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1 **How does the resuspension of the biofilm alter the functioning of the**
2 **benthos-pelagos coupled food web of a bare mudflat in Marennes-Oléron**
3 **Bay (NE Atlantic)?**

4

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38

39 **Abstract**

40 Intertidal mudflats are ecosystems submitted to natural hydrodynamical forcings during each
41 tide. When the offshore water flows at high tide, a proportion of the biofilm produced at low
42 tide can be resuspended in the water column and interact with the pelagic food web. As a
43 consequence, the resuspension creates a link between the benthos and the pelagos, modifying
44 their properties and the stability of the meta-ecosystem they form together. The aim of this
45 study is to describe the consequences of the microbial biofilm resuspension on the pelagic
46 food web, and to investigate the question of the stability of the benthos-pelagos coupling
47 resulting from the biofilm resuspension. Two food webs were considered, corresponding to
48 different hydrodynamical conditions in summer condition: one allowing the biofilm massive
49 resuspension, and one without resuspension, but with particle sedimentation. The Monte-
50 Carlo Markov Chain Linear Modelling was used to estimate the unknown flows of the food
51 web. The comparison of the Ecological Network Analysis indices for the two food webs
52 allowed defining their respective differences of structure and functioning. The results showed
53 that the massive resuspension of the microbial biofilm stimulates pelagic primary production
54 and microbial food web via a higher bacterivory. The higher activity of the whole system
55 coupled with both a drop in the specialization of the trophic pathways and a low cycling
56 activity demonstrated that when massive resuspension occurs, the system is disturbed. In
57 contrast, when sedimentation occurs, the food webs show functioning features pointing out to
58 a higher stability of the whole system.

59

60 **Keywords:** intertidal mudflat, biofilm resuspension, stability, meta-ecosystem

61

62

63 **1. Introduction**

64 The structure and the functioning of food webs affect the emergent properties and thus the
65 stability of the ecosystem. As a consequence, describing the emergent properties of the
66 ecosystem is a prerequisite for establishing their stability. The literature on the subject is
67 diverse and can lead to controversial interpretations and conclusions. However, some trends
68 can be observed such as equilibrium between two extremes that allows the ecosystem to act
69 like a buffer to external perturbations. For instance, the coexistence of weak and strong
70 interactions is assumed to bring stability to the ecosystem (McCann et al., 1998), or the
71 asymmetry in the ecosystem ensures a higher stability (Rooney et al., 2006), or an ecosystem
72 that presents a balance between Ascendency and redundancy is supposed to be more stable
73 (Ulanowicz, 2003). Moreover, Levin (1999) proposed that a stable ecosystem pattern is
74 composed of subsystems strongly intraconnected but weakly interconnected. At larger scale,
75 this theory is transposable to the concept of the meta-ecosystem defined by Loreau et al.
76 (2003) as a set of ecosystems connected by spatial flows. A set of ecosystems strongly
77 intraconnected weakly interconnected thus form a stable meta-ecosystem. In this study, we
78 propose to consider the benthos and the pelagos as systems connected by spatial flows at high
79 tide to form a stable meta-system. We have used this concept in order to describe and to
80 understand the effects of the benthos-pelagos coupling on the properties of the food webs and
81 its consequences on the stability of the Brouage mudflat meta-system.

82 As bare intertidal mudflat, Brouage mudflat, is characterized by the development of a
83 microbial biofilm at the surface of the sediments at diurnal low tide. This biofilm is usually
84 mainly composed of brown micro-algae (diatoms) which constitute the microphytobenthos
85 (Cariou-Le Gall and Blanchard, 1995) and prokaryotes, all of them linked by a matrix of
86 extracellular polymeric substances (EPS) (Decho, 2000). The production of the biofilm is
87 integrated to the benthic food web via the deposit feeders, especially *Peringia ulvae* (Haubois

88 et al., 2005; Pascal et al., 2008a; Pascal et al., 2009), via the facultative suspension feeders
89 and via the meiofauna (Pascal et al., 2009; Pascal et al., 2008b; Pascal et al., 2008c). The
90 meio- and macrofauna are not only involved in the regulation of the microphytobenthos
91 biomass via the grazing, but also via the bioturbation and the biostabilisation of the sediment
92 whose effects are coupled with physical factors (tides and swell) (Blanchard et al., 2001).
93 When the tidal flow arises, the microphytobenthos biomass decreases at the surface of the
94 sediments (Guarini et al., 2000) for two reasons: i) the downward ‘migration’ of motile
95 diatoms into the sediments (Consalvey et al., 2004; Guarini et al., 2000; Herlory et al., 2004;
96 Ni Longphuir et al., 2009) and ii) the resuspension of a part of the diatom stock into the
97 water column. The resuspension of the microphytobenthic biofilm is controlled by a complex
98 interaction between physical and biological forcing. The physical resuspension of the
99 microphytobenthos depends on the bed shear stress which is induced by the tidal current
100 and/or the wind-waves (Blanchard et al., 2002; De Jonge and Van Beuselom, 1992). The
101 erodability of the sediment is strongly variable in space and in time (Tolhurst et al., 2006) and
102 depends on biological factor modifying sediment properties such as macrofauna activities and
103 microbial biofilm setting up (Herman et al., 2001; Orvain et al., 2004). The
104 microphytobenthos resuspension also depends on biological factors such as the ageing of the
105 biofilm (Orvain et al., 2004) and the content of exopolysaccharids (EPS) (Orvain et al.,
106 present issue). When the microphytobenthic biofilm is in its exponential growth phase, it
107 stabilizes the sediments and counteracts the bioturbation due to macrofauna which favors its
108 resuspension (Orvain et al., 2004). In contrast, when the biofilm reaches its senescent phase,
109 the roughness of the biofilm as well as bacterial biofilm degradation are enhanced and the mat
110 is more easily resuspended (Orvain et al., 2004). The microphytobenthic diatom that are
111 resuspended in the water column are integrated to the pelagic food web and can be ingested
112 by suspension feeders, in the case of the Brouage mudflat especially by *Crassostrea gigas*, a

113 cultivated species (Riera and Richard, 1996) and *Cerastoderma edule* (Sauriau and Kang,
114 2000).

115 In this study new *in situ* observations and experimentations were taken into account,
116 especially on the resuspension of the biofilm (Orvain et al., present issue) and the
117 consequences on the pelagic food web are evaluated by using a model describing trophic
118 pathways. Erosion experiments allowed to determine the critical shear velocity necessary
119 regarding the resuspension of benthic micro-organisms and resuspension rates (Dupuy et al.,
120 present issue) . The Lagrangian and Eulerian field surveys followed the future of the
121 resuspended particles in the water column, respectively following the water mass or at a fixed
122 point (Guizien et al., 2013). Moreover grazing experiments and viral lysis experiments
123 (Montanié et al., present issue) were performed in order to determine the effect of
124 resuspension of benthic organisms on the pelagic food web *sensu largo* (*i.e.* including virus).
125 These refinements were incorporated in the framework of a trophic-flow model to better
126 unravel the impact of the biofilm resuspension on the food web functioning by deciphering
127 the contribution of each flow in the contribution in the functioning during high-tide phase. At
128 high tide, the rise of the tide and the chemical/physical/biological processes associated with
129 the increase of the water level on the Brouage mudflat create spatial flows linking benthic and
130 pelagic parts. Consequently, it can be considered as a ‘meta-ecosystem’ defined by Loreau et
131 al., (2003) as a set of ecosystems which are linked by spatial biotic and/or abiotic flows across
132 the ecosystem boundaries. We especially focused on one question: How does the resuspension
133 of the microbial biofilm at high tide modifies the stability of ecosystem in respect to the meta-
134 ecosystem pattern? We explored this question by comparing the network organization of two
135 distinct food web models representing 2 scenarii of a summer situation. In the first model
136 scenario, the hydrodynamic conditions were extreme and sufficient to induce the resuspension
137 of the microphytobenthos (physical mass erosion, when bed shear stress $BSS > 3 \text{ cm.s}^{-1}$ on

138 Brouage mudflat). In this case the velocity of current stays superior to the critical sinking
139 velocity, thus no sedimentation is possible. While in the second case the physical forcing was
140 too weak to induce any resuspension, only limited and extremely low erosion of *chl a*
141 (biological erosion when $BSS < 3 \text{ cm.s}^{-1}$) induced by the bioturbation of the macrofauna can
142 be observed (Orvain et al., present issue). Moreover the settling of pelagic particles (organic
143 or not) could occur and the sinking velocity enhanced by the pelletisation (Orvain et al.,
144 present issue). The missing flows of the food web (i.e. flows which were not measured *in situ*)
145 were estimated by the Monte Carlo Markov Chain Linear Inverse Modelling (MCMC-LIM)
146 (Van den Meersche et al., 2009). This mathematical method explores a solution space defined
147 by constraints issued from *in situ* measurement and values issued from the literature. All
148 solutions proposed by the MCMC-LIM were used to calculate several ecological network
149 analysis (ENA) indices, describing the emergent properties of the ecosystem.

150

151 **2. Material and Methods**

152 2.1. The study area

153 The Brouage intertidal mudflat is located at the French Atlantic coast in the bay of Marennes-
154 Oléron (figure 1). The bay covers 150 km² and the Brouage mudflat, at the eastern part of the
155 bay, represents 68 km² at low tide. The averaged bottom slope is relatively flat (1:1000) and
156 the tidal area is large (up to 4 km). The sediment consists of silt and clay particles (95% <63
157 μm) (Pascal et al., 2009). The current speeds in the bay range from 0.2 to 0.6 m.s⁻¹ and the
158 bed shear stress from 1.5 to 4 Pa (Bassoullet et al., 2000; Le Hir et al., 2000). The zone of
159 interest is located in the middle of the Brouage mudflat and is characterized by a typical ridge
160 and runnel bedform (Gouleau et al., 2000).

161

162 2.2. Inverse modelling

163 Two summer food web models were performed: the first one simulated a high-tide situation
164 with massive suspension of micro-organisms in the water column (resuspension model), and
165 the second one also at high tide, where the physical forcing was not sufficient to induce
166 resuspension (sedimentation model). As a consequence, an insignificant quantity of particles
167 is suspended via biological factors as macrofauna bioturbation and its counterparts by a strong
168 sedimentation of organic matter.

169 The inverse modelling can be divided into 3 steps: (i) determine the species that compose the
170 food web, and all possible flows between them. Twenty-one compartments were listed (Table
171 1) linked by 115 or 118 flows for the models with and without resuspension, respectively. (ii)
172 determine the mass balance of each compartment and constrains flow values by *in situ*
173 measurements. (iii) limit possible values of flows by biological constraints.

174

175 2.2.1. Considered compartments and flows

176 2.2.1.1. *Resuspension and sedimentation*

177 A portable erodimeter (Guizien et al., 2012) was used to estimate the erosion shear stress of *in*
178 *situ* cohesive sediments. An increased shear stress (by small steps, each timed to last about 10
179 minutes) was applied to the mud surface and the suspension of micro-organisms inhabiting in
180 the sediment was monitored by changes in water column micro-organisms concentration.
181 From these experiments, it was defined that resuspension of the microorganisms and diatoms
182 took place when the shear bed velocity was higher or equal to 3 cm.s^{-1} . Sedimentation could
183 not occur at higher current velocity.

184 Sedimentation was only considered in the model without resuspension, because the lower
185 current velocity ($< 3 \text{ cm.s}^{-1}$) allowed particles to settle down on the bottom during the slack
186 water. The sedimentation rate was estimated from the formula $D = W_s * C$ where D is expressed
187 in $\text{mgC.m}^{-2}.\text{h}^{-1}$, C is the concentration of particles in the water column (mgC.m^{-3}) and W_s the

188 sinking velocity of particles ($\text{m}\cdot\text{h}^{-1}$) (Krone, 1962). Concentration of both pelagic bacteria and
189 chlorophyll *a* were measured *in situ*. The minimal limit for the concentration of the particulate
190 carbon corresponded to the pelagic particulate carbon produced during high tide. For defining
191 its maximal limit we considered that the import of carbon into the water column was equal to
192 the amount of the benthic particulate carbon resuspended in the water column and not
193 consumed. Consequently, it was assumed that the particulate carbon present in the water
194 column at high tide, when resuspension occurred was likely to be found in a similar quantity
195 at high tide $n+1$.

196

197 *2.2.1.2. The microphytobenthos*

198 Primary production of the microphytobenthos is linked to the biomass of diatoms present in
199 the biofilm and to light conditions (Macintyre et al., 1996). During immersion, the turbidity of
200 the overlying water, stopping the penetration of light (Alpine and Cloern, 1988) inhibits
201 benthic primary production (Denis and Desreumaux, 2009; Migné et al., 2009). Moreover,
202 just before the flood return, the diatoms move down into the sediment (Herlory et al., 2004;
203 Round and Palmer, 1966). In our models, no microphytobenthic production was considered.
204 The only input to the microphytobenthos compartment is thus an import of carbon which
205 comes from the production of the previous diurnal low tide by the microphytobenthos,
206 and which was not consumed during low tide. The import of carbon to the high tide
207 corresponded to the export of carbon determined for microphytobenthos in a low tide model
208 and was equal to $31.9 \text{ mgC}\cdot\text{m}^{-2}$ per high tide (Saint-Béat et al., 2013). Moreover the secretion
209 of EPS, related to the activity of photosynthesis and migration (Underwood and Paterson,
210 2003), was supposed negligible at high tide (Hanlon et al., 2006). This was confirmed by a
211 survey of EPS concentration in a tidal mesocosm during a tidal cycle showing a fall of EPS
212 concentration in the biofilm during high tide (Agogué et al., present issue)

213 9.7mgC of benthic diatoms were resuspended per high tide (Dupuy et al., present issue); they
214 constitute a flow from the benthos to the pelagos that enhances the phytoplanktonic biomass
215 after resuspension (Brito et al., 2012; Koh et al., 2006). In this way, the microphytobenthos
216 constitutes a food resource for the secondary producers in pelagic and benthic ecosystems
217 (Guarini et al., 1998; Riera and Richard, 1996; Yoshino et al., 2012).

218

219 *2.2.1.3. Benthic bacteria*

220 Biofilms (i.e an assemblage of benthic diatoms and bacteria) were reconstituted in a tidal
221 mesocosm: the production and the biomass of the bacteria were measured during 5 days at
222 low and high tides (Agogu e et al., present issue). . The benthic bacterial production was
223 estimated by tritiated thymidine incorporation (Garet and Moriarty, 1996), which was
224 converted to numbers of cells using the ratio of 1.96×10^{17} cells per mol of thymidine
225 determined for this study. A mean increase of 24.3% of the bacterial production in
226 comparison to the bacterial production at low tide was observed in mesocosm experiments.
227 The bacterial biomass was obtained from the mean cell volume calculated with Furhman's
228 formula (1981) and converted in carbon units from the formula $133.754 \times V^{0.438}$ (V in μm^3)
229 (Romanova and Sazhin, 2010). The carbon contain in a bacterium was thus estimated as equal
230 to $79 \text{ fg C. cell}^{-1}$ for a mean biovolume of $0.28 \mu\text{m}^3$. During erosion experiments at the
231 threshold velocity considered in this study, 58.2 mgC per high tide issued from the benthic
232 bacteria were suspended (Dupuy et al., present issue). A part of the suspended bacteria were
233 damaged or dead during the erosion process (40%) (Mallet et al., present issue), and thus they
234 integrated the pelagic particulate organic carbon compartment. On the contrary the remaining
235 suspended benthic bacteria, still active, were considered to increase the pelagic bacteria
236 biomass (Mallet et al., present issue).

237

238 2.2.1.4. *Infauna (meiofauna and macrofauna)*

239 The microphytobenthos is the preferential resource of the benthic fauna but in case of
240 unavailability of microphytobenthos, bacterivory becomes significant (Pascal et al., 2009). At
241 high tide, bacterivory was supposed to be higher than the low tide values: the values of low
242 tide used in the previous model (Saint-Béat et al., 2013) were thus integrated to high tide
243 models as minimal values. The obligate as well as facultative suspension feeders were
244 assumed to feed on particles from bacteria to mesozooplankton (Self and Jumars, 1988;
245 Taghon, 1982).

246

247 2.2.1.5. *Phytoplankton*

248 The primary production of the phytoplankton was estimated for six other sites in Marennes-
249 Oléron Bay based on *in situ* measurement of chlorophyll *a* water concentration, salinity,
250 temperature and depth profiles of light attenuation (Struski and Bacher, 2006). The
251 phytoplanktonic primary production is influenced by the erosion of sediment, limited light
252 penetration and by the resuspension of benthic diatoms which likely participate to the
253 phytoplanktonic production (Macintyre et al., 1996). In order to prevent any bias in the
254 estimation of the planktonic primary production, we constrained it by minimal and maximal
255 primary production values measured in summer for the different stations of the bay. These
256 stations are characterized by different hydrological conditions and are thus characterized by
257 different resuspension and turbidity, and consequently by a different light penetration.
258 Constraining the phytoplanktonic production by a range of possible values allowed to adjust
259 the probability density function for gross primary production according to the needs of the
260 food web based on the situation considered (i.e. with or without resuspension).

261

262 2.2.1.6. *Pelagic bacteria*

263 The summer abundance and the summer production of the pelagic bacteria were measured *in*
264 *situ* (Ory et al., 2011). Bacteria were counted by epifluorescence microscopy after being fixed
265 with 0.02 μ m filtered formaldehyde (2% final concentration) and staining for 30 min with
266 Sybr Green I (for more details see Noble and Fuhrman, 1998; Ory et al., 2011). The
267 measurement of AMPase (V_{\max}), which is considered as an indicator of the bacterial
268 production, was used to estimate the bacterial production from the equation $\log BP =$
269 $0.9271 * \log V_{\max} + 5.3641$ ($r^2=0.67$, $n=10$, $p=0.003$). Pelagic bacteria being assumed to
270 contain 16 fgC per cell (Labry et al., 2002), the bacterial production was thus expressed in
271 carbon.

272 Experiments on viral lysis were conducted to test the interactions between bacteria,
273 heterotrophic nanoflagellates (HNF) and viruses in the water column. In artificial incubations,
274 they were re-combined to mimic the field assemblage with respect to the natural viral to
275 bacterial ratio (VRB) and the bacteria to flagellates ratios. Fractionation allowed creating
276 experimental recombined treatments and then differentiating between the direct and indirect
277 interactions of the presence/absence of the virus and HNF. Through *in vitro* experiments,
278 bacterial losses induced by viruses and flagellates were estimated by comparing the reduction
279 of the bacteria cell production (MBP) between the different experimental assemblages.

280

281 *2.2.1.7. Benthic and pelagic viruses*

282 Viral lysis was estimated from viral production (i.e. net increase of viral abundance divided
283 by the time of the experiment) within 2 L bottle incubations in the presence or absence of
284 benthic particulates in order to determine the effect of the biofilm resuspension on the viral
285 lysis. Bacterial mortality due to viral lysis was calculated from the viral production divided by
286 the burst-size viruses (i.e. number of viruses produced by a bacterium at burst-time) which
287 was estimated as 33 in this study (Montanié, pers. comm.). The quantity of viruses produced

288 per time unit was converted into carbon considering that one virus contains 0.2 fgC
289 (Magagnini et al., 2007; Suttle, 2005).

290 The viral lysis of benthic bacteria at high tide was considered to be similar to the one at low
291 tide, thus we considered that 40 % of the bacterial production was lost by viral lysis (Saint-
292 Béat et al., 2013). At high tide, the benthic viruses were suspended and integrated into the
293 pelagic virus compartment. 1.29 mgC per high tide of virus per m² were resuspended in the
294 water column at the critical shear bed velocity of 3cm.s⁻¹ (Dupuy et al., present issue)
295 determined by the erosion experiment (see above).

296

297 *2.2.1.8. Ciliates and heterotrophic Nanoflagellates*

298 The biomasses were expressed in carbon from a conversion factor of 19 µgC.µm⁻³ (Putt and
299 Stoecker, 1989) by considering equivalent spherical diameter (ESD). The abundances and
300 biomass of Ciliates (ESD < 50 µm) and heterotrophic nanoflagellates (2µm < ESD < 10µm)
301 were estimated *in situ*. The seawater was filtered onto 0.8 µm Nucleopore black filter. The
302 ciliates and nanoflagellates were enumerated by epifluorescence microscopy. Cells were first
303 fixed by the glutaraldehyde and the paraformaldehyde and stained with the lugol 1% and
304 DAPI respectively.

305 In the models, phytoplankton and pelagic bacteria are prey of the compartments ciliates and
306 nanoflagellates, which are themselves the preys of ciliates. The nanoflagellates also
307 potentially graze the viruses (Bettarel et al., 2005; Manage et al., 2002).

308

309 *2.2.1.9. Mesozooplankton*

310 Mesozooplankton (200µm < ESD < 400µm) play a central role in the pelagic food web in the
311 Marennes-Oléron Bay (Sautour and Castel, 1998) and show a variable diet (Vincent and
312 Hartmann, 2001). The resources of mesozooplankton, as confirmed by bottle grazer

313 experiments, in the area of Brouage mudflat are phytoplankton, either directly or indirectly
314 via ciliates and the heterotrophic nanoflagellates (Azémar et al., 2007). This diet can be
315 completed by the ingestion of detritic matter (David et al., 2006).

316 The abundance and the biomass of the mesozooplankton were estimated during study period.
317 The mesozooplankton was sampled using a 200µm mesh WP2 net, preserved in buffered
318 formaldehyde with Na(BO₃)₄ (final concentration 5%) and counted under binocular
319 microscope. The biomasses were expressed in carbon by multiplying the dry weight by 0.4
320 (Simard et al., 1985). These measurements were completed by bottle grazer experiments to
321 test the effects of the biofilm suspension on the grazing of mesozooplankton. Water from the
322 erodimeter (after erosion experiments) was mixed with filtered pelagic water (200 µm, in
323 order to exclude mesozooplankton) in different proportions (20, 40 or 70%). This mix was
324 transferred in 1.13 L Nalgene bottles and and incubated during 12 or 24 h in presence/absence
325 (temoin) of mesozooplankton predators collected *in situ*. The resuspended biofilm in the water
326 disturbs the trophic interactions of the mesozooplankton, especially through an inhibition of
327 the grazing of phytoplankton and heterotrophic nanoflagellates by the mesozooplankton
328 (Hartmann, pers. comm.). Thus in the model with the resuspension no flow between
329 phytoplankton and nanoflagellates towards mesozooplankton was considered.

330

331 *2.2.1.10. Grazing Fishes*

332 Main species able to graze on mudflat at high tide are mullets (*Liza ramada* and *Liza aurata*).
333 Observed individuals arrive on the mudflat with an empty stomach, while they leave it with a
334 full stomach (Carpentier et al., present issue). Thus the mullets were considered as a vector of
335 carbon export. Since, the abundance of individuals going about the Brouage mudflat at high
336 tide could not be measured *in situ*, grazing traces left by mullets on mudflat were considered
337 as a proxy of their grazing pressure. Presence of traces was estimated from pictures of one

338 square meter quadrats (expressed by surface of sediment removed by mullets by square
339 meter). In addition, experiments on the feeding behavior of mullets were conducted in
340 mesocosms to assess the volume of sediment ingested per individual at each tide (Como et al.,
341 present issue)). The coupling with field pictures finally allowed estimating the density of
342 fishes per square meter.

343

344 *2.2.1.11. Imports and exports*

345 For all benthic compartments, we considered that the production during the previous low tide
346 was not totally consumed, thus imports of carbon from the diurnal low tide were taken into
347 account. These import values corresponded to the mean export values of the low tide model
348 (Saint-Béat et al., 2013). Export was considered for both models regarding the
349 microphytobenthos and the macrofauna, while export was considered only in the model
350 without resuspension regarding the benthic particulate carbon and the dissolved particulate
351 carbon. For the pelagic compartment, no import from the open sea was considered in the
352 model with resuspension and an import from the open sea of pelagic particulate carbon was
353 considered in the model without resuspension. We supposed that the production of the
354 pelagos was totally consumed during the high tide, thus no export from the bay to the open
355 sea of carbon was considered except for the pelagic particulate carbon, when the suspension
356 occurred.

357

358 *2.2.2. Equations*

359 The second step characterizes the mass balances of each compartment (listed in Table S1) and
360 flows measured in the field. These two elements (*i.e.* mass balance and equations) were
361 written within an equation: $A * x = b$ where x was vector that contained possible flows, the
362 matrix A expressed the mass balance and the field observation as a combination of

363 coefficients of the carbon flows and the vector b contained value of mass balances and values
364 of known flows (Vézina, 1989). The mass balances correspond to the report of inputs and
365 outputs for each compartment of the food web. By default, a compartment is considered to be
366 at the equilibrium (*i.e.* a constant biomass). Concerning the model with suspension we needed
367 to consider standing stock of the benthic particulate carbon and the benthic dissolved carbon
368 in deficit. Indeed, for these two compartments, there was a net change in mass equal to
369 resuspension term for particulate carbon and equal to the minimal value necessary to the
370 running of model for the dissolved organic carbon. In the case without resuspension, we
371 considered that the biomass loss of pelagic bacteria was equal to the value of the
372 sedimentation. The other sets of equations corresponded to the values of flows, which were
373 measured *in situ*.

374

375 2.2.3. Inequalities

376 At the last step, some biological constraints were added to the mass balances and flow values.
377 These constraints were obtained from the literature and limit the possible solutions of flows to
378 realistic values. The information was added to the model with the inequality: $G * x \leq h$,
379 where x remains the vector containing flows, G is a matrix that contains the coefficients of the
380 biological constraints and the vector h is composed of values of biological constraints
381 (Vézina, 1989). For the benthic compartments the set of inequalities of the low tide model
382 (Saint-Béat et al., 2013) was used. When the constraints corresponded to a value of flows, the
383 value of this constraint was updated according to the time of high tide (8h). The inequalities
384 for the pelagic compartments were grouped in the Table 2.

385 The sedimentation flows values were limited, considering two different sinking velocities,
386 which is different according to the particle size (De La Rocha and Passow, 2007). The
387 minimal sinking velocity corresponded to the sinking velocity of a single isolated particle. We

388 considered a minimal sinking velocity of 0.05 m.d^{-1} for free bacteria (Lapoussière et al.,
389 2011), 0.25 m.d^{-1} for chlorophyll *a* (Lapoussière et al., 2011) and 2.32 m.d^{-1} for particulate
390 carbon (Burns and Rosa, 1980). The maximal sinking velocity referred to the sinking velocity
391 of ‘marine snow’, that are defined as organic aggregates with a diameter $> 0.5 \text{ mm}$ (Alldredge
392 and Silver, 1988). The maximum sinking velocity chosen for this study was 16 m.d^{-1} (Turner,
393 2002). We considered that pelagic dissolved carbon can fall with the aggregates formed by
394 ‘marine snow’ and represents one third of the total carbon in aggregates (Alldredge, 2000).

395

396 2.2.4. Calculation of solutions

397 The generated matrices (A, b, G and h) define a multi-dimensional space delimiting possible
398 solutions of the flows (x). The MCMC-LIM mirror (Van den Meersche et al., 2009) was used
399 to sample through that solution space in an attempt to map it completely. The MCMC-LIM,
400 based on the mirror technique defined by Van Den Meersche et al.(2009) and updated for
401 LIM use by van Oevelen et al. (2010), calculates several solutions and allows a direct
402 characterization of the uncertainty. This modelling technique brings the advantage of
403 calculating a range of possible values for each flow (i.e. a probability density function). For
404 each model (with resuspension and without resuspension), 500, 000 iterations with a jump of
405 0.5 were calculated. The length of jump and the number of iterations were determined to
406 cover the solution space as completely as possible. In this study the simulations were realized
407 with a MATLAB[®] translation conceived by Alain Vézina and Lauriane Campo of the R-
408 CRAN project package LIM-Solve created by Van den Meersche et al. (2009).

409

410 2.2.5. Network analysis

411 From the 500,000 solutions estimated by MCMC-LIM, seven ecological network analysis
412 (ENA) indices were calculated. These indices allow assessing the structure and the

413 functioning of the two food webs. The magnitude of cycling within the system was described
414 by the Finn cycling Index (*i.e.* FCI). This index represents the fraction of flows involved in
415 the cycling (Finn, 1976). A cycle represents a series of transfers between components in an
416 ecosystem beginning and ending in the same compartment without going through the same
417 compartment twice. The FCI is estimated by the ratio T_c/TST , where TST is the total system
418 throughput (*i.e.* sum of all flows) and T_c the amount devoted to cycling. Various global
419 indices describe the developmental and organizational state of the ecosystem (Ulanowicz,
420 1986). The TST measures the activity of the whole ecosystem. The TST can be considered as
421 the total power generated within the system (Baird et al., 1998). The AMI value is indicative
422 of the specialization of flows in the network (Ulanowicz, 2004). The probability of flows
423 between two compartments increases with the AMI value, and thus with the specialization of
424 flows. The Ascendency (A) which represents the state of organization within the ecosystem
425 (Ulanowicz, 1986), is described as the product of the TST and the average mutual information
426 (*i.e.* AMI). The development capacity (DC) is defined as the upper limit of Ascendency. The
427 relative Ascendency is the ratio A/DC and estimates the proportion of the network that is
428 organized and thus efficient. The $(DC - A)$ difference estimates the inefficient part of the
429 network, corresponding to the overheads (*i.e.* overheads on imports, exports and dissipation)
430 and redundancy, that measures the uncertainty associated to the presence of multiple or
431 parallel pathways among the compartments (Ulanowicz and Norden, 1990). The internal
432 Ascendency (A_i) and internal development capacity (DC_i) refer to internal exchanges alone
433 and exclude the exogenous flows.

434 These indices were estimated using MATLAB[®] routine written by Carole Lebreton and
435 Markus Schartau (GKSS Research Centre, Geesthacht, Germany) to calculate the index value
436 for every solution estimated by the LIM-MCMC.

437

438 2.2.6 Statistical test

439 Since the distribution of the data did not follow a normal distribution a non-parametric test
440 was used. The significance of the differences between the indices calculated for both
441 networks with and without resuspension was controlled by the Wilcoxon test ($\alpha = 0.01$). The
442 tested hypothesis was that the two data sets were issued from a continuous distribution with
443 equal medians. Statistical tests is possible because using the LIM-MCMC technique on
444 500,000 solutions, 500,000 values of each ENA index were also calculated, as consequence
445 we can use statistical tests which are not usually possible in such a context of food web
446 modelling using static methods and at this level of functional diversity.

447

448 **3. Results**

449 3.1. Flow values

450 Some differences in flow values between the two conditions (i.e. with or without suspension)
451 were observed (Table S2). The pelagic primary production was higher with resuspension. On
452 the whole, consumption rates remained the same irrespective of the condition, except for the
453 bacterivory of heterotrophic nanoflagellates (doubled with resuspension), the bacterivory of
454 nematodes (consumption without resuspension was 7 times higher than the value during
455 resuspension), as well as herbivory of deposit-feeders (about twice higher without
456 resuspension than with resuspension) and consumption on nematodes by grazing fishes that
457 both doubled without suspension. The exudation of DOC by benthic bacteria increased
458 without suspension contrary to the exudation of DOC by pelagic bacteria that was five times
459 higher during resuspension. The mortality of phytoplankton (*i.e.* phyTOppc) was higher when
460 resuspension occurred. The egestion of nematodes without suspension was twice the egestion
461 during resuspension. The export of carbon from benthic compartment was higher without
462 suspension.

463

464 3.2. Compartment activities

465 Significant differences appeared according to the condition considered (Figure 2). The benthic
466 activity was stimulated by the sedimentation of micro-organisms of the water column. In
467 contrast, the resuspension of micro-organisms inhabiting in the sediment stimulated the
468 pelagic activity.

469 Several pelagic compartments were affected by the resuspension of micro-organisms. The
470 phytoplankton (phy), the pelagic non-living compartments (*i.e.* particulate compartment (ppc)
471 and dissolved organic carbon (pdc)) as well as the pelagic bacteria (bcp) had a higher activity
472 in the case of resuspension. On the contrary the microphytobenthos, the benthic bacteria, the
473 benthic non-living compartments were more active when sedimentation occurred.

474

475 3.3. Diet and consumption

476 Herbivory tended to represent a more important part in the pelagic system (Table 3). In
477 contrast, bacterivory was higher in the benthic compartment. The resuspension of the micro-
478 organisms to the water column had an effect on bacterivory, herbivory and the ratio between
479 them. In the pelagic part, the resuspension favored the bacterivory. On the contrary, the
480 herbivory was favored in the case without resuspension. The herbivory and bacterivory in
481 benthos were both higher without resuspension.

482 The ratios showed that the herbivory was dominant in the pelagos. Nevertheless, when
483 resuspension occurred, the decline in the ratio (almost divided by 2) was due to a fall of
484 herbivory as well as a rise in bacterivory. A fall in the ratio was observed regarding the
485 benthos due to a decline in the bacterivory lower than in herbivory.

486 None of the compartment was affected by the resuspension (Figure 3). Conversely, the diet of
487 nematodes was drastically altered during the resuspension phase (B). Whatever the

488 resuspension occurred or not, the contribution of the microphytobenthos as a food item for
489 nematodes did not change (about 15%). On the contrary, benthic bacteria and detritus
490 contributed to nematodes diet almost equally in the case without resuspension (40 and 30%,
491 respectively), while it mainly shifted to benthic particulate (about 80%) in resuspension
492 situation.

493 The detritus contributed only slightly to the diet of deposit feeders. This group fed mainly on
494 microphytobenthos and benthic bacteria. The contribution of each of these two groups
495 changed with the resuspension. While the consumption on the benthic bacteria remained the
496 same between resuspension and sedimentation phases, it corresponded to a higher
497 contribution to the deposit-feeder diet during resuspension.

498 The facultative suspension feeders fed on the planktonic and benthic species. The contribution
499 of the phytoplankton to the diet of this group was higher when the resuspension occurred.
500 Consequently, the microphytobenthos was merely consumed. In contrast, in the case without
501 resuspension, the microphytobenthos contributed to 40% of the consumption and the
502 phytoplankton for 20%. The contribution of pelagic and particulate carbon tended to be lower
503 with the resuspension.

504 The resuspension tended to have some consequences on the diet of the heterotrophic
505 nanoflagellates and mesozooplankton (Figure 4). The diet of the heterotrophic nanoflagellates
506 was more diversified during resuspension because of the contribution of virus (vvp). The
507 contribution of pelagic bacteria (bcp) was three times higher in the case of resuspension.
508 Consequently the contribution of the phytoplankton (phy) decreased. The most affected
509 compartment was the mesozooplankton. Without resuspension the mesozooplankton fed
510 equally on the phytoplankton, heterotrophic nanoflagellates, pelagic particulate carbon (ppc)
511 and ciliates. During the resuspension, the consumption on both heterotrophic nanoflagellates
512 and phytoplankton was inhibited.

513

514 3.4. ENA indices

515 Significant differences between values of the indices of the two situations were observed
516 (Figure 5). The TST was about 3 times higher when the resuspension occurred. The
517 Ascendency followed the same trend. However, a lower organization of the system (i.e. lower
518 AMI value) was observed. The higher relative Ascendency, coupled with a lower AMI value
519 observed in the case of resuspension, suggested a lower diversity of flows. The overheads
520 based on the imports, exports, respiration and redundancy of the system were lower during
521 resuspension. The internal normalized Ascendency tended to be similar for the two situations.
522 The proportion of flows involved in the cycling (i.e. FCI value) was lower during
523 resuspension event.

524

525 **4. Discussion**

526 4.1. Activity of the benthic and the pelagic compartments

527 The benthos was more active than the pelagos regarding simulation without resuspension; in
528 contrast the pelagic activity was higher during resuspension. This fact can be explained by a
529 large import of particulate carbon to the pelagic particulate compartment. Without this import
530 of pelagic carbon, the pelagic activity was equal to the benthic activity during resuspension.
531 The higher benthic activity was previously shown in the model of the Brouage mudflat food
532 web. In fact, the higher activity of the benthos was observed irrespective of the model
533 considered in previous studies by regarding annual budget (Leguerrier et al., 2004) or by
534 deciphering seasonal budgets (Degré et al., 2006). However, in our model, the ranking of the
535 compartments was modified. The main difference concerned the benthic bacteria and the
536 microphytobenthos. The benthic bacteria dominated the ecosystem; they were followed by the
537 benthic non-living detritus compartments. Surprisingly, the microphytobenthos was ranked

538 only 8th. The difference with previous models is the time-scale considered: a mean year
539 (Leguerrier et al., 2004) or a mean month (Degré et al., 2006) which is in dramatic contrast to
540 the small scale mean immersion period integrated in our model. During immersion, because
541 of darkness due to sediment burying, the microphytobenthos production was null (Blanchard,
542 2006). As a consequence, the carbon input to this compartment exclusively originated from
543 the photosynthesis performed during the previous diurnal low tide, which might explain its 8th
544 rank in our model. The first pelagic compartments were ranked 4th and 5th and corresponded
545 to the phytoplankton and the dissolved organic carbon, respectively.

546 The resuspension of the microbial biofilm stimulated the activity of the phytoplankton, the
547 non-living compartments (detritus) and the pelagic bacteria. This stimulation was not only the
548 consequence of the input of new matter in the water column. The phytoplankton showed a
549 higher gross primary production when the resuspension of the microbial biofilm occurred.
550 Pelagic primary production was not imposed to the model; it was only constrained by minimal
551 and maximal values of pelagic production found for different hydrological conditions in
552 Marennes-Oléron Bay. The higher production was somewhat surprising because the
553 resuspension also generates a high turbidity and the reduction of the light penetration which
554 dramatically reduces phytoplankton photosynthesis (Billerbeck et al., 2007; Porter et al.,
555 2010). When buried in the sediments, the microphytobenthos can remove nutrients from the
556 overlying water and the sediment pore water (Macintyre et al., 1996). Such activity tends to
557 reduce the nutrient fluxes from the sediments to the water column which can limit the
558 phytoplankton production (Sarker et al., 2009; Sloth et al., 1996). When the
559 microphytobenthos resuspension occurs, the nutrient fluxes to the water column increase
560 which has a positive effect on the phytoplankton production even if light is limiting (Porter et
561 al., 2010). Paradoxically, the import of microphytobenthic diatoms to the water column
562 contributes itself positively to the production of the phytoplankton (Macintyre et al., 1996).

563 By enriching water in particulate and dissolved carbon, which sustained a higher bacterial
564 activity as previously reported (Cotner et al., 2000; Poremba et al., 1999; Sloth et al., 1996),
565 the resuspension also stimulated heterotrophic production.

566 On the contrary, the settling of pelagic micro-organisms to the bottom of the water column
567 had smaller but significant consequences on the benthic compartments. In our model, the
568 input of pelagic fresh matter to the benthos increased the stock of available carbon for higher
569 trophic levels but it did not affect the production of the different compartments. The higher
570 activity observed for the benthic compartments (mpb, bdc, bcb, bpc) (Figure 2) was linked to
571 the deposit of pelagic diatoms, dissolved carbon, pelagic bacteria and particulate carbon
572 respectively at the surface of the sediments. The photosynthetic production of the pelagic
573 diatoms settled at the bottom of the water column during immersion is more probably limited
574 by the penetration of light than by the nutrient availability. It is supposed that, in contrast to
575 the light reaching the surface of the sediments (Billerbeck et al., 2007; Macintyre et al., 1996),
576 nutrients are often not a limiting factor for the photosynthesis in the intertidal sediments
577 (Migné et al., 2004; Serôdio and Catarino, 2000). The high turbidity reported in the bay of
578 Marennes-Oléron (Raillard and Mesenguen, 1994) likely stops the light penetration to the
579 sediment surface and strongly impairs the photosynthesis of pelagic diatoms. The effect of the
580 settling on the benthic bacterial production is more obvious. The bacterial production depends
581 on the substrate supply including organic carbon (Sander and Kalff, 1993). For instance in
582 Kiel Bight, the settling of detritus stimulates the benthic bacterial production (Meyer-Reil,
583 1983). Consequently, it is very likely that the benthic bacterial production is stimulated in the
584 Brouage mudflat during sedimentation.

585

586 4.2. Herbivory *versus* bacterivory

587 The massive resuspension event impacted the pelagic microbial food web. It stimulated the
588 bacterivory of the pelagos as reported before for heterotrophic nanoflagellates (Garstecki et
589 al., 2002). A higher quantity of carbon flowed through the virus (viral lysis was doubled) and
590 consequently more virus were consumed by heterotrophic nanoflagellates. The increase of
591 pelagic bacterial abundance and production doubled the bacterivory rate of heterotrophic
592 nanoflagellates. In contrast, the resuspension tended to decrease the pelagic herbivory. In spite
593 of a higher gross primary production and a direct input of benthic diatoms biomass to the
594 water column, the phytoplankton was integrated to a lower proportion to the pelagic food
595 web. Indeed, the grazing of phytoplankton by the mesozooplankton had been shown to be
596 inhibited during catastrophic erosion event (Hartmann, pers.comm.). Consequently, our
597 models showed that a lower part of the phytoplankton was consumed in the model with
598 resuspension, inducing a greater mortality of this compartment. This result of the models (*i.e.*
599 higher phyTOppc when resuspension occurs) is coherent with previous results of resuspension
600 experiments (Porter et al., 2010). It thus appears that in conditions of resuspension, the
601 phytoplankton indirectly participated to the enrichment of the water column in dissolved
602 organic carbon and to the pelagic bacterial production.

603 The bacterivory dominated the benthic compartment during immersion irrespective of the
604 resuspension. At high tide, benthic diatoms moves down the sediment and cannot perform
605 photosynthesis because of the absence of light (Cartaxana et al., 2011). Hence, the benthic
606 food web must be sustained by the input of carbon coming from the photosynthetic
607 production of the previous emersion and by the bacterial production. In our model, we
608 supposed that the meiofauna and the macrofauna showed a constant consumption along the
609 day irrespective of immersion/emersion periods. This hypothesis was based on the assumption
610 that the meiofauna and the deposit feeders had alternative resources since the
611 microphytobenthos was not sufficient to sustain their respective metabolism. Detritus (van

612 Oevelen et al., 2006) bacteria were possible alternative resource for benthic fauna (Pascal et
613 al., 2009; van Oevelen et al., 2006). Some isotopic analyses at the Brouage mudflat showed
614 that the benthic detritus contributes to 11% in maximum to the deposit-feeders consumption
615 (Richard, comm. pers.). We supposed that the alternative feeding resource was the benthic
616 bacteria (see result section .

617 Previous studies on the bacterivory rates of the nematodes, the foraminifera and *Peringia*
618 *ulvae* in the Brouage mudflat indeed showed that bacteria can constitute a significant
619 alternative resource to the microphytobenthos under some conditions (Pascal et al., 2008a;
620 Pascal et al., 2008b; Pascal et al., 2008c). When there was no resuspension, the herbivory and
621 the bacterivory were both stimulated, although the bacterivory was stimulated in a larger
622 proportion due to the higher activity of the nematodes. The bacterivory thus remained
623 dominant in the benthic compartment irrespective of the physical forcing. The Sylt- Rømø
624 Bight in the North of Germany is composed of a mosaic of habitats including a mudflat. Its
625 benthic food web is based on microphytobenthos and macrophytes. In this benthic ecosystem,
626 the herbivory dominates the bacterivory (Baird et al., 2004). Indeed, herbivory is more than
627 two times higher than bacterivory. Thus the ratio herbivory/bacterivory of the Sylt-Rømø
628 Bight displays an opposite tendency than the ratio estimated for the Brouage mudflat. This
629 opposite tendency may be linked to the fact that this ratio was obtained from the food web for
630 the whole bay on a long term. As a consequence, habitats with high and low primary
631 production were associated, thus the available carbon issued from the primary production was
632 more important. Moreover, the food web considered in Baird et al. (2004) represents a mean
633 day as a consequence the difference between low tide and high tide was not visible and the
634 effect of the season was not considered contrary to present simulations, which focused on
635 summer conditions and high tide only In this study, that considered the summer period, little
636 carbon issued from the primary production at low tide was available. The consideration of the

637 food web for the whole year at the Brouage mudflat should abate the seasonal difference and
638 change the trend of herbivory/bacterivory ratio.

639

640 4.3. Functioning of the Brouage food web

641 For comparing the functional indices from our model to others, we took care of selecting
642 ecosystem models that coupled the pelagic and benthic compartments. Moreover the non-
643 living compartments must be separated from bacteria, otherwise the ENA indices would be
644 biased (Johnson et al., 2009). Values of relative Ascendency and internal relative Ascendency
645 were in general higher to those previously reported. Relative Ascendency ranged from 33.4
646 (Monaco and Ulanowicz, 1997) to 49.5 for the Chesapeake Bay (Baird et al., 1991) and the
647 internal Ascendency from 31.2 for the Delaware (Monaco and Ulanowicz, 1997) to 44.1 for
648 the Sundays Bay (Scharler and Baird, 2005). The cycling estimated without resuspension was
649 higher to the FCI (i.e. Finn Cycling Index) estimated in the Sylt- Rømø Bight (= 17.2%) and
650 close to the value of Sundays Estuary (Scharler and Baird, 2005). The differences between
651 our study and previous ones are most probably based on the shorter time scale in our models.
652 In the aforementioned studies, the ecosystems considered are estuaries which are subjected to
653 the tidal rhythm and thus which are controlled by strong temporal/physical forcing. It was
654 demonstrated how physical parameters can influence the ecological properties described by
655 the ENA indices (Niquil et al., 2012). The consequences of physical forcing like the
656 resuspension are smoothed when the considered networks use flows averaged over a mean
657 day, more representative of normal conditions without waves. Additionally, the biological
658 processes change according to the immersion and the emersion periods which impacts the
659 carbon budget (Migné et al., 2009). Consequently, when emersion and immersion are
660 considered separately (i.e. short time scale), it allows more precisely deciphering the
661 biological and physical processes that control the functioning of the food web.

662 When the massive resuspension of the microbial biofilm occurred, the enrichment of the
663 water column by the benthic particulate carbon (i.e. $3.584\text{gC}\cdot\text{m}^{-2}$.per high tide) mainly
664 supported the increased activity of the whole system and the decreased organization of the
665 network decreased. The higher value of Ascendency ($2\cdot 10^4\text{ mgC}\cdot\text{m}^{-2}$.per high tide against
666 $0.6\cdot 10^4\text{ mgC}\cdot\text{m}^{-2}$.per high tide during sedimentation) was the consequence of a higher TST
667 ($10000\text{ mgC}\cdot\text{m}^{-2}$.per high tide during resuspension and $3500\text{ mgC}\cdot\text{m}^{-2}$.per high tide during
668 sedimentation), in spite of a drop down in the specialization of the trophic way (measured by
669 AMI) This is a characteristic observation for a so-called “pulse eutrophication”, an intermittent
670 increase of organic matter supply combined with physical factors (Patrício et al ., 2004).
671 Moreover a high value of Ascendency derived from a very high TST, could disturb the
672 internal stability of the system (Ulanowicz, 2003). The lower overheads suggest a lower
673 resistance to the perturbation as proposed by Ulanowicz (2003). Thus the resuspension
674 decreased the resistance of the system to a perturbation. We propose that the massive
675 resuspension event in the Brouage mudflat could be defined as a “pulse eutrophication” event
676 that regularly disturbs the meta-ecosystem. On the contrary the biological erosion coupled
677 with a high sedimentation tended to reduce the perturbation in the meta-system.

678 During the massive resuspension, the lower proportion of cycling (i.e. lower value of FCI)
679 coupled with a high internal relative Ascendency (close to 50%) can be explained by the
680 limited integration to the planktonic food web of the non-living carbon suspended in the water
681 column. Indeed, in spite of a higher pelagic bacterial production and a higher detritivory, a
682 low quantity of carbon was recycled. As a consequence, almost all the carbon suspended in
683 the water column (i.e. $3.534\text{ gC}\cdot\text{m}^{-2}$.per high tide) was exported. Note that the export value
684 was not constrained in the model, thus this value reflected a real property of the network. The
685 larger the difference between the cycling and the internal relative Ascendency, the less
686 organized and more under pressure a system would be (Baird et al., 2007; Baird et al., 1991).

687 Thus the Brouage mudflat was less organized (confirmed by lower value of AMI) and
688 submitted to a higher stress during the resuspension. A similar relation (i.e. great difference)
689 between FCI and internal relative Ascendency was found for the mussel-bed in the Rømø-Sylt
690 Bight (Baird et al., 2007) and in an upwelling area (Baird et al., 1991). Baird et al (1991)
691 brought a significant nuance to the stress sense, by the distinction between ecosystems which
692 are under physically or chemically pressure. Indeed, the two constraints do not refer to the
693 same time scale. A chemical stress is in general recent and it has an exogenous origin to the
694 considered ecosystem. In contrast, physical perturbations are older and the ecosystem can
695 have adapted to it. These differences explain how a low cycling value can be coupled with a
696 high internal relative Ascendency (Baird et al., 1991). During the massive resuspension phase,
697 and as expected, the Brouage mudflat obviously showed the characteristics of a system that is
698 physically perturbed.

699 When massive resuspension did not occur, the Brouage mudflat was characterized by a high
700 specialization (i.e. high AMI) and by a relative Ascendency close to 60%. Such value
701 illustrates a state closed to the equilibrium between the efficient and the fraction of the
702 network that has not yet been organized (Bodini and Bondavalli, 2002); it is based on
703 redundancy in the imports, the exports, the dissipation and on internal redundancy (Baird et
704 al., 2004). The equilibrium between both parts (relative Ascendency and overheads) is
705 supposed to bring sustainability to the ecosystem (Ulanowicz et al., 2009); the inefficient part
706 being used as a reserve that brings the necessary flexibility for the ecosystem sustainability.
707 Moreover the high internal relative Ascendency is a strong sign that the system is relatively
708 mature (Baird et al., 1991). The lower difference between internal relative Ascendency and
709 FCI supposed a higher organization and a less disturbed system (Baird et al., 2007). Hence,
710 without massive resuspension of the microbial biofilm, the Brouage system seems to be
711 relatively mature and stable.

712

713 4.4. Conclusion: the stability of the Brouage meta-system

714 As defined by Loreau (2003), a meta-ecosystem corresponds to the different ecosystems
715 which are linked together by spatial flows of energy and matter. The rise of the tide and the
716 chemical/physical/biological processes, which are associated with the increase of the water
717 level on the mudflat can be considered as spatial flows. Here, we considered two different
718 events according to the hydrodynamical conditions: 1) the massive resuspension of benthic
719 matter in the water column 2) the sedimentation of pelagic matter on the mudflat sediments
720 associated to a biological resuspension induced by macrofauna activities. As described above,
721 their respective impact on the functioning of the benthic and the pelagic food webs strongly
722 differs. The massive resuspension tends to disturb the Brouage meta-system while the
723 sedimentation stabilizes it. These opposite consequences can be explained by the difference in
724 the intensity of the flows. When the massive resuspension occurs, the sum of flows from the
725 sediments to the water column was strong (about 3654 mgC.m^{-2} per immersion) while during
726 the sedimentation, it was only 10% of the flow during resuspension. The interaction between
727 the benthic and the pelagic compartments also appeared weaker during sedimentation than
728 during massive resuspension. As suggested by Levin (1999), a highly modular system
729 (composed of strongly connected sub-systems which are connected by weak links) is a stable
730 system. This concept could be transposed to the meta-ecosystem. We observed that the
731 sedimentation constitutes a weak link between the two subsystems benthos and pelagos. In
732 contrast the massive resuspension constitutes a strong link between benthos and pelagos. To
733 conclude the stabilizing pattern of Levin is observed when sedimentation occurs and not
734 during massive resuspension event. This conceptual step appears essential for the better
735 understanding of (meta-)ecosystem structure and functioning in order to improve our
736 prediction for their sustainability.

737 Despite its visible destabilizing effect, the massive resuspension brought some benefits to the
738 Brouage meta-system. It stimulated the pelagic microbial food web by increasing both
739 phytoplanktonic and bacterial production, and by stimulating bacterivory. Because of the
740 coupling of beneficial and destabilizing effects, massive resuspension show features
741 characteristic of an intermediate disturbance (reviewed in Shea et al., 2004). An intermediate
742 disturbance can be defined as an event that alters the specific niche availability, for instance
743 by removing the biomass or changing the nutrient availability, while it maintains the general
744 biodiversity (Shea et al., 2004). A complementary and extensive study of the long term
745 massive resuspension frequency and its consequences on the Brouage meta-system would
746 allow to confirm the intermediate disturbance hypothesis.

747

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Compartments	Abbreviations
Benthos	
Microphytobenthos	mpb
Benthic bacteria	bcb
Meiofauna	mfb
Nematodes	nem
Deposit-feeders	dep
Suspension-feeders	sus
Facultative suspension-feeders	suf
Omnivorous species	omn
Carnivorous species	car
Benthic viruses	vrb
Benthic particulate carbon	bpc
Benthic dissolved carbon	bdc
Pelagos	
Phytoplankton	phy
pelagic bacteria	bcp
Heterotrophic nanoflagellates	hnf
Ciliates	cil
Mesozooplankton	mes
Grazing fishes	gfi
Pelagic viruses	vrp
Pelagic particulate carbon	ppc
Pelagic dissolved carbon	pdc

Table 1: List of compartments and used abbreviations.

Processes	Compartments	Lower limit	Upper limit	References
Gross Growth Efficiency	HNF, CIL, MES	10%	40%	Straile, 1997
Net Growth Efficiency	BCB, BCP	11%	61%	DelGiorgio and Cole, 1998
	MFB	30%	50%	van Oevelen et al. 2006
	NEM	60%	90%	
	MAC	50%	70%	
Assimilation Efficiency (loss to the det)	HNF,CIL,MES	50%	90%	Vézina and Platt, 1988
	MFB	57%	97%	van Oevelen et al. 2006
	NEM	6%	30%	
	MAC	40%	75%	
	GFI	50%	90%	Leguerrier et al., 2004
Excretion (loss to doc)	HNF,CIL,MES	10% of ingestion	100% of respiration	min: Vézina and Pace, 1994 max: Vézina and Platt, 1988
	PHY	10%NPP 5%GPP	55%NPP 50%GPP	Breed et al., 2004 Vézina and Platt, 1988
Respiration	HNF,CIL,MES	20% of ingestion	-	Breed et al., 2004
	PHY, MPB	5% GPP	30%GPP	Vézina and Platt, 1988
	MES	biomass*4.8*W ^{-0.25}	biomass*14*W ^{-0.25}	min: Hemmingsen, 1960
	CIL, HNF	biomass*0.6*W ^{-0.25}	biomass*1.7*W ^{-0.25}	max: Moloney and Field, 1989
Consumption / Biomass	GFI	3%	8%	Bruslé, 1981
Gross primary production (mgC.m ⁻² .h ⁻¹)	PHY	10	50	Struski and Bacher, 2006
Loss of doc for pelagic bacteria (mgC.m ⁻² .h ⁻¹)	BCP	0.012	-	in this study(with suspension)
		0.005	-	
Bacterivory by HNF	HNF	-	49% of the bacterial production	in this study (with suspension)
	HNF	-	45% of the bacterial production	in this study (without suspension)
Respiration (mgC.m ⁻² .h ⁻¹)	GFI	0.226	3.628	min: derived from Killen et al., 2010 max: derived from Brett, 1965

1066

1067 **Table 2:** List of biological constraints used for the food web model. NPP: Net Primary
1068 Production, GPP: Gross Primary Production. W: body mass in pgC. Net Growth Efficiency =
1069 (consumption–detritus production-respiration)/ (consumption-detritus production), Gross
1070 Growth Efficiency=(consumption-loss to det-loss to doc-respiration)/ (consumption-loss to
1071 det-loss to doc- production).

1072

1073

	Benthic		Pelagic	
	With resuspension	Without resuspension	With resuspension	Without resuspension
Herbivory (mgC.m ⁻² .HT ⁻¹)	20.4 ± 0.1	39.7 ± 7.3	28.7 ± 11.2	33.8 ± 9.8
Bacterivory (mgC.m ⁻² .HT ⁻¹)	85.9 ± 5.8	123.7 ± 42.7	14.3 ± 5.8	8.1 ± 3.2
Ratio herbivory/bacterivory	0.2 ± 0.01	0.35 ± 0.1	2.9 ± 3.1	5.6 ± 4.9

1074

1075

1076 **Table 3:** Mean values of herbivory and bacterivory in the benthos and the pelagos according
1077 to the resuspension of the biofilm. HT⁻¹= per High Tide. These values correspond to the mean
1078 and the standard deviation calculated from the 500,000 iterations calculated by the inverse
1079 analyses. For each compartment (*i.e.* benthos and pelagos), values were significantly different
1080 with or without resuspension (Wilcoxon test, p<0.05) according to the condition considered.

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1082

1083 **Figures captions**

1084 **Figure 1:** Map of the study site: the Brouage mudflat within the Marennes-Oléron Bay.

1085

1086 **Figure 2:** Histogram presenting the activity of the compartments composing the food web.
1087 The activity corresponds to the sum of inflows and is expressed in $\text{mgC}\cdot\text{m}^{-2}$ per high tide. A)
1088 corresponds to the sum of the activity of all compartments for the benthos and the pelagos
1089 according to the 2 modeled situations. B) and C) refer to the activity of each compartment of
1090 the benthos and of the pelagos. Compartments are sorted by top down activity in order to
1091 determine which ones of the compartments have higher contribution to the activity of the
1092 whole ecosystem according to the situation considered (i.e. sedimentation or resuspension).
1093 See table 1 for the abbreviations of the compartments.

1094

1095 **Figure 3:** Diet of the meiofauna and macrofauna. A) Top diagrams refer to the case without
1096 resuspension and B) down diagrams refer to the case where the resuspension occurred. The
1097 contribution corresponds to the fraction that represents the consumption on a prey in
1098 comparison to the total consumption. The contribution of each species to the compartment
1099 consumption was estimated from the mean value of each flow.

1100

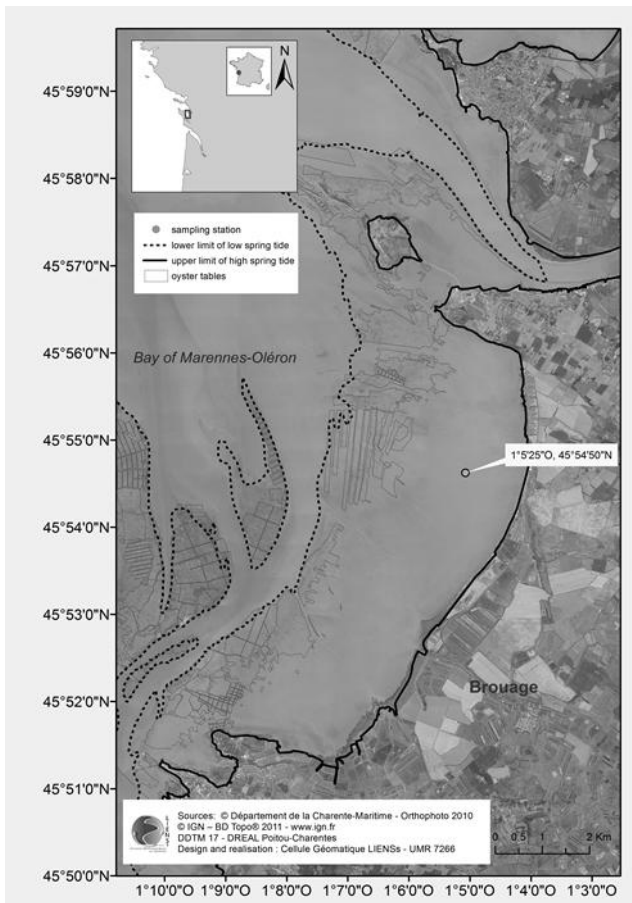
1101 **Figure 4:** Diet of heterotrophic nanoflagellates (hnf), ciliates (cil) and mesozooplankton
1102 (mes). A) top diagrams refer to the simulation without resuspension and B) down diagrams
1103 refer to the simulation with resuspension. The contribution corresponds to the fraction that
1104 represents the consumption on a specific compartment in comparison to the total diet. The
1105 contribution of each species to the compartment consumption was estimated from the mean
1106 value of each flow.

1107

1108 **Figure 5:** Boxplots displaying the values of different ENA indices: the total System
1109 Throughput (TST), the Ascendency, the overheads, the relative Ascendency (A/DC), the
1110 Average mutual Information (AMI), the internal relative Ascendency (A_i/DC_i) and the Finn
1111 Cycling index (FCI). The indices were calculated from the 500,000 solutions coming from the
1112 MCMC-LIM method. Red crosses correspond to outliers. Medians of all these indices were
1113 significantly different for the two seasons (Wilcoxon test, H_0 was rejected, p -value < 0.01).

1114

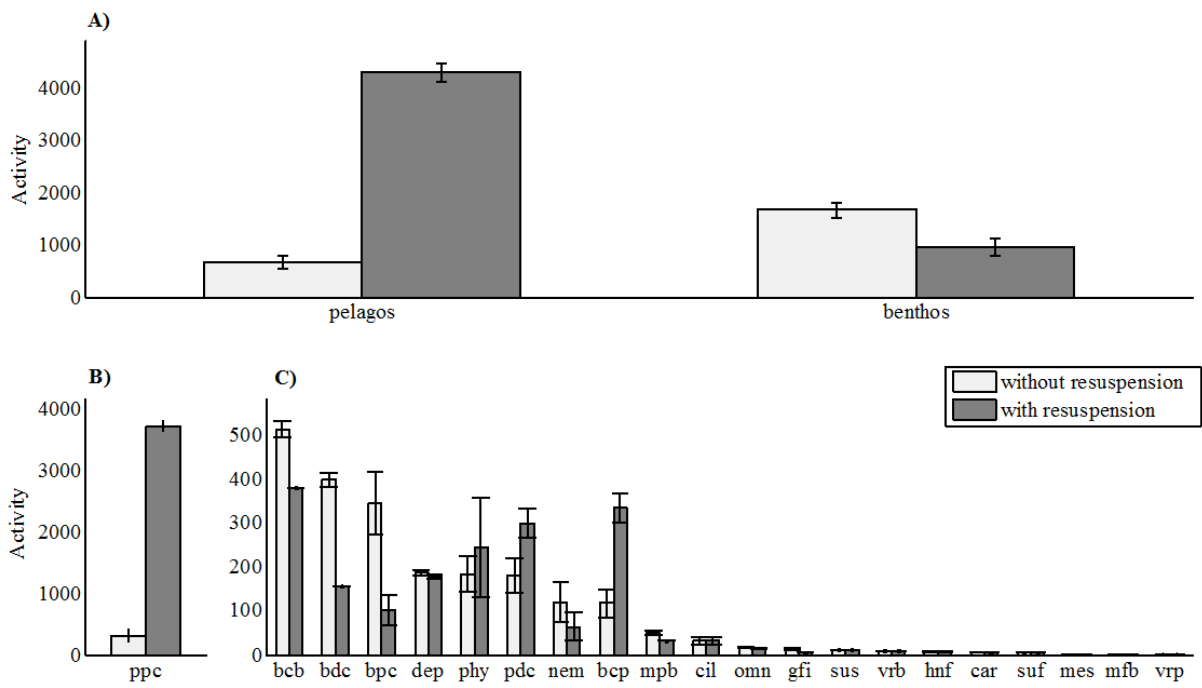
1115 Figure 1



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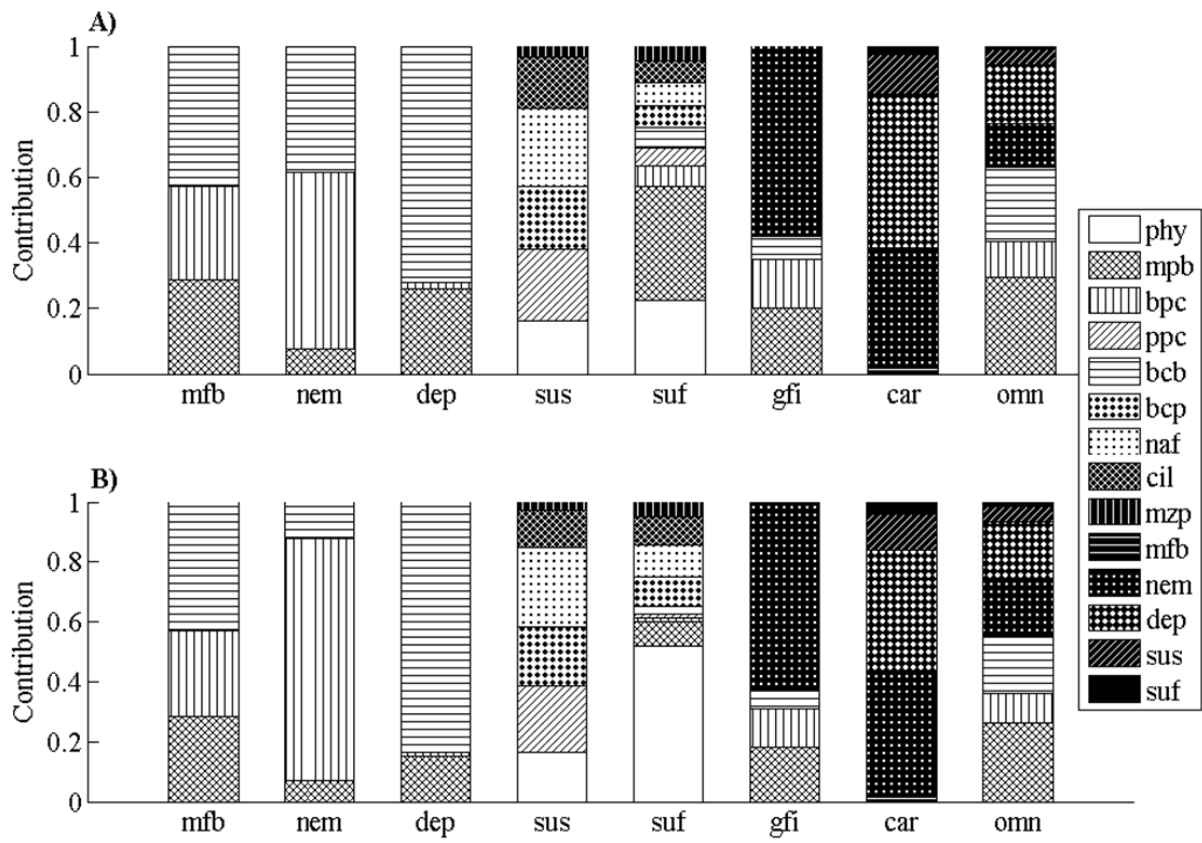
1118 Figure 2



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1121 Figure 3

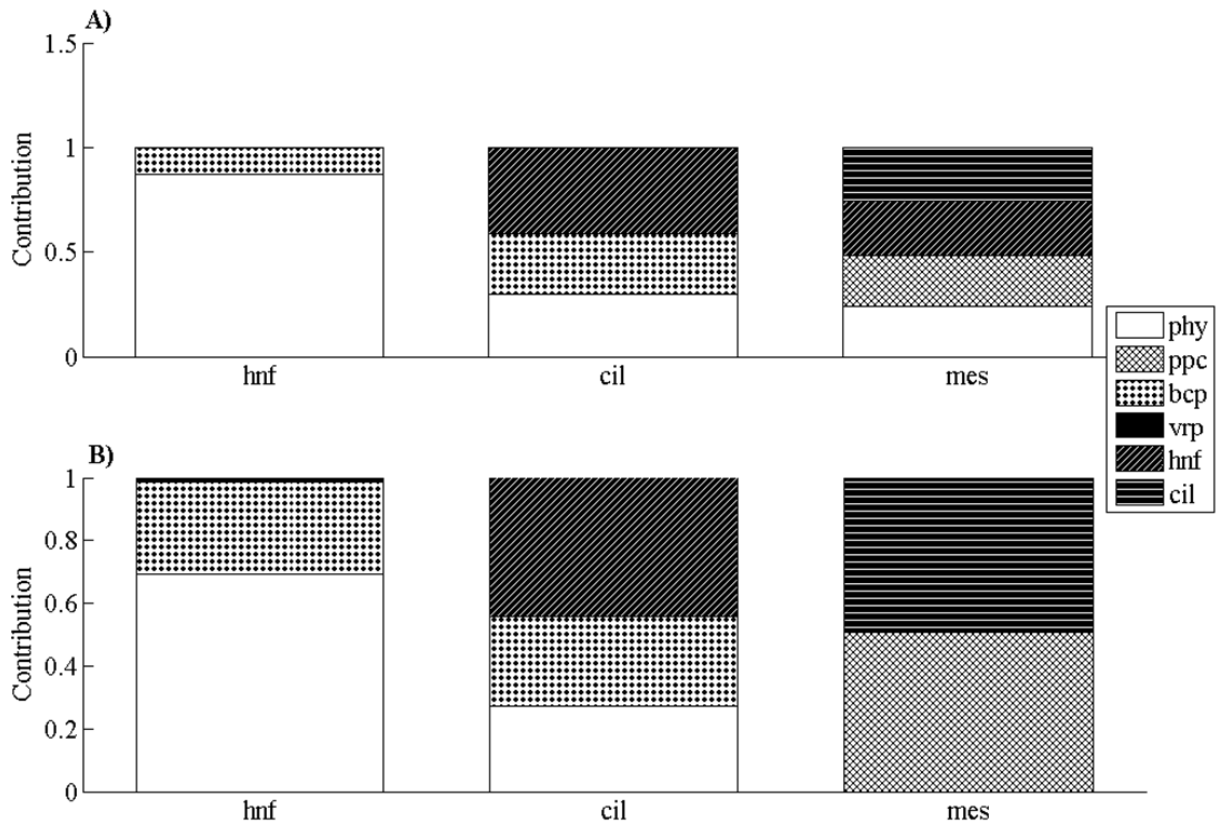


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1124 Figure 4

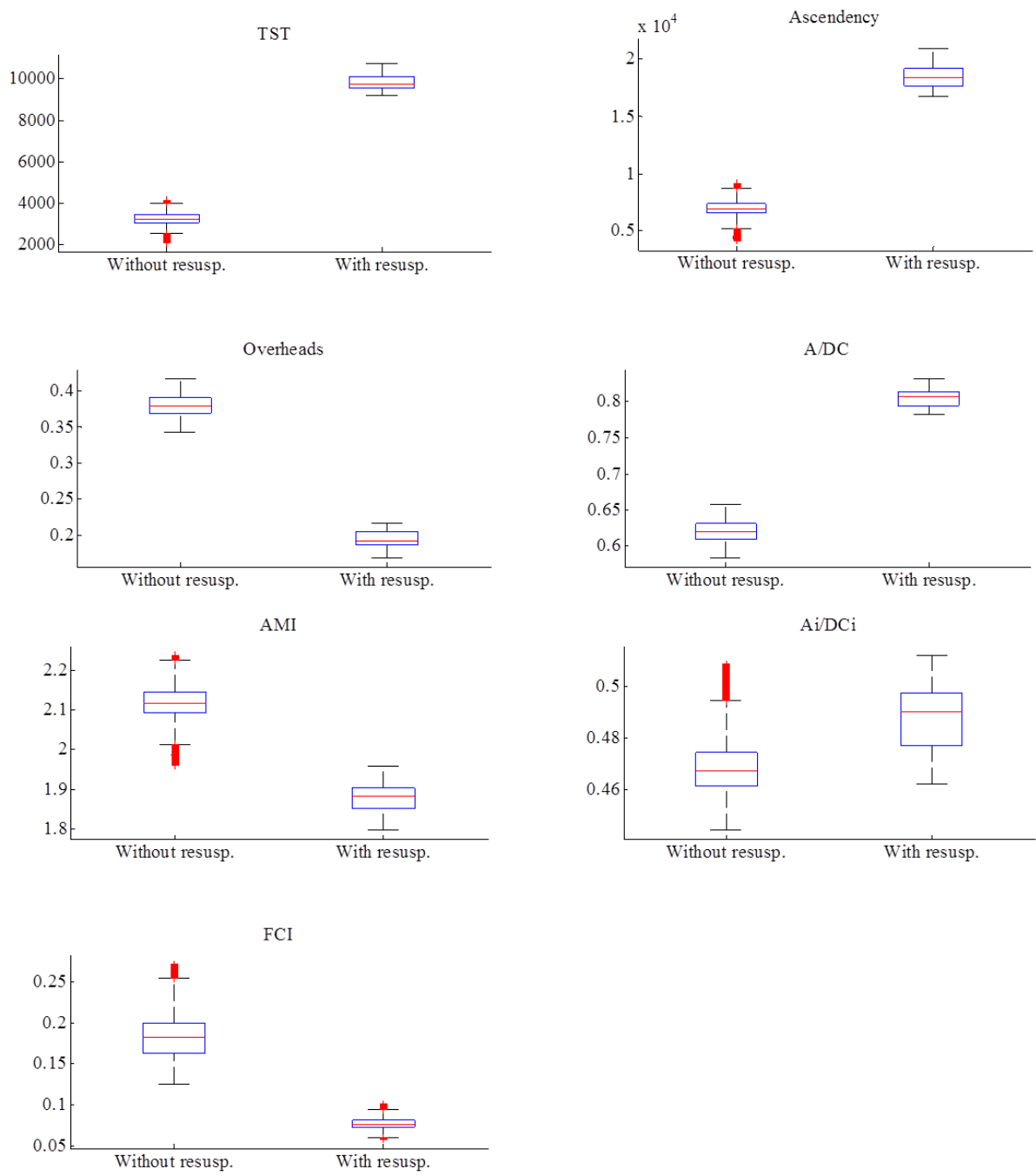
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1128 Figure 5



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