Sediment stability: can we disentangle the effect of bioturbating species on sediment erodibility from their impact on sediment roughness?

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Abstract :

Benthic organisms, in particular bioturbators, can influence erosion processes either by affecting sediment roughness through their mere presence and/or activities, or by modulating sediment characteristics (e.g., silt content, granulometry) and thus altering its erodibility. To date, it was not possible to distinguish the influence of bioturbating species on sediment roughness from their impact on sediment erodibility. Consequently, uncertainties remain regarding the role played by benthic species on sediment dynamics. In this study, we used a canal flume which allows to record the bed shear stress at the surface of a non-cohesive sediment (4% of mud) during erosion experiments, thus allowing to disentangle the influence of bioturbators, here the common cockle Cerastoderma edule, on the two erosion mechanisms. In order to assess the influence of bioturbating species on sediment stability in different environmental situations, we additionally tested for the effects of three factors, i.e. bivalve density, availability of suspended food (i.e. phytoplankton presence) and microphytobenthos (MPB) occurrence, which may modulate the behavior of cockles. We observed that cockles promote the erosion of the surficial layer by increasing its roughness as a consequence of their sediment reworking activity and/or presence at the sediment surface (emerging shell). In contrast, we calculated similar critical bed shear stress for erosion with and without bivalves suggesting that cockles have a minor influence on the erodibility of non-cohesive substrates with a low silt content. The destabilizing effect of cockles increased with the bivalve density whereas it was attenuated by the presence of phytoplankton. We hypothesize that the magnitude of cockles' bioturbation activity was lower when a high proportion of suspended food is available. High concentrations of suspended food may also have enhanced the filtration and biodeposition rates of cockles, thus rapidly leading to the 'muddification' of the sediment bed and consequently counteracting with the own destabilizing effect of the bivalves. Finally, the sole presence of MPB did not significantly affect the resuspension dynamics of non-cohesive sediments with a low proportion of mud.

Highlights

► The role of cockles on non-cohesive sediment dynamics was tested. ► The influence of cockles on sediment erodibility and bed roughness was disentangled. ► Cockles increased the sediment bed roughness and, to a lesser extent its erodibility. ► The destabilization effect of cockles increased with their density. ► Phytoplankton and microphytobenthos presence limited the cockle destabilizing role.

1. Introduction

40

41   Over the last 50 years, numerous studies have assessed the influence of various benthic organisms, i.e.

42   macrozoobenthos (e.g., Hillman et al., 2019; Kristensen et al., 2013), macrophytes (e.g., Lawson et al.,

43   2012; Madsen et al., 2001) and microphytobenthos (e.g., Sutherland et al., 1998; Yallop et al., 1994), on

44   sediment dynamics, mainly through measurements of critical bed shear stress for erosion and resuspension

45   fluxes of sediment particles. These studies showed that benthic organisms have diverse impacts on the

46   stability of cohesive sediments, both promoting and hampering their erosion (see Grabowski et al., 2011;

47   Le Hir et al., 2007 for review). The biota-mediated effects were mainly observed on the erosion of the

48   biogenic fluff layer, i.e. at intermediate current flow before the sediment bed failure ("mass erosion")

49   which occurs at higher current flow (Cozzoli et al., 2020; Orvain et al., 2003b; Orvain, 2005).

50   With regard to the role of macrozoobenthic organisms, there was an emphasis on the effects of the

51   common cockle *Cerastoderma edule* (e.g., Andersen et al., 2010; Ciutat et al., 2007; Eriksson et al., 2017;

52   Li et al., 2017; Neumeier et al., 2006). Indeed, this suspension-feeding bivalve is widespread in semi-

53   sheltered areas from the Barents Sea to West African lagoons (Bazaïri et al., 2003; Hayward and Ryland,

54   1995; Honkoop et al., 2008) where it can be dominant in terms of abundance and biomass (Beukema

55   1976, Rakotomalala et al. 2015). Cockles are also efficient bioturbators i.e. organisms which mix the

56   sediment matrix as a result of their feeding, locomotor and burrowing activities (Kristensen et al., 2013).

57   In particular, cockles crawl at the sediment surface, migrate upside-down in the first few centimeter of the

58   sediment column, and "clap" their valves when buried in the sediment column (Flach, 1996). These

59   activities cause sediment particle movements, i.e. sediment reworking, and also enhance solute exchanges

60   between pore- and overlying waters, i.e. biorrigation (Flach, 1996; Mermillod-Blondin et al., 2004;

61   Swanberg, 1991). In this way, cockles regulate key sediment properties that govern their stability, such as

62   roughness, particle size distribution, compaction, bulk density or moisture content (Grabowski et al.,

63   2011).

64   The influence of cockles on sediment dynamics depend on the structure of their population, i.e. individual

65   size and population density. Large organisms show a higher bioturbation potential as compared to small

66   conspecific and thus their destabilizing role in sediments is enhanced (Cozzoli et al., 2019, 2018;

67   Rakotomalala et al., 2015). Similarly, the disrupting effect of cockles increases with an increase in their

68   population size; although this density-dependent effect is non-linear with no increase in the destabilizing

69   effect above a maximum density threshold (Ciutat et al., 2006; Cozzoli et al., 2020). Yet, experimental

70   erosion studies testing the effects of bioturbator density on sediment dynamics processes were usually

71   performed with populations of one size class whereas the length-frequency distribution of natural

72   population in the field shows a gaussian distribution (e.g., Boldina and Beninger, 2013 for an example

73   with cockles). Recently, metabolic theories in ecology (Brown et al., 2004) have been applied to scale

74 individual and population metabolic rates of bioturbators with their biomass at a state temperature.

75 Metabolic rates were then used to describe the effect of bioturbators on sediment resuspension (Cozzoli et

76 al., 2018). In this way, it has been possible to accurately evaluate the influence of organisms taking into

77 account their individual influence and density. This size scaling approach of metabolic rates can be used to

78 predict the potential of several bioturbating species on sediment resuspension in different environmental

79 context (Cozzoli et al., 2020, 2019). Nonetheless, this approach has some limits. In particular, at high

80 density, intraspecific competition can lower individual bioturbation potentials (Duport et al., 2006) and

81 lead to an overestimation of the influence of bioturbator population on sediment resuspension (Cozzoli et

82 al., 2018).

83 Despite the large number of studies that have been conducted, there remains uncertainties with regard to

84 the role of *C. edule* in sediment erosion processes. First, there are discrepancies between laboratory and

85 field investigations. Several laboratory flume experiments have highlighted a destabilizing effect of

86 cockles on cohesive and non-cohesive sediments with a low proportion of silts. Bivalves reduced the

87 critical threshold τ_{crit} for erosion and enhance the erosion of fine particles (e.g., Ciutat et al., 2006; Cozzoli

88 et al., 2020; Neumeier et al., 2006; Rakotomalala et al., 2015). In contrast, field studies did not show any

89 direct destabilizing effect of cockles (Andersen et al., 2010; Donadi et al., 2014). Inconsistencies in results

90 between *ex-* and *in-situ* studies may be related to an alteration of the behavior of cockles used during

91 laboratory experiments that were more disturbed than their conspecifics in the field (Andersen et al.,

92 2010). Second, there is a methodological barrier in link with the erosion devices that have been used so far

93 (i.e. annular flume canal, cohesive strength meter, EROMES flume, etc.). The devices do not allow for a

94 complete mechanistic understanding of the role play by benthic organisms, such as cockles *C. edule,* in

95 sediment dynamics processes because it was not possible to measure the bed shear stress during erosion

96 experiment. The latter was typically estimated from calibration curves obtained from other sediment

97 samples (e.g., Ciutat et al., 2007; Orvain et al., 2003b; Widdows et al., 1998). Yet, sediment stability

98 depends on both the erodibility of the sediment and the bed shear stress induced by hydrodynamic forcing

99 (Le Hir et al., 2007 and references therein). Erodibility is defined as the resistance of a sediment to erosion

100 when it is submitted to hydrodynamics forcing and depends on the sediment nature, i.e. cohesiveness,

101 granulometry, percentage of silt, etc. On the other hand, the bed shear stress is a friction force representing

102 the intensity of flow-turbulent fluctuations in the bottom boundary layer. (Le Hir et al., 2007 and

103 references therein). The bioturbation of benthic animals can affect sediments' characteristics and thus

104 influence their erodibility (Cozzoli et al., 2018, 2020; Orvain et al., 2003b). Their mere presence and/or

105 activity can also influence the bed roughness, modifying the relationship between the current velocity and

106 the bed shear stress (Friedrichs et al., 2000). Consequently, the calibration curves used so far to estimate

107 the bed shear stress were probably biased by differences in local roughness caused by bioturbating
108 organisms.
109 In this study, we used a canal flume which permits to continuously record the pressure up- and
110 downstream the sediment-water interface (Guizien et al., 2012; Le Hir et al., 2008) allowing to estimate
111 the bed shear stress for each sediment sample (Guizien et al., 2012). Using this device, we could
112 disentangle the influence of cockles *C. edule* on sediment erodibility from their influence on sediment
113 roughness Such information will definitively be of great interest in a modelling perspective. Experiments
114 were conducted in non-cohesive sediments with a low proportion of silt (i.e. 4%) since studies on the
115 influence of macrofauna-mediated processes in these environments remains scarce (but see Cozzoli et al.,
116 2020; Harris et al., 2015; Joensuu et al., 2018; Li et al., 2017). Indeed, non-cohesive sediments are typical
117 of high-energy environments and physical processes used to be considered most effective than biological
118 ones in influencing the dynamics of these sediments. However, recent findings suggested that macrofauna
119 can also play a significant role on the resuspension dynamics of non-cohesive sediments (e.g., Dairain et
120 al., 2020; Harris et al., 2015; Joensuu et al., 2018). Finally, we contextualized our study and assessed the
121 interest of our methodology under different simulated environmental scenarios by testing for the separate
122 and combined effect of three factors, i.e. density and metabolic rates of cockle populations, change in food
123 availability (i.e. phytoplankton) and microphytobenthos occurrence, that may modulate the influence of
124 bivalves on sediment dynamics (Andersen et al., 2010; Maire et al., 2006; Rakotomalala et al., 2015).

2. Materials and methods

2.1. Design of the experiment

We conducted a fully crossed factorial experiment in mesocosm conditions in which we tested the separate and combined influence of cockle density ("Density of cockles"), enrichment of the water column with phytoplankton ("Phytoplankton", 2 levels: "With phytoplankton" and "Without phytoplankton") and enrichment of the sediment surface with MPB ("MPB", 2 levels: "Without MPB" and "With MPB") on sediment stability (i.e. sediment erodibility and roughness). Three densities of cockles were studied: 0 ind. m^{-2} ("no cockles"); 288 ind. m^{-2} (i.e. 2 cockles per experimental plot, "low density") and 720 ind. m^{-2} (i.e. 5 cockles per experimental plot, "high density"). By combining the three factors, the experiment consisted of 12 treatments. Each treatment was replicated three times.

2.2. Experimental setup

2.2.1. Sampling of *Cerastoderma edule* and sediment

Cockles were collected by hand in a sandy area in Arcachon Bay (44°34'N, 1°14'W), France. Back in the laboratory, they were maintained in a seawater open circuit pending experimentation. Cohesive and non-cohesive sediments were collected in *Baie des Veys*, (49°21'′N, 1°08'′W) and in *Banc d'Arguin*, (49°35'′N, 1°14'′W), France, respectively. Relatively dense populations of cockles inhabit these two areas. Back in the laboratory, sediments were sieved through a 2 mm mesh to retain macrofauna and debris. Then a mixture of 50 % cohesive and 50 % non-cohesive sediments was prepared and kept for approximatively a week in the dark before being introduced in the experimental plots (see 2.2.3). The sediment mixture finally consisted of slightly muddy sand (sand = 95.4 %, mud = 4.4 %, gravel = 0.2 % and D_{50} = 287.5 µm). Cockles colonize a wide range of sedimentary environments and the granulometry of the sediment mixture is considered to be similar to those of natural areas colonized by *C. edule* (Cozzoli et al., 2013; Huxham and Richards, 2003).

2.2.2. Microphytobenthos culture

Natural microphytobenthos (MPB) biofilms were collected on a mudflat at low tide 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 2.2.1). The inoculum was kept under an 18:6 h obscurity-light regime (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 2.2.3) (Orvain et al., 2003a).

2.2.3. Incubation procedure

156   The experimental plots consisted of PVC tubes (internal diameter = 9.4 cm, height = 22 cm). Each

157   incubation experiment lasted nine days. On day 1, the experimental plots were filled with the prepared

158   sediment mixture (sediment column of 21 cm). On day 2, cockles of similar size (total length = 24–29

159   mm; Supplement S1) were added in each experimental plot. The plots were then placed in a mesocosm in

160   a semi-diurnal tidal cycle (one diurnal emersion phase). On day 3, a 1-cm layer of sediment not enriched

161   or enriched with MPB was added to the surface of the sediment cores. From day 2 to day 9, an 18:6 h

162   night-day alternation regime was applied using cool white lamps (light intensity = 46.5 µmol photons m^2

163   s^{-1}). The day phase corresponded to the diurnal emersion phase. Erosion experiments were conducted on

164   day 9, corresponding to an MPB growth of six days. The incubation period lasted eight days in the

165   treatments without cockles: the 1-cm layer of sediment not enriched or enriched with MPB was added on

166   day 2, and the erosion experiment was performed on day 8. The influence of the enrichment of the water

167   column with phytoplankton on the impact of cockles on sediment dynamics was tested by feeding cockles

168   in half of the experimental treatments with a monospecific suspension of laboratory-reared *Isochrysis*

169   *galbana* (approx. 5000 cells mL^{-1}) during the mesocosm incubation time.

170   Air-bubbling systems were added in the mesocosm to keep the water fully oxygenated. Approximatively

171   10 % of the total volume of the mesocosm seawater volume was renewed each day. The seawater

172   temperature over the incubation period averaged 12.0 ± 0.4 °C and the salinity 31.7 ± 0.8 (mean ± SD,

173   daily measurement).

2.2.4. Microphytobenthos photosynthetic parameters

175   At the end of the 6-day incubation period, and before the erosion experiment, the superficial MPB

176   chlorophyll *a* fluorescence in each experimental plot was measured using a Pulse Amplitude Modulated

177   (PAM) fluorimeter (IMAGING-PAM *M-series,* Walz). The experimental plots were placed in the dark for

178   ca. 5 min before a low frequency light was applied to determine the minimum level of fluorescence F_0. A

179   saturating light pulse was then applied to determine the maximum fluorescence F_m. The effective quantum

180   yield of the photosystem II ("yield") was then determined as follows:

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

181   The yield is a measure of the PSII maximum energy conversion efficiency and thus is related to the

182   oxidized state of the PSII (Kromkamp et al., 1998). F_0 was used to estimate the photosynthetically active

183   chlorophyll *a* biomass (hereafter referred as "Chlorophyll *a* biomass"; mg Chl a m^{-2}) within the sediment

184   photic layer using the standard curve: *Chlorophyll a biomass* = 12.142 F_0 - 0.2012. The thickness of the

185   sediment photic layer was ca. 200 µm (Morelle et al., 2018). In this way, we quantified the chlorophyll *a*

186   biomasses at the microscale and the values obtained were low compared to the MPB biomasses usually

187   measured in the top centimeter of the sediment column (usually > 100 mg m^{-2}). Nonetheless, the relative

188   comparison of chlorophyll *a* biomasses based on F_0 is a good proxy to evaluate the potential productive

189   chlorophyll *a* stock and MPB growth performances in the photic layer (Honeywill et al., 2002; Kromkamp

190   et al., 1998).

191   **2.2.5. Erosion procedure**

192   After 6 days of incubation (see 2.2.3), we performed erosion experiments. We used a recirculating

193   straight flume (length= 1.2 m long, width = 0.08 m, height = 0.02 m; see Guizien et al., 2012 and Orvain

194   et al., 2014 for a description of the "erodimeter"), in which a unidirectional flow was generated by a pump.

195   Experimental plots were removed from the tidal mesocosm approximatively 20 min before the start of the

196   erosion experiment. Sediment cores were cut to a ca. 7-cm depth and placed in the flume with the

197   sediment surface flush with the bottom of the flume. The latter was then carefully filled with seawater and

198   a current flow was applied. The seawater in the flume was enriched with a monospecific suspension of

199   laboratory-reared *I. galbana* (approx. 5000 cells mL^{-1}) when cockles were fed with phytoplankton during

200   the incubation period (see 2.2.3). A frequency device connected to the recirculating pump was used to

201   gradually increase the current flow from 0 up to ca. 72.5 cm s^{-1} in up to 20 steps. Each step lasted five

202   minutes.

203   The flow discharge was monitored using an electromagnetic flowmeter (Promag 10P, Endress+Hauser). A

204   multiprobe (DS5, Hydrolab) with turbidity and fluorescence sensors made it possible to continuously

205   record turbidity and to estimate the concentration of chlorophyll *a* in the water. Calibration curves enabled

206   us to calculate the concentrations of suspended particulate matter ("suspended matter"; g L^{-1}) and

207   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 =

208   0.998 for suspended matter and chlorophyll *a*, respectively). A trap downstream the sediment sample also

209   allowed us to measure the erosion of sand particles. The total volume of the sand trap was 17.7 cm^3;

210   erosion experiments were shortened if the sand trap was filled before the maximal current speed was

211   reached (ca. 72.5 cm s^{-1}). Finally, the pressure upstream and downstream the sediment sample was

212   recorded using a pressure sensor (deltabar P70, Endress+Hauser).

213   **2.2.6. Erosion data treatment**

214   The bed shear stress (τ) was determined for each sample following Guizien et al. (2012). First, the

215   difference of pression between the up- and downstream parts of a smooth section over an increasing

216   current flow was recorded and used to estimate the head loss and thus the bed shear stress (τ_0) at the

217   surface of the smooth section. Then, differences of pressures between the up- and downstream parts of the

218   sediment samples were recorded and compared to the profile obtained for the smooth section. Differences

219   in bed shear stress between the "smooth" and the "sediment samples" profiles result from the sediment

220   roughness:

$$\tau_{rough} = \tau_{smooth} + \frac{S1}{2S3}\left(\Delta h_{caps} - \Delta h_{core}\right)$$

221   where τ_{rough} is the bed shear stress above a sediment sample, τ_{smooth} is the bed shear stress above a smooth

222   section, $S1$ is the tunnel cross-section area, $S3$ is the core area, Δh_{caps} is the head loss for a hydraulically

223   smooth section (i.e. differential pressure) and Δh_{core} is the measured head loss for a rough sediment

224   sample. In this way, bed shear stresses determined in this study account for the bed deformation and for

225   the presence of physical objects that could protrude at the sediment-water interface, such as cockle shells.

226   Accordingly, shear velocities U^* were calculated as follows:

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

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

228   The relationship between U^* and the depth-averaged current velocity was then used to estimate the

229   roughness length z_0 (cm) for each sample. The relationship between the two variables was estimated using

230   a simple linear regression (Supplement S2). It can deviate from linearity because of the deformation of the

231   sediment surface at high current flows and/or due to movements of the cockles. Therefore, linear

232   regressions were applied on reduced ranges of current flows that only included the linear part of the curve.

233   The linear regression slope determined for each sample allowed us to integrate the so-called von Karman-

234   Prandtl "law of the wall":

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

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

235

236   where k is the von Karman's constant (k = 0.41) and h the height of the flume tunnel (h = 2 cm)

237   (Supplement S2).

238   Then, we determined critical erosion thresholds for the chlorophyll a of MPB biofilms and the sand

239   fraction of the sediment column as the intercept of the best linear regression of non-null chlorophyll a

240   concentration in the water column and sand volume, respectively, against $\log_{10}(U^*+1)$ (Supplement S3):

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

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

9

241   where U^*_{crit} is the critical shear velocity for erosion (m s^{-1}), y is the chlorophyll *a* concentration in the

242   water column (µg L^{-1}) or the thickness of eroded sand (cm) (Supplement S3). The critical bed shear stress

243   τ_{crit} for the chlorophyll *a* of the MPB biofilm and the sandy fraction of the sediment column were

244   calculated as follows:

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

245   With regard to the mud fraction of the sediment column, it was graphically possible to distinguish the

246   erosion of the biogenic fluff layer from the erosion of the sediment bed (Supplement S4). During the

247   erosion of the fluff layer, only small quantities of mud particles were eroded and resuspended. In contrast,

248   during the erosion of the sediment bed, we observed an exponential increase of mud particles in the water

249   column (Supplement S4). Therefore, both critical erosion thresholds of the biogenic fluff layer and of the

250   sediment bed were determined following the procedure described above.

251   Finally, mean erosion rates of the MPB biofilm, mud and sand fractions at the sediment-water interface

252   were calculated over the three steps following the critical erosion incipient point:

$$flux = (C_{crit+3} - C_{crit})(V/S)$$

253   Where C_{crit} is the concentration of particles when the critical erosion threshold is attained, C_{crit+3} is the

254   concentration of particles after three steps following the critical erosion incipient point, V is the volume of

255   water in the flume canal and S is the surface area of the test section. Regarding the mud fraction, only

256   fluxes that occurred after the erosion of the biogenic fluff layer were calculated. The Matlab computing

257   environment (v. 2019a, MathWorks) was used. A detailed example of this analysis can be found in the

258   Supplementary data (Supplements S2-S4).

2.2.7. Estimation of the metabolic rate of the cockle population

260   Following erosion experiments, the cockles were placed in a seawater open circuit for 24 h before being

261   dissected. The total length of each cockle was measured using a digital caliper. The measured size was

262   rounded down to the nearest mm. The shell was then opened by cutting the posterior adductor muscle, all

263   soft tissues were extracted, dried for at least 48 h at 60 °C and finally weighed (dry weight, DW). DW

264   were converted in Ash-Free Dry Weight (AFDW) using a conversion factor of 0.8 (pers. obs.). AFDW

265   were used to calculate basal individual metabolic rate, i.e. metabolic rate of organisms under resting

266   conditions, following Brey (2010) and using a J/AFDW ratio of 21.5 (Brey et al., 2010). Metabolic rates

267   were calculated for a water temperature of 12°C. Basal metabolic rates are less than active metabolic rates

268   which include additional energy for locomotion, feeding, burrowing, etc. activities. However, active

269   metabolic rates are usually constant multiple of basal metabolic rates (Savage et al., 2004).

270 Individual metabolic rates are proxies of the level of activity of bioturbators (Cozzoli et al., 2019, 2018)

271 and can be used to upscale the influence of individual bioturbators to the population level. Indeed, the

272 contribution of individual cockles to sediment resuspension can be described as a function of their used

273 energy and be modelled by size scaling laws of individual metabolic rate irrespectively of the sedimentary

274 environment (Cozzoli et al., 2020). Thereby, we also estimated the metabolic rates of the population of

275 cockles by taking into account the density of bivalves in the experimental plots (density of cockles in

276 experimental plots = 0, 288 and 720 ind. m^{-2}).

277 At 12°C, the metabolic rates of the cockle populations in experimental plots inhabited by two (density =

278 288 ind. m^{-2}) and five (density = 720 ind. m^{-2}) cockles were 80.1 ± 4.5 and 172.8 ± 10.7 mW m^{-2} (mean ±

279 SE), respectively (Supplement S1). The difference in the metabolic rates of the cockle populations was

280 statistically significant (Wilcoxon test, $p < 0.001$; Supplement S1).

281 **2.3. Statistical analyses**

282   The influence of cockle density, enrichment of water with phytoplankton and enrichment of the surface

283 of the sediment plots with MPB on (1) the biomass and effective quantum yields of the photosystem II of

284 the MPB in the photic layer after 6 days of incubation, (2) critical bed shear stress τ_{crit} of the different

285 sediment fractions (chlorophyll a, mud and sand) and (3) fluxes of sandy particles at the sediment-water

286 interface of the experimental plots during the erosion experiments were assessed using a permutational

287 multivariate analyses of variances (PERMANOVA) (Anderson, 2001; McArdle and Anderson, 2001)

288 without data transformation. The design consisted of three factors: "Density of cockles" (3 levels: "no

289 cockles", "low density" and "high density"), "Phytoplankton" (2 levels: "Without phytoplankton" and

290 "With phytoplankton") and "MPB" (2 levels: "Without MPB" and "With MPB"). We tested the separate

291 and combined effects of the three factors on among-replicate variability (i.e. dispersion) using the

292 PERMDISP procedure (Anderson, 2006).

293 We also used analyses of covariance (ANCOVA) to investigate potential differences in the relationship

294 between the metabolic rate of the cockle populations and (1) the biomass of MPB effective quantum

295 yields of the photosystem II of at the sediment surface of experimental plots, (2) the critical bed shear

296 stress of the different sediment fractions and (3) the fluxes of mud, chlorophyll a and sand particles at the

297 sediment-water interface of experimental plots with the "Phytoplankton" and "MPB" factors as

298 categorical independent variables. Shapiro-Wilk and Levene tests were used to check for the normality of

299 the data and homogeneity of the variances, respectively. All statistical analyses were performed with the

300 free computing environment R (R Core Team, 2019).

3. Results

3.1. Microphytobenthos biomass

3.1.1. Biomass of chlorophyll *a*

Following the 6-day incubation period, chlorophyll *a* biomass ranged 0.052–0.42 and 0.33–1.27 mg m^{-2} in the photic sediment layer of the plots "Without MPB" and "With MPB", respectively (Fig. 1A). Biomasses of MPB in the plots that have been enriched with benthic microalgae were significantly higher than in plots not enriched with MPB (Fig. 1A, Table 1). At high density, cockles reduced significantly the biomass of the MPB biofilms (Fig. 1A, Table 1). In contrast, there was no significant influence of the "Phytoplankton" factor on the MPB biomass (Fig. 1A, Table 1). There was an interacting effect between the "Phytoplankton", "Density of cockles" and "MPB" factors on MPB biomasses (Table 1). However, pairwise comparisons did not reveal significant differences between entities.

The biomass of chlorophyll *a* in the photic layer of the sediment column decreased significantly with an increase in the metabolic rate of the cockle populations (Fig. 1A; ANCOVA, $p < 0.01$). The "MPB" and "Phytoplankton" factors significantly influenced this relationship in an interactive way (Fig. 1A; ANCOVA, , $p < 0.05$). Indeed, the relationship between both variables in the plots "With MPB" did not vary irrespectively of the enrichment of the water column with phytoplankton (Fig. 1A; ANCOVA, $p = 0.96$). In contrast, "Without MPB" and "With phytoplankton" there was no significant relationship between the chlorophyll *a* biomass and the metabolic rate of the cockle populations (ANCOVA, $p = 0.35$) while chlorophyll *a* biomasses decreased significantly with an increase in the metabolic rate of the cockle populations in the plots "Without MPB" and "Without phytoplankton" (Fig. 1A; ANCOVA, $p < 0.01$).

3.1.2. Effective quantum yield of the photosystem II

The effective quantum yields of the photosystem II (PSII) ranged 0.24–0.45 and 0.44–0.51 in the sediment photic layer of the plots "Without MPB" and "With MPB", respectively (Fig. 1B). There was no significant effect of the "Phytoplankton" and "Density of cockles" factors on the effective quantum yield of the PSII (Fig. 1B, Table 1). Conversely, effective quantum yields of the PSII were significantly higher in the sediment surface of the plots "With MPB" as compared to those "Without MPB" (Fig. 1B, Table 1). The effective quantum yield of the PSII did not vary significantly with the metabolic rate of the cockle populations in the plots "With phytoplankton" (Fig. 1B; ANCOVA, $p = 0.29$). In contrast, it was negatively correlated with the metabolic rates of the cockle populations in the plots "Without phytoplankton" (Fig. 1B; ANCOVA, $p < 0.01$). This relationship did not depend on the enrichment with MPB (without vs. with MPB) (Fig. 1B; ANCOVA, $p = 0.09$).
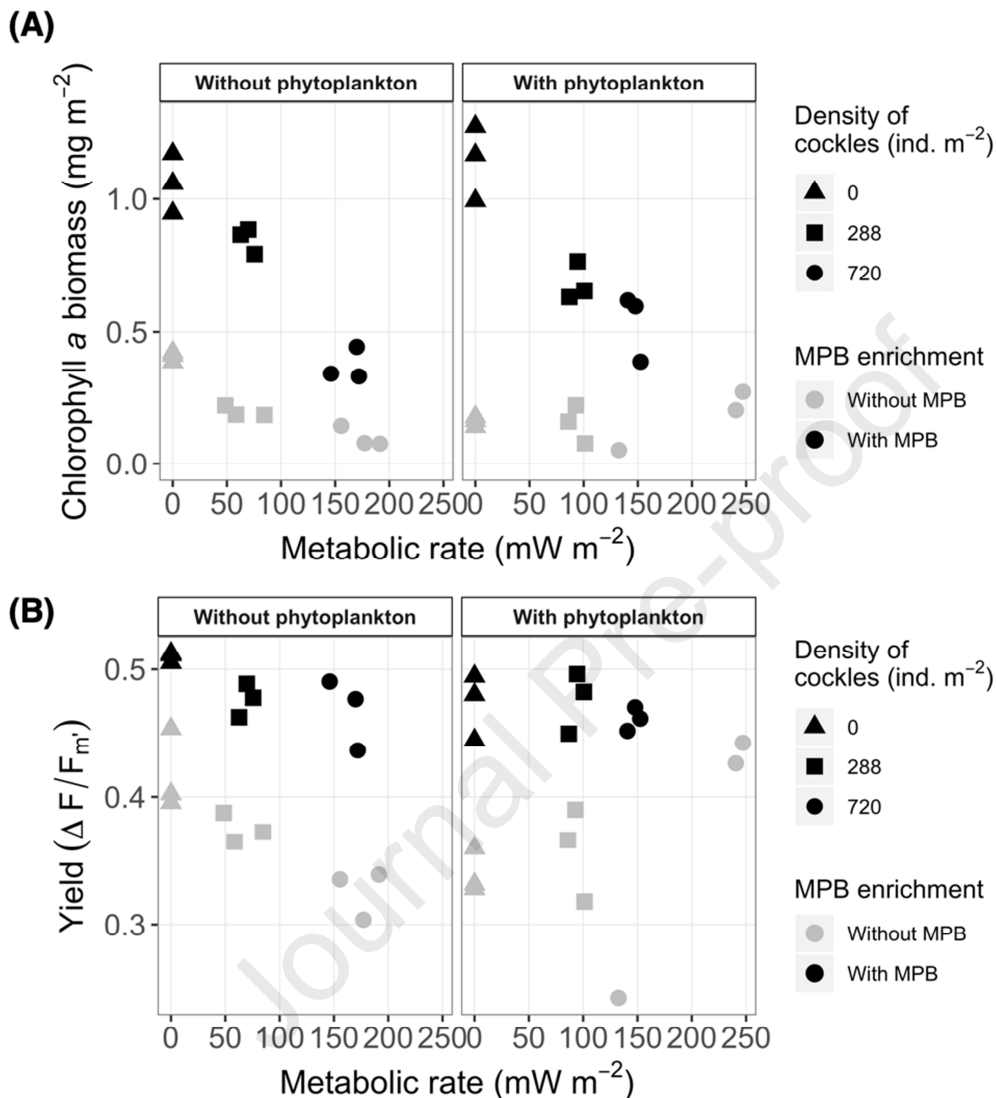
Fig. 1 Influence of the density of cockles *Cerastoderma edule* and enrichment of the water column with phytoplankton ("Without phytoplankton" and "With phytoplankton") on the relationship between (A) the biomass of chlorophyll *a* and (B) associated mean effective quantum yields of photosystem II ("yield") measured in the photic sediment layer of experimental plots not enriched and enriched with microphytobenthos (MPB; "Without MPB" and "With MPB", respectively) and the metabolic rates of the cockle populations

332

3.2. Sediment resuspension dynamics

The concentrations of suspended matter and chlorophyll *a* in the water column were recorded as proxies of the erosion of the mud fraction (i.e. fine particles) and biofilms of MPB, respectively. The thickness of sand eroded was also recorded. These three fractions of the sediment column showed a similar

13

337 resuspension pattern characterized by an exponential increase of the mass of sediment eroded with an

338 increase in the current flow (Fig. 2). Overall, the erosion of the different fractions of the sediment column

339 were initiated at lower current velocities when cockles inhabited the experimental plots. In contrasts, there

340 was no separate effect of the "Phytoplankton" nor of the "MPB" factors on sediment resuspension

341 dynamics in the absence of cockles (Fig. 2).

342 With regards to the mud fraction, we first observed the erosion of a biogenic fluff layer at low current

343 velocities (ca. 10-30 cm s^{-1}) except for one of the "Low density"-"With phytoplankton"-"Without MPB"

344 sample. The typical erosion of the biogenic fluff layer was clearly followed by a mass erosion of the

345 sediment bed at the highest current flows (Fig. 2A). For this fraction, we also reported an interactive effect

346 between the "Density of cockles" and "Phytoplankton" factors. "Without phytoplankton", there was a

347 clear decrease in the current velocity needed to initiate the erosion with an increase in the density of

348 cockles. "With phytoplankton", cockles also enhanced the erosion of mud particles, but we did not

349 observe such strong differences in the current velocity needed to initiate mud particle erosion between

350 plots inhabited by a "low" and "high" density of cockles (Fig. 2A).

351 Concerning to the erosion of MPB biofilms, we noted that the enrichment of the water column with

352 phytoplankton and the resulting high concentrations of chlorophyll *a* made difficult to detect any increase

353 in the quantities of chlorophyll *a* caused by the erosion of the MPB biofilms (Fig. 2B). Nonetheless,

354 "Without phytoplankton", the resuspension of MPB biofilms followed the erosion of fine particles

355 (Supplement S5). We also observed that cockles enhanced the erosion of MPB in a density-dependent

356 way. This density effect was more noticeable in plots "With MPB" than in those "Without MPB" (Fig.

357 2B).

358 Finally, there was an interactive effect between the "Density of cockles", "Phytoplankton" and "MPB"

359 factors on the resuspension of sand particles. Cockles enhanced the resuspension of sand particles in a

360 density-dependent way in all treatments, expected in the "Without phytoplankton" and "With MPB"

361 treatment in which cockles at low and high density had a similar effect on the current velocity needed to

362 initiate   the   erosion   of   sand   particles   (Fig.   2C).

363
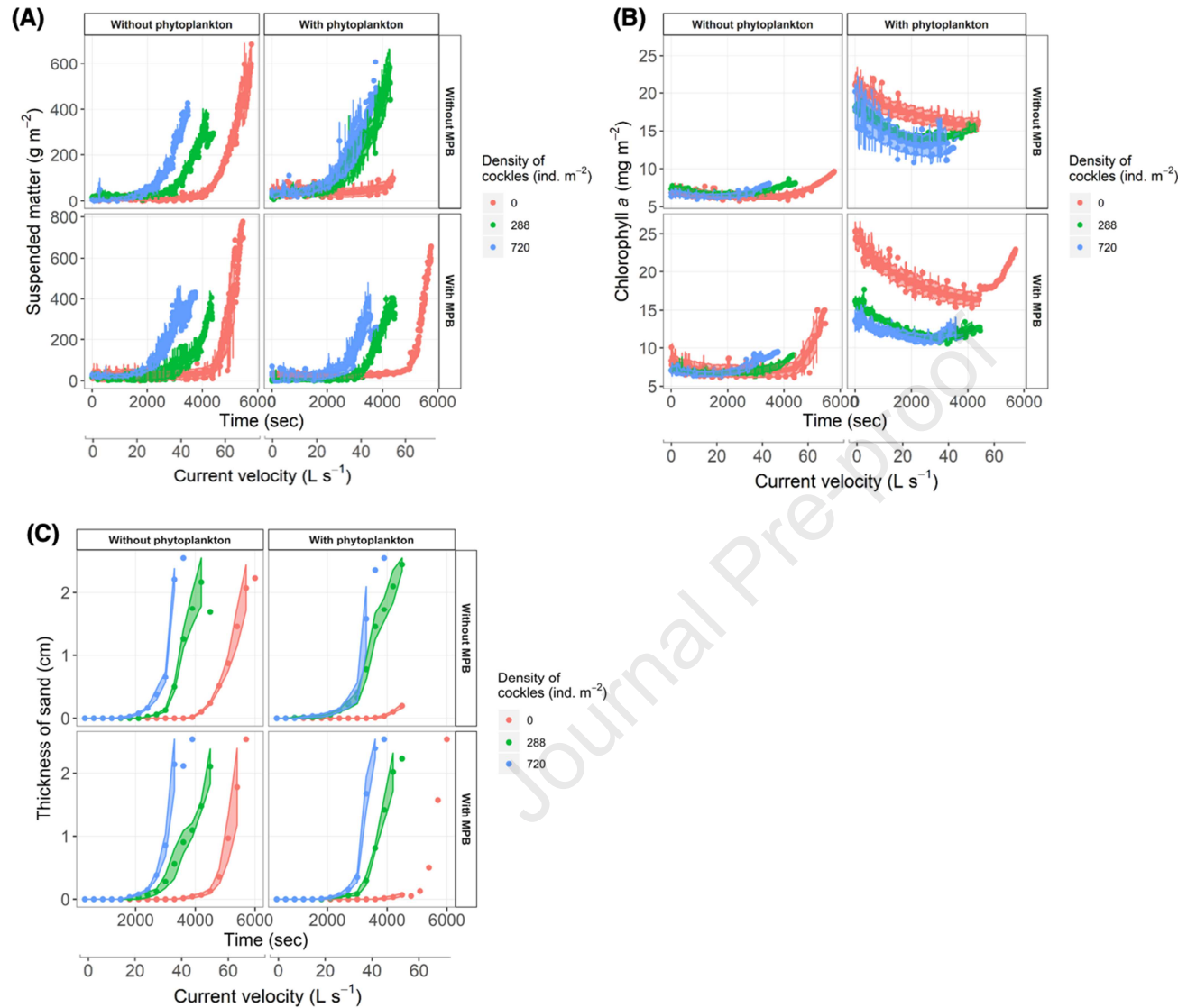
Fig. 2 Temporal changes in the resuspension dynamics of (A) the mud fraction ("Suspended matter"), (B) the chlorophyll *a* of microphytobenthic biofilms and (C) the sand fraction of sediment columns not enriched and enriched with microphytobenthos (MPB; "Without MPB" and "With MPB", respectively) and inhabited by cockles *Cerastoderma edule* at different densities. The influence of the enrichment of the water column with phytoplanktonic organisms was also tested ("Without phytoplankton" and "With phytoplankton"). Mean eroded masses are plotted. Coloured areas represent the standard error around the mean. *N* = 3 for each experimental condition. For all plots "Without cockles" -"With phytoplankton"-

15

369   "Without MPB" and two plots "Without cockles" -"With phytoplankton"-"With MPB", erosion experiments were stopped before mass erosion
370   occurred.

3.3. Shear velocity dynamics

371
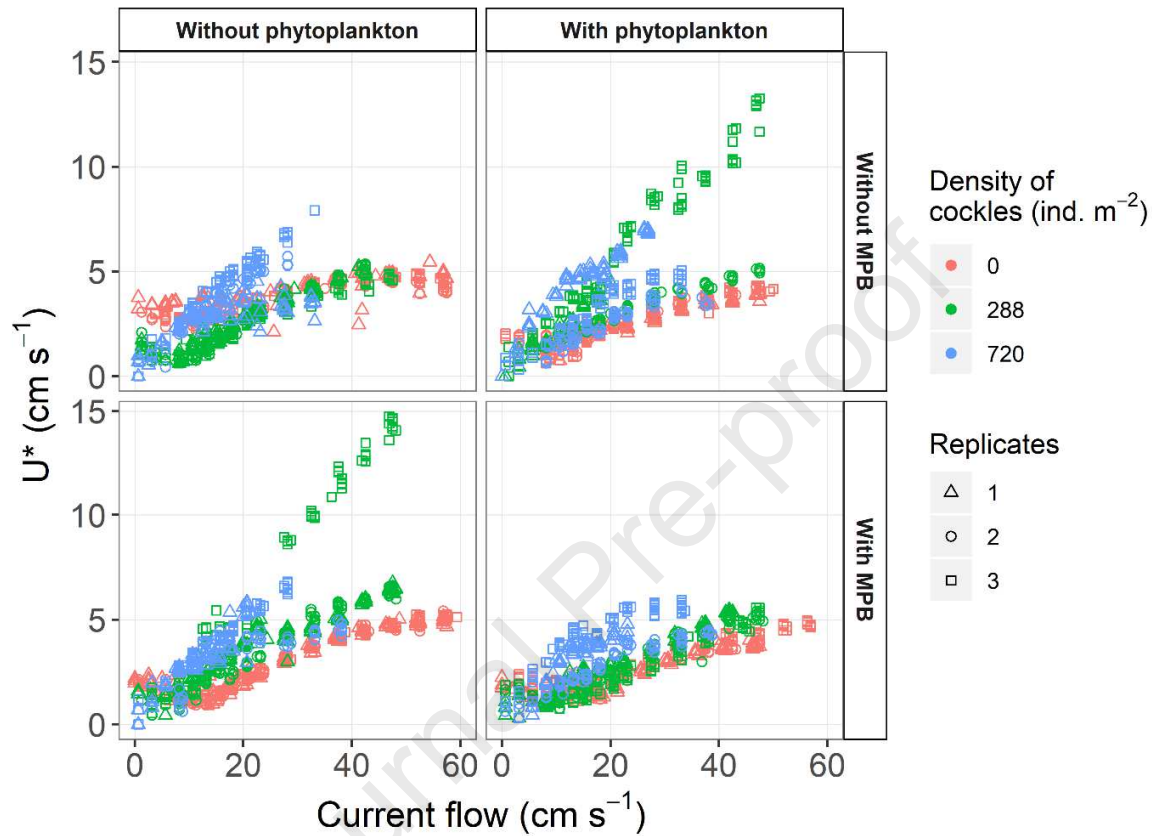
372 Fig. 3 shows the dynamics of the shear velocity (U^*, cm s^{-1}) at the sediment surface of experimental

373 plots as a function of the current flow for the different treatments. At the sediment surface of the "no

374 cockles" plots, U^* initially decreased with an increase in the current flow (ca. 0-15 cm s^{-1}). This initial

375 decrease in U^* is an artefact in the pressure measurement. Air bubbles were initially present on the

376 rooftop side of the flume. The initial increase in the water current in the flume drove out these bubbles and

377 influenced the head loss between the upstream and downstream parts of the samples. As a result, we

378 recorded a decrease in U^*. After this initial decrease in U^* and for a current flow > ca. 10-15 cm s^{-1}, we

379 recorded an increase in U^* with the current flow. Finally, U^* reached a stable value above a current flow

380 of ca. 45 cm s^{-1}. The dynamics of U^* in the "no cockles" plots did not depend on the enrichment of water

381 with phytoplankton nor on the enrichment of the sediment surface with MPB. At the sediment surface of

382 the plots inhabited by cockles, the dynamics of U^* was different. For most of the samples there was no

383 initial decrease in U^*, except for cockles at low density in the plots "Without phytoplankton" and

384 "Without MPB". Instead, U^* constantly increased with an increase in the current flow. Although the

385 presence of cockles modified the dynamics of U^* along the current flow gradient, i.e. the shaped of the

386 curve, there was no density effect. Additionally, we did not observe an interactive influence of the

387 "Phytoplankton" and "MPB" factors on the dynamics of U^*.

388 The presence of cockles in the sediment plots also increased the values of U^*. The influence of cockles on

389 U^* values depended on the "Phytoplankton" and "MPB" factors. "With phytoplankton" and "Without

390 MPB", U^* reached higher values at the surface of the plots inhabited by cockles compared with values

391 recorded without cockles. A similar pattern was observed "Without phytoplankton" and "With MPB".

392 Interestingly, "With phytoplankton" and "With MPB", U^* reached higher values only at the surface of

393 plots inhabited by a high density of cockles compared to values recorded without cockles or with a low

394 density of cockles. A similar trend was also noticed for plots "Without phytoplankton" and "Without

395 MPB".

3.4. Roughness length

396

397 The roughness length averaged 0.13 ± 0.02, 0.70 ± 0.17 and 1.13 ± 0.22 mm in the plots without

398 cockles, inhabited by a low density (i.e. 288 ind. m^{-2}) and a high density (i.e. 720 ind. m^{-2}) of cockles,

399 respectively (mean ± SE) (Fig. 4). There was a significant effect of the "Phytoplankton" and "Density of

400 cockles" factors on z_0 whereas there was no significant effect of the "MPB" factor (Table 1). "With

401 phytoplankton", cockles significantly increased z_0, but there was no density-dependent effect whereas

402 "Without phytoplankton" z_0 increased with an increase in the density of cockles (Fig. 4, Table 1).

17

403   z_0 increased with an increase in the metabolic rate of the cockle populations (ANCOVA, $p < 0.01$). There

404   was no significant influence of the "Phytoplankton" nor the "MPB" factors on this relationship

405   (ANCOVA, $p = 0.052$ and $p = 0.55$, respectively).

406

407   **Fig. 3** Dynamics of the shear velocity U* (cm s^{-1}) across a gradient of current flows (cm s^{-1}) at the
408   sediment surface of experimental plots not enriched and enriched with microphytobenthos (MPB;
409   "Without MPB" and "With MPB", respectively) and placed in a tidal mesocosm not enriched and
410   enriched with phytoplankton ("Without phytoplankton" and "With phytoplankton", respectively). The
411   influence of cockles *Cerastoderma edule* at three densities (0, 280 and 720 ind. m^{-2}) was also evaluated.
412   Three individual replicates for each treatment are plotted.

413
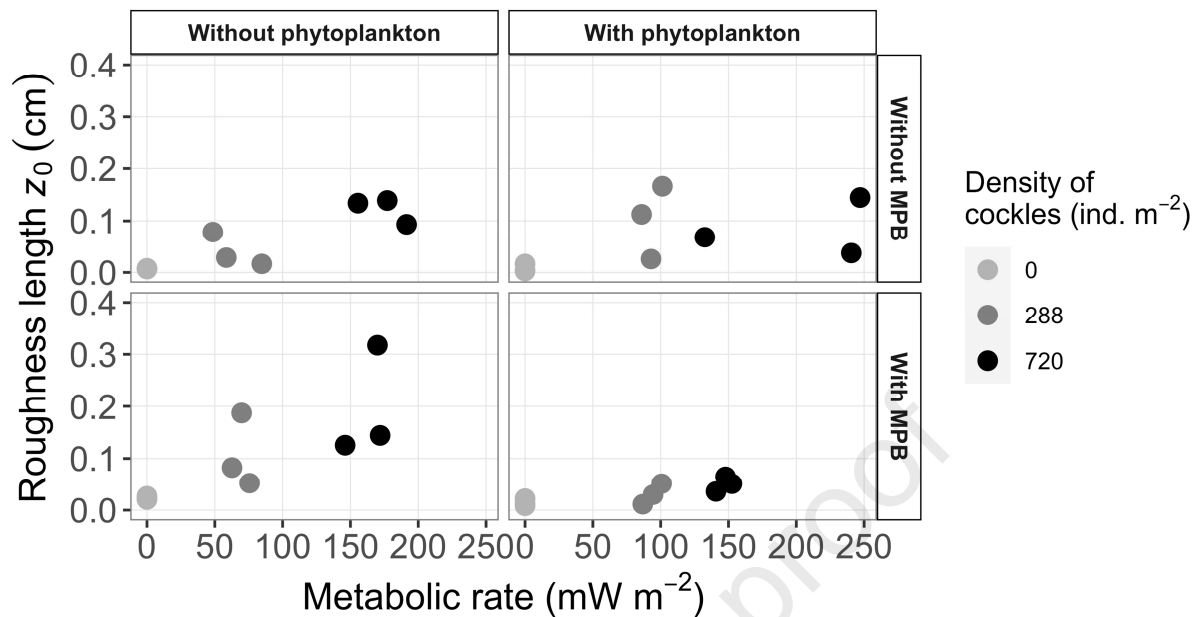
Fig. 4 Influence the enrichment of the water column with phytoplankton ("Without phytoplankton" and "With phytoplankton") on the relationship between the roughness length z_0 measured at the surface of sediment columns not enriched and enriched with microphytobenthos (MPB; "Without MPB" and "With MPB", respectively) and the metabolic rates of cockles *Cerastoderma edule* populations.

418

3.5. Critical bed shear stress

3.5.1. Mud fraction

Critical bed shear stresses (τ_{crit}) were determined for the erosion of the biogenic fluff layer and of the sediment bed (Fig. 5A and 5B). For one sample, we did not observe the erosion of the biogenic fluff layer but only mass erosion.

τ_{crit} for the biogenic fluff layer and the sediment bed ranged 0.05–2.21 and 0.70–7.10 Pa, respectively. There was no separate influence of the "Phytoplankton" and "MPB" factors and no interactive effect between them on τ_{crit} for the biogenic fluff layer (Fig. 5A, Table 1). In contrast, the presence of cockles significantly reduced τ_{crit} for the biogenic fluff layer. There was also an interactive effect between the "Density of cockles" and "Phytoplankton" factors on τ_{crit} with the cockles reducing τ_{crit} to a higher extent "Without phytoplankton" than "With phytoplankton". τ_{crit} decreased significantly with an increase in the metabolic rate of the cockle populations (Fig 5A; ANCOVA, $p < 0.05$). This relationship was not significant "With phytoplankton" where it was significant "Without phytoplankton" (ANCOVA, $p < 0.05$).

There was no separate influence of the "Phytoplankton", "Density of cockles" and "MPB" factors on τ_{crit} for the sediment bed, but we observed an interaction between these factors (Fig. 5B, Table 1). However, pairwise comparisons did not show any significant differences between entities. Finally, there was no significant relationship between τ_{crit} for the sediment bed and the metabolic rate of the cockle populations, independently of the enrichment with phytoplankton or MPB (Fig. 5B; ANCOVA, $p = 0.79$).

3.5.2. Chlorophyll *a*

For five samples, the current flow applied at the sediment surface of the experimental plots during the erosion experiment was too weak to initiate any significant increase in the chlorophyll *a* concentration in the water column. Thus, it was not possible to determine τ_{crit} for these samples. Considering the large number of missing values, we did not conduct PERMANOVA analyses and only provide qualitative results on the effect of the three tested factors. τ_{crit} for the chlorophyll *a* of MPB biofilms ranged 0.72–6.84 Pa (Fig. 5C). In the plots "Without MPB", there was no apparent effect of cockles on τ_{crit}. In contrasts, "With MPB", cockles reduced τ_{crit}, without density-dependent effect. There was no significant relationship between τ_{crit} and the metabolic rate of the cockle populations (ANCOVA, $p = 0.33$).

3.5.3. Sand fraction

τ_{crit} for the sand fraction ranged 0.37–2.46 Pa (Fig. 5D). There was no significant effect of the "Phytoplankton" and "MPB" factors (Table 1). In contrast, the erosion of sand particles in the plots inhabited by cockles at a low density was initiated at lower τ_{crit} than in the plots without cockles or inhabited by a high density of bivalves (Fig. 5D, Table 1). There was no significant relationship between τ_{crit} and the metabolic rate of the cockle populations, irrespectively of the enrichment with phytoplankton or MPB (ANCOVA, $p = 0.33$).
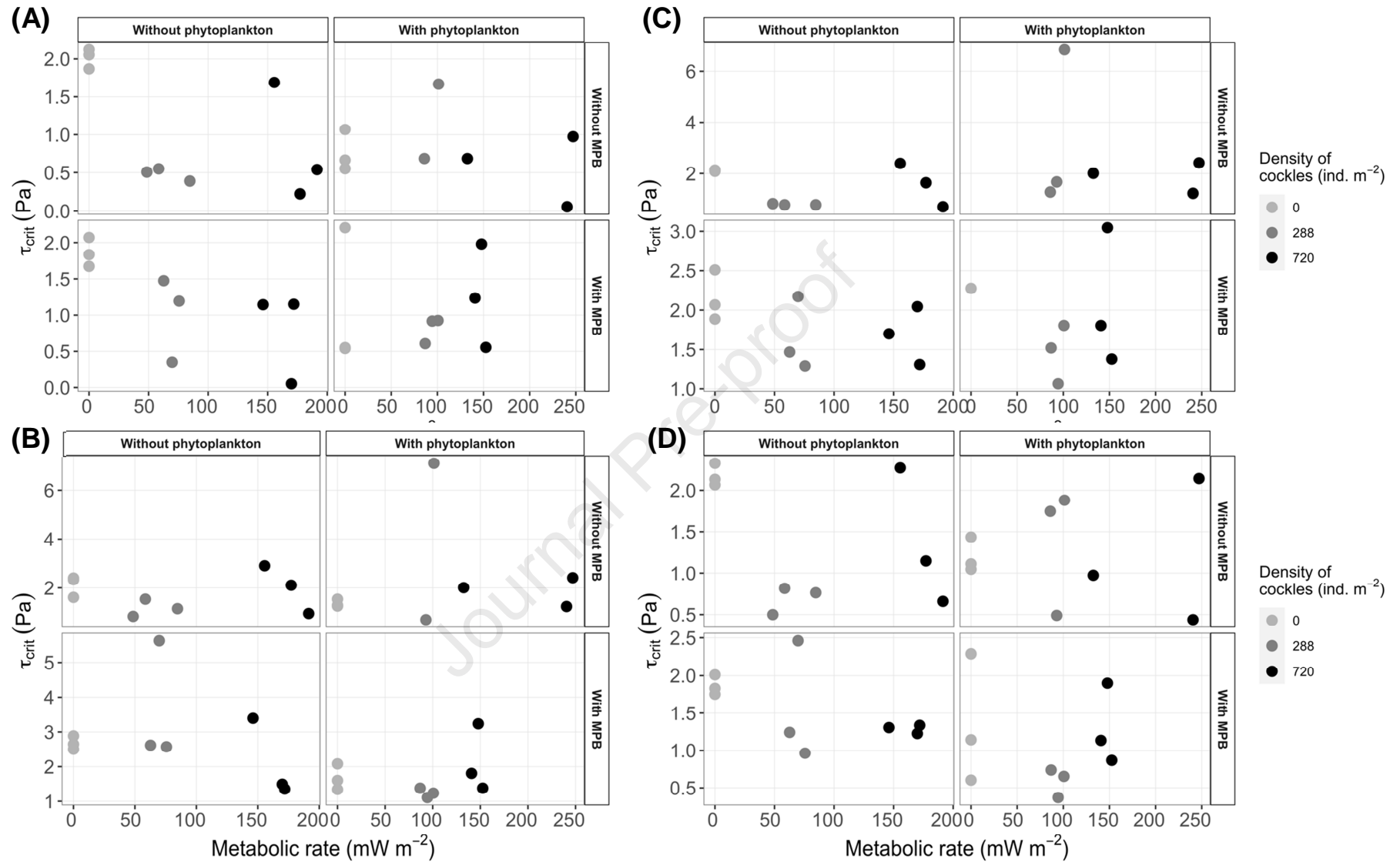
Fig. 5 Influence of the enrichment of the water column with phytoplankton and of the sediment surface with microphytobenthos ("MPB") on the relationship between the critical bed shear stress τ_{crit} (Pa) for (A) the biogenic fluff layer, (B) the sediment bed, (C) the biofilm of microphytobenthos and (D) the sand fraction of the sediment column and the metabolic rates of the cockle populations.

21

457 **3.6. Sediment fluxes**

458 **3.6.1. Mud fraction**

459 Erosion fluxes of fine particles (mud fraction, "suspended matter") during the erosion of the biogenic

460 fluff layer could not be determined for seven samples since the erosion of this layer was immediately

461 followed by the erosion of the sediment bed. For another sample, there was no erosion of a biogenic fluff

462 layer and fluxes of fine particles were then 0 g m^{-2} s^{-1}. Only qualitative results on the effect of the "Density

463 of cockles", "MPB" and "Phytoplankton" factors are thus provided. Fluxes of fine particles ranged 0–0.45

464 g m^{-2} s^{-1} (Fig. 6A). There was no apparent influence of the "MPB" factor on the fluxes of fine particles

465 during the erosion of the biogenic fluff layer (Fig. 6A). In contrast, cockles enhanced the fluxes of fine

466 particles at the sediment-water interface of the plots "With phytoplankton" (Fig. 6A). However, there was

467 no significant relationship between the fluxes of fine particles during the erosion of the biogenic fluff

468 layer and the metabolic rate of the cockle populations (Fig. 6A; ANCOVA, $p = 0.76$).

469 **3.6.2. Chlorophyll *a***

470 There was no erosion of the MPB biofilm for five samples so that no chlorophyll *a* fluxes could have

471 been determined. Therefore, only qualitative results on the effect of the "Density of cockles", "MPB" and

472 "Phytoplankton" factors are provided. Fluxes of chlorophyll *a* ranged 0.00–8.29 µg m^{-2} s^{-1} (Fig. 6B). For

473 the plots "Without MPB", chlorophyll *a* fluxes were on average higher at the sediment-water interface of

474 the plots inhabited by cockles than without cockles. In the plots "With MPB", there was no apparent trend

475 regarding the effect of cockles on chlorophyll *a* fluxes. Nonetheless, fluxes of chlorophyll *a* significantly

476 increased with an increase in the metabolic rates of the cockle populations (ANCOVA, $p < 0.05$).

477 **3.6.3. Sand fraction**

478 Fluxes of sand ranged 3.61–98.60 µm s^{-1} (Fig. 6C). There was no significant influence of the

479 "Phytoplankton", "Density of cockles" and "MPB" factors on the flux of sand particles and no interactive

480 effect between them (Fig. 6C, Table 1). There was no significant relationship between the flux of sand and

481 the metabolic rate of the cockle populations, irrespectively of the enrichment with phytoplankton or with

482 MPB (ANCOVA, $p = 0.74$).
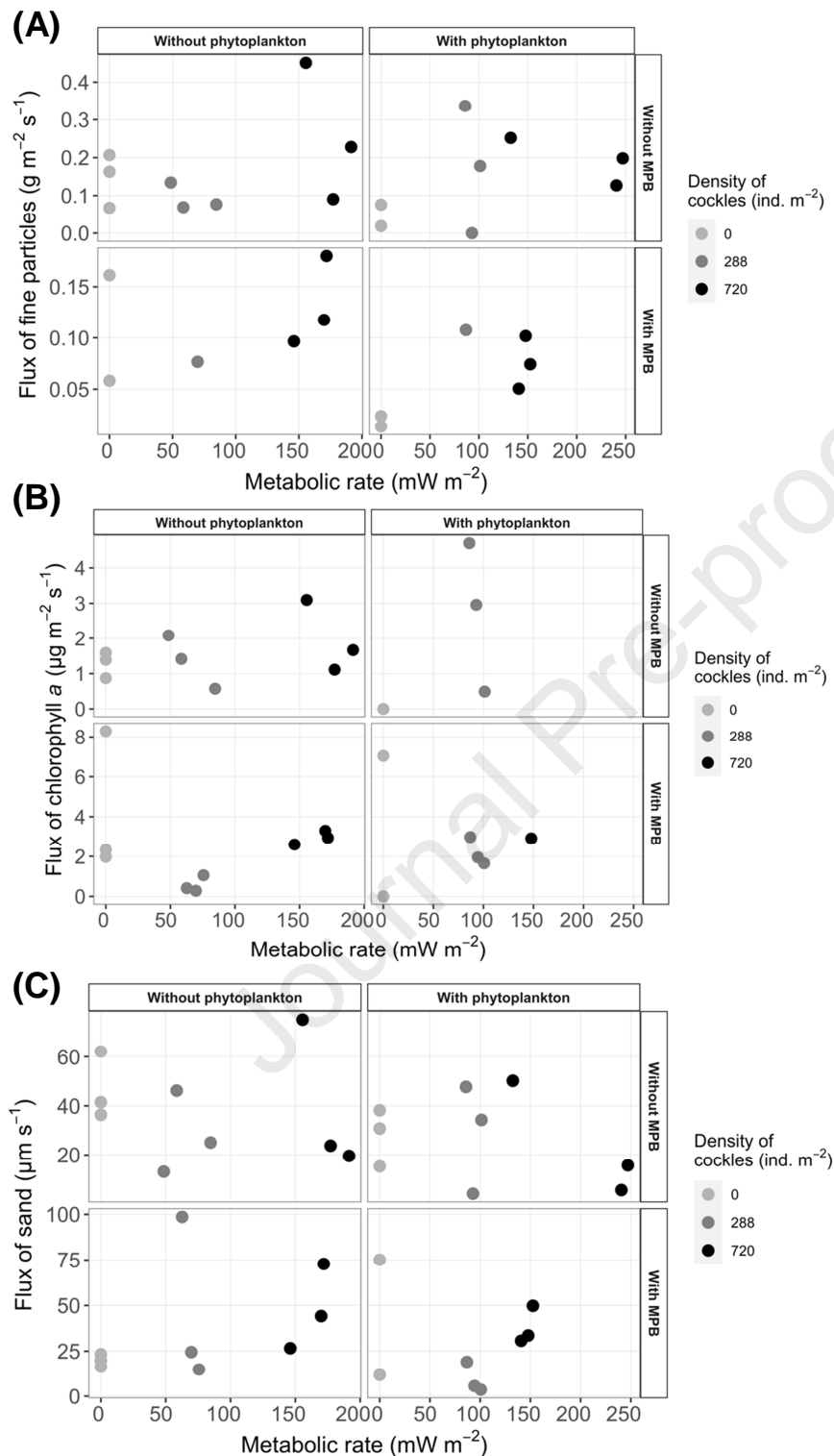
Fig. 6 Influence of the enrichment of the water column with phytoplankton and of the sediment surface with microphytobenthos ("MPB") on the relationship between the (A) fluxes of fine particles during the erosion of the biogenic fluff layer, (B) fluxes of chlorophyll a, and (C) fluxes of sand particles and the metabolic rates of the cockle populations .

23

487 **Table 1** Results of PERMANOVA analyses testing the influence of the enrichment of the water column
488 with phytoplankton ("Phytoplankton"), the occurrence of cockles at different densities ("Density of
489 cockles") and the enrichment of the sediment surface of experimental plots with microphytobenthos
490 ("MPB") on different parameters quantified before and during erosion experiments. P(perm) in bold
491 indicate significant effects ($p < 0.05$). * denotes significant differences in dispersion (PERMDISP
492 analysis, $p < 0.05$).

	df	*Pseudo-F*	P(perm)
Chlorophyll *a* biomass			
Phytoplankton (1)	1	0.66	0.42
Density of cockles (2)	2	70.72	**< 0.01***
MPB (3)	1	441.68	**< 0.01***
(1) x (2)	2	6.73	**< 0.01***
(1) x (3)	1	3.26	0.08*
(2) x (3)	2	28.21	**< 0.01***
(1) x (2) x (3)	2	5.73	**<0.05**
Effective quantum yield of photosystem II			
Phytoplankton (1)	1	1.46	0.24
Density of cockles (2)	2	1.64	0.21
MPB (3)	1	77.76	**< 0.01***
(1) x (2)	2	3.00	0.07
(1) x (3)	1	0.01	0.93
(2) x (3)	2	0.02	0.98*
(1) x (2) x (3)	2	1.16	0.34*
Roughness length z_0			
Phytoplankton (1)	1	4.87	**<0.05**
Density of cockles (2)	2	13.50	**< 0.01***
MPB (3)	1	0.40	0.58
(1) x (2)	2	3.31	**< 0.05**
(1) x (3)	1	7.19	**<0.01***
(2) x (3)	2	0.18	0.55*
(1) x (2) x (3)	2	1.50	0.26*
Critical bed shear stress			
Biogenic fluff layer – muddy fraction			
Phytoplankton (1)	1	1.52	0.23
Density of cockles (2)	2	4.64	**< 0.05**
MPB (3)	1	1.15	0.29
(1) x (2)	2	4.51	**< 0.05**
(1) x (3)	1	0.17	0.68
(2) x (3)	2	0.15	0.85
(1) x (2) x (3)	2	1.77	0.19*
Sediment bed – muddy fraction			
Phytoplankton (1)	1	0.71	0.43
Density of cockles (2)	2	0.30	0.79*
MPB (3)	1	0.42	0.54
(1) x (2)	2	0.44	0.67*
(1) x (3)	1	3.61	0.68
(2) x (3)	2	0.05	0.07*
(1) x (2) x (3)	2	3.90	**<0.05***
Sand			
Phytoplankton (1)	1	2.96	0.10

24

Density of cockles (2)	2	3.36	**0.05**
MPB (3)	1	0.001	0.97
(1) x (2)	2	1.27	0.31
(1) x (3)	1	0.79	0.39
(2) x (3)	2	0.04	0.96
(1) x (2) x (3)	2	3.07	0.06*
Fluxes of sediment			
Sand			
Phytoplankton (1)	1	2.00	0.17
Density of cockles (2)	2	0.46	0.64
MPB (3)	1	< 0.01	0.99
(1) x (2)	2	0.32	0.73
(1) x (3)	1	< 0.01	0.99
(2) x (3)	2	0.67	0.52
(1) x (2) x (3)	2	1.60	0.22*

493

4. Discussion

4.1. Effect of cockles on sediment stability

4.1.1. Overall effect of cockles

Depending on their bioturbation mode, intensity of activity and environmental condition, benthic organisms can have various impacts on non-cohesive ranging from no effect (Li et al., 2017) to a destabilizing (Needham et al., 2013) or stabilizing effect (Joensuu et al., 2018). Our results support a destabilizing effect of the common cockle *Cerastoderma edule* in non-cohesive sediments. In particular, the resuspension dynamics profiles (Fig. 2) highlight that cockles enhance the resuspension of both mud and sand particles from the surficial sediment layer. The resuspension of sediment particles was indeed initiated at lower current velocities in the presence of cockles. In sharp contrast, Li et al. (2017) did not show any significant effect of cockles on the resuspension dynamics of fine particles in a similar environment. The densities of cockles being similar in the two studies, such a discrepancy may be due to differences in the experimental set-ups, especially regarding the duration of the acclimation period i.e. the time allowed for cockles to settle and bury into their new environments before erosion experiments start. Li et al. (2017) conducted erosion experiments following a 2-day settling period whereas cockles were presently left for 6 days in the sediment plots before we performed erosion experiments. This longer acclimation period may allow cockles to significantly alter the sediment erodibility and/or roughness. Additionally, Li et al. (2017) placed cockles in a pure sand while we used a sediment containing a small proportion of silt (4%). Although both sediments were non-cohesive, this small proportion of cohesive particles may have influence biota-mediated processes (Cozzoli et al., 2020).

4.1.2. Effect of cockles on sediment roughness and erodibility

The use of a flume allowing to record the pressure between the upstream and downstream parts of sediment samples (Le Hir et al., 2008) associated to the calculation method developed by Guizien et al. (2012) enabled us to accurately estimate the bed shear stress at the sediment surface of plots with diverse topographies. By doing so, critical thresholds τ_{crit} for erosion that take into account the sediment roughness were calculated. We also estimated the roughness length from the dynamics of the shear velocity across a gradient of current flows for each sample. As a result, we highlighted that the destabilizing effect of cockles results from both their impact on sediment erodibility and roughness. The significant effect of cockles on the roughness length z_0 indicates that cockles modify the surface topography of the sediment they inhabit and increase its roughness. Indeed, the locomotor, burrowing and feeding activities of cockles cause the reworking of sediments and thus alter the topography of their surface (Flach, 1996; Li et al., 2017). Additionally, some organisms were not fully buried or emerged at the sediment surface while

26

526 migrating vertically in the sediment column (pers. obs.). Thus, cockles could also have modified the

527 topography of the sediment bed by their mere presence (Anta et al., 2013). As a result of their effect on the

528 sediment topography, cockles changed the relationship between the bed shear stress and hydrodynamics.

529 This relationship could also have been modulated by other activities of cockles, such as filtration. For

530 instance, the siphons of cockles were often visible at the sediment surface during erosion experiments

531 (pers. obs.) suggesting that the bivalves were actively filtering. Bivalves can also produce exhalant jets

532 which can interfere with the current flow and may influence the bed shear stress as well (Jonsson et al.,

533 2005; van Duren et al., 2006).

534 Although the methodology employed in this study allowed to quantify the effect of bioturbators on both

535 sediment erodibility and bed roughness, it remains difficult to estimate the relative contribution of both

536 processes on sediment dynamics. We demonstrated a significant effect of cockles, as considered as a

537 categorical factor, on the critical thresholds τ_{crit} for erosion of the fluff layer and the sand fraction of the

538 sediment column. Nonetheless, the *F-value* associated to the influence of cockles in these analyses were

539 much lower than those calculated when assessing the effect of cockles on the roughness length z_0.

540 Thereby, we suggest that the destabilizing impact of cockles is largely driven by effects on sediment

541 roughness. This is in agreement with Ciutat et al. (2007) who reported important changes in the bed shear

542 stress of cohesive sediments. The latter could be caused by modifications of the sediment topography, and

543 thus roughness. In contrast, Li et al. (2017) noted that cockles display different behaviors in non-cohesive

544 vs. cohesive environments with cockles generally less active in cohesive than in non-cohesive sediments.

545 This had consequences on the topography of the sediment surface that was less disturbed in the cohesive

546 environment than in the non-cohesive one. Yet, Li et al. (2017) showed a significant destabilizing effect of

547 cockles only in the cohesive sediment. The relative importance of sediment erodibility and roughness on

548 sediment dynamics in this case might have been different from what is observed here in a non-cohesive

549 sediment with a low proportion of silt. Indeed, the destabilizing effect of cockles observed by Li et al.

550 (2017) might have been mainly mediated by changes in the erodibility of the cohesive sediment. To our

551 opinion, an important next step will consist of developing a method that will clearly evaluate to which

552 extent erodibility and roughness respectively modulate sediment dynamics in both non-cohesive and

553 cohesive environments.

554 **4.2. Modulation of the influence of cockles on sediment stability**

555 In natural environments, it is likely that various abiotic and biotic parameters modulate the influence of

556 bioturbators on sediment erosion processes (Andersen, 2001; Kristensen et al., 2013). Among the diverse

557 factors that could interfere with the role of cockles on sediment dynamics, we focused on three parameters

558 that greatly vary both temporally and spatially, i.e. bivalve density, MPB occurrence and suspended food

559 (i.e. phytoplankton) availability.

560 Similarly to Ciutat et al. (2007) we noted an increase of the destabilizing effect of cockles with an increase

561 in their density. This effect was even greater by taking into account the metabolic rates of the cockle

562 population. Metabolic rates are based on metabolic theories observing that the mass/size of organisms

563 affect biological structures and processes, i.e. all the organismal activities needing energy and involving

564 matter transformation, depend on temperature and are proportional to the organism mass/size in a size

565 scaling way (Brown et al., 2004; van der Meer, 2006; West, 1997). Recently, Cozzoli et al. (2020, 2018)

566 demonstrated that the metabolic rates of bioturbators could be used as an accurate descriptor of the

567 activity levels of these organisms and allows to predict their influence on sediment resuspension in

568 different environments. Indeed, metabolic rates of bioturbator populations can be derived from individual

569 estimation, taking into account the individual effect of organisms and their density (Cozzoli et al., 2020,

570 2019, 2018). This novel approach may be more accurate to evaluate the influence of natural populations

571 with organisms of heterogenous sizes than taking into account their sole density. Our results also suggest

572 that there was no switch in the relative importance of erodibility and roughness on dynamics of this non-

573 cohesive sediment with an increase in the bivalve density and metabolic rate. Indeed, there was a strong

574 correlation between the roughness length z_0 and the metabolic rate of cockle populations whereas only τ_{crit}

575 for the biogenic fluff layer was significantly correlated with the metabolic rate of cockle populations.

576 The enrichment of the sediment column with phytoplankton also slightly modulated the sediment

577 resuspension dynamics in the presence of bivalves. Indeed, the density-dependent effect of cockles on

578 sediment resuspension was less clear when the water column was enriched with phytoplankton, i.e.

579 cockles at high and low density had a similar impact on sediment resuspension. There was also no positive

580 correlation between the critical bed shear stress for the fluff layer and the metabolic rates of the cockle

581 populations in plots enriched with phytoplankton whereas this correlation was significant without

582 phytoplankton. The high availability of food may have influence the levels of activity of cockles, with the

583 bivalves less active (in term of locomotion and burrowing) when phytoplankton was at high concentration.

584 This hypothesis is in accordance with the work of Maire et al. (2007) who highlighted a reduced sediment

585 reworking activity of the bivalve *Abra ovata* when food was highly available. Here, the high concentration

586 of phytoplankton in the water column may also have enhanced the filtration activity of cockles and thus

587 the rapid deposition of feces and pseudo-feces onto the sediment surface (Navarro and Widdows, 1997).

588 This resulting biodeposition may have led to a "muddification" (Soissons et al., 2019) of the sediment and

589 an increase resistance to hydrodynamics forcing.

590 We also observed that the enrichment of the sediment surface of the experimental plots with

591 microphytobenthos (MPB) did not modulate the stability of non-cohesive sediments both in the presence

592 and absence of cockles. Given the extensive literature that unravels a stabilizing role of MPB (e.g.,
593 Holland et al. 1974; Yallop et al. 1994; Miller et al. 1996), our results may be surprising. However, MPB
594 stabilizing effects have been mainly reported for cohesive substrates and notably in sandy mud
595 environments (Ubertini et al., 2015). Conversely, in non-cohesive environments, only a very thick
596 microbial mat could interfere with sediment erosion processes (Yallop et al., 1994). The microbial mat in
597 our experimental plots was thus probably insufficiently developed to counteract the hydrodynamics stress
598 at the sediment surface and thus to efficiently lower the sediment erosion potential. In the presence of
599 cockles, we also quantified a lower MPB biomass of biofilms at the sediment surface. Cockles have been
600 previously shown to have contrasting effects on the development of benthic microalgae biofilms
601 depending on the respective intensities of their bioturbation processes, i.e. bioirrigation vs. sediment
602 reworking. The porewater transport generated by cockles can indeed stimulate nutrient fluxes at the
603 sediment-water interface on which MPB relies (Eriksson et al., 2017; Swanberg, 1991), while particle
604 reworking activities can mechanically disrupt MPB biofilms and interfere with their growth
605 (Rakotomalala et al., 2015). Our results clearly emphasize that the sediment reworking activity of cockles
606 was the main process influencing the development of MPB in this study.

607 Finally, we evidenced that the combined availability of suspended-food and MPB may modulate the
608 influence of cockles on non-cohesive sediment dynamics. Indeed, cockles seemed to have a lower impact
609 on sediment roughness and thus a reduced destabilizing effect when suspended food (i.e. phytoplankton)
610 and MPB biofilms were together at high availability. Although this trend was not statistically significant
611 (Fig. 2 and Fig. 3), the reasons behind this pattern remain unclear.

612 ## 5. Conclusion

613   The influence of burrowing organisms on sediment dynamics have been assessed through numerous
614 field and laboratory studies. Nonetheless, the mechanistic understanding of how bioturbating organisms
615 affect the erosion of sediments, i.e. both their erodibility and roughness, is still limited. Our lab
616 investigation highlighted a significant destabilizing effect of the common cockle *Cerastoderma edule* on
617 non-cohesive sediments with a low silt content (4%). This was a direct consequence of cockles' effect on
618 the sediment bed topography and roughness rather than changes in the sediment erodibility. We also
619 demonstrated that the cockle-mediated impact on sediment dynamics depend on several environment
620 factors. First, the destabilizing effect of *C. edule* increased with an increase in the bivalve density. This
621 pattern was even more apparent taking into account the metabolic rates of the cockle population. Second,
622 the presence of suspended food limited the destabilizing role of cockles. High availability of suspended
623 food may lower the bioturbation potential of cockles and/or promote their filtering activity and
624 biodeposition. Finally, we noted that while MPB biofilms did not temper the destabilizing role of cockles

625   at low availability of suspended food, the bivalve's impact on sediment roughness may have been minimal

626   when both phytoplankton and MPB biofilms are present. The understanding of how environmental drivers

627   may influence the role of macrofauna in both non-cohesive and cohesive substrates remains scarce and the

628   latter results are thus of particular interest. To our knowledge only the influence of intraspecific

629   competition (e.g., Ciutat et al., 2006; Cozzoli et al., 2020; Kristensen et al., 2013), and more recently

630   parasitism (Dairain et al., 2020), on macrofauna organisms and their knock-on effect on sediment

631   dynamics have been assessed so far. We thus argue for an identification of abiotic and biotic drivers of

632   macrofauna-mediated processes on sediment dynamics. In particular, the evaluation on how and to what

633   extent stress factors of major concern, such as global climate change or metal and organic contaminations,

634   influence the behavior of bioturbators could lead to develop accurate and site-specific calibrated models

635   predicting the importance of macrofauna in sediment erosion processes in a near future.

Compliance with ethical standards

Declarations of interest

None.

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845

Highlights

- The role of cockles on non-cohesive sediment dynamics was tested

- The influence of cockles on sediment erodibility and bed roughness was disentangled

- Cockles increased the sediment bed roughness and, to a lesser extent its erodibility

- The destabilization effect of cockles increased with their density

- Phytoplankton and microphytobenthos presence limited the cockle destabilizing role

Declaration of interests

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

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