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1 **Modelling the functioning of a coupled Microphytobenthic-EPS-bacterial system in**
2 **intertidal mudflats**

3 **Rakotomalala C^{1*}, Guizien K², Grangeré K¹, Lefebvre S³, Dupuy C⁴, Orvain F¹**

4 **Abstract**

5 A mechanistic and biogeochemical model was developed to analyze the interactions between
6 microphytobenthos (MPB), bacteria and nutrients in a tidal system. Behavioral vertical
7 migration was hypothesized as being controlled by exogenous factors (tide and light) but also
8 by endogenous factors (carbon and nitrogen requirements). The secretion of Extracellular
9 Polymeric Substances (EPS) during photosynthesis (overflow metabolism) and migration of
10 diatoms was also formulated. Similarities in MPB dynamics between observations and
11 simulations support the assumption that carbon and nitrogen ratios are additional key processes
12 behind the vertical migration of diatoms in the sediment. The model satisfactorily reproduced
13 the three growth phases of the MPB development observed in a mesocosm (the lag phase, the
14 logarithmic growth, and the plateau). Besides, nutrient availability, which could be induced by
15 faunal bioturbation, significantly determined the extent of MPB biomass and development. The
16 plateau phase observed in the last days of simulations appeared to be attributed to a nutrient
17 depletion in the system, emphasizing the importance of nutrient availability. The model,
18 although improvable especially on the formulation of the EPS excretion and bacteria
19 development, already updated understanding of several aspects of benthic-system functioning
20 during experimental conditions.

21 *Key words:* Microphytobenthos, migration, carbon and nitrogen ratio, biogeochemical model

22 *Highlights:*

- 23 - A biogeochemical model of a benthic system was developed
- 24 - A focus on MPB primary production was investigated in model simulations
- 25 - This study highlighted that internal C/N ratio plays a key role in the MPB development
- 26 - Nitrogen availability is a driver of MPB migration and production

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28 *Declarations of interest:* none

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66 **1. Introduction**

67 A significant part of the primary production in estuarine systems is sustained by
68 microphytobenthos (MPB) (Cloern et al., 2014; Underwood and Kromkamp, 1999) which
69 photosynthetic activity takes place within a thin layer of the sediment (photic zone) with less
70 than 1mm thickness in muddy substrata (Kromkamp et al., 1998; Serôdio et al., 1997). MPB
71 can be resuspended in the water column and contributes to planktonic biomass (de Jonge and
72 Van Beusekom, 1992; Ubertini et al., 2015) making benthic-pelagic coupling a critical process
73 in coastal systems. Consequently, MPB constitutes major contributor to carbon and energy flow
74 within food webs in intertidal zones (Gaudron et al., 2016) and subtidal zones (Kang et al.,
75 2015).

76 Epipellic diatoms, denominated as MPB in this study, represent the dominant constituent of
77 benthic microautotrophs in muddy flats (Barranguet et al., 1996). It is assumed that growth of
78 MPB in the sediment is temporally restricted to few hours during diurnal low tides (Guarini et
79 al., 2000a), a period which is characterized by extreme variations of environmental factors.
80 Temperature may reach more than 40°C in summer during midday emersion in some location
81 and can have deleterious impact on benthic microalgae growth (Béchet et al., 2017; Blanchard
82 et al., 1996). MPB functioning is well adapted to such extreme conditions such as vertical
83 migration (Consalvey et al., 2004) and/or physiological photoprotection to excessive light
84 (Barnett et al., 2015). Development of benthic diatoms in the sediment is accompanied by
85 production of mucilaginous substances, commonly denominated as “Extracellular Polymeric
86 Substances” (EPS) predominantly composed of carbohydrates which was reported to facilitate
87 the migration of cells (Smith and Underwood, 1998). The EPS also have role in retaining
88 moieties through hydrophilic properties (McKew et al., 2011) and in sediment physical
89 properties protecting against sediment erosion (Underwood and Paterson, 1993). Furthermore,
90 EPS secretion can fuel the bacterial compartment (Agogue et al., 2014).

91 Despite the knowledge on MPB and its importance in coastal ecosystems, specific model of
92 MPB development remains scarce compared to phytoplankton (Bernard, 2011; Geider et al.,
93 1998; Ross and Geider, 2009; Shimoda and Arhonditsis, 2016). This induced the use of
94 phytoplanktonic-adapted models to simulate the microphytobenthic compartment (Blackford,
95 2002; Hochard et al., 2010). Models describing MPB development using forcing factors such
96 as light and tide (Pinckney and Zingmark, 1993; Savelli et al., 2018; Serôdio and Catarino,
97 2000) or light, temperature and hydrodynamic disturbances (Mariotti and Fagherazzi, 2012)
98 were developed. Specific behavioral and physiological adaptations of benthic microalgae were

99 rarely taken into account albeit the model developed by Guarini et al. (2000b) which remains a
100 reference model to date. Vertical migration, a key process in MPB functioning, is based on a
101 chronobiological behavior induced by two exogenous factors namely tide and light in the study
102 of Guarini et al. (2000b) as demonstrated by several studies (Consalvey et al., 2004; de Brouwer
103 and Stal, 2001; Mitbavkar and Anil, 2004). However, exogenous factors alone **may not be**
104 sufficient to explain the MPB vertical migration as resuspension of MPB has been observed
105 without sediment erosion (Guarini et al., 2008; Mariotti and Fagherazzi, 2012) and vertical
106 migration of MPB in the subtidal zone have been attributed to endogenous factors (Ní
107 Longphuirt et al., 2009). In addition, analyzes conducted by Kingston (2002) revealed a
108 downward migration stimulated by nutrient supply which could be enhanced by faunal
109 bioturbation (D'Hondt et al., 2018; Swanberg, 1991). Vertical migration could, therefore, be
110 controlled by internal requirements, either in terms of carbon at the surface with light or in terms
111 of nitrogen deeper at potentially nutrient-enriched sediment (Kingston, 2002). It is thus
112 important to respond to the lack of models integrating the critical processes of MPB
113 development. There is also a clear challenge in incorporating the nitrogen cycle and diagenetic
114 mechanisms for better simulating the primary production of MPB and exchanges of carbon and
115 nitrogen with other elements of the biogeochemical cycle at the sediment-water interface
116 (Hochard et al., 2012).

117 The purpose of this study was to analyze the functioning of a benthic system composed of
118 epipellic diatoms and bacteria using a biogeochemical model which integrated critical features
119 of MPB development in the sediment. Precisely, this study explored the hypothesis that MPB
120 vertical migration is controlled by both endogenous factors (carbon and nitrogen requirements)
121 and exogenous factors (light and tide). Moreover, EPS metabolic routes during photosynthesis
122 and vertical migration of MPB (de Brouwer et al., 2006; Smith and Underwood, 2000; Staats
123 et al., 2000) were modelled and analyzed. MPB development was analyzed under different
124 extents of nutrients. The dynamics of MPB development and EPS production measured during
125 a 10-day experiment in a tidal mesocosm were used to evaluate the model. Sensitivity analyses
126 of the model were also performed.

127 **2. Material and methods**

128 **2.1. Model description**

129 The model developed herein is based on MPB model of Guarini et al (2000b) and on
130 phytoplankton quota model of Geider et al. (1998). Quota models were specifically dedicated
131 to account for dynamic C/N ratios in phytoplankton (see Ross and Geider 2009 and references

132 therein) and consist in a system of 4 ordinary differential equations (functional and reserve
133 carbon, nitrogen and chl *a* content). We adopted a simpler modeling strategy by using nitrogen
134 as the basic unit and carbon, involved in MPB photosynthesis, as an accessory variable but in
135 two separate ODEs with a C/N ratio expected to be lower compared to that of Ross and Geider
136 (2009).

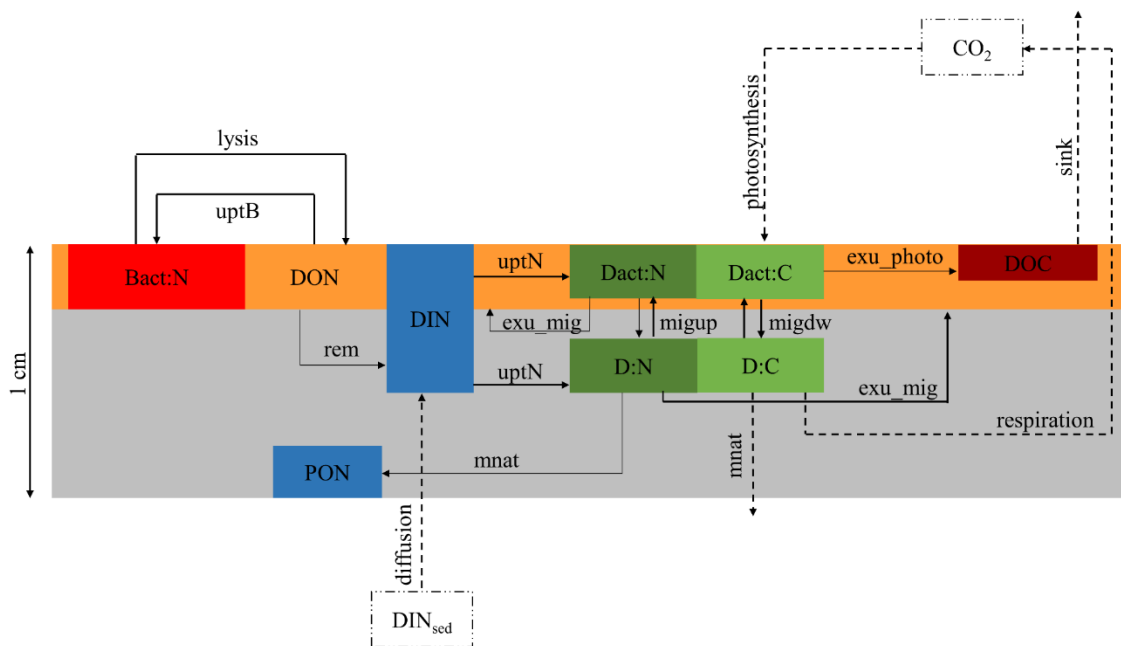
137 The assimilation of nitrogen and the respiration of carbon were assumed to occur in the
138 modelled photic and aphotic layers while the assimilation of carbon through photosynthesis
139 only took place in the photic layer at low tide during daylight. Such dissociation of carbon
140 metabolism with light and nitrogen metabolism with and without light have been also
141 highlighted by Jauzein et al. (2011) for phytoplankton. Consequently, MPB was modeled as
142 photosynthetically active (Dact:C and Dact:N) and inactive (D:C and D:N) biomass. Tide (6h
143 low tide with light -18h high tide in the dark), ambient temperature (ca 16°C), and constant light
144 (140 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) were the forcing variables of the model. CO₂ was not modeled as it
145 was considered as non-limiting in the system. Upward migration was supposed to be driven by
146 light, tide, and carbon requirements, while downward migration was only controlled by nitrogen
147 requirements. At the surface, the benthic diatoms assimilated carbon during photosynthesis and
148 nitrogen until carbon was in excess compared to nitrogen content (threshold value q_{C2N}
149 ca~3.5). Inversely, in the aphotic layer, diatoms assimilated nitrogen and respired carbon until
150 the carbon content became insufficient (threshold value q_{N2C} ca~1) then moved upward at low
151 tide and in the presence of light. In this study, photosynthesis was limited only by light and
152 temperature in the photic zone, nitrogen limitation provoking migration down the aphotic zone.

153 Processes, such as EPS production by benthic diatoms and interaction with bacteria, were
154 recently integrated in a biogeochemical model (Hochard et al., 2010). Some authors highlighted
155 the excretion of EPS by diatom cells related to an overflow metabolism, adhesion, and
156 locomotion (de Brouwer et al., 2006; Orvain et al., 2003; Smith and Underwood, 1998).
157 Exudation of EPS during photosynthesis was integrated in the model as Dissolved Organic
158 Carbon (DOC). Conversely, EPS release during vertical migration was also modelled as a
159 release of dissolved organic nitrogen (DON) and a loss of carbon outside the system.

160 In the present model, bacteria development was simply integrated and limited by the
161 availability of DON. An inhibition effect of EPS (DOC) on bacterial development in the biofilm
162 (Agogu e et al., 2014; Doghri et al., 2017) was also taken into account. Bacterial mortality was
163 attributed to viral lysis (Le Chevanton et al., 2013; Siem-J rgensen et al., 2008).

164 Simple formulations were adopted to represent the mineralization of PON (Particulate
 165 Organic Nitrogen) into DON and DON into DIN (Dissolved Inorganic Nitrogen: NH_4^+ , NO_3^- ,
 166 and NO_2^-). For now, the processes of nitrification/denitrification in relation to oxygen
 167 consumption were not detailed in this model, because the model was simplified to be in line
 168 with the dataset available for comparison. Moreover, this study focused on innovative
 169 mechanisms linking vertical migration to the C/N internal balance of MPB and not on the
 170 detailed dynamics of oxygen, ammonium and nitrates as this is the case in other models of MPB
 171 primary production in relation with early diagenesis of organic matter (Hochard et al., 2012,
 172 2010).

173 The concept and processes integrated in the model were summarized in the Fig. 1. Details
 174 on model equations and parameters were developed in the appendix. The model developed
 175 herein was implemented in the numerical tool Eco3M (Baklouti et al., 2006). The code was
 176 developed in FORTRAN 90-95 and used Euler explicit method as solving methods. The code
 177 was under Cecill License.



178
 179
 180 *Fig. 1: Conceptual framework of the model of a benthic system constituted by MPB, Bacteria*
 181 *and nutrients in the first centimeter of sediment expressed in carbon and nitrogen respectively.*
 182 *MPB is distributed in active (Dact:N and Dact:C) or inactive layers (D:N and D:C). An*
 183 *overflow of carbon (DOC) is secreted during photosynthesis. Vertical migration represents the*
 184 *link between the two compartments, during which glycoproteins are secreted and directly fuel*
 185 *the first nutrient compartment (Dissolved Organic Nitrogen or DON). Bacteria (Bact:N) relies*

186 on DON and which development is inhibited by the photosynthesis-related carbon excretion
187 DOC. Dissolved Inorganic Nitrogen (DIN), on which the MPB relies on, represents the second
188 nutrient compartment. The Particulate Organic Nitrogen (PON) resulted from natural mortality
189 of MPB cells. The scale of the boxes in the graph is not representative of reality. Sinks are
190 represented by dashed arrows. Forcing variables are represented by dashed boxes.

191 **2.2. Test case: the mesocosm study of Orvain et al. (2003)**

192 Model performance was tested in comparison with the experimental study of Orvain et al.,
193 (2003) which analyzed the dynamics of benthic diatoms and associated extracellular
194 carbohydrates excretion. In this experimental study, a natural community of diatoms was
195 maintained in controlled conditions consisting of 6h diurnal low tide and 18h nocturnal high
196 tide during 10 days in two different tanks. Erosion of sediment and MPB during rising and ebb
197 tides were avoided in the mesocosm experiments (Orvain et al., 2003). Both processes were
198 thus not integrated in the model. The mesocosm was maintained at ambient temperature (ca
199 16°C) and constant irradiance (PAR=140 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) during diurnal phases. Sediment
200 was sieved through 1mm mesh prior to diatoms culture to remove macrofauna. However,
201 meiofauna (nematoda and foraminifera) were still present in the sediment. Chl *a* and EPS (Low
202 and High Molecular Weight) contained in the 1 cm of sediment were assayed at the beginning
203 of diurnal emersion and just before diurnal immersion during 10 days. Each assay in each tank
204 were performed in triplicate. Nutrients (urea, ammonium, nitrate/nitrite and phosphate) content
205 was also measured at the beginning and at the end of the experiments over the first and the
206 second centimeter depth.

207 **2.3. Sensitivity analysis**

208 2.3.1. Initial conditions

209 Values of photosynthetically active microphytobenthic biomasses (Dact:C and Dact:N) and
210 the photosynthesis-related EPS (DOC) compartments were set to zero with the assumption that
211 neither photosynthesis nor EPS production have taken place at the beginning of the experiments.
212 As the silty mud (100% of fine mud <63 μm) was collected *in situ* and manipulated thereafter,
213 the algal cells were supposed to be in the state of carbon excess as after an emersion phase (C/N
214 = 1.94:0.1). Two other MPB initial states were tested and related simulations were presented in
215 supplementary material (SM1). The value of ammonium and nitrate recorded at the beginning
216 of the experiment, expressed in the same unit as in the model, was used as initial values of DIN
217 compartment in the first centimeter (0.343 mol N m⁻³). As neither bacteria, nor DON, nor PON
218 were assessed during the experiments and as the model appears not to be sensitive on the

219 variation of the initial conditions of those three compartments, values were set arbitrary to 1, 0,
220 and 5 mol N m⁻³ respectively as initial conditions.

221 2.3.2. Nutrient diffusion

222 At the beginning as well as at the end of the experiments of Orvain et al., (2003),
223 concentrations of DIN (ammonium, nitrite, and nitrate) were higher in the second centimeter
224 (0.563 to 0.312 mol N m⁻³ respectively) than in the first centimeter (0.343 to 0.036 mol N m⁻³).
225 Nutrient diffusion from deeper layers was likely going on in the experiments and has been
226 already modelled in another study (Hochard et al., 2010). The hypothesis that nutrient input
227 maintaining the growth of diatoms until the 10th day could arise from the deeper layer was then
228 tested. Diffusion of nutrients (DIN) controlled by the gradient known as Fickian chemical
229 diffusion, between the deeper layer and the first centimeter of sediment, was thus integrated in
230 the model (Scenario A) as in Lavery et al. (2001). Moreover, solute fluxes depending on
231 sediment porosity and tortuosity (Boudreau, 1996) were also integrated in the Fickian
232 formulation of the present study (Appendix Table 4). The DIN in the second centimeter was
233 hypothesized to linearly decrease from the value at the beginning of the mesocosm culture
234 (0.563 mol N m⁻³).

235 Ecological role of meiofauna was reviewed (Schratzberger and Ingels, 2018) mentioning
236 nutrient input and enhanced nutrient cycling due directly or indirectly to meiofauna functioning,
237 which enhance diatoms development (D'Hondt et al., 2018). The paucity of studies quantifying
238 the whole nutrient increase in the sediment due to meiofauna prompted us to test some values
239 to integrate the processes. Two levels of biodiffusion simulations were thus tested by
240 multiplying the diffusion coefficient by a factor 5 (Scenario B) and a factor 10 (Scenario C).
241 Equation and parameters of diffusion were given in the appendix (Table 4 and 5).

242 2.3.3. C/N ratio threshold values

243 Sensitivity analysis of the intra-cellular quota C/N thresholds triggering the upward
244 (qC2N=3.5) and downward (qN2C=1) migration was also conducted. The two parameters were
245 varied about -50%, -30%, +30%, and +50%.

246 2.4. Statistical tests

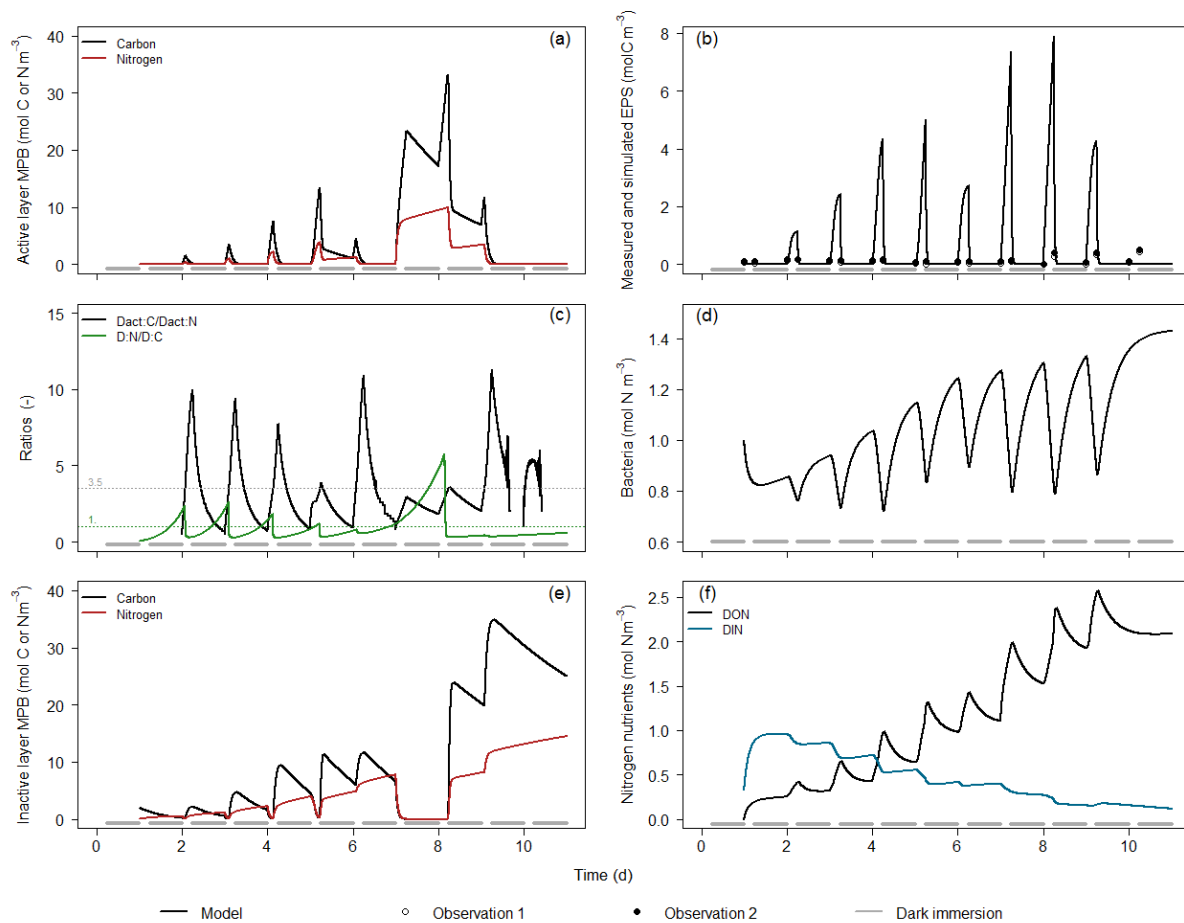
247 The Taylor diagram (Taylor, 2001) was used to evaluate the performance of the model,
248 which graphically groups the correlation between simulations and observations, the RMS error
249 represented by the radial distance from the observation, and the standard deviation of the

250 dynamics represented by the radial distance from the origin. Simulations with high value of the
251 correlation coefficient, low value of the RMS error as well as dispersion equivalent to the
252 observations reflects a very good fit. The experimental measurements of chl *a* and EPS from
253 the study of Orvain et al. (2003) were converted in carbon concentration using ratios of C/chl *a*
254 = 45 and Glucose/C = 15.

255 **3. Results**

256 **3.1. Functioning of the benthic system model**

257 Vertical migration of MPB was simulated and depicted by upward migration to the active
258 layer at the beginning of nearly each diurnal emersion and downward migration to the inactive
259 layer until dark immersion (Fig. 2a and e). Precisely, carbon requirement brought cells to the
260 surface to accumulate carbon until the later became in excess then nitrogen requirement induced
261 them to go back to the sediment, where carbon content progressively decreased through
262 respiration while nitrogen content increased. Carbon and nitrogen transfers between active (Fig.
263 2a) and inactive layers (Fig. 2e) were reproduced by an inverse pattern between them. The 6
264 first days, both N/C and C/N ratio in the inactive and active layer (Fig. 2c green and black line)
265 exceeded the threshold values ($q_{N2C} = 1$ and $q_{C2N} = 3.5$) respectively resulting in daily
266 upward and downward migration of cells (Fig. 2a and e). Diatom migration from the inactive
267 to the active layer occurred when cells were nitrogen enriched (Fig. 2c green line) except for
268 the day 6, 9, and 10. The exponential development of diatoms was modelled at the surface as
269 depicted by the abrupt increase in the carbon content of MPB (black line) after 6 days of latency
270 and moderate growth period (Fig. 2a). Diatoms remained at the surface during 2 days then MPB
271 growth drastically dropped to literally stop thereafter resulting in an empty active layer (Fig.
272 2a) and a maximum concentration of carbon and nitrogen in the inactive layer the last two days
273 (Fig. 2f).



275

276 *Fig.2: Simulated functioning of the benthic system. Temporal dynamics of: (a, e) the carbon*
 277 *(black line) and the nitrogen (blue line) concentrations of MPB in the active (a) and inactive*
 278 *(e) layers; (b) the photosynthesis-related DOC (line) confronted with the measured EPS HMW*
 279 *(points); (c) the C/N ratio in the active layer (black) and the N/C ratio in the inactive layer;*
 280 *(d) the bacterial biomass, (f) the dissolved inorganic nitrogen DIN (red) and the dissolved organic*
 281 *nitrogen DON (black) in the first centimeter of sediment. Gray line in each graph represents*
 282 *dark immersion periods in the system while space in between represents emersion phase with*
 283 *light.*

284 While DIN availability overall decreased in the system until near-depletion, both bacterial
 285 biomass and DON increased (Fig. 2d and f black). All three compartments (DIN, bacterial
 286 nitrogen content and DON) exhibited daily oscillations. During the 6 hours of diurnal emersion
 287 when MPB was photosynthetically active, bacterial biomass and DIN decreased while DON
 288 increased. During 18 hours dark immersion, decrease of DON concentration (Fig. 2f black) was
 289 observed whereas inverse pattern was simulated for bacteria (Fig. 2d black). At the same time,

290 DIN concentration (Fig. 2f blue) slightly increased during 6 days and decreased thereafter when
291 maximum concentration of nitrogen in the inactive layer was observed.

292 It was noteworthy that biomass of bacterial decline during diurnal emersion was
293 proportional to the DOC increase (Fig. 2b line), as expected from bacterial growth inhibition
294 by DOC. However, as soon as DOC was hydrolyzed during immersion, bacterial growth
295 outcompeted viral lysis of bacteria and bacterial biomass increased again. DOC variation
296 followed photosynthetic activity depicted by active diatom carbon content, and therefore the
297 DOC increase was larger in days 7 and 8 than during the 6 days of latency and moderate growth
298 period. This was only partially in agreement with pronounced increase of EPS-HMW (Fig. 2b
299 points) observed the 3 last days in Orvain et al. (2003) experiments. Moreover, the extent of
300 simulated DOC was largely higher compared to observed EPS concentrations.

301 **3.2. Sensitivity analysis**

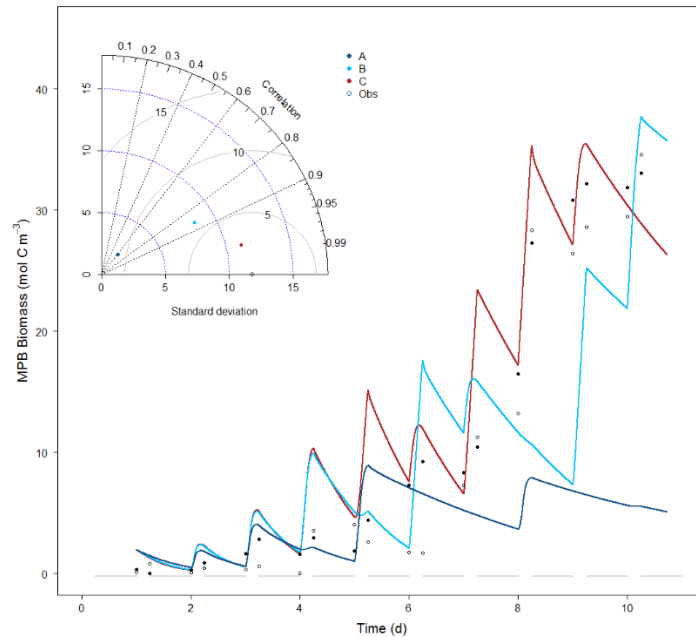
302 **3.2.1. Nutrient availability**

303 In the mesocosm study by Orvain et al. (2003), the temporal variation of MPB growth
304 showed 3 distinct phases of development. The lag phase lasted about 3 days and was followed
305 by continuous increase being the greatest between the 8th and the 9th day and stabilized over the
306 last day (Fig. 3, points).

307 Dynamics of modelled carbon in the 1st cm of sediment (pooling active and inactive layers)
308 over the 10 days simulation was substantially lower when integrating chemical diffusion alone
309 (Fig. 3 blue curve). When diffusion was limited to Fickian diffusion, the model underestimated
310 the MPB biomass as illustrated by RMSE higher than 10 (Fig. 3, left graph, blue point). The lag
311 phase was well reproduced however the two last phases of MPB growth during an experimental
312 configuration were not reproduced. Simulated pattern showed lower correlation with observed
313 patterns ($R \sim 0.6$) and low standard deviation ($\sim 2 \text{ mol C m}^{-3}$) reflecting lower spatial variability.

314 With a biodiffusion of nutrients 5 times greater than the Fickian diffusion, concentration of
315 carbon was higher than simulations conducted with chemical diffusion (Fig. 3 cyan curve).
316 Enhanced nutrient availability resulted in daily growth of MPB with a cyclic succession of high
317 production followed by lower production the next day. The exponential phase happened one
318 day later compared to observations. The model did not fit well the observed pattern during the
319 6h productive period (Fig. 3, left graph, cyan point) with lower spatial variability depicted by
320 low standard deviation ($\sim 8 \text{ mol C m}^{-3}$) compared to standard deviation of measurements (~ 12

321 mol C m⁻³). However, simulated pattern was closer to data than the previous simulation with
322 better correlation (R~0.87) and lower RMSE (~6).



323

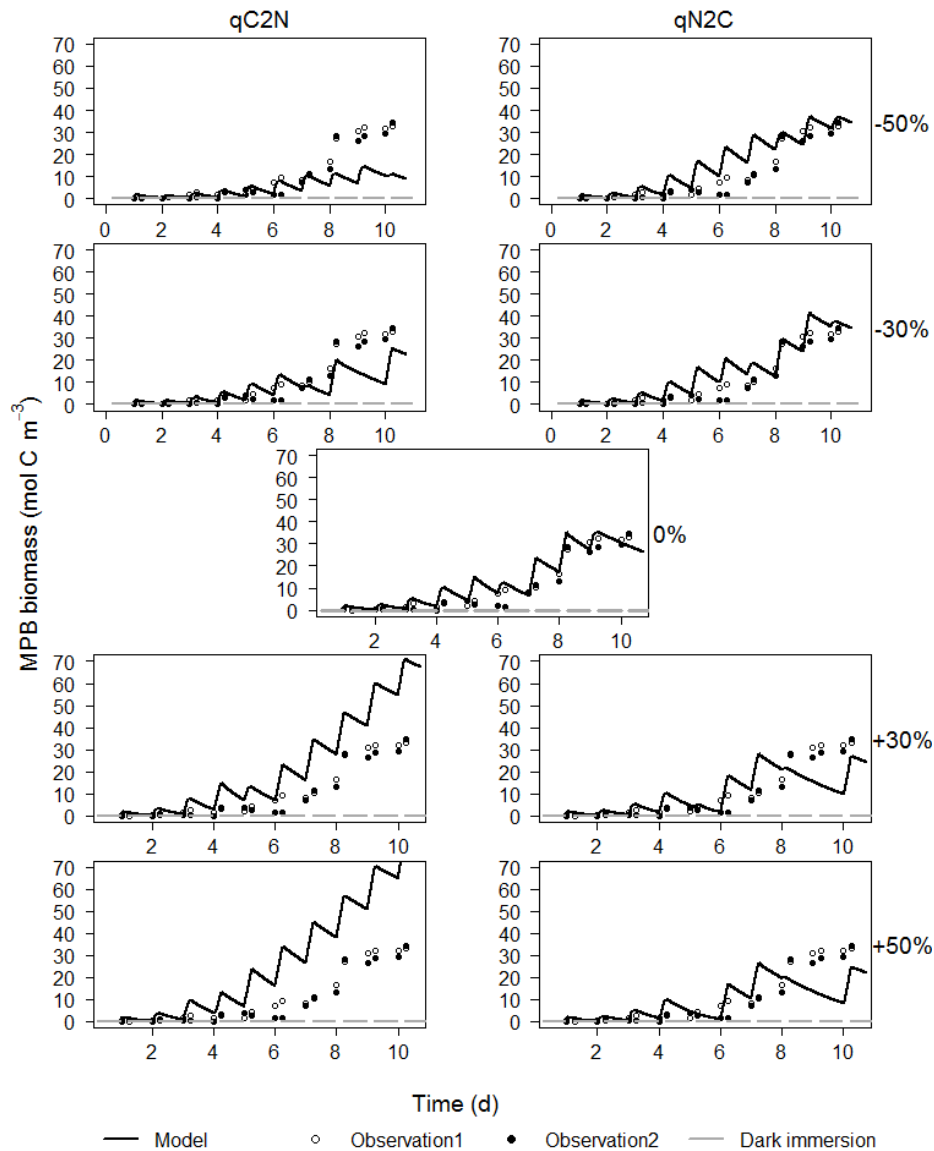
324 *Fig. 3: Simulated MPB biomass (lines) in the first centimeter of sediment under three*
325 *different extent of diffusion: chemical diffusion (blue), and bio-diffusion 5 times (cyan) and 10*
326 *times (red) greater than the chemical diffusion. The points represent the MPB biomass*
327 *calculated from the study of Orvain et al. (2003). Gray line represents dark immersion periods*
328 *in the system. The left graph represents the Taylor diagram showing the difference between the*
329 *observed MPB and the simulated MPB under three different diffusion extent. Gray and blue*
330 *dashed curves represent respectively the RMSE and the standard deviation of observed and*
331 *simulated dynamics.*

332 With enhanced refueling of DIN compartment (10 times the chemical diffusion), the
333 dynamics of the MPB (Fig. 3, red curve) was similar to that of measurements showing the three
334 specific phases of MPB development during experimental conditions. Moreover, this 3rd test
335 better simulated the amplitude of variation than the two previous simulations with almost the
336 same standard deviation as observation, and displayed the lowest RMSE (~2) and the best
337 correlation (R~0.98) among all simulations (Fig. 3, left graph red point).

338 **3.2.2. Physiological thresholds triggering vertical migration**

339 Varying the threshold parameters triggering the downward (q_{C2N}) and upward (q_{N2C}) of
340 diatom cells in the sediment led to different dynamics of MPB in the system, however the
341 latency phase was systematically reproduced (Fig. 5).

342 Decreasing the value of the downward migration threshold (q_{C2N}) resulted in MPB
343 biomass lower than what was observed (Fig. 5, q_{C2N} -30% and -50%). Moreover, the moderate
344 and exponential growth were not reproduced depicted by lower SD value ($\sim 5 \text{ mol C m}^{-3}$)
345 compared to the SD of observation and the reference ($\sim 12 \text{ mol C m}^{-3}$) (Supplementary Material
346 [SM2](#) Fig. 1 and 2). The extent of the carbon increment was more pronounced when the same
347 threshold value was increased (Fig. 5, q_{C2N} +30% and +50%) however the dynamics of MPB
348 growth showed almost constant daily growth and again did not displayed the two last growth
349 phases of MPB which was reflected by higher SD (between 20 and 25 mol C m^{-3}) regarding
350 observed and reference simulation patterns (Supplementary Material [SM2](#) Fig. 1 and 2).



351

352 *Fig. 5: Simulations (lines) of diatom dynamics in the first centimeter of sediment obtained*
 353 *while analyzing the sensitivity of the model by varying the $qC2N$ and the $qN2C$ by -50%, -30%,*
 354 *0%, +30%, and +50% as 0% corresponds to best simulation with a biodiffusion 10 times higher*
 355 *than the chemical diffusion. Measurements (points) were also represented on each graph. Gray*
 356 *line represents dark immersion periods in the system.*

357 Earlier upward migration (lower values of $qN2C$) induced again daily photosynthetic
 358 activity which slightly overestimated the simulation of reference as well as the observation (Fig.
 359 5, $qN2C$ -30% and -50%). However, simulations better fitted the observations mainly when the
 360 threshold value was decreased by 30%, which showed almost the same SD as observation and
 361 the simulation of reference and the lowest RMSE values (Supplementary Material SM2 Fig. 1
 362 and 2). Simulated MPB biomass was characterized by cycles of high growth followed by 2 to

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363 3 days of decrease when upward migration was delayed (higher values of qN2C) (Fig.5 qN2C
364 +30% and +50%). The patterns of these last simulations had the lowest correlation coefficient,
365 low SD value and high RMSE compared to observation and the simulation of reference
366 (Supplementary Material SM2 Fig. 1 and 2).

367 **4. Discussion**

368 **4.1. Exogenous Vs endogenous factors controlling MPB vertical migration**

369 A model of a benthic system which simulates physiological functioning of MPB,
370 concomitant development of bacteria, and fluctuation of nutrients in the first centimeter of
371 sediment was developed in this study. Simulations obtained from the model realistically
372 reproduced the dynamics of MPB biomass measured in the first centimeter of sediment in
373 laboratory experiments (Orvain et al., 2003). The model succeeded in reproducing the vertical
374 migration of epipellic diatoms which follows the periodicity of tide and light as encountered in
375 laboratory (Perkins et al., 2010) and also *in situ* (Blanchard et al., 2001). Cyclic simulated
376 carbon assimilation during daytime emersion followed by carbon decrease during dark
377 immersion regulated the upward and downward migration of cells between an active layer,
378 where photosynthesis outcompeted respiration, and an inactive layer, where photosynthesis did
379 not occur thus respiration dominated. The model was set up with the hypothesis that intra-
380 cellular C/N quota determines the vertical migration of epipellic diatoms cells in the sediment
381 together with tide and light. Debate is still open about the main factors driving the vertical
382 migration of MPB in the sediment and this modelling approach offers some opportunities to
383 discuss them. In their study, Consalvey et al. (2004) and Saburova and Polikarpov (2003)
384 recapitulated factors that likely induce vertical migration of MPB which include exogenous and
385 endogenous processes. Light was shown to be the “zeitgeber” (Mitbavkar and Anil, 2004) of
386 the chronobiologic behavior, and especially the upward migration. However, Kingston (2002)
387 has also showed that nutrients and carbon gradients at the surface could explain the downward
388 migration of diatoms cells. Our results substantiate that exogenous factors (light and tide) and
389 mainly endogenous factor (C/N ratio) control diatom migration. In densely packed biofilm, high
390 competition for nutrients (Orvain et al., 2003) and increase of carbon content in MPB at the
391 surface lead to an unbalanced C/N ratio in cells which migrate down to the sediment where
392 higher availability of nutrients in reduced form is encountered (Magni and Montani, 2006),
393 supporting the assumption of more favorable nutrient conditions at depth (Saburova and
394 Polikarpov, 2003). In addition, accumulation of intracellular nutrient has been observed for
395 benthic microalgae (Garcia-Robledo et al., 2016). Nutrient uptake at the surface and especially

396 in the aphotic layer were well simulated since an increase of MPB nitrogen content occurred
397 mainly during dark immersion. Saburova and Polikarpov (2003) already illustrated decoupled
398 photosynthesis and cells division associated to high concentration of DIN in the sediment. Thus,
399 decoupled assimilations of C and N integrated in the model appeared to be realistic and could
400 reflect reality. Adjustment of the intracellular C/N gradient is thus achieved through vertical
401 migration which allowed efficient benthic microalgae functioning. The same patterns has been
402 observed with phytoplankton with varying C/N ratio during light period under N-sufficient
403 condition (Jauzein et al., 2011). The same decoupling of nitrogen and carbon assimilation has
404 also been reported for marine microalgae including diatoms (Clark and Flynn, 2002; Jauzein et
405 al., 2008; Schartau et al., 2007). Flynn and Fasham (2002) also suggested a link between
406 phytoplankton migration cycle and intercellular nitrogen content.

407 Choosing the carbon and the nitrogen requirements to predict vertical migration of epipellic
408 diatom represents new approach which in our knowledge has not been applied to benthic system
409 models yet. This may explain the decrease of the chl *a* concentration almost 2h before the end
410 of the light period (Cartaxana et al., 2016). The downward migration is thus highly driven by
411 endogenous processes in diatoms cells. Elemental requirements could also explain the
412 resuspension of MPB in the water column without sediment erosion encountered in the study
413 of Guarini et al. (2008) and what Mariotti and Fagherazzi (2012) designated as chronic
414 detachment. As long as N in the diatom cells is sufficient, MPB continues carbon photo-
415 assimilation even during rising tide. When the C/N ratio is unbalanced again with cells that are
416 in excess of N and the carbon stock is insufficient for respiration, the cells migrate back up to
417 the surface during low tide and daylight hours. This finding could also be the factor involved in
418 the presence of incipient diatom cells hours before ebb tide (Cartaxana et al., 2016) depicted as
419 the initial lag phase of MPB upward migration (Coelho et al., 2011).

420 In addition to vertical migration, photoprotection or even photoinhibition could be
421 encountered when MPB is subjected to high light (Cartaxana et al., 2011) and could explain a
422 downward migration before the end of the exposure low tide periods. Extreme temperature
423 clearly impairs microalgae growth and viability (Béchet et al., 2017), whose effect could be
424 synergetic with that of light (Laviale et al., 2015). Savelli et al. (2018) showed the relevant role
425 of the thermoinhibition on the summer primary production of MPB. However, as neither
426 temperature ($\sim 16^{\circ}\text{C}$) nor light intensity ($120 \mu\text{mol photons m}^{-2}$) during the mesocosm
427 experiment did not reach extreme values, the model is suited for experimental conditions.
428 However, it should be noted that MPB growth limited by temperature and light was already

429 formulated in the model (Appendix Table 3). And compared to Guarini et al. (2000b), the value
430 of optimum temperature were modified (20°C instead of 25°C) to better fit field data
431 (unpublished data, Guizien K., Personal communication) in Marennes Olérons Bay during field
432 survey (Orvain et al., 2014).

433 Sensitivity analysis conducted on the two threshold values of migration showed that they
434 were sensitive and greatly determined the dynamics of MPB. Varying those values supposed
435 either nitrogen or carbon assimilation is shorter or longer and resulted in different simulations.
436 The effect of elemental requirements was hidden by chronobiological growth of MPB when
437 cell were photosynthetically active longer at the surface and when cells migrated earlier at the
438 surface (Fig. 5, qC2N+30%, qC2N +50%, qN2C-30%, and qN2C-50%). In contrast, when cells
439 assimilated nitrogen longer in the sediment or when they migrated earlier down to the sediment,
440 nitrogen assimilation lasted longer and was followed by important MPB growth, thus the effect
441 of internal requirement overtook the chronobiological effect in MPB growth.

442 The internal C/N ratio of MPB then highly controls its dynamics in the sediment. The
443 modeled C/N ratio in this study fluctuated between 1 and 3.5 with a constant PAR (140 μmol
444 photons $\text{m}^{-2} \text{s}^{-1}$). In a different approach, Ross and Geider (2009) improved the initial model of
445 Geider et al. (1998) which simulated total carbon and nitrogen contents of planktonic
446 microalgae whose ratio oscillated between 5 to 6 and 7 to 13 with a forcing PAR of 60 and 1200
447 μmol photons $\text{m}^{-2} \text{s}^{-1}$ respectively. The difference comes especially from the carbon simulated
448 in Ross and Geider (2009) which represents the total carbon content whereas the carbon
449 simulated herein represents only a part of the total carbon which is involved directly in the
450 photosynthesis process leading to a C/N ratio value lower than in the literature.

451 This modeling exercise helped to explain processes on which questions remained open.
452 However, the reproduction of the same growth dynamics of MPB during an experimental
453 condition highlighted the importance of C/N ratio balance in its functioning. Further
454 investigations of the fate of C/N ratios in epipelagic diatoms cells and the empirically estimated
455 C/N thresholds driving the vertical migration need to be conducted to improve the model
456 robustness.

457 **4.2. Bacteria, EPS, and MPB dynamics**

458 Synergistic temporal variations of MPB, bacteria, and nutrients were required to obtain
459 realistic reproduction of MPB growth observed during the experimental investigation by Orvain
460 et al. (2003). The model succeeded in maintaining the three-phased growth of MPB. Moreover,
461 decrease of bacterial biomass during daytime exposure was depicted while an important

462 increase was observed during dark immersion. Orvain et al. (2014) observed in natural
463 condition a negative correlation between bound EPS exuded by MPB and bacteria in the
464 sediment **only during growth phase**. Such findings have been reiterated during experimental
465 investigations (Agogu   et al., 2014; Doghri et al., 2017). The formulation of bacterial
466 development in the model integrated the inhibition effect of photosynthetic overflow DOC. This
467 negative correlation seemed to be more straightforward in these studies and this hypothesis
468 seemed to explain the observed alternating opposition of growth between bacteria (during
469 immersion nocturnal periods) and MPB (during daylight low-tide). However, positive effect of
470 bacteria on diatoms growth could also be encountered depending on species (Jauffrais et al.,
471 2017). Further analysis should be conducted to seek out the potential effect of bacteria on MPB
472 at the community level. Bacterial loss in marine system has been attributed to mortality through
473 viral lysis (Fischer et al., 2003; Tsai et al., 2013) which was the case in this study.

474 Competition between MPB and bacteria on nutrients was temporally delayed as bacteria
475 relied on DON while the MPB relied on DIN. The DON then fueled the DIN through bacterial
476 mineralization (Boh  rquez et al., 2017) which could partly explain the opposed short-term
477 dynamics of bacteria and MPB. Risgaard-Petersen et al. (2004) found lower bacterial activity
478 in the presence of MPB attributed to direct competition on nutrients but could also be combined
479 with the previously mentioned inhibition effect of MPB on bacteria. As the same MPB growth
480 pattern was obtained during the experiment and with the model, interactions between bacteria
481 and MPB in the model appears realistic **despite the absence of bacteria biomass measurement**
482 **during the study of Orvain et al. (2003)**. The inhibition effect of MPB on bacterial growth
483 appeared to encompass both complex interaction between them and their direct competition on
484 nutrients. However, formulation needs to be improved and validated, by refining the DIN
485 composition (ammonium, nitrates, nitrites...), by integrating the competition for ammonium
486 between MPB and bacteria, and by taking into account other processes related to the
487 regeneration of nutrients from organic matter as in Hochard et al. (2010).

488 **4.3. EPS nature Vs EPS function**

489 Diatoms DOC production was modelled based on their functions overflow release during
490 photosynthesis and should strictly corresponds to highly assimilable carbohydrates molecules.
491 Orvain et al. (2003) stated that the insoluble EPS (HMW) was more associated with the diatoms
492 and represented an overflow of carbon during photosynthesis in nutrient-depleted situation.
493 Moreover, photosynthesis is a processes involved in EPS production (Smith and Underwood,
494 2000; Staats et al., 2000). Both modelled EPS (DOC) and measured EPS HMW displayed daily

495 fluctuation characterized by secretion during daytime exposure. Sudden drop was simulated
496 during the successive dark immersion periods. Tidal and diel dynamics of EPS were in
497 accordance with study of Agogu  et al. (2014). Carbon exudation by MPB is associated with
498 what Schartau et al. (2007) called carbon overconsumption or overflow metabolism (de
499 Brouwer and Stal, 2001). The maximum overflow metabolism was simulated in day 8 before a
500 downward migration of MPB in this study. They found that the first excretion happened during
501 the growth phase while the second excretion took place under nutrient-depleted condition
502 (Orvain et al., 2003). Other studies have also found higher production of EPS during the
503 stationary phase (Agogu  et al., 2014; Pierre et al., 2014; Staats et al., 2000). In our study,
504 important photosynthesis-related EPS were modelled during strong growth with the maximum
505 value the day 8, whereas the second mode happening during nutrient-depleted stationary phase
506 was not maintained the two last days of simulation. [Modified EPS extraction protocols](#)
507 [\(Takahashi et al., 2009\)](#) showed that colloidal fraction were glucose-rich probably because of a
508 [metabolic route related to photosynthesis](#). The latter could fit with the description of the
509 photosynthetic related EPS modelled in this study. Colloidal EPS fractions were found to have
510 biochemical composition related to carbon storage and were known to be a carbon source for
511 heterotrophic bacteria [\(Cook et al., 2007; Pierre et al., 2014\)](#).

512 The second type of EPS was released during MPB migration as DON and as a loss of carbon
513 outside the modelled system [\(Boh rquez et al., 2017\)](#). EPS compounds include a variety of
514 molecules nature and weight some consisting of glycoproteins [\(Pierre et al., 2014\)](#). Orvain et
515 al. (2003) described the LMW fraction as remnants of algal cells during movement. Moreover,
516 [Ser dio et al., \(1997\)](#) recorded migratory pattern which was maintained when cultures were
517 darkened. MPB cell must have internal reserves allowing them to synthesize EPS during a
518 relative long period, even in absence of light. By the same token, [Smith and Underwood \(1998\)](#)
519 mentioned the hypothesis of migration-specific EPS production by epipellic diatoms. “Cells
520 locomotion requirement” in their study can be associated to C/N ratio modelled in this study
521 and which forced the upward or the downward migration. Furthermore, our hypothesis of EPS
522 produced while cells migrate within the sediment thus appears realistic. The presence of
523 nitrogen in EPS were identified [\(Agogu  et al., 2014; Pierre et al., 2014\)](#) supporting the
524 expression in DON of the migration-related EPS in the model.

525 However, the differentiation of the EPS related to photosynthesis (carbon) and migration
526 (nitrogen and carbon) in this study may not be roughly sketched since EPS production seems to
527 be accompanied by high secretion of monomers (rhamnose, fucose, galactose, uronic acids ...)

528 as well as proteins (Agogu  et al., 2014; Takahashi et al., 2009). Moreover, further analysis
529 should be conducted to better account for the potential effect of varying salinity on EPS
530 production. High tolerance to varying salinity was observed with an epipellic diatom species in
531 controlled conditions where vertical migration was avoided (Juneau et al., 2015). However,
532 stimulated EPS production was observed with high salinity in natural conditions (Orvain et al.,
533 2014) which has protective role on MPB cells (Steele et al., 2014). The incorporation of the
534 EPS secretion in the model implementation must be thus improved and better evaluated.

535 **4.4. Importance of nutrient availability**

536 MPB development was highly limited by nutrients. Daily variation of MPB concentration
537 was mainly attributed to endogenous factors, however, nutrient depletion was the main factor
538 driving the plateau phase of MPB dynamics. In our study, the diffusion of nutrients from the
539 deeper layer was mandatory to reproduce the typical 3 phase growth pattern of MPB. High
540 variability of the diffusivity coefficient in the sediment was reported in the literature (Li and
541 Gregory, 1974). However, the chosen value in this study was of the same order of magnitude
542 as the diffusivity coefficient often used in the literature (ca. $1.9 \times 10^{-9} \text{ m}^2 \text{ s}^{-1}$) (Bola ek and Graca,
543 1996). The dynamics of observed MPB biomass along the 10-day experiment were
544 underestimated with chemical diffusion alone. Integration of nutrient availability, hypothesized
545 to be enhanced by faunal activity, greatly ameliorated the quality of the simulations. The best
546 simulation was obtained with a biodiffusion 10 fold higher than the chemical diffusion. Faunal
547 induced diffusion of nutrients by the benthic fauna was important in our simulations especially
548 when the nutrient concentration at the surface was low. The sensitivity analysis to biodiffusion
549 highlighted that the lower the nutrient concentrations, the more important the biodiffusion.
550 Faunal activities can indeed impact dissolved nutrient loads (Heilskov et al., 2006; Laverock et
551 al., 2011) in a system which enhances primary productivity (Cad e, 1993; Chennu et al., 2015).
552 As meiofauna (nematodes and foraminifera), was still observed in the experimental system
553 (Orvain et al., 2003), nutrient supply could have resulted from processes such as bio-irrigation,
554 nutrient release, and enhanced bacterial activity (Schratzberger and Ingels, 2018). Active
555 bioturbator may create burrows in the sediment that enhance irrigation of solutes such as
556 ammonium and nitrate (Aller and Aller, 1992; Christensen et al., 2000). Moreover, secretion of
557 nutrients by meiofauna (D'Hondt et al., 2018) could also take place as found with macrofauna
558 (Cad e, 1993; Gardner et al., 2006). Hence, integrating the bio-irrigation related to the
559 meiofauna activities, as conducted by Butensch n et al. (2016), should be performed to better
560 analyze the biogeochemical functioning of estuarine benthic systems.

561 The model developed herein is suited to reproduce development of MPB in controlled
562 conditions. The model could also be directly used to analyze benthic system functioning in
563 natural conditions only if all influencing compartments were taken into account. Indeed, MPB
564 consumption by macrofauna and nutrient availability due to faunal activity was required when
565 the model was used to analyze the functioning of Marennes-Oléron (France) mudflat and which
566 gave satisfactory dynamics of the MPB compared to measurements (unpublished data, Guizien
567 K., Personal communication). Moreover, *in situ* application of the model will require accurate
568 tidal and light cycles. Light attenuation in the water column should be taken into account for
569 low turbidity zone such as subtidal system, while hypothesizing development of MPB during
570 diurnal low tide could reflect natural condition of a system with high turbidity of the water
571 column, encountered in most of intertidal mudflats.

572 **5. Conclusion**

573 A model was developed in this study which simulates the functioning of a biogeochemical
574 benthic system constituted of MPB and associated EPS release, bacteria, and nutrients.
575 Simulations highlighted that MPB dynamics was highly limited by nutrient availability in the
576 surficial sediment. Observed three-phased MPB dynamics was only reproduced by integrating
577 an enhanced nutrient flux attributed to meiofauna activity. Moreover, this study figures among
578 the first attempts in integrating EPS production, MPB and bacterial development in a benthic
579 system model. The model also used a new approach by taking into account the carbon and
580 nitrogen requirements as major drivers in vertical migration of MPB. This was made possible
581 by decoupling carbon and nitrogen metabolisms. Formulation of MPB functioning in this study
582 will improve integration of MPB into biogeochemical models, such as in the study of Hochard
583 et al. (2010), to better analyze the functioning of benthic estuarine ecosystems.

584

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867

868 Contribution of all authors

869 1- C.R., F.O., K.G., S.L., and C.D. conceived and designed the study.

870 2- The initial biogeochemical model with MPB and the secretion of EPS was conceived
871 and designed by K.G., S.L., and F.O.

872 3- The coupling between EPS and bacteria was formulated by the 3 initial model
873 conceptors and C.D.

874 4- The model development and parameterization was performed by C.R., K.G., F.O., S.L.
875 and K.G.

876 5- All authors contributed to writing, reviewing and editing of the paper

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878 Competing interest: The authors declare that they have no conflict of interest.

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Appendix

893 Table 1: Dependents: each pool is an average over the 1 cm of sediment

<i>Dependent name</i>	<i>Dependent meaning</i>	<i>Unit</i>
State variables		
<i>[Dact : C]</i>	Energetic carbon pool in active diatom i.e. at mud surface	mol C m ⁻³
<i>[Dact : N]</i>	Nitrogen pool in active diatoms i.e. at mud surface	mol N m ⁻³
<i>[D : C]</i>	Energetic carbon pool in inactive diatoms i.e. below the mud surface	mol C m ⁻³
<i>[D : N]</i>	Nitrogen pool in inactive diatoms i.e. below the mud surface	mol N m ⁻³
<i>[PON]</i>	Particulate organic nitrogen pool	mol N m ⁻³
<i>[DOC]</i>	Dissolved organic carbon pool	mol C m ⁻³
<i>[DON]</i>	Dissolved organic nitrogen pool	mol N m ⁻³
<i>[DIN]</i>	Dissolved inorganic nitrogen pool	mol N m ⁻³
<i>[Bact : N]</i>	Nitrogen pool in bacteria	mol N m ⁻³
Forcing variables		
<i>E_{PAR}</i>	Light intensity	W m ⁻²
<i>T</i>	Mud surface temperature	°C
<i>h</i>	Tide detection [0,1]	-
<i>DIN_{sed}</i>	Dissolved inorganic nitrogen pool over the 2nd cm depth	mol N m ⁻³

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903 Table 2: Model equations

$$\frac{d[Dact: C]}{dt} = \varphi(\infty, [Dact: C]) - \varphi([Dact: C], [D: C]) + \varphi([D: C], [Dact: C]) - \varphi([Dact: C], \infty)_E - \varphi([Dact: C], \infty)_R - \varphi(\infty, [DOC]) \quad (1)$$

$$\frac{d[Dact: N]}{dt} = \varphi([DIN], [Dact: N]) - \varphi([Dact: N], [D: N]) + \varphi([D: N], [Dact: N]) - \varphi([Dact: N], [DON]) \quad (2)$$

$$\frac{d[D: C]}{dt} = \varphi([Dact: C], [D: C]) - \varphi([D: C], [Dact: C]) - \varphi([D: C], \infty)_E - \varphi([D: C], \infty)_R - \varphi([D: C], \infty)_M \quad (3)$$

$$\frac{d[D: N]}{dt} = \varphi([DIN], [D: N]) + \varphi([Dact: N], [D: N]) - \varphi([D: N], [Dact: N]) - \varphi([D: N], [DON]) - \varphi([D: N], [PON]) \quad (4)$$

$$\frac{d[PON]}{dt} = \varphi([D: N], [PON]) - \varphi([PON], [DON]) \quad (5)$$

$$\frac{d[DOC]}{dt} = \varphi(\infty, [DOC]) - \varphi([DOC], \infty)_S \quad (6)$$

$$\frac{d[DON]}{dt} = \varphi([Dact: N], [DON]) + \varphi([D: N], [DON]) - \varphi([DON], [Bact: N]) + \varphi([Bact: N], [DON]) + \varphi([PON], [DON]) - \varphi([DON], [DIN]) \quad (7)$$

$$\frac{d[DIN]}{dt} = +\varphi([DON], [DIN]) + \varphi(\infty, [DIN]) - \varphi([DIN], [D: N]) - \varphi([DIN], [Dact: N]) \quad (8)$$

$$\frac{d[Bact: N]}{dt} = \varphi([DON], [Bact: N]) - \varphi([Bact: N], [DON]) \quad (9)$$

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905 $\varphi([X], [Y])$ represents the flux transfer from compartment [X] to compartments [Y]

906 $\varphi([X], \infty)$ represents the flux lost from compartment [X]

907 $\varphi(\infty, [X])$ represents the flux input to compartment [X]

908 Table 3: Specific functions for light and temperature limitation used in the model equations

$L_L = \tanh\left(\frac{E_{PAR}}{K_{PAR}}\right)$	Light limitation
$L_T = \left(\frac{T_{max} - T}{T_{max} - T_{opt}}\right)^\beta e^{\left[-\beta\left(\frac{T_{max}-T}{T_{max}-T_{opt}}-1\right)\right]}$	Temperature limitation (Blanchard et al., 1996)

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933 Table 4: Model fluxes formulations

photosynthesis	$\varphi(\infty, [Dact: C]) = P_{max} \frac{[Dact: N]}{[Dact: N] + K_1} L_L L_T$	Inorganic carbon assimilation fueling epipelagic diatoms energetic carbon pool as a result of photosynthesis
exu_photo	$\varphi(\infty, [DOC]) = \gamma_p \varphi(\infty, [Dact: C])$	Sugar exudation overflowing during photosynthesis
migdw	$\varphi([Dact: C], [D: C]) = (1 - \alpha_1) \frac{\nu}{2} \left[1 + \tanh \left(\frac{\frac{[Dact:C]}{[Dact:N]} - qC2N}{\delta_{CN}} \right) \right] [Dact: C]$	Diatoms downward migration when diatoms internal quota of carbon to nitrogen $\frac{[Dact:C]}{[Dact:N]}$ exceeds a threshold value qC2N
	$\varphi([Dact: N], [D: N]) = (1 - \alpha_1) \frac{\nu}{2} \left[1 + \tanh \left(\frac{\frac{[Dact:C]}{[Dact:N]} - qC2N}{\delta_{CN}} \right) \right] [Dact: N]$	
exu_migl	$\varphi([Dact: C], \infty)_E = \frac{\alpha_1}{1 - \alpha_1} \varphi([Dact: C], [D: C])$	Exudation of glyco-proteins during downward migration
	$\varphi([Dact: N], [DON]) = \frac{\alpha_1}{1 - \alpha_1} \varphi([Dact: N], [D: N])$	
uptN	$\varphi([DIN], [D: N]) = \frac{\alpha_2}{2} \frac{[DIN]}{[DIN] + K_N} \frac{[D: C]}{[D: C] + K_C} L_T$	Inorganic nitrogen assimilation by inactive diatoms when below mud surface
	$\varphi([DIN], [Dact: N]) = \frac{\alpha_2}{2} \frac{[DIN]}{[DIN] + K_N} \frac{[Dact: C]}{[Dact: C] + K_C} L_T$	Inorganic nitrogen assimilation by active diatoms at the surface
respiration	$\varphi([Dact: C], \infty)_R = \gamma \varphi([DIN], [Dact: N])$	Active and inactive diatoms respiration
	$\varphi([D: C], \infty)_R = \gamma \varphi([DIN], [D: N])$	
migup	If $h=0$ and $E_{PAR}>0$	

	$\varphi([D:C], [Dact:C]) = (1 - \alpha_1) \frac{\nu}{2} \left[1 + \tanh \left(\frac{\left[\frac{[D:N]}{[D:C]} \right] - qN2C}{\delta_{CN}} \right) \right] [D:C]$ <p>Otherwise</p> $\varphi([D:C], [Dact:C]) = 0$	Diatoms upward migration when internal quota of nitrogen to carbon $\left[\frac{D:N}{D:C} \right]$ exceeds a threshold value $qN2C$ and the tide is low during the day
	<p>If $h=0$ and $E_{PAR} > 0$</p> $\varphi(D:N, Dact:N) = (1 - \alpha_1) \frac{\nu}{2} \left[1 + \tanh \left(\frac{\left[\frac{[D:N]}{[D:C]} \right] - qN2C}{\delta_{CN}} \right) \right] [D:N]$ <p>Otherwise</p> $\varphi(D:N, Dact:N) = 0$	
exu_mig2	$\varphi([D:C], \infty)_E = \left(\frac{\alpha_1}{1 - \alpha_1} \right) \varphi([D:C], [Dact:C])$	Exudation of glyco-proteins during upward migration
	$\varphi([D:N], [DON]) = \left(\frac{\alpha_1}{1 - \alpha_1} \right) \varphi([D:N], [Dact:N])$	
mnat1	$\varphi([D:N], [PON]) = \mu_m [D:N]$	Loss of nitrogen pool in inactive diatoms due to natural mortality
mnat2	$\varphi([D:C], \infty) = \mu_m [D:C]$	Loss of carbon pool in inactive diatoms due to natural mortality
diffusion	$\varphi([DIN_{SED}], [DIN]) = D_0 \frac{\varphi_d [DIN_{SED}] - [DIN]}{\theta^2 \cdot 0.01^2}$	Chemical diffusion of nutrients from the second cm depth layer
uptB	$\varphi([DON], [Bact:N]) = \alpha_3 \frac{[DON]}{[DON] + K_b} L_T e^{(-\beta_1 [DOC])}$	DON assimilation by bacteria
rem1	$\varphi([PON], [DON]) = \alpha_{rem} [PON] e^{[\beta_2 (T - T_{opt}^B)]}$	Bacterial enzymatic activities transforming PON

		into DON
rem2	$\varphi([DON], [DIN]) = \alpha_{rem}[DON]e^{[\beta_2(T-T_{opt}^B)]}$	Bacterial enzymatic activities transforming DON into DIN
lysis	$\varphi([Bact:N], [DON]) = \alpha_4[Bact:N]$	Bacteria mortality due to viral lysis
sink	$\varphi([DOC], \infty)_S = \mu[DOC]$	Loss of DOC exported to water column at high tide through hydrolysis and diffusion

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945 Table 5: Parameters used in the model

Parameter name	Parameter meaning	Unit	Value	References
K_{PAR}	Light saturation constant	W m^{-2}	100	Guarini et al., 2000
T_{max}	Diatom lethal temperature	$^{\circ}\text{C}$	38	Blanchard et al. (1996)
T_{opt}	Diatom optimal growth temperature	$^{\circ}\text{C}$	20	Inspired from Blanchard et al. (1996)
β	Exponential curvature	No unit	0.1	Inspired from Blanchard et al. (1996)
P_{max}	Maximum photosynthetic rate	$\text{mol C m}^{-3} \text{ s}^{-1}$	$120.3 \cdot 10^{-5}$	Guarini et al., 2000
K_1	Photosynthesis half-saturation value of internal pool of nitrogen in active diatoms	mol N m^{-3}	1	Assumed
γ_{P}	Proportion of photosynthesized carbon overflow as carbohydrate EPS	No unit	0.38	Inspired from Smith and Underwood, 1998
α_1	Proportion of exudation required for vertical migration	No unit	0.05	Inspired from Smith and Underwood, 1998
v	Maximal migration rate	s^{-1}	0.5	Assumed
q_{C2N}	Maximal value for internal C/N quota in active diatoms	No unit	3.5	Assumed
δ_{CN}	Slope of the sensitivity curve for downward and upward migration	No unit	0.1	Assumed
α_2	Maximum diatom DIN uptake rate	$\text{mol N m}^{-3} \text{ s}^{-1}$	$2 \cdot 10^{-5}$	Assumed
K_{N}	Diatom DIN uptake half-saturation value for DIN in inactive diatoms	mol N m^{-3}	0.5	Assumed

K_C	Diatom DIN uptake half-saturation value for energetic carbon pool in inactive diatoms	mol C m^{-3}	10	Assumed
γ	Stoichiometric proportion of diatoms energetic carbon pool consumed through respiration to uptake DIN	No unit	4	Assumed
q_{N2C}	Minimum value for internal C/N quota in inactive diatoms	No unit	0.7	Assumed
μ_m	Diatoms natural mortality rate	s^{-1}	$3 \cdot 10^{-9}$	Assumed
α_3	Maximum DON uptake rate for bacteria	$\text{mol N m}^{-3} \text{ s}^{-1}$	$4.8 \cdot 10^{-5}$	Synthesis based on Degré et al., 2006, Leguerrier et al., 2003, 2004, and Pascal et al. 2009
K_B	Bacteria DON uptake half-saturation value for DON	mol N m^{-3}	0.2	Assumed
β_1	Bacteria DON uptake inhibition factor due to carbohydrate EPS overflow during photosynthesis	No unit	0.1	Assumed
α_{rem}	DIN remineralization rate through bacterial enzymatic activity	s^{-1}	$4.63 \cdot 10^{-7}$	Assumed
β_2	Temperature sensitivity parameter of bacterial enzymatic activity	No unit	0.0405	Ory, 2010 and Ory et al. (2011)
T_{opt}^B	Optimal temperature of bacterial enzymatic activity	$^{\circ}\text{C}$	30	Ory, 2010 and Ory et al. (2011)
α_4	Bacterial mortality rate	s^{-1}	$3 \cdot 10^{-5}$	Ory, 2010 and Ory et al. (2011)
μ	DOC resuspension rate	s^{-1}	$8 \cdot 10^{-4}$	Assumed
D_0	Diffusivity coefficient	$\text{m}^{-2} \text{ s}^{-1}$	$1.4 \cdot 10^{-9}$	Lavery et al., 2001
φ_d	Sediment porosity	No unit	0.89	Measured
θ^2	Tortuosity of the sediment	No unit	1.11	Chatelain, 2010
C:chl <i>a</i>	Carbon and chl <i>a</i> ratio	$\text{mgC mg chl } a$	45	Guarini et al., 2000
Glucose:C	Glucose and carbon ratio	g Glucose gC^{-1}	15	Calculated

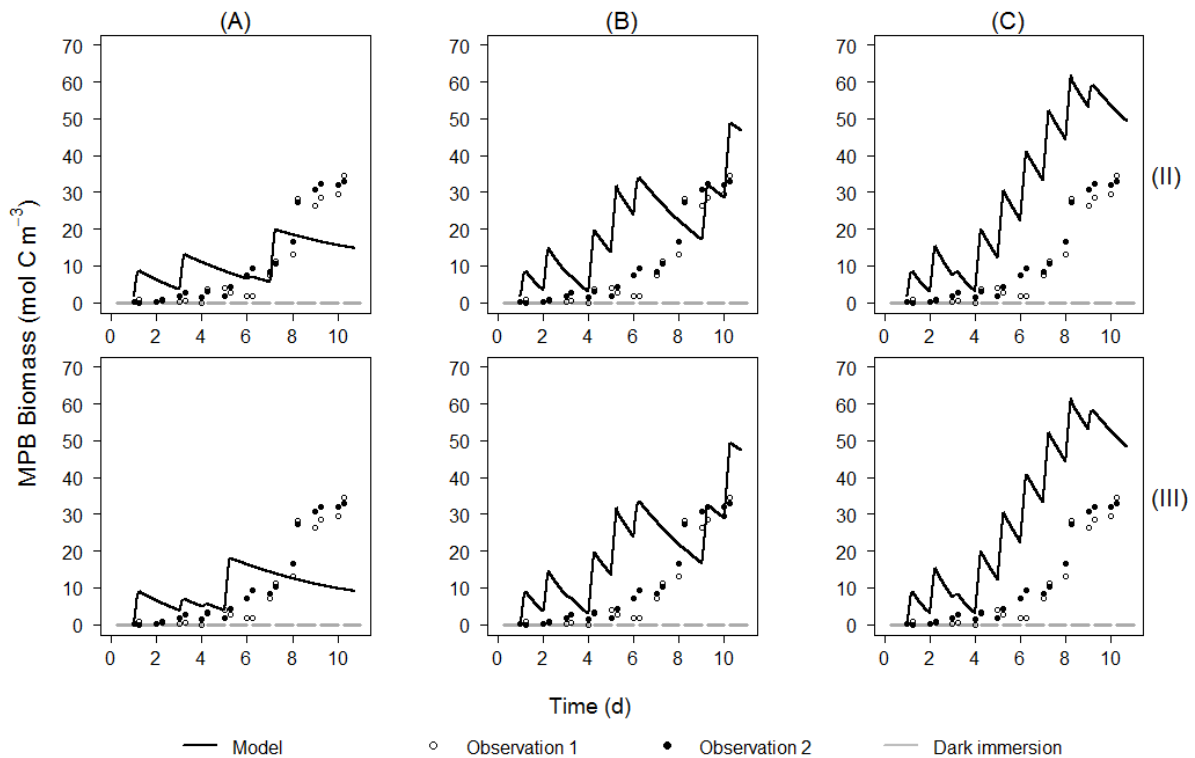
947 ***Bibliography of the appendix***

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Supplementary Material SM1

977 Fig. 1: Simulated MPB concentration (lines) in the first centimeter of sediment under three
978 different types of diffusion: chemical diffusion (A), bio-diffusion 5 times (B) and 10 times (C)
979 greater than the chemical diffusion and under two other MPB initial state: (D:C/D:N)init. = 1
980 (II) and (D:C/D:N)init. = 0.05 (III). Points correspond to MPB biomass from the study of Orvain
981 et al. (2003). Gray line represents dark immersion periods in the system



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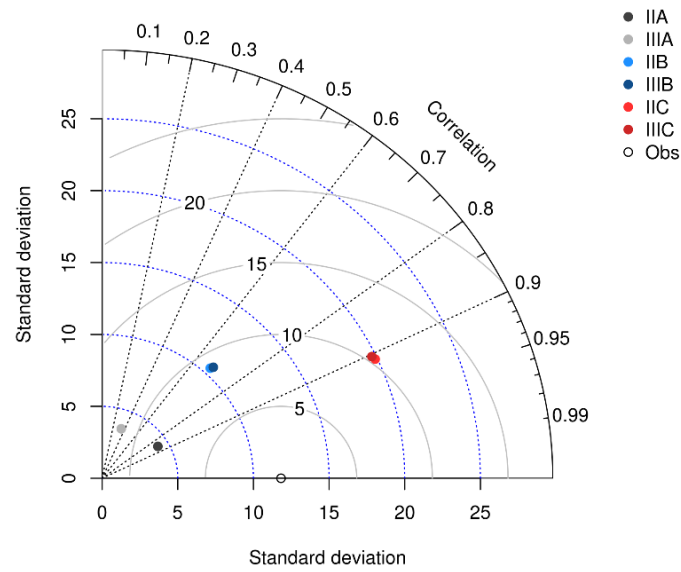
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990 Fig. 2: Taylor diagram showing the difference between observed and simulated MPB under
991 different diffusion and different initial state.

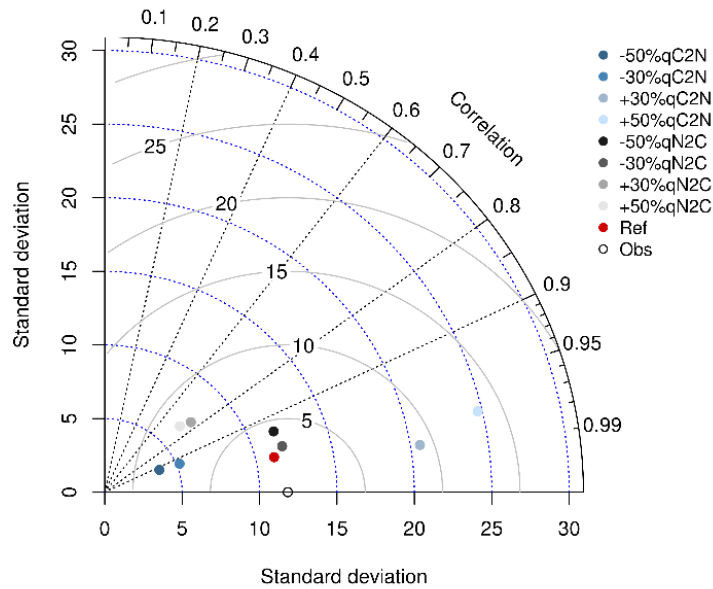


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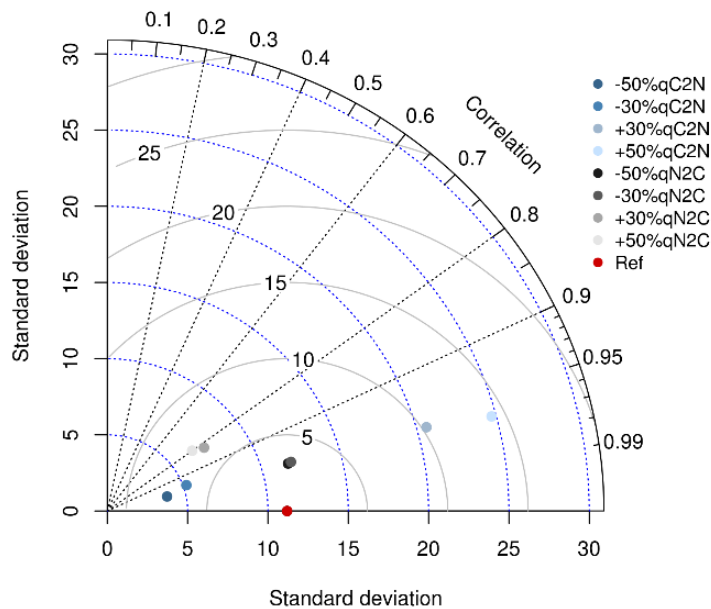
Supplementary Material SM2

1011 Fig. 1: Taylor diagram showing the difference between the observed and simulated MPB
1012 when different values of $qC2N$ and $qN2C$ were tested.



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1014 Fig. 2: Taylor diagram showing the difference between the simulated MPB of reference and
1015 simulated MPB when different values of $qC2N$ and $qN2C$ were tested.



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