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1 **Modelling the Effect of *Cerastoderma edule* Bioturbation on**
2 **Microphytobenthos Resuspension Towards the Planktonic Food**
3 **Web of Estuarine Ecosystem**

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32 Abstract

33 Microphytobenthos (MPB) represents an important food source for primary consumers in
34 estuarine ecosystems and the availability of MPB as food items results from complex
35 physical, chemical, and biological interactions. In Baie des Veys (Lower Normandy, France),
36 the common cockle *Cerastoderma edule* constitutes the major bioturbator in the ecosystem in
37 terms of biomass. In this ecosystem, cockle bioturbation is a key process regulating the MPB
38 erosion flux in the water column. This bivalve intensely modifies the top layer of the sediment
39 by increasing the sediment erodibility and the fluxes of suspended chlorophyll *a* through the
40 valve movements. More precisely, cockle bioturbation destabilizes the sediment surface by
41 creating a biogenic layer that is easily eroded with tidal hydrodynamic forces. Associated
42 MPB can then be exported to the water column to fuel higher trophic levels of the planktonic
43 food web. The aim of this study was to develop a numerical model that reproduces the export
44 of MPB associated to the biogenic layer erosion. Kinetics of suspended MPB, in response to
45 increasing stress, were obtained from flume experiments in lab controlled conditions and *in*
46 *situ* natural conditions. Following this, the suspended MPB were analyzed to respectively
47 parameterize the model by 1) a calibration approach, and 2) an independent validation. The
48 analysis has highlighted that the higher the biomass of cockles, the higher the MPB
49 resuspension rates. Our model consistently reproduces the tendency encountered in laboratory
50 analysis and with *in situ* natural conditions. During the validation, a small site-specific lack of
51 adjustment was identified, but, among the macrozoobenthic community, the model can be
52 significantly improved by considering the bioturbation activities of another ecosystem
53 engineer, *Pygospio elegans*. This study thus provides reliable estimates of the daily food
54 availability from benthic primary consumers in an estuarine system where cockles dominate
55 the bioturbating assemblage. This model can be inserted in various model designs (0D, 1D-
56 vertical or 3D).

57 Keywords: sediment transport, erodibility, modelling, microphytobenthos, *Cerastoderma*
58 *edule*, bioturbation

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72 1. Introduction

73 Numerical modelling represents a useful tool to overcome complexity and temporal variations
74 of marine ecosystems. It has been used to reproduce physical transport on tidal flat temporal
75 pattern in estuarine system (e.g. Toorman 2002). Such complex models simulate the temporal
76 pattern of tidal flats through hydrodynamic disturbances which integrate sediment suspension
77 and circulation (Cancino and Neves, 1999; Chao et al., 2008; Clarke and Elliott, 1998;
78 Warner et al., 2008). Moreover, sediment erosion may also be mediated by biological
79 activities (Kristensen et al., 2012; Orvain et al., 2012; Widdows and Brinsley, 2002; Willows
80 et al., 1998; Wood and Widdows, 2002). Biology can affect the sediment properties through
81 faunal bioturbation process described by the same authors. Bioturbation is a key process in
82 coastal system and greatly modifies the physical properties of the sediment (Andersen et al.,
83 2010; Ciutat et al., 2006). Macrofauna bioturbation can stabilize or destabilize the sediment
84 depending on the species. Macrozoobenthos changes the erodibility of the sediment. This
85 process of ecosystem functioning has been modelled by simulating the bioturbation effect of
86 macrofauna on sediment stability (Orvain, 2005; Orvain et al., 2003; Willows et al., 1998).
87 Orvain et al. (2012) have validated a model of bioturbation effect of two macrofauna species
88 (*Scrobicularia plana* and *Peringia ulvae*) on sediment erodibility. They stated that the effect
89 of bioturbation on sediment properties remains a species-specific process. Moreover,
90 Kristensen et al. (2012, 2013) clearly showed that faunal erosion impacts must preferably be
91 evaluated in biomass units when developing bioturbation/erosion laws, however erosion laws
92 remain species-specific (Kristensen et al., 2012; Orvain et al., 2012). Species such as the
93 bivalve *Scrobicularia plana* have strong erosion impact in the sediments they inhabit while
94 *Peringia ulvae* have strong surface effects, especially when compared in biomass unit.
95 *Peringia ulvae* also have strong grazing effects on microphytobenthic biofilms (Orvain, 2005;
96 Orvain et al., 2014) and the important surface area can be rapidly covered, even by one single
97 individual (Orvain et al. 2012).

98 Moreover, the study of the benthic autotrophic compartment has also been modeled with
99 special focus on the role of microphytobenthos (MPB) resuspension and the dynamics of its
100 biomass (Guarini et al., 2008; Mariotti and Fagherazzi, 2012). Export of MPB in the water
101 column is a key process that maintains the biofilm development and avoids the saturation of
102 MPB development in the sediment (Blanchard et al., 2001). A realistic simulation of
103 resuspension of MPB biofilm can be obtained only if this process is not associated to the
104 strong erosion of the underlying sediment (Guarini et al. 2008). The mass bed erosion is a
105 strong event that has a too drastic influence on chlorophyll *a* biomass dynamics to let develop
106 the biofilm at a sustainable equilibrium state. The model developed by Guarini et al. (2008)
107 represents detachment process that continually and moderately affects the benthic marine
108 MPB biofilms under low hydrodynamic forces. In nature, such chronic detachment of benthic
109 microalgae can be assumed to be equivalent to the commonly named “fluff layer erosion” by
110 Shimeta et al. (2002) and Orvain et al. (2003), mainly related to bioturbation activities
111 (Orvain et al., 2004). Mariotti and Fagherazzi (2012) have developed a model of growth and
112 resuspension of MPB biofilm development under hydrodynamic disturbances. The chronic
113 detachment of MPB biofilm was integrated in a simple manner in the model, which
114 corresponds to the resuspension of MPB described by Guarini et al. (2008). They have also
115 integrated the erosion of the sediment in the model, which occurs in a case of high
116 hydrodynamic forcing, and traditionally considered as “bed erosion” (type Ib or type II

117 erosion, according to the definition by Amos et al. (1992). Mariotti and Fagherazzi (2012)
118 have pointed out that the intensity, the frequency of hydrodynamic disturbances, and the time
119 scale dynamic of MPB growth are decisive factors for MPB temporal pattern.

120 The common cockles (*Cerastoderma edule*) move in their environment and rework the
121 sediment particles, modifying the chemical and physical properties of their habitats (Hedman
122 et al., 2011). There is some controversy about the effect of this species on sediment
123 erodibility. The destabilizing (Ciutat et al., 2006, 2007) or stabilizing (Andersen et al., 2010)
124 effect of cockles has been counteracted. Nonetheless, Andersen et al. (2010) have highlighted
125 the stabilizing effect of MPB biofilm, such as other studies have found in absence of fauna
126 (Sutherland et al., 1998; Underwood and Paterson, 1993). Also, they explained the lack of
127 destabilizing effect of cockles in their results as the direct consequence of the entirely buried
128 position of cockle during the experiments. They then stated that the position of the cockle in
129 the sediment can increase the bed roughness. Otherwise, species-specific behavior such as
130 filtration, valve movement, and burying activity, common to the cockle, disturbs the sediment
131 and leads to the erosion of sediment at a lower shear stress as compared to an undisturbed
132 sediment. Experiments conducted by Jonsson et al. (2005) also support the assumption that
133 cockles directly consume a part of suspended algal matter, playing a key role by disturbing
134 turbulence in the benthic boundary layer. Cockles can thus be considered as an engineer
135 species that physically disturbs sediment and water column allowing MPB availability in the
136 ecosystem.

137 To the best of our knowledge, there is a dearth of modelling the export of MPB in the water
138 column associated to sediment erosion due to macrofaunal bioturbation. We need to bridge
139 the gap between modelling the chronic detachment of MPB and the fluff layer erosion in a
140 bioturbated system, to better evaluate the role of these ecosystem engineers. The purpose of
141 this study was to assess the predictability of MPB erosion by using bioturbation/erosion laws
142 that have only been used in the past for modelling sediment transport (Orvain et al., 2012) in a
143 bioturbated system. More specifically, we aimed at refining the way to model the ‘chronic’
144 fluff layer erosion and the associated MPB under the bioturbation action of the bivalve
145 *Cerastoderma edule* in the Baie des Veys (Normandy-France), where this species drastically
146 dominates the wild macrofaunal community (Ubertini et al., 2012). The objective of this study
147 was to model the erosion rate of MPB in response to various body sizes and densities of
148 cockles and thereby determine the food availability of benthic primary producers for the
149 cockles and associated suspension-feeders in estuarine ecosystems. The model of fluff layer
150 erosion has been parameterized with experimental data by following a 2-step approach: 1)
151 calibration of erosion parameters related to bioturbation on the basis of experimental data in
152 controlled lab conditions, cockle density and body size, and 2) validation performed with *in*
153 *situ* data from three locations in the Baie des Veys (Normandy-France). The validation step
154 was conducted without readjusting the parameters to assess the model fitness to independent
155 *in situ* data. The residuals between modelled and observed data were computed to discuss
156 fitting adjustment.

157

158 2. Data

159 2.1 Laboratory experiments

160 Experiments were conducted to determine the effects of cockle bioturbation on the
161 resuspension rates of microphytobenthic biofilm in the water column. Density effect of
162 juveniles (0.25 - 1.4 cm) and adult cockles (2.2 - 2.7 cm) were experimented. Erosion was
163 conducted with the Erodimeter flume. Details of the functioning of the flume are explained in

164 Le Hir et al. (2008). The device allowed the imposition of controlled bed shear velocities (u^*
165 ca 1.40 - 4 cm s⁻¹) on sediment cores of microphytobenthos and cockle culture. Tested
166 velocities were incrementally increased every 5 minutes, constituting the forcing factor for the
167 model developed later. Probes connected to the flume recorded continually: i) the flow
168 discharge; ii) the pressure upstream and downstream the sediment core; iii) the turbidity; and
169 iv) the suspended Chlorophyll *a* biomass (calibrated with the fluorimetry). Following the
170 method of Guizien et al. (2012), the bed shear stress (τ_b , Pa or kg m⁻¹ s⁻²) was calculated. The
171 recorded fluorescence was also converted in quantity of chlorophyll (Chl a_{probe} , $\mu\text{gChl } a \text{ L}^{-1}$)
172 in the water column. Chl a_{meas} , which represents the quantity of eroded chlorophyll *a* per unit
173 of area ($\mu\text{gChl } a \text{ m}^{-2}$) was deduced with the product of chlorophyll *a* concentration ($\mu\text{gChl } a$
174 L^{-1}) and the volume of the Erodimeter (L) over the surface of the core (m²). Water was
175 sampled at 3 different flows (1.65, 2.97, 3.94 cm s⁻¹), was filtered with Whatman filters (GF/C
176 47 mm), and treated to determine the concentration of suspended matter (in g L⁻¹) and the
177 concentration of suspended chlorophyll *a* (in $\mu\text{g L}^{-1}$).

178 179 2.2 Chlorophyll *a* correction

180 Studies conducted by Jonsson et al. (2005) have shown direct consumption of a part of
181 suspended matter exported in the water column by cockles. A high resolution camera was
182 placed over the sediment cores during the erosion experiments. Time during which an active
183 filtration occurred (t_{fil} , s) was then deduced from siphon movement. Given that cockles
184 filtered a certain quantity of suspended chlorophyll *a* during the experiments, the filtration
185 relationship developed by Rueda et al. (2005) was used to quantify the microphytobenthic
186 chlorophyll *a* consumed during the experimental time. The rate at which the cockle filters
187 (Chl a_{fil} , $\mu\text{gChl } a \text{ m}^{-2} \text{ s}^{-1}$) depends on the clearance rate (CR, $\text{L m}^{-2} \text{ s}^{-1}$) and the chlorophyll *a*
188 concentration in the water (Chl a_{probe} , $\mu\text{gChl } a \text{ L}^{-1}$). We used the recorded chlorophyll *a* in the
189 flume to estimate the filtration rate.

$$190 \quad \text{Chl } a_{fil} = \text{Chl } a_{probe} \times CR \quad (1)$$

191 The clearance rate (CR, $\text{L m}^{-2} \text{ s}^{-1}$), in agreement with the cockle growth model by Rueda et al.
192 (2005), was deduced from the biomass of cockle (biomass, gDWcockle m⁻²) and the rate at
193 which an organism of 1g of dry weight filters the chlorophyll *a* biomass (A_{cr} , L gDWcockle^{-1}
194 s⁻¹).

$$195 \quad CR = A_{cr} \times \text{Biomass} \quad (2)$$

196 The total amount of suspended chlorophyll *a* (Chl a_{tot} , $\mu\text{gChl } a \text{ m}^{-2}$) is thereafter corrected by
197 artificially adding the cumulative sum of filtered chlorophyll *a* (Chl a_{fil}) during the period of
198 active filtration (t_{fil} , s) to the measured chlorophyll *a* (Chl a_{meas} , $\mu\text{gChl } a \text{ m}^{-2}$).

$$199 \quad \text{Chl } a_{tot} = \text{Chl } a_{meas} + \text{Chl } a_{fil} \times t_{fil} \quad (3)$$

200 Corrections were made due to the fact that the model will reproduce the resuspension of MPB
201 without the filtration process of cockle. The model development presented herein is based on
202 data from the aforementioned experiments and the model was thus calibrated with the total
203 resuspended chlorophyll *a* (Chl a_{tot}). Parameters and equations of filtration activity of cockles
204 are summarized in Tab. 1.

205 206 2.3 Validation data

207
208 Independent datasets were obtained from a temporal survey of the cockle population dynamic
209 in the Baie des Veys (Lower-Normandy France) in June and September 2012, January and
210 April 2013. The survey was conducted at low tide at 3 sites in the Baie des Veys (Fig. 1i): A,
211 B, and C.

212 Two series of samplings were conducted per site and per date. The first series consists of
213 analyzing the macrofaunal composition and the chlorophyll *a* content of the sediment (Fig.

214 lii, gray circles). Samplings were made in 5 stations per site (Fig. 1ii). Quadruplicate samples
215 of macrofauna and Chlorophyll *a* content were made per station. Analysis of each sample was
216 conducted separately. Macrofauna were sampled with a 0.25 m² quadrat of 0.15 m depth, then
217 were extracted from the sediments with sieve of 1mm mesh size. Thereafter, macrofauna
218 species were identified and counted. The chlorophyll *a* content of the sediment was
219 determined by sampling the surface layer with a disc of 20 cm diameter and 1 cm depth.
220 Sediment sample was homogenized and freeze-dried during 12h. Following the method
221 conducted by Welschmeyer (1994), chlorophyll *a* was extracted with acetone during 24 hours
222 at dark from 200g of dried sediment. Chlorophyll *a* was then measured with fluorometer
223 whose values were expressed in quantity of chlorophyll *a* per g of sediment ($\mu\text{gChl } a$
224 gDWsediment^{-1}).

225 The second series consists of sampling sediment cores to analyze the erodibility of the
226 sediment (Fig. 1ii, black circles). Samplings were conducted on-site in 3 stations chosen
227 randomly among the 5 stations (Fig. 1ii). Three sediment cores were sampled in each station
228 for the flume experiments (Erodimeter). In total, 9 extra sediment cores were sampled each
229 date. The same experimental procedure as during laboratory experiments was adopted, during
230 which resuspended chlorophyll *a* was continuously measured. The filtered chlorophyll *a* in
231 the recirculating flume was estimated in the same way as in laboratory experiments, and when
232 cockles were present in the sediment core. The total resuspended chlorophyll *a* was used for
233 the validation step. Cockle specimens from the erosion experiments were thereafter captured
234 at the end of the experiments and individually weighed to provide the biomass of cockles
235 responsible of bioresuspension in the flume. Since the core of sediment used with the flume
236 experiment was sampled *in situ*, other macrofauna species were present in the sediment.

237 Among the 36 erosion experiments, only 18 experiments with live and active cockles were
238 analyzed and were used to validate the model. Thus, the corresponding samples of
239 macrofauna and chlorophyll *a* in the sediment were considered for further analyses.

240 Kruskal-Wallis nonparametric tests were conducted to analyze temporal and spatial
241 differences between sites regarding chlorophyll *a* content and macrofauna composition
242 (because the conditions for parametric ANOVA were not fulfilled).

243

244 3. Model development

245 3.1 Conceptualization

246 Fig. 2 represents concepts and processes which are taken up in this study. The water column
247 constitutes one single compartment. The second compartment is represented by the sediment
248 where cockles are present. The link between the two compartments is represented by the flux
249 due to erosion (E_{btb}). Filtration by cockles ($\text{Chl } a_{\text{fil}}$) is also represented in Fig. 2 and was used
250 to determine the total suspended chlorophyll *a* as explained earlier. Two bioturbation effects
251 of cockle on the sediment are considered in the present study: (1) the increase of bed
252 roughness, and (2) the bioresuspension of MPB due to valve adduction. Cockle effect on bed
253 roughness was not modelled but the bed shear stress, affected by cockles, was measured and
254 directly used as the forcing variable. A 0-dimension model design was chosen to be developed
255 on the basis of the aforementioned bio-destabilizing effects of cockles on sediment. Fluxes
256 resulting from advection and diffusion exchanges are neglected in our approach.

257

258 3.2 Model equations

259 In this study, three state variables are used and units are given in Tab. 2: the suspended
260 chlorophyll *a* (SChl *a*), the suspended matter (SPM), and the biogenic matrix (Q_{btb}). Previous
261 works of Orvain et al. (2003) describe the total suspended matter with the following equation:

$$262 \frac{dSPM}{dt} = E_{\text{bed}} + E_{\text{btb}} - D \quad (4)$$

263 E_{bed} , E_{btb} , and D are respectively the bed eroded flux, the bioresuspension flux and the
 264 deposition flux. First, type Ia erosion (E_{btb}) occurred in relation to detached aggregates
 265 produced by bioturbation activities, and then Type Ib or II ‘catastrophic’ erosion (E_{bed}) takes
 266 place at the moment when the critical bed shear stress ($\tau_{crit-bed}$) is reached resulting in a
 267 massive increase of suspended matter (Orvain et al., 2003). This process also refers to the
 268 classical bed erosion (type Ib) related to consolidation effects or sand/mud mixtures (Amos et
 269 al., 1992). The superficial bioresuspension (E_{btb}) requires a low shear stress comparable to the
 270 hydrodynamic forcing during a flood/ebb tide.

271 However, the erosion of the underlying bed sediment requires a greater shear velocity and is
 272 correlated with the burying activity of cockles. Since the goal of our study is to model the
 273 resuspension of MPB associated to the fluff layer (Type Ia), the value of the Type Ib and II
 274 bed erosion (E_{bed}) was artificially removed in the model, and the experimental dataset was
 275 restricted to the first part of the curve before catastrophic erosion. The process of catastrophic
 276 erosion is related to wind-induced stress in coastal ecosystems. This phenomenon is, however,
 277 out of the scope of the present study, in which we focus on chronic MPB erosion related to
 278 cockle bioturbation and not sediment transport or MPB long-term dynamics. We suppose that,
 279 within the range of experienced shear velocities, the deposition of matter is directly
 280 resuspended in the water column. The Eq. 4 is then simplified as follows and is used as the
 281 next step of model development.

$$\frac{dSPM}{dt} = E_{btb} \quad (5)$$

282 The value of the bioresuspension critical shear stress ($\tau_{crit-fluff}$, Pa or $\text{kg m}^{-1} \text{s}^{-2}$) is determined
 283 differently depending two situations. In a case of an overlap of the 2 types of erosion (Ia and
 284 Ib), means of SPM were directly linearized.

$$SPM = a \times u^* + b \quad (6)$$

285 where u^* (u^* , cm s^{-1}) corresponds to the current velocity.

286 In a case when a plateau of SPM is reached (erosion type Ia), mean values were first power
 287 transformed and thereafter linearized.

$$10^{SPM} = a \times u^* + b \quad (7)$$

288 The zero value of SPM corresponds to the value at which the erosion is initiated at the critical
 289 shear velocity ($u_{crit-fluff}$, cm s^{-1}). The corresponding critical shear stress ($\tau_{crit-fluff}$) is deduced
 290 from a linear relationship between the critical shear velocity, corresponding to the initiation
 291 point of erosion, and the seawater density ρ (kg m^{-3}).

$$\tau_{crit-fluff} = \rho \times u_{crit-fluff}^2 \quad (8)$$

292 As long as erosion takes place, the quantity of sediment contained within the biogenic matrix
 293 diminishes. The variation of the bioturbated sediment (the third state variable) over time
 294 depends on the erosion flux.

$$\frac{dQ_{btb}}{dt} = -E_{btb} \quad (9)$$

295 The extent of sediment resuspension (E_{btb} , $\text{gDWsediment m}^{-2} \text{s}^{-1}$) depends, in part, on the
 296 physical forcing factor mainly represented by the shear stress τ_f (Pa). The Partheniades
 297 formulation (1965) modified by Orvain et al. (2003) is then used to calculate the sediment
 298 resuspension flux E_{btb} which is a product of the excess of shear stress ($\tau_f/\tau_{crit-fluff}-1$), the
 299 erosion coefficient α (s^{-1}), and the amount of bioturbated sediment (Q_{btb} , $\text{gDWsediment m}^{-2}$).

$$E_{btb} = \alpha \times Q_{btb} \times \left(\frac{\tau_f(t)}{\tau_{crit-fluff}} - 1 \right) \quad (10)$$

300 when $\tau_f(t) > \tau_{crit-fluff}$ if not $E_{btb}=0$

301 Before the erosion (so given as initial condition $t = 0$), the suspended matter (SPM) is equal to
 302 0 and quantity of bioturbated sediment ($Q_{btb (t=0)}$, $\text{gDWsediment m}^{-2}$) is obtained from the
 303 product of the traces height of cockle on the sediment h_{btb} (m), and the dry density within
 304 traces ρ_{fluff} ($\text{gDWsediment m}^{-3}$).

311
$$Q_{btb(t=0)} = h_{btb} \times \rho_{fluff} \quad (11)$$

312 Experimental results (see section 4.1) showed that the biomass of cockles represents a
 313 relevant factor that determines the cockle bioturbation on sediment. The bioturbated sediment
 314 depends linearly on the biomass of cockle (Biomass, g DW cockle m⁻² as a forcing variable)
 315 and the bioturbated volume of sediment per g of cockle A_{btb} (m³ g⁻¹ DW cockle). The process
 316 is traduced conceptually with the trace height which represents the depth of the bioturbated
 317 sediment if the material uniformly covers the surface area at the beginning of the erosion.

318
$$h_{btb(t=0)} = A_{btb} \times Biomass \quad (12)$$

319 During the erosion, the trace height decreases according to the variation of the bioturbated
 320 sediment (Q_{btb}, gDWsediment m⁻²).

321
$$h_{btb} = \left(\frac{Q_{btb}(t)}{\rho_{fluff}} \right) \quad (13)$$

322 The first state variable SChl *a* (µgChl *a* m⁻²) is obtained by converting the suspended matter
 323 (SPM) into suspended chlorophyll *a* with a conversion factor sedtochla. The equation (5) then
 324 becomes:

325
$$\frac{dSChl a}{dt} = E_{btb} \times sedtochla \quad (14)$$

326 The mentioned conversion factor sedtochla represents the slope of the linear relationship
 327 between suspended matter and the chlorophyll *a*, both obtained from water filtration
 328 mentioned earlier (see the end of the section 2.1).

329 Equations and parameters of the developed model are summarized in the Tab. 2.

330 3.3 Model parameterization and validation

331 Simulations of suspended MPB in the water column under the influence of cockle
 332 bioturbation were performed with the determination of two parameters. The first parameter is
 333 A_{btb} (Eq. 12) which represents the bioturbated volume of sediment per g of cockle. The second
 334 parameter is α (Eq. 10): the erosion coefficient and corresponds to the rate at which the
 335 bioturbated sediment is eroded. Parameterization of the model is performed using the
 336 minimization with the Simplex method (Nelder and Mead, 1965) by minimizing the ordinary
 337 least squares criterion (Sum of Squared Error).

338
$$SCE = \sum (SChl a - Chl a_{tot})^2 \quad (15)$$

339 Simultaneous estimation of the two parameters was performed by minimizing the error (SCE)
 340 to simulate the chronic detachment of MPB in the water column.

341 Then, different approaches were conducted to evaluate how the model fits the measurements.
 342 Modelling efficiency (ME), as described in Vanclay and Skovsgaard (1997) was calculated
 343 with the following equation:

344
$$ME = 1 - \frac{\sum (SChl a - Chl a_{tot})^2}{\sum (SChl a - \overline{Chl a_{tot}})^2} \quad (16)$$

345 Where Chl *a*_{tot} represents the observations and SChl *a* the corresponding predictions. $\overline{Chl a_{tot}}$
 346 stands for the mean of the observations. A ME equals to 1 shows that the model fits well with
 347 the observation. A ME equals to zero means that the model is not better than a simple average
 348 and a negative value corresponds to bad fit.

349 Theil's inequality coefficient can be also used to evaluate the accuracy of the simulations. The
 350 same equation used by Lo et al. (2011) was used to calculate the coefficient.

351
$$U = \sqrt{\frac{\sum (Chl a_{tot} - SChl a)^2}{\sum Chl a_{tot}^2}} \quad (17)$$

352 A value of U equals to zero represents perfect simulations. U equals to 1 represents
 353 simulations which is not better than considering unchanging variable. U higher than 1
 354 represents bad simulations.

355 Test of equivalence (Robinson and Froese, 2004) using a null hypothesis was also conducted
356 with the R software package ‘equivalence’ (Robinson et al., 2005). The robust two one sides
357 test for equivalence was used on simulated and observed data.

358 To explain discrepancies between model results and measurement residuals between all total
359 suspended chlorophyll *a* (Chl a_{tot}) and all respective simulated chlorophyll *a* (SChl *a*) were
360 confronted with biomasses of macrofaunal major species and also confronted with chlorophyll
361 *a* content in the sediment.

362

363 4. Results

364 4.1 Laboratory experiments and chlorophyll *a* correction

365 The percentage of resuspended benthic chlorophyll *a* is linearly correlated with the cockle
366 biomass ($r^2 = 0.78$, $p < 0.001$) (Fig.3) which reflects how the matrix of sediment susceptible of
367 being eroded responds to the biomass of the burrowing bioturbator. Formation of bioturbated
368 sediment is thus a function of cockle biomass in a system where cockle is the dominant
369 bioturbator species.

370 The measurement of chlorophyll *a* in the water column traduces the quantity of MPB
371 exported in the water column associated to the erosion of the biogenic matrix. Chlorophyll *a*
372 resuspension in the water column increases with increasing shear stress and increasing
373 biomass of cockle. Suspended chlorophyll *a* during experiments with adult cockles is much
374 higher than with juvenile individuals (Fig.4a).

375 The analyses of the kinetics of chlorophyll *a* have shown two types of erosion that occurred
376 during the flume experiments (Fig.4a): fluff layer (or ‘chronic erosion’, type Ia according to
377 the definition by Amos et al. 1992) and bed erosion (Type Ib or II ‘catastrophic erosion’).
378 Only fluff layer erosion (type Ia) occurred for juvenile bioturbators, except in the case of 1
379 experiment at the highest density (Fig. 4a). The fluff layer erosion (Ia) was characterized by a
380 low sediment flux as shown by the slope of the curve during the first phases of the
381 experiment. This type of erosion occurred also at low critical shear stress ($\tau_{crit-fluff}$ ca 0.007 to
382 1.69 Pa) and with low biomass of bioturbators. The bed erosion was not reached for most of
383 the experiments with juveniles (with a lower biomass compared to adult cockles). The bed
384 erosion (type Ib) requires higher bed shear stress ($\tau_{crit-bed}$ ca. 0.79 to 2.33 Pa), and is
385 accompanied by an important export of matter traduced by a more important slope of
386 suspended matter (Fig. 4a). In intertidal ecosystem, such high hydrodynamic forces can be
387 qualified of ‘catastrophic erosion’ since it can only be encountered during extreme
388 phenomenon (in case of wind-induced stress).

389 The total resuspended chlorophyll *a* (Fig. 4b) was estimated by artificially adding the quantity
390 of chlorophyll *a* filtrated by the cockle during the erosion experiment to the chlorophyll *a*
391 recorded by the probes (Fig. 4a). The maximum values of corrected suspended chlorophyll *a*
392 is 2 times greater than those recorded by the probe. However, on average, about 10% of
393 suspended chlorophyll *a* was filtrated by the cockle during the fluff layer erosion. In this
394 work, the total amount of suspended chlorophyll *a* (Chl a_{tot}) during the fluff layer erosion is
395 used to perform the model parameterization of MPB resuspension under cockle bioturbation.

396

397 4.2 Model calibration

398 The bed shear stress measurements (τ_f , Pa) from each separate experiment were used as a
399 forcing variable of the model (Fig.5c). The model was applied using the same bioturbator
400 biomasses as the ones used during the laboratory experiments. Experimental results which
401 consist of the total suspended chlorophyll *a* kinetics (Chl a_{tot}) is represented in the Fig. 5a.
402 The corresponding simulations of suspended MPB in the water column (SChl *a*) is shown in

403 the Fig. 5b. The sigmoidal pattern of resuspended chlorophyll *a* is very well reproduced by
404 the model (Fig. 5b). Moreover, the model realistically reproduces the lower scale of juvenile
405 bioturbation impact on MPB erosion. The erosion of the biogenic matrix of sediment is
406 indirectly represented by the evolution of the trace height over time in Fig. 6, **with a**
407 **maximum depth of eroded sediment of ca. 1 mm**. This figure represents the variation
408 through time of the quantity of sediment and associated MPB from modeled sediment matrix
409 under the bioturbation of cockle (represented by the depth of bioturbated matrix sediment
410 uniformly distributed). A decrease of the modeled trace height over the incremental
411 hydrodynamic forces was observed. At the end of the simulation, almost all the available
412 MPB in the bioturbated matrix was resuspended in the water column as observed with the Fig.
413 6.

414 Modelling efficiency shows reasonable values on how the model reproduces the MPB
415 bioresuspension (Tab. 3). Theil's inequality coefficient is also acceptable for the calibration
416 step (Tab. 3). Moreover the test of equivalence rejected the null hypothesis of inequality with
417 strict and relaxed tests (Tab. 4). The Q-Q plot (Fig. 5d) indicates some acceptable skewness
418 and dispersion between observations and simulations.

419

420 4.3 Biotic and abiotic characteristics of sampling sites

421 The 3 sampled sites (A, B, and C) are different in terms of sediment properties, MPB
422 biomasses and species assemblages. Analysis of macrofauna assemblage was conducted in the
423 sampled sites. 10 major species were identified during the survey (Tab. 5). Analysis showed
424 that the cockle dominates the assemblage in term of biomass in Baie des Veys about 98% all
425 the time of the survey. The analysis also showed that about 3/4 of the macrofauna assemblage
426 is constituted by species that actively rework sediment through movements (Tab. 5). Only two
427 species are supposed to have a stabilizing effect on the sediment. Statistical analyses
428 (Kruskal-Wallis) show significant differences in chlorophyll *a* content between sites ($p < 0.01$)
429 and during the period of survey ($p < 0.05$).

430 Site A is characterized by a sandy mud substrate. Average biomass of cockle ranges between
431 46 (in January 2013) to 403 (in April 2013) in gAFDW m^{-2} (Tab. 5). Deposit feeding annelid
432 *Scoloplos armiger* is the second dominant species with a biomass ranging between 0.15 to
433 1.15 gAFDW m^{-2} followed by the *Pygospio elegans*, in which biomass varies from 0 to 0.03
434 gAFDW m^{-2} . Statistical analysis shows a significant temporal variation of the chlorophyll *a*
435 content in the sediment in site A ($p < 0.001$). Analyses of the sediment chlorophyll *a* content
436 represented the lowest value ($1.50 \mu g g^{-1}$) in April 2013 and a maximum value ($5.6 \mu g g^{-1}$) in
437 September 2012 (See Fig.7).

438 The sediment in site B was the muddiest of the three sites. The cockle always dominates the
439 macrofauna, having a maximum biomass in January 2013 ($791 gAFDW m^{-2}$) and a minimum
440 biomass in April 2013 ($110 gAFDW m^{-2}$). Macrofaunal assemblage analysis at this second
441 site showed a complex composition compared to site A (Tab. 5). 3 among the 4 principal
442 bioturbator species are clearly deposit-feeders, consuming MPB directly in the biofilm (*Abra*
443 *tenuis*, *Macoma balthica* and *Peringia ulvae*). Analysis of chlorophyll *a* included within the
444 top centimeter of the sediment reveals the highest value among the sampling sites. The
445 highest ($13.4 \mu g g^{-1}$) and the lowest value ($4.88 \mu g g^{-1}$) of chlorophyll *a* in the sediment are
446 observed respectively in January 2013 and in April 2013 in the site B. A significant temporal
447 variation of the chlorophyll *a* content in the sediment (Fig. 7) was observed in the second site
448 ($p < 0.05$).

449 The last site (C) is the sandiest station located in the middle of the bay (closer to the river
450 mouth) and where the highest biomass of cockles was recorded over the sampling period
451 (Tab. 5). Cockle biomasses show a maximum value in January 2013 (2595 gAFDW m⁻²) and
452 a minimum value in June 2012 (226 gAFDW m⁻²). Several species constitute the macrofaunal
453 assemblage but at a lower scale compared to the second site (lower biomasses). Presence of
454 bioturbator (*Scoloplos armiger*) and MPB consumer and bioturbator such as *Macoma balthica*
455 was also noticed in this site. No significant temporal variation of chlorophyll *a* content in the
456 sediment (Fig. 7) was highlighted by statistical analysis in the third site ($p>0.05$).

457 4.4 Model validation

458 Statistical analysis showed a significant spatial variability between the three sites. Thus, the
459 validation of the model was performed site per site and with independent *in situ* data. The
460 Fig. 8 represents the measurements of resuspended MPB at the three sites compared to the
461 predicted resuspended MPB (Fig.8 A, B and C – Observations - Models). Time increases also
462 suppose an increase in hydrodynamical forces over time (the real bed shear stress τ_f measured
463 during experiments).

464 Fig.8 shows that the model of suspended MPB displayed satisfying agreement with the
465 dynamics of *in situ* bioresuspension in all seasons and in all locations. However, minor
466 discrepancies are observed. The model slightly underestimates (Fig.8A – Q-Q plots) and
467 overestimates (Fig.8 B and C - Q-Q plots) the bioresuspension. The modelling efficiency
468 value shows a good agreement between observations and simulations as shown in the Tab. 3
469 for the 3 sites. Theil's inequality coefficient also show acceptable performance of the model.
470 However, test of equivalence gives less favorable statement than the previous results and
471 accepts the null hypothesis of inequality (Tab. 4) with both strict and relaxed tests for all sites.
472 Contrary to calibration test of the model, the model using only cockle biomass to predict
473 resuspension of microphytobenthos in the field. However, the lowest p-value was obtained in
474 site B, which highlighted a moderate cockle biomass (Tab. 5). We explored some possibilities
475 to improve the quality of adjustment during validation procedure, by analyzing the remained
476 residuals between observed and predicted field data, especially in sites A and C, which
477 showed the highest discrepancies between predicted and observed data.

478 All residuals of suspended chlorophyll *a* were calculated and were confronted to sediment
479 chlorophyll *a* content and biomasses of macrofauna species to determine if the lack of fitting
480 of the model could be explained by a specific stock of MPB in the sediment or specific
481 macrofauna species. When plotted against chlorophyll *a* content, residuals did not show any
482 tendency (Figure not shown). Analysis with macrofauna did not show any tendency either,
483 except for the species *Pygospio elegans* (Fig.9). At low biomass of this bioturbator, the
484 residuals of resuspended chlorophyll *a* were close to 0. When the biomass increased (in the
485 range of low values of *Pygospio* biomass $\sim 10^2$ mgAFDW.m⁻²), the residuals of suspended
486 chlorophyll *a* increased as a function of bioturbator density. After the critical value $\sim 10^2$
487 mgAFDW.m⁻², the relationship shifted from a positive function to a negative one. At very
488 high *P. elegans* biomass ($> 10^3$ mgAFDW.m⁻²), the residuals of suspended chlorophyll *a* were
489 negative.

490 5. Discussion

491 5.1 Effect of cockle on biological stabilization and destabilization of sediment

492 Biological stabilization and destabilization figure among key processes that determine the
493 extent of sediment erosion in estuaries. In most cases, biostabilization of the sediment has
494 been attributed to MPB development. This is the case in the observations reported by
495 Andersen et al. (2010), made during their erosion experiments. EPS (Extracellular Polymeric
496 Substances) production takes place during motion of diatoms and has been stated to bond fine
497 grains of sediment, thereby increasing the stability of the sediment (Tolhurst et al., 2006;
498 Underwood and Paterson, 1993). Consequently, biostabilization of the sediment should lead
499 to a difference between the outputs of the model and the *in situ* measurements of suspended
500 chlorophyll *a*. When residuals of suspended chlorophyll *a* were plotted against chlorophyll *a*
501 content of sediment, the later does not explain the observed discrepancy (slight overestimation
502 of the model) between *in situ* data and simulations. Thus, biostabilization could be weakened
503 by important faunal activity. Moreover, Orvain et al. (2007) did not observe either any
504 stabilizing effect of MPB during their *in situ* analysis because the impact of macrofauna
505 activity on sediment was significant.

506 In the case of cockles, opposite results have been observed about stabilizing (Andersen et al.,
507 2010; Donadi et al., 2013a) and destabilizing effects (Ciutat et al., 2006, 2007; Neumeier et
508 al., 2006) of this species on sediment. In our case, cockles enhance the erosion of sediment,
509 allowing for the export of associated MPB. Cockles were fully buried within the sediment bed
510 during erosion experiments, and surface irregularities were not provoked by the protruding
511 shell but by the fluff layer formation of sediment surface. Change of roughness with cockle
512 shells and sudden valve adduction during filtration, lead to more matter eroded to the water
513 column. Our finding concurs with Neumeier et al. (2006), who report a way in which cockles
514 create irregularities on sediment. Such irregularities constitute weak points where erosion
515 starts.

516 Differences were observed in the effect of adult and juvenile cockles on the process of MPB
517 resuspension (Fig. 4), which are due to the extent of bioturbation depending on the biomass.
518 The higher the biomass, the higher the sediment reworked, and thus, the higher the
519 resuspension of associated chlorophyll *a*. Sediment changes due to adult cockles are more
520 important than with juvenile bioturbator. Bioturbation of adult cockles is also correlated to
521 valve adduction during filtration at which time important erosion of sediment was noticed.
522 Experimental results confirm that bioresuspension is greater with high biomass of bioturbator
523 and is easily exported in the water column at low shear stress.

524 5.2 Model of MPB resuspension under cockle bioturbation

525 The model that we developed reproduces the resuspension of MPB associated with fluff layer
526 erosion due to destabilization activity of the cockle. The model represents a simple
527 monospecific bioturbator system. Biomass dependence of bioturbated matrix formation is
528 well integrated in our model of fluff layer erosion and associated MPB (Eq. 11 and 12). The
529 model uses a reduced number of parameters: the biomass specific bioturbation coefficient A_{btb}
530 (Eq. 12) and the coefficient of erosion α (Eq. 10). Those parameters were estimated and
531 provide satisfying calibration results (Fig. 5).

532 This study shows that, combined with bed shear stress (τ_f), the biomass of the main
533 bioturbator can be the only factor involved in the bioresuspension of the MPB in sandy-mud
534 ecosystems. The model apparently determines the resuspension process of MPB without
535 recourse to a complex hydrodynamic model (e.g. Le Hir et al., 2000). Our study joins

536 statement of Wood and Widdows (2002) that physical forces (tides) represents the driven
537 factor of sediment erosion and biological component (macrofauna bioturbation) is able to
538 drastically accentuate the process, especially in a highly changing system. The model
539 simulates the erosion of the bioturbated surface of the sediment that contains important
540 biomass of microalgae. This study points to the significant impact of the common cockle on
541 the erosion of benthic diatoms in the water column which does not require high shear stress
542 with (mean of $\tau_{\text{crit-fluff}}$ equals to 0.81 +/-0.86 Pa). Measurements conducted from 2009 and
543 2013 in the Baie des Veys (Lower Normandy, France) show that the cockle represents the
544 major dominant species in terms of biomass (more than 98%). The common cockle thus
545 plays a decisive role on sediment erodibility in the bay scale. Analyses of model performance
546 (Tab. 3) and tests of equivalence (Tab. 4) for the experimental data show that simulated
547 resuspended MPB was reasonably similar to observed values both with strict and relaxed
548 tests.

549 This study also reveals that the modified Partheniades formulation of Orvain et al. (2003),
550 which describes the fluff layer erosion (Eq. 10), was applicable to a few bioturbator species
551 with different behaviors (*Peringia ulvae*, *Scrobicularia plana*, *Macoma balthica* and
552 *Cerastoderma edule*). The difference lays on the fluff layer creation, in other words to the
553 species-specific bioturbation process. Orvain (2005) explains that the difference in
554 bioturbation intensity is due to different mechanisms of bioturbation. The fluff layer
555 formation was asymptotically related to bioturbator biomasses, for species like *P. ulvae*
556 (Orvain et al., 2003) and *M. balthica* (van Prooijen et al., 2011; Willows et al., 1998), while it
557 is linearly correlated to the density of *S. plana* (Orvain, 2005) and biomass of the cockle, *C.*
558 *edule* in our case. Sediment reworking, burrowing activity and continuous valve adduction
559 during filtration of cockle represent key processes on the resuspension of MPB in the water
560 column. Change of roughness and turbulences caused by cockle in the surface when subjected
561 to hydrodynamic forces were taken into account through the forcing variable of the model τ_f
562 represented. However, it is not within the scope of the mechanistic model that we developed.
563 Consequently, the erosion fluxes are proportional to cockle biomasses when the cockle
564 dominates the macrofaunal assemblages.

565 Then, the same parameters were used (without adjustment) to validate the model with
566 independent *in situ* measurements (Fig. 8). The application *in situ* shows optimistic results as
567 shown with the model performance indexes (Tab. 3). The general tendency of the suspended
568 MPB kinetics is well reproduced by the model (Fig. 8 A-B-C) mainly for the site B where a
569 high value of ME is observed. The results of equivalence tests should be taken with caution.
570 Promising results is still observed with the site B with a low value of p-value despite the non-
571 rejection of the inequality in all sites. It is important to notice that other macrofauna were
572 present in the sediment which was not the case for the experimental design of calibration test.
573 Several processes were not taken into account in our formulation such as bioturbation by
574 other species (mainly in site B with diversified macrofauna composition), interaction between
575 bioturbation effects and consumption by other species. The use of the model directly *in situ*
576 and when cockle is not the main bioturbator is not recommended. The site with moderate
577 biomass of cockles (site B) showed a better quality of adjustment during validation test.

578 5.3 Integration of faunal community and food availability for upper consumers

579 Our study reveals that the biomass of cockle is among the main factors that explain the MPB
580 resuspension in the Baie des Veys. Fig. 6 highlights that the depth of sediment that is actually
581 eroded because of cockle bioturbation can reach only 1 millimeter at most. We have put forth
582 an analysis to determine the limits of the model by determining if the slight discrepancy of the
583 model may be explained by specific macrofauna assemblage. Residual analysis on suspended
584 chlorophyll *a* showed that *Pygospio elegans* could explain the slight underestimation and
585 overestimation of the model simulations compared to measurements (Fig. 9). On one hand,
586 the deposit feeding behavior of this polychaete could induce MPB resuspension, at biomasses
587 of about 10^2 mg AFDW m^{-2} in our case (Fig. 9). On the other hand, they become very
588 efficient at actively capturing resuspended microalgae in a suspension-feeding activity and
589 could stabilize sediment due to bioreef structure at biomasses $> 10^2$ mg AFDW m^{-2} in our
590 case (Fig. 9). In their analyses, Orvain et al. (2007) have also found such contrasting effects
591 with another species, the gastropod *Peringia ulvae*. Further studies need to be conducted to
592 better evaluate the impact of *P. elegans* on sediment erodibility, cascade effects on MPB
593 development, and availability for suspension-feeders after resuspension.

594 Improvements can thus be done with the model developed herein. A possible approach is to
595 conduct analysis based on functional groups (Pearson, 2001) and to combine species with a
596 similar bioturbation effect. For species with a similar impact as cockle, we can use the same
597 set of equations, and biomass could be sufficient for the reproduction of MPB
598 bioresuspension. Consequently, a species-specific model can be converted into a functional
599 group model. Applied together, these 2 models could take into account a broad effect of
600 community on sediment stability and consequently on MPB availability in estuarine
601 ecosystem.

602 Ubertini (2012) observed evidence of enhancement of MPB development around the cockle
603 burrow in absence of hydrodynamic forces especially for adult individuals. This process joins
604 the facilitation of primary production by cockle noticed by Donadi et al. (2013b). This
605 specific engineering mechanism by cockles could explain the discrepancies between studies
606 on cockle bioturbation, since this species could simultaneously have 2 differing interactions:
607 1) a sediment-stabilizing effect of cockles promoted by the facilitation of MPB primary
608 production, and 2) a chronic detachment of a part of the MPB standing stock by reworking
609 effects of the sediment surface during feeding-related movements (the process modelled
610 herein). In addition, cockles can have a third effect by modifying the bed roughness and
611 increases the turbulent mixing in the benthic boundary layer. These changes also have a
612 positive effect on the erosion flux by affecting the bed shear stress dynamics (τ_f). Another
613 possible improvement of the model is to integrate the facilitation of MPB development and
614 primary production by cockle.

615 Analyzing MPB availability in estuarine system is crucial. Indeed, Lefebvre et al. (2009)
616 noticed that macrofauna species switch their food source from phytoplankton to MPB
617 differently. Moreover, Kang et al. (2006) demonstrated the importance of MPB during critical
618 period and during phytoplankton shortfall. The contribution of MPB to suspension feeder diet
619 was also highlighted over successive years (Grangeré et al., 2012).

620 6. Conclusion

621 This study has allowed us to characterize the cockle behavior and to model the capacity of
622 this species in facilitating mud resuspension and associated MPB. We found that in a system

623 where cockle dominates significantly the macrofaunal assemblage, biomass of cockle
624 represents a relevant factor that determines the MPB resuspension. A model of MPB
625 bioresuspension was calibrated with experimental data. The use of the model directly *in situ* is
626 not recommended especially when cockle is not the main bioturbator and further
627 improvement was discussed. The model represents a baseline in the simulation of benthic
628 food availability for upper consumers as filter-feeders.

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774

775 Fig.1 Sampling sites location (i). Quadruplicate samples of macrofauna and chlorophyll *a*
776 content of the sediment were conducted per station per site (ii grey circle). Triplicate samples
777 of sediment cores were also conducted in three randomly chosen station per site (ii black
778 circles).

779
780 Fig.2 Conceptualization of the model of MPB resuspension under cockle bioturbation. Simple
781 arrow represents flux between the two compartments: the bioturbated layer (Q_{btb} ,
782 $gDW_{sediment} m^{-2}$), the suspended matter (SPM, $gDW_{sediment} m^{-2}$). Sediment erosion is
783 accompanied with MPB resuspension ($SChl a$, $\mu gChl a m^{-2}$). The link between the two
784 compartments is represented by the erosion flux (E_{btb} , $gDW_{sediment} m^{-2} s^{-1}$). The filtration
785 rate of cockle ($Chl a_{fil}$, $\mu gChl a m^{-2} s^{-1}$) was used to estimate the total amount of suspended
786 MPB in the water column.

787
788 Fig. 3 Linear regression between cockle biomass and percentage of resuspended chlorophyll *a*
789 from the total microphytobenthic biomass in the sediment ($r^2=0.78$).

790
791 Fig. 4 Chlorophyll *a* concentration recorded in the Erodimeter (a) and cumulative chlorophyll
792 *a* concentration after filtration correction (b) as a function of time and depending on cockle
793 biomass. Shear stress (τ_f , Pa) increases over time.

794
795 Fig. 5 Observed resuspended chlorophyll *a* (a) and predicted eroded chlorophyll *a* (b) as a
796 function of time and depending on cockle biomass. Shear stress increases over time (c). Q-Q
797 plot between observed and predicted suspended chlorophyll *a* (d). The solid line represents
798 $Y=X$ relationship. The kinetics of chlorophyll *a* was restricted to the fluff layer erosion phase.

799
800 Fig. 6 Height (m) of the bioturbated surface layer variation through time as a function of
801 cockle biomass ($gDW_{cockle} m^{-2}$)

802
803 Fig. 7 Chlorophyll *a* content of the top centimeter of the sediment in three sites (A, B, and C)
804 in June and September 2012 and January and April 2013.

805
806 Fig. 8 Observed suspended chlorophyll *a* (Observations) and predicted suspended chlorophyll
807 *a* (Models) as a function of time and depending on the biomass of cockles in three location
808 (A, B, C) in the Baie des Veys-France. The solid line represents $Y=X$ relationship between
809 observed and predicted suspended chlorophyll *a* and Q-Q plots were built with averaged per-
810 step data (during 5 min) of observed and modeled erosion kinetics (Q-Q Plots).

811
812 Fig. 9 Residuals of suspended chlorophyll *a* plotted against *Pygospio elegans* biomass (log
813 transformed). The residuals represent the differences between the flume chlorophyll *a* data
814 and the simulated chlorophyll *a*. Each residual observation is obtained from the averaged
815 residuals of resuspended chlorophyll *a* of one experiment (at all time steps).