockles as a categorical factor (i.e. without vs. with un- or parasitised cockles), and irrespectively of the presence of the parasite *B. minimus*, we highlight a more equivocal impact of this bivalve in sandy sediments. Indeed, cockles reduced significantly the critical erosion threshold for the biogenic fluff layer. Cockles also tend to reduce the critical threshold for the erosion of sand particles, even though not statistically significantly (but $p = 0.06$). The influence of cockles on sediment erodibility was slightly more pronounced when we used the biomass of cockle populations as a continuous explanatory variable. The critical erosion thresholds of the biogenic fluff layer and of the sand fraction decreased significantly with an increase in the biomass of cockle populations. In addition to their impact on sediment roughness, cockles also modulate the erodibility of sandy sediments and overall enhance their erosion. Even so, it is not yet possible to quantify the relative importance of these two processes (roughness vs. erodibility) for sediment resuspension dynamics.

Finally, the decrease in the critical erosion threshold with an increase in the biomass of cockle populations also confirms the reduced deleterious effect of parasitised cockles on sediment erodibility compared to unparasitised organisms. Similarly to what was observed for sediment roughness, the lower impact of parasitised cockles on sediment erodibility could be related to a reduced mobility and bioturbation rate, particularly a reduced sediment reworking activity. Parasitised cockles therefore negatively interfere with sediment cohesiveness to a lesser extent than unparasitised organisms.

4.4. Interactive effect of parasitised cockles and microphytobenthos

4.4.1. Influence of parasitised 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 the experimental plots enriched with MPB highlights the good physiological status of MPB biofilms. Irrespectively of their parasitic status, cockles had significant effect on the physiological status of microphytobenthic organisms. In contrast, we observed a decrease in the chlorophyll *a* biomass in the photic layer with an increase in the biomass of cockle populations. Therefore, both unparasitised and parasitised cockles have a deleterious impact on the growth of benthic microalgae, but this effect depends on the presence of the parasite *B. minimus*. Indeed, this parasite limits the deleterious effect of its host on the growth of benthic microalgae. As mentioned above, the bioturbation activity of cockles could be lowered by *B. minimus*, in which case parasitised cockles would disrupt MPB biofilms to a lesser extent than unparasitised organisms. Indeed, through their sediment reworking activity, cockles mechanically disrupt MPB biofilms thereby increasing chlorophyll *a* erosion rates (Rakotomalala et al., 2015). By doing so, this bivalve could facilitate the resuspension of MPB in the water column, which would then be 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 studies concluded that cockles promote MPB growth. Indeed, the bioturbation generated by this bivalve can stimulate remineralisation of organic matter and fluxes of inorganic nutrients at the sediment-water interface (Mermillod-Blondin and Rosenberg, 2006; Swanberg, 1991). In so doing, cockles fuel the growth of benthic microalgae (Eriksson et al., 2017; Swanberg, 1991). Although here we show that cockles did interfere with the growth of MPB, we nonetheless suggest that these results are not incompatible with the results of previous studies showing a stimulating effect of *C. edule* on MPB. Indeed, we placed cockles in a sandy sediment with a small quantity of fine particles that might contain a very small proportion of organic matter available for remineralisation and the recycled nutrients on which benthic microalgae rely, compared to a cohesive sediment. Therefore, the influence of cockles on MPB growth might depend on the environment. In this context, parasitised and unparasitised cockles might have contrasting effects depending on the sedimentary environment. In organic-enriched sediments, unparasitised cockles would stimulate the growth of benthic microalgae to a greater extent than parasitised organisms, with a potential effect on sediment stability. However, this remains to be investigated in future studies. Finally, we would like to point out that, as ecosystem engineers, cockles can modify their environment. In particular, in turbid waters cockles can promote the deposition of fine particles at the sediment surface, leading to "muddification" of sandy environments (Soissons et al., 2019). In this case, cockles might promote the growth of MPB, with consequences for sediment stability. In our experimental context, water turbidity was very low making this cascade effect, however, unlikely.

4.4.2. Indirect effects of parasitised cockles on sediment stability

In the MPB enriched plots, parasitised and unparasitised cockles have differential impacts on the resuspension dynamics of fine particles, MPB biofilms and sand particles. The erosion of the different sediment fractions was delayed when the experimental plots were inhabited by parasitised cockles compared to erosion in the plots with unparasitised bivalves. Parasitised cockles have a less detrimental effect on the growth of MPB biofilms than their unparasitised conspecifics. Moreover, the MPB growth was similar in plots without cockles and inhabited by parasitised cockles. Thus, it may be suggested that the reduced destabilising effect of parasitised cockles on sandy sediments compared to that of unparasitised organisms is due to a stabilisation effect by MPB biofilms. However, the resuspension kinetics of fine particles, MPB biofilms and sand particles were similar in experimental plots not enriched and enriched with MPB. The enrichment of the sediment surface with MPB did not neither influence the critical erosion thresholds and sediment fluxes for the different sediment fractions. Thus, in the present study, we 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 by increasing the critical erosion threshold (Le Hir et al., 2007 and references therein). However, these studies mostly focused on cohesive sediments. The role of MPB on the dynamics of sandy sediments has been comparatively 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 contain larger sediment particles that might not stick together as easily than the fine particles that comprise cohesive sediments. Moreover, these sediments are mainly colonised by epipelic diatoms whereas epipsammic diatoms dominate non-cohesive environments. Epipsammic diatoms do not actively migrate in the sediment column and are considered to be less efficient in stabilising sediments than the epipelic diatoms that colonise cohesive sediments (Holland et al., 1974; Paterson and Hagerthey, 2001; Vos et al., 1988). Therefore, evidence of a stabilisation effect of MPB in sandy sediments has only been reported after the development of a thick MPB mat (Yallop et al., 1994). In the present study, chlorophyll *a* biomasses in experimental plots enriched with MPB were low 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 may have been underestimated (the PAM fluorimeter measures the chlorophyll *a* fluorescence in the sediment photic zone and consequently does not account for benthic algae which migrate downwards in the sediment column), we suggest that the quantity of MPB that had developed at the sediment surface of the experimental plots enriched with MPB was not sufficiently high to stabilise the sediment. Indeed, the high proportion of sand may have prevented the development of a protective biofilm by epipelic diatoms. Consequently, the less destabilising effect of parasitised cockles *C. edule* on sandy sediment cannot be explained by a stabilisation effect due to the MPB biofilm.

The reasons behind the different effects of parasitised cockles on the erosion kinetics of sandy sediment depending on the presence of a MPB biofilm remain unclear. Nonetheless, it should be mentioned that biomasses of parasitised cockles placed in the experimental plots not enriched with MPB varied more than the biomass of conspecifics in the plots enriched with MPB. Accordingly, some parasitised cockles in plots not enriched with MPB may have had similar bioturbation rates (Cozzoli et al., 2018) to those of unparasitised organisms. Organisms can vary in their response to parasitism, some specimens being more sensitive to this stress factor than others (Minchella, 1985). Due to the low number of replicates, the large inter-variability in biomass between parasitised cockles in plots not enriched with MPB 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 parasitised and unparasitised bioturbating organisms on the erosion dynamics of a sandy sediment we were able to reveal 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 parasitised cockles on sediment erodibility and hydrodynamics appears reduced compared to unparasitised organisms. This pattern could be attributed to the parasite reducing the bioturbation potential of its host as a result of an altered physiological state. Consequently, parasitism also modulates the interaction between cockles and microphytobenthic organisms. Indeed, parasitised organisms have a less negative effect on MPB growth than unparasitised individuals. Nonetheless, the biomasses of MPB biofilms that developed at the water interface of sediment columns remained too low to efficiently stabilise this sandy sediment, irrespective of the presence of parasitised and unparasitised cockles. The stabilisation effect of microphytobenthic organisms has mainly been reported in cohesive sediments. Indeed, cohesive sediments are characterised by a smaller grain size than sandy sediments. By producing EPS, microphytobenthic organisms can thus more efficiently bind sediment grains together and thereby increase the stability of cohesive sediments (Grabowski et al., 2011; Yallop et al., 1994). In sandy environments, a highly turbid water column and a high deposition rate by cockles could nonetheless increase the mud content of the sediment surface (Soissons et al., 2019) and thus enhance colonisation by epipelic diatoms. Therefore, the feedback loop between parasitism, cockles and MPB may modulate the stability of cohesive or "muddified" sandy sediments to a greater extent than observed in this study, but this remains to be investigated in future studies.

CRediT authorship contribution statement

Annabelle Dairain: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - original draft, Visualization. **Olivier Maire:** Conceptualization, Supervision, Project administration, Resources, Funding acquisition, Writing - review & editing. **Guillaume Meynard:** Methodology, Investigation. **Francis Orvain:** Conceptualization, Methodology, Software, Supervision, Project administration, Resources, Funding acquisition, Writing - review & editing.

Declaration of competing interest

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.139307.

References

Aller, R.C., 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall, P.L., Tevesz, M.J.S. (Eds.), Animal-Sediment Relations. Springer US, Boston, MA, pp. 53–102.

Aller, R.C., 1988. Benthic fauna and biogeochemical processes in marine sediments: the role of burrow structures. In: Blackburn, T.H., Sorensen, J. (Eds.), Nitrogen Cycling in Coastal Marine Environments, pp. 301–338.

Andersen, T.J., 2001. The role of fecal pellets in sediment settling at an intertidal mudflat, the Danish Wadden Sea. In: McAnally, W.H., Mehta, A.J. (Eds.), Coastal and Estuarine Fine Sediment Processes, pp. 387–401 Amsterdam.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol 26, 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62, 245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x.

Austen, I., Andersen, T.J., Edelvang, K., 1999. The influence of benthic diatoms and invertebrates on the erodibility of an intertidal mudflat, the Danish Wadden Sea. Estuar. Coast. Shelf Sci. 49, 99–111. https://doi.org/10.1006/ecss.1998.0491.

Baudrimont, M., de Montaudouin, X., 2007. Evidence of an altered protective effect of metallothioneins after cadmium exposure in the digenean parasite-infected cockle (*Cerastoderma edule*). Parasitology 134, 237–245. https://doi.org/10.1017/S0031182006001375.

Bazaïri, H., Bayed, A., Glémarec, M., Hily, C., 2003. Spatial organisation of macrozoobenthic communities in response to environmental factors in a coastal lagoon of the NW African coast (Merja Zerga, Morocco). Oceanol. Acta 26, 457–471. https://doi.org/10.1016/S0399-1784(03)00041-0.

Beukema, J.J., 1976. Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. Neth. J. Sea Res. 10, 236–261. https://doi.org/10.1016/0077-7579(76)90017-X.

Brey, T., 2010. An empirical model for estimating aquatic invertebrate respiration. Methods Ecol. Evol. 1, 92–101. https://doi.org/10.1111/j.2041-210X.2009.00008.x.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789. https://doi.org/10.1890/03-9000.

Brustolin, M.C., Thomas, M.C., Mafra, L.L., da Cunha Lana, P., 2016. Bioturbation by the sand dollar *Encope emarginata* (Echinoidea, Mellitidae) changes the composition and size structure of microphytobenthic assemblages. Hydrobiologia 779, 183–192. https://doi.org/10.1007/s10750-016-2815-6.

Ciutat, A., Widdows, J., Readman, J., 2006. Influence of cockle *Cerastoderma edule* bioturbation and tidal-current cycles on resuspension of sediment and polycyclic aromatic hydrocarbons. Mar. Ecol. Prog. Ser. 328, 51–64. https://doi.org/10.3354/meps328051.

Ciutat, A., Widdows, J., Pope, N.D., 2007. Effect of *Cerastoderma edule* density on near-bed hydrodynamics and stability of cohesive muddy sediments. J. Exp. Mar. Biol. Ecol. 346, 114–126. https://doi.org/10.1016/j.jembe.2007.03.005.

Cozzoli, F., Bouma, T., Ysebaert, T., Herman, A.P.M.J., 2013. Application of non-linear quantile regression to macrozoobenthic species distribution modelling: comparing two contrasting basins. Mar. Ecol. Prog. Ser. 475, 119–133. https://doi.org/10.3354/meps10112.

Cozzoli, F., Bouma, T.J., Ottolander, P., Lluch, M.S., Ysebaert, T., Herman, P.M.J., 2018. The combined influence of body size and density on cohesive sediment resuspension by bioturbators. Sci. Rep. 8, 3831. https://doi.org/10.1038/s41598-018-22190-3.

Cozzoli, F., Gjoni, V., Del Pasqua, M., Hu, Z., Ysebaert, T., Herman, P.M.J., Bouma, T.J., 2019. A process based model of cohesive sediment resuspension under bioturbators' influence. Sci. Total Environ. 670, 18–30. https://doi.org/10.1016/j.scitotenv.2019.03.085.

Dairain, A., de Montaudouin, X., Gonzalez, P., Ciutat, A., Baudrimont, M., Maire, O., Legeay, A., 2018. Do trace metal contamination and parasitism influence the activities of the bioturbating mud shrimp *Upogebia* cf. *pusilla*? Aquat. Toxicol. 204, 46–58. https://doi.org/10.1016/j.aquatox.2018.08.019.

Dairain, A., Legeay, A., de Montaudouin, X., 2019. Influence of parasitism on bioturbation: from host to ecosystem functioning. Mar. Ecol. Prog. Ser. 619, 201–214. https://doi.org/10.3354/meps12967.

de Montaudouin, X., Bachelet, G., Sauriau, P.-G., 2003. Secondary settlement of cockles *Cerastoderma edule* as a function of current velocity and substratum: a flume study with benthic juveniles. Hydrobiologia 503, 103–116. https://doi.org/10.1023/B:HYDR.0000008493.83270.2d.

de Montaudouin, Xavier, Blanchet, H., Kisielewski, I., Desclaux, C., Bachelet, G., 2003. Digenean trematodes moderately alter *Hydrobia ulvae* population size structure. J. Mar. Biol. Assoc. U. K. 83, 297–305. https://doi.org/10.1017/S0025315403007112h.

de Montaudouin, X., Thieltges, D.W., Gam, M., Krakau, M., Pina, S., Bazairi, H., Dabouineau, L., Russell-Pinto, F., Jensen, K.T., 2009. Digenean trematode species in the cockle *Cerastoderma edule*: identification key and distribution along the north-eastern Atlantic shoreline. J. Mar. Biol. Assoc. U. K. 89, 543. https://doi.org/10.1017/S0025315409003130.

Desclaux, C., de Montaudouin, X., Bachelet, G., 2002. Cockle emergence at the sediment surface: "favourization" mechanism by digenean parasites? Dis. Aquat. Org. 52, 137–149. https://doi.org/10.3354/dao052137.

Dobson, A., Lafferty, K.D., Kuris, A.M., Hechinger, R.F., Jetz, W., 2008. Homage to Linnaeus: how many parasites? How many hosts? Proc. Natl. Acad. Sci. 105, 11482–11489. https://doi.org/10.1073/pnas.0803232105.

Donadi, S., Weerman, E.J., van der Heide, T., van der Zee, E., van de Koppel, J., Olff, H., Piersma, T., van der Veer, H.W., Klemens Eriksson, B., 2013. Non-trophic interactions control benthic producers on intertidal flats. Ecosystems 16, 1325–1335. https://doi.org/10.1007/s10021-013-9686-8.

Eriksson, B.K., Westra, J., van Gerwen, I., Weerman, E., van der Zee, E., van der Heide, T., van de Koppel, J., Olff, H., Piersma, T., Donadi, S., 2017. Facilitation by ecosystem engineers enhances nutrient effects in an intertidal system. Ecosphere 8, e02051. https://doi.org/10.1002/ecs2.2051.

Flach, E.C., 1996. The influence of the cockle, *Cerastoderma edule*, on the macrozoobenthic community of tidal flats in the Wadden Sea. Mar. Ecol. 17, 87–98. https://doi.org/10.1111/j.1439-0485.1996.tb00492.x.

Friedrichs, M., Graf, G., Springer, B., 2000. Skimming flow induced over a simulated polychaete tube lawn at low population densities. Mar. Ecol. Prog. Ser. 192, 219–228. https://doi.org/10.3354/meps192219.

Ginetsinskaya, T.A., 1988. Trematodes, Their Life Cycles, Biology and Evolution, Amerind Publishing Company. Amerind Publishing Company, New Delhi.

Grabowski, R.C., Droppo, I.G., Wharton, G., 2011. Erodibility of cohesive sediment: the importance of sediment properties. Earth-Sci. Rev. 105, 101–120. https://doi.org/10.1016/j.earscirev.2011.01.008.

Graf, G., Rosenberg, R., 1997. Bioresuspension and biodeposition: a review. J. Mar. Syst. 11, 269–278. https://doi.org/10.1016/S0924-7963(96)00126-1.

Guizien, K., Orvain, F., Duchêne, J.-C., Le Hir, P., 2012. Accounting for rough bed friction factors of mud beds as a result of biological activity in erosion experiments. J. Hydraul. Eng. 138, 979–984. https://doi.org/10.1061/(ASCE)HY.1943-7900.0000627.

Harris, R.J., Pilditch, C.A., Hewitt, J.E., Lohrer, A.M., Van Colen, C., Townsend, M., Thrush, S.F., 2015. Biotic interactions influence sediment erodibility on wave-exposed sandflats. Mar. Ecol. Prog. Ser. 523, 15–30. https://doi.org/10.3354/meps11164.

Hayward, P.J., Ryland, J.S., 1995. Handbook of the Marine Fauna of North-west Europe. Oxford University Press, Oxford.

Holland, A.F., Zingmark, R.G., Dean, J.M., 1974. Quantitative evidence concerning the stabilization of sediments by marine benthic diatoms. Mar. Biol. 27, 191–196.

Honeywill, C., Paterson, D., Hagerthey, S., 2002. Determination of microphytobenthic biomass using pulse-amplitude modulated minimum fluorescence. Eur. J. Phycol. 37, 485–492. https://doi.org/10.1017/S0967026202003888.

Honkoop, P.J.C., Berghuis, E.M., Holthuijsen, S., Lavaleye, M.S.S., Piersma, T., 2008. Molluscan assemblages of seagrass-covered and bare intertidal flats on the Banc d'Arguin, Mauritania, in relation to characteristics of sediment and organic matter. J. Sea Res. 60, 255–263. https://doi.org/10.1016/j.seares.2008.07.005.

Huxham, M., Richards, M., 2003. Can postlarval bivalves select sediment type during settlement? A field test with *Macoma balthica* (L.) and *Cerastoderma edule* (L.). J. Exp. Mar. Biol. Ecol. 288, 279–293. https://doi.org/10.1016/S0022-0981(03)00023-6.

Jensen, K.T., Mouritsen, K.N., 1992. Mass mortality in two common soft-bottom invertebrates, *Hydrobia ulvae* and *Corophium volutator* - the possible role of trematodes. Helgoländer Meeresunters 46, 329–339. https://doi.org/10.1007/BF02367103.

Joensuu, M., Pilditch, C.A., Harris, R., Hietanen, S., Pettersson, H., Norkko, A., 2018. Sediment properties, biota, and local habitat structure explain variation in the erodibility of coastal sediments. Limnol. Oceanogr. 63, 173–186. https://doi.org/10.1002/lno.10622.

Jones, S.E., Jago, C.F., 1993. *In situ* assessment of modification of sediment properties by burrowing invertebrates. Mar. Biol. 115, 133–142. https://doi.org/10.1007/BF00349395.

Jonsson, P.R., Andé, C., 1992. Mass mortality of the bivalve *Cerastoderma edule* on the swedish west coast caused by infestation with the digenean trematode *Cercariae cerastodermae* I. Ophelia 36, 151–157. https://doi.org/10.1080/00785326.1992.10430365.

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O., Banta, G.T., 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar. Ecol. Prog. Ser. 446, 285–302. https://doi.org/10.3354/meps09506.

Kristensen, E., Magalhães Neto, J., Lundkvist, M., Frederiksen, L., Pardal, M.Â., Valdemarsen, T., Flindt, M.R., 2013. Influence of benthic invertebrates on the erodibility of estuarine cohesive sediments: density- and biomass-specific responses. Estuar. Coast. Shelf Sci. 134, 80–87. https://doi.org/10.1016/j.ecss.2013.09.020.

Kromkamp, J., Barranguet, C., Peene, J., 1998. Determination of microphytobenthos PSII quantum efficiency and photosynthetic activity by means of variable chlorophyll fluorescence. Mar. Ecol. Prog. Ser. 162, 45–55. https://doi.org/10.3354/meps162045.

Kuris, A.M., Hechinger, R.F., Shaw, J.C., Whitney, K.L., Aguirre-Macedo, L., Boch, C.A., Dobson, A.P., Dunham, E.J., Fredensborg, B.L., Huspeni, T.C., Lorda, J., Mababa, L., Mancini, F.T., Mora, A.B., Pickering, M., Talhouk, N.L., Torchin, M.E., Lafferty, K.D., 2008. Ecosystem energetic implications of parasite and free-living biomass in three estuaries. Nature 454, 515–518. https://doi.org/10.1038/nature06970.

Le Hir, P., Monbet, Y., Orvain, F., 2007. Sediment erodability in sediment transport modelling: can we account for biota effects? Cont. Shelf Res. 27, 1116–1142. https://doi.org/10.1016/j.csr.2005.11.016.

Li, B., Cozzoli, F., Soissons, L.M., Bouma, T.J., Chen, L., 2017. Effects of bioturbation on the erodibility of cohesive versus non-cohesive sediments along a current-velocity gradient: a case study on cockles. J. Exp. Mar. Biol. Ecol. 496, 84–90. https://doi.org/10.1016/j.jembe.2017.08.002.

Longshaw, M., Malham, S.K., 2013. A review of the infectious agents, parasites, pathogens and commensals of European cockles (*Cerastoderma edule* and *C. glaucum*). J. Mar. Biol. Assoc. U. K. 93, 227–247. https://doi.org/10.1017/S0025315412000537.

MacIntyre, H.L., Geider, R.J., Miller, D.C., 1996. Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. Estuaries 19, 186. https://doi.org/10.2307/1352224.

Magalhães, L., Freitas, R., de Montaudouin, X., 2015. Review: *Bucephalus minimus*, a deleterious trematode parasite of cockles *Cerastoderma* spp. Parasitol. Res. 114, 1263–1278. https://doi.org/10.1007/s00436-015-4374-6.

Magalhães, L., de Montaudouin, X., Freitas, R., Daffe, G., Figueira, E., Gonzalez, P., 2017. Seasonal variation of transcriptomic and biochemical parameters of cockles (*Cerastoderma edule*) related to their infection by trematode parasites. J. Invertebr. Pathol. 148, 73–80. https://doi.org/10.1016/j.jip.2017.05.009.

Maire, O., Duchêne, J.C., Grémare, A., Malyuga, V.S., Meysman, F.J.R., 2007. A comparison of sediment reworking rates by the surface deposit-feeding bivalve *Abra ovata* during summertime and wintertime, with a comparison between two models of sediment reworking. J. Exp. Mar. Biol. Ecol. 343, 21–36. https://doi.org/10.1016/j.jembe.2006.10.052.

Malham, S.K., Hutchinson, T.H., Longshaw, M., 2012. A review of the biology of European cockles (*Cerastoderma* spp.). J. Mar. Biol. Assoc. U. K. 92, 1563–1577. https://doi.org/10.1017/S0025315412000355.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297. https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2.

Mermillod-Blondin, F., Rosenberg, R., 2006. Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. Aquat. Sci. 68, 434–442. https://doi.org/10.1007/s00027-006-0858-x.

Mermillod-Blondin, F., Rosenberg, R., François-Carcaillet, F., Norling, K., Mauclaire, L., 2004. Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. Aquat. Microb. Ecol. 36, 271–284. https://doi.org/10.3354/ame036271.

Miller, D.C., Geider, R.J., MacIntyre, H.L., 1996. Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. II. Role in sediment stability and shallow-water food webs. Estuaries 19, 202–212. https://doi.org/10.2307/1352225.

Minchella, D.J., 1985. Host life-history variation in response to parasitism. Parasitology 90, 205. https://doi.org/10.1017/S0031182000049143.

Montserrat, F., Van Colen, C., Provoost, P., Milla, M., Ponti, M., Van den Meersche, K., Ysebaert, T., Herman, P.M.J., 2009. Sediment segregation by biodiffusing bivalves. Estuar. Coast. Shelf Sci. 83, 379–391. https://doi.org/10.1016/j.ecss.2009.04.010.

Morelle, J., Orvain, F., Claquin, P., 2018. A simple, user friendly tool to readjust raw PAM data from field measurements to avoid over- or underestimating of microphytobenthos photosynthetic parameters. J. Exp. Mar. Biol. Ecol. 503, 136–146. https://doi.org/10.1016/j.jembe.2018.02.007.

Moulin, F.Y., Guizien, K., Thouzeau, G., Chapalain, G., Mülleners, K., Bourg, C., 2007. Impact of an invasive species, *Crepidula fornicata*, on the hydrodynamics and transport properties of the benthic boundary layer. Aquat. Living Resour. 20, 15–31. https://doi.org/10.1051/air:2007012.

Mouritsen, K.N., 2002. The parasite-induced surfacing behaviour in the cockle *Austrovenus stutchburyi*: a test of an alternative hypothesis and identification of potential mechanisms. Parasitology 124, 521–528. https://doi.org/10.1017/S0031182002001427.

Mouritsen, K.N., Haun, S.C.B., 2008. Community regulation by herbivore parasitism and density: trait-mediated indirect interactions in the intertidal. J. Exp. Mar. Biol. Ecol. 367, 236–246. https://doi.org/10.1016/j.jembe.2008.10.009.

Mouritsen, K.N., Jensen, K.T., 1994. The enigma of gigantism: effect of larval trematodes on growth, fecundity, egestion and locomotion in *Hydrobia ulvae* (Pennant) (Gastropoda: Prosobranchia). J. Exp. Mar. Biol. Ecol. 181, 53–66. https://doi.org/10.1016/0022-0981(94)90103-1.

Mouritsen, K.N., Poulin, R., 2002. Parasitism, community structure and biodiversity in intertidal ecosystems. Parasitology 124, S101–S117. https://doi.org/10.1017/S0031182002001476.

Needham, H.R., Pilditch, C.A., Lohrer, A.M., Thrush, S.F., 2011. Context-specific bioturbation mediates changes to ecosystem functioning. Ecosystems 14, 1096–1109. https://doi.org/10.1007/s10021-011-9468-0.

Neumeier, U., Lucas, C.H., Collins, M., 2006. Erodibility and erosion patterns of mudflat sediments investigated using an annular flume. Aquat. Ecol. 40, 543–554. https://doi.org/10.1007/s10452-004-0189-8.

Nowell, A.R.M., Jumars, P.A., Eckman, J.E., 1981. Effects of biological activity on the entrainment of marine sediments. Mar. Geol. 42, 133–153. https://doi.org/10.1016/0025-3227(81)90161-4.

Orvain, F., Le Hir, P., Sauriau, P.-G., 2003a. A model of fluff layer erosion and subsequent bed erosion in the presence of the bioturbator, *Hydrobia ulvae*. J. Mar. Res. 61, 821–849. https://doi.org/10.1357/002224003322981165.

Orvain, F., Galois, R., Barnard, C., Sylvestre, A., Blanchard, G., Sauriau, P.-G., 2003b. Carbohydrate production in relation to microphytobenthic biofilm development: an integrated approach in a tidal mesocosm. Microb. Ecol. 45, 237–251. https://doi.org/10.1007/s00248-002-2027-7.

Orvain, F., Sauriau, P.-G., Sygut, A., Joassard, L., Le Hir, P., 2004. Interacting effects of *Hydrobia ulvae* bioturbation and microphytobenthos on the erodibility of mudflat sediments. Mar. Ecol. Prog. Ser. 278, 205–223. https://doi.org/10.3354/meps278205.

Orvain, F., Sauriau, P.-G., Bacher, C., Prineau, M., 2006. The influence of sediment cohesiveness on bioturbation effects due to *Hydrobia ulvae* on the initial erosion of intertidal sediments: a study combining flume and model approaches. J. Sea Res. 55, 54–73. https://doi.org/10.1016/j.seares.2005.10.002.

Orvain, F., Guizien, K., Lefebvre, S., Bréret, M., Dupuy, C., 2014. Relevance of macrozoobenthic grazers to understand the dynamic behaviour of sediment erodibility and microphytobenthos resuspension in sunny summer conditions. J. Sea Res. 92, 46–55. https://doi.org/10.1016/j.seares.2014.03.004.

Ouellette, D., Desrosiers, G., Gagne, J., Gilbert, F., Poggiale, J., Blier, P., Stora, G., 2004. Effects of temperature on *in vitro* sediment reworking processes by a gallery biodiffusor, the polychaete *Neanthes virens*. Mar. Ecol. Prog. Ser. 266, 185–193. https://doi.org/10.3354/meps266185.

Pascal, L., 2017. Rôle de l'espèce ingénieure *Upogebia pusilla* dans le fonctionnement biogéochimique des écosystèmes intertidaux à herbier (*Zostera noltei*) du bassin d'Arcachon. University of Bordeaux, Bordeaux, France.

Pascal, L., Maire, O., Deflandre, B., Romero-Ramirez, A., Grémare, A., 2019. Linking behaviours, sediment reworking, bioirrigation and oxygen dynamics in a soft-bottom ecosystem engineer: the mud shrimp *Upogebia pusilla* (Petagna 1792). J. Exp. Mar. Biol. Ecol. 516, 67–78. https://doi.org/10.1016/j.jembe.2019.05.007.

Paterson, D.M., 1989. Short-term changes in the erodibility of intertidal cohesive sediments related to the migratory behavior of epipelic diatoms. Limnol. Oceanogr. 34, 223–234.

Paterson, D.M., Black, K.S., 1999. Water flow, sediment dynamics and benthic biology. In: Nedwell, D.B., Raffaelli, D.G. (Eds.), Advances in Ecological Research: Estuaries, pp. 155–193.

Paterson, D.M., Hagerthey, S.E., 2001. Microphytobenthos in constrasting coastal ecosystems: biology and dynamics. Ecological Comparisons of Sedimentary Shores. Ecological Studies (Analysis and Synthesis). Reise K, Berlin, Heidelberg.

Premo, K., Tyler, A., 2013. Threat of predation alters the ability of benthic invertebrates to modify sediment biogeochemistry and benthic microalgal abundance. Mar. Ecol. Prog. Ser. 494, 29–39. https://doi.org/10.3354/meps10561.

Preston, D.L., Mischler, J.A., Townsend, A.R., Johnson, P.T.J., 2016. Disease ecology meets ecosystem science. Ecosystem 19, 737–748. https://doi.org/10.1007/s10021-016-9965-2.

Przeslawski, R., Zhu, Q., Aller, R., 2009. Effects of abiotic stressors on infaunal burrowing and associated sediment characteristics. Mar. Ecol. Prog. Ser. 392, 33–42. https://doi.org/10.3354/meps08221.

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rakotomalala, C., Grangeré, K., Ubertini, M., Forêt, M., Orvain, F., 2015. Modelling the effect of *Cerastoderma edule* bioturbation on microphytobenthos resuspension towards the planktonic food web of estuarine ecosystem. Ecol. Model. 316, 155–167. https://doi.org/10.1016/j.ecolmodel.2015.08.010.

Rhoads, D.C., Young, D.K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28, 150–178.

Riethmueller, R., Hakvoort, J.H.M., Heineke, M., Heymann, K., Kühl, H., Witte, G., 1998. Relating erosion shear stress to tidal flat surface colour. In: Black, K.S., Paterson, D.M., Cramp, A. (Eds.), Sedimentary Processes in the Intertidal Zone, pp. 283–293 London.

Soissons, L.M., Gomes a Conceição, T., Bastiaan, J., van Dalen, J., Ysebaert, T., Herman, P.M.J., Cozzoli, F., Bouma, T.J., 2019. Sandification vs. muddification of tidal flats by benthic organisms: a flume study. Estuar. Coast. Shelf Sci. 228. https://doi.org/10.1016/j.ecss.2019.106355.

Stal, L.J., 2010. Microphytobenthos as a biogeomorphological force in intertidal sediment stabilization. Ecol. Eng. 36, 236–245. https://doi.org/10.1016/j.ecoleng.2008.12.032.

Sturdivant, S.K., Díaz, R.J., Cutter, G.R., 2012. Bioturbation in a declining oxygen environment, *in situ* observations from Wormcam. PLoS One 7, e34539. https://doi.org/10.1371/journal.pone.0034539.

Sutherland, T.F., Grant, J., Amos, C.L., 1998. The effect of carbohydrate production by the diatom *Nitzschia curvilineata* on the erodibility of sediment. Limnol. Oceanogr. 43, 65–72. https://doi.org/10.4319/lo.1998.43.1.0065.

Swanberg, I.L., 1991. The influence of the filter-feeding bivalve *Cerastoderma edule* L. on microphytobenthos: a laboratory study. J. Exp. Mar. Biol. Ecol. 151, 93–111.

Thieltges, D.W., Krakau, M., Andresen, H., Fottner, S., Reise, K., 2006. Macroparasite community in molluscs of a tidal basin in the Wadden Sea. Helgol. Mar. Res. 60, 307–316. https://doi.org/10.1007/s10152-006-0046-3.

Thomas, F., Poulin, R., 1998. Manipulation of a mollusc by a trophically transmitted parasite: convergent evolution or phylogenetic inheritance? Parasitology 116, 431–436.

Thomas, F., Poulin, R., de Meeus, T., Guegan, J.-F., Renaud, F., 1999. Parasites and ecosystem engineering: what roles could they play? Oikos 84, 167–171. https://doi.org/10.2307/3546879.

Ubertini, M., Lefebvre, S., Gangnery, A., Grangeré, K., Le Gendre, R., Orvain, F., 2012. Spatial variability of benthic-pelagic coupling in an estuary ecosystem: consequences for microphytobenthos resuspension phenomenon. PLoS One 7, 1–17. https://doi.org/10.1371/journal.pone.0044155.

Ubertini, M., Lefebvre, S., Rakotomalala, C., Orvain, F., 2015. Impact of sediment grain-size and biofilm age on epipelic microphytobenthos resuspension. J. Exp. Mar. Biol. Ecol. 467, 52–64. https://doi.org/10.1016/j.jembe.2015.02.007.

Vos, P.C., de Boer, P.L., Misdorp, R., 1988. Sediment stabilization by benthic diatoms in intertidal sandy shoals: qualitative and quantitative observations. In: de Boer, P.L., van Gelder, A., Nio, S.D. (Eds.), Tide-Influenced Sedimentary Environments and Facies. Extended Versions of Papers Presented at the Symposium on Classic Tidal Deposits, Held August 1985 in Utrecht, Netherlands, pp. 511–526 Dordrecht.

Widdows, J., Brinsley, M., 2002. Impact of biotic and abiotic processes on sediment dynamics and the consequences to the structure and functioning of the intertidal zone. J. Sea Res. 48, 143–156. https://doi.org/10.1016/S1385-1101(02)00148-X.

Widdows, J., Navarro, J.M., 2007. Influence of current speed on clearance rate, algal cell depletion in the water column and resuspension of biodeposits of cockles (*Cerastoderma edule*). J. Exp. Mar. Biol. Ecol. 343, 44–51. https://doi.org/10.1016/j.jembe.2006.11.011.

Yallop, M.L., de Winder, B., Paterson, D.M., Stal, L.J., 1994. Comparative structure, primary production and biogenic stabilization of cohesive and non-cohesive marine sediments inhabited by microphytobenthos. Estuar. Coast. Shelf Sci. 39, 565–582. https://doi.org/10.1016/S0272-7714(06)80010-7.