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1 **Linking behaviours, sediment reworking, bioirrigation and**
2 **oxygen dynamics in a soft-bottom ecosystem engineer: the mud**
3 **shrimp *Upogebia pusilla* (Petagna 1792)**

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15

16 **Highlights:**

17 Behaviours control bioturbation processes

18 Sediment reworking is induced by “Burrowing”

19 About 60 % of the volume of reworked sediment occurs around burrow walls

20 Bioirrigation and oxygen dynamics are induced by “Ventilating”

21 “Ventilating” is induced by a 12-25% O₂ saturation and indirectly cued by “Burrowing”

22 **Abstract**

23 Despite the role of bioturbation in controlling biogeochemical processes taking place
24 at the sediment-water interface, little is still known about how animal behaviours influence
25 sedimentary biogeochemical processes. In the present work, we used the mud shrimp
26 *Upogebia pusilla* as model organism to assess the effect of behaviour types/intensities on
27 sediment reworking, bioirrigation and sediment oxygen dynamics based on three sets of
28 seasonal experiments. We identified four main behaviours: “Resting”, “Walking”,
29 “Ventilating” and “Burrowing”. Mud shrimp were much more active (*i.e.*, not “Resting”)
30 during summer than during winter and to a lesser extent spring due to elevated temperature.
31 There were three distinct components of sediment reworking. The first one consisted in the
32 expulsion of sediment particles from the burrow to the sediment-water interface, the second
33 one to the transfer of sediment downward within the burrow and the third one to the transport
34 and compaction of sediment across burrow walls. Temporal changes in the intensities of all
35 components correlated tightly since they all resulted from “Burrowing”. The temporal
36 dynamics of porewater exchange and oxygen dynamics were clearly discontinuous and in
37 direct relation with “Ventilating”. However, other behaviours, and especially “Burrowing”
38 were also involved in the control of this dynamics through the modulation of oxygen
39 availability within the burrow, which is cuing the onset of ventilation at a 12-25 % saturation
40 threshold. These results underline the importance of taking into account changes in animal
41 behaviour types/intensities at the appropriate temporal scales when assessing the impact of
42 bioturbation on biogeochemical processes taking place at the sediment-water interface.

43 **Keywords:**

44 Behavior, Seasonal changes, Bioturbation, Sediment reworking, Bioirrigation, Oxygen
45 dynamic

46 **1. Introduction**

47 In marine soft-sediment, organic matter mineralization is controlled by the balance
48 between redox reactions, organic matter sedimentation and transport (*i.e.*,
49 advection/diffusion) processes (Aller, 2014). In the absence of macrofauna, this leads to a
50 vertically stratified dominance of specific organic matter mineralization pathways (typically
51 following the sequence of O₂, NO₃⁻, Mn- and Fe-oxides, SO₄²⁻ and CO₂, Froelich et al., 1979)
52 controlled by diffusive transport. A large majority of the uppermost layer of marine
53 sediments is however inhabited by burrow dwelling infauna which profoundly disrupt this
54 balance through bioturbation (*sensu* Kristensen et al., 2012). Bioturbation encompasses two
55 distinct processes, namely sediment reworking (*i.e.*, the movements of sediment particles and
56 associated organic matter) and burrow ventilation, which causes bioirrigation (*i.e.*, the
57 exchange of water and solute between the overlying water column and porewater). The effect
58 of sediment reworking on organic matter mineralization is highly dependent on sediment
59 reworking types. Downward conveyor-belt feeders can for example quickly transfer
60 particulate organic matter deep in the sediment column where mineralization is less efficient.
61 Conversely, upward conveyor-belt feeders counteract the burying of particulate organic
62 matter by repeatedly bringing it back to the sediment-water interface. Through bioirrigation,
63 bioturbating infauna increases the transport of the most energetically favorable electron
64 acceptor (*i.e.*, oxygen) in deep and otherwise anoxic sediment layers enhancing aerobic
65 mineralization of organic matter. Additionally, oxygen oxidizes reduced inorganic
66 metabolites produced during anaerobic processes lowering their porewater concentration and
67 generating a reservoir of potential oxidants, both improving conditions for the anaerobic
68 mineralization of organic matter as well (Volkenborn et al., 2016).

69 A lot of *in-* and *ex-situ* experiments have been conducted to assess the functional
70 consequences of bioturbation (Fanjul et al., 2015; Mermillod-Blondin et al., 2004;

71 Papaspyrou et al., 2007; Pascal et al., 2016b). Overall, their results suggest that bioturbation
72 increases the sediment capacity for organic matter mineralization and thus enhances carbon
73 and nutrient cycling (Aller, 1994; Kristensen et al., 2012; Lohrer et al., 2004; Mermillod-
74 Blondin and Rosenberg, 2006; Meysman et al., 2006). For most of them these studies are
75 based on: (1) the comparison between bioturbated and unbioturbated sediment, and (2)
76 relatively short term (typically several days or weeks) experiments. They thus establish an
77 operational link between the presence of bioturbating species and their functional
78 consequences but fail to provide relevant information on the processes at play and on the
79 spatial and temporal scales at which they operate.

80 The elementary processes constitutive of bioturbation usually take place at small (*i.e.*,
81 typically less than a few cm and s) spatial and temporal scales. From a spatial standpoint,
82 bioturbation generates microenvironments where the nature and the intensity of
83 biogeochemical processes are modified (Kristensen et al., 2012; Meysman et al., 2006). From
84 a temporal standpoint, it induces short-term oscillations in redox conditions affecting the
85 microbial communities responsible for organic matter mineralization (Aller, 2014). Such
86 oscillations result from the fact that bioturbation is caused by intermittent activities associated
87 with different behaviours of benthic macrofauna. This qualitative link has been
88 acknowledged for a long time (*e.g.*, Kristensen et al., 2012; Meysman et al., 2008). However,
89 direct quantitative assessments have been achieved only recently due to technological
90 difficulties in “penetrating” the sediment column. Corresponding studies have mostly dealt
91 with bioirrogation in relation with several technological developments such as image analysis
92 (Grémare et al., 2004; Hollertz and Duchêne, 2001; Jordana et al., 2000), pressure captors
93 (Wethey et al., 2008; Wethey and Woodin, 2005; Woodin et al., 2016) and planar optodes
94 (Jovanovic et al., 2014; Przeslawski et al., 2009; Timmermann et al., 2006) allowing for the
95 simultaneous high-frequency recording of behaviours, hydraulic activities and associated

96 consequences in terms of oxygenation (Volkenborn et al., 2012a, 2012b). Studies are clearly
97 less advanced regarding sediment reworking. To our knowledge, the only available study
98 quantitatively linking sediment reworking and feeding activity in benthic macrofauna is the
99 one by Maire et al. (2007) carried out on the deposit-feeding bivalve *Abra ovata*. This
100 particular species induces sediment reworking within only the top few centimeters of the
101 sediment column and mostly through a biodiffusive mode resulting from its feeding activity
102 (Bernard et al., 2016; Maire et al., 2007). There is thus still a clear need to carry out similar
103 studies on different kinds of species transporting sediments over larger spatial scales (*e.g.*
104 through non-local transport) and presenting a larger variety of behaviours potentially
105 generating bioturbation. The overall aim of the present study was therefore to establish a
106 qualitative and quantitative link between the behaviour, bioturbation processes and sediment
107 biogeochemical processes in a large bioturbating species.

108 We selected a mud shrimp as model organism. Mud shrimp are considered among the
109 most influential ecosystem engineers in marine soft-bottom ecosystems (Atkinson and
110 Taylor, 2005; Cadée, 2001; Pillay and Branch, 2011). They dig large and complex burrows
111 which extend deep (*i.e.*, down to 2 m) within the sediment column and connect to the
112 overlying water by several distant openings (Coelho et al., 2000; Kinoshita, 2002; Nickell
113 and Atkinson, 1995). The maintenance and ventilation of their burrows result in strong
114 sediment reworking and bioirrigation that profoundly affect the physical (*e.g.*, granulometry,
115 porosity and permeability), chemical (*e.g.*, organic carbon content, oxygen concentration) and
116 biological (*e.g.*, structure and diversity of both prokaryotic and eukaryotic communities)
117 properties of the sediment (Aller and Dodge, 1974; Berkenbusch et al., 2000; Bird et al.,
118 2000; Laverock et al., 2011; Pillay et al., 2007). By doing so, mud shrimp deeply affect the
119 biogeochemical functioning of benthic ecosystems (D'Andrea and DeWitt, 2009; Pascal et
120 al., 2016b; Pillay et al., 2007; Ziebis et al., 1996). Numerous studies have already been

121 dedicated to the autecology of mud shrimp including the assessments of their behaviours and
122 time allocation patterns between behaviours (*e.g.*, “Wander”, “Ventilate”, “Burrow”, “Rest”;
123 Stamhuis et al., 1996), sediment reworking, and bioirrigation rates (Berkenbusch and
124 Rowden, 1999; Branch and Pringle, 1987; Dworschak, 1981; Dworschak et al., 2006; Pascal
125 et al., 2016b; Rowden et al., 1998; Stamhuis et al., 1997), and effects on spatio-temporal
126 changes in the oxygenation of their burrows and surrounding sediments (Forster and Graf,
127 1995; Volkenborn et al., 2012b). These studies have however been mainly carried out on
128 deposit-feeding mud shrimp even though one cannot exclude that feeding types may have a
129 significant effect on how time is allocated between behaviours (Stamhuis et al., 1996).
130 Moreover, they have mostly focused on the direct relationship between burrow ventilation
131 and bioirrigation and largely ignored the assessment of the relationship between behaviour
132 types and sediment reworking. In addition, the assessments of sediment reworking rates have
133 been mostly restricted to the quantification of the expulsion of sediment at the sediment-
134 water interface and have largely neglected the component of sediment reworking taking place
135 below sediment surface, around burrow walls. To our knowledge, these studies (but see
136 Pascal et al., 2016b) have also largely ignored seasonal changes in time allocation patterns,
137 and bioirrigation rates.

138 The present study aimed at filling these gaps by focusing on a suspension-feeding
139 mud shrimp and investigating how behaviour (types and time allocation) affects (1) sediment
140 reworking, (2) bioirrigation and (3) oxygen dynamics within its burrow. This first required to
141 achieve comprehensive descriptions of the behaviours, between-behaviour time allocation
142 pattern and sediment reworking of our biological model: *Upogebia pusilla* (Petagna 1792).
143 This suspension-feeding mud shrimp occurs all along the East Atlantic coast from Norway to
144 Mauritania (De Saint Laurent and Le Boeuf, 1979; Hayward and Ryland, 1990) and in the
145 Mediterranean Sea (Dworschak, 1987a). It presents dense populations in the Arcachon Bay

146 (i.e., our study site; Pascal et al., 2016a) where it significantly affects benthic biogeochemical
147 processes (Pascal et al., 2016b).

148 **2. Material and methods**

149 *2.1. Collection and maintenance of animals and sediment*

150 Three sets of controlled laboratory experiments were carried out in winter (January),
151 spring (April) and summer (August) 2014. During each season, 30 adult specimens of the
152 mud shrimp *Upogebia pusilla* were collected at low tide in an intertidal *Zostera noltei*
153 meadow (44° 40.782' N, 1° 08.321' W) of the Arcachon Bay (Southwest coast of France)
154 using a bait piston pump. Mud shrimp were immediately isolated in individual containers.
155 Back at the laboratory, they were measured (Total Length from the tip of the rostrum to the
156 tip of the telson, ± 1 mm) and weighted (Blotted Wet Weight, ± 0.1 mg). Twenty undamaged
157 mud shrimp (4.6 ± 0.4 cm in TL and 1.9 ± 0.3 g in BW) were selected. They were then
158 individually introduced in (1) 10 thin aquaria (25 (L) \times 1.9 (W) \times 50 (H) cm) for the
159 assessments of burrow characteristics, behaviour, sediment reworking and oxygen dynamics,
160 and (2) 10 sediment cores (9.4 cm inner diameter, 40 cm long) for the assessment of
161 bioirrigation. Ten other cores were kept without mud shrimp and used as controls. Thin
162 aquaria and sediment cores were previously filled with a 30 cm layer of sieved (500 μ m
163 mesh) muddy sand sediment collected at the sampling site at each season (consistently D_{50} :
164 159 μ m, organic carbon: 0.35 % DW). Mud shrimp were not fed during experiments.
165 Experiments started 48 h after mud shrimp introduction, which allowed for the construction
166 of a whole (i.e., open-ended) burrow during all seasons. All aquaria and sediment cores were
167 kept in a dark thermo-regulated room (at 12, 16 and 22 °C in January, April and August,
168 respectively, corresponding to the measured seawater temperature during field sampling)
169 during the whole experiment durations (a month). All the aquaria and sediment cores were

170 fuelled with a continuous natural seawater flow ($\sim 0.25 \text{ L min}^{-1}$, same temperature as above)
171 to ensure a good oxygenation of experimental enclosures.

172 The use of thin aquaria clearly constitute a compromise between the necessity of
173 getting a visual access to the lumen of the burrows in view of assessing mud shrimp
174 behaviour, and possible artefacts due to space limitation. There are nevertheless several
175 rationale suggesting that these artefacts remain limited in the case of the present study: (1)
176 care was taken to use small mud shrimp that are likely less affected by space limitation, (2) at
177 the beginning of the experiment (i.e., 48h after mud shrimp addition) burrows shapes and
178 characteristics were fully consistent with those previously reported for *U. pusilla*
179 (Dworschak, 1983), (3) those characteristics were similar to those assessed through resin
180 casting for individual burrows from the sampled field population (see Table 1 and
181 supplementary material Table S3), and (4) at the end of the winter and to a lesser extent
182 spring experiments significant portions of the burrow lumens remained hidden thereby
183 suggesting that aquarium width probably does not constitute a limiting factor.

184 ***2.2.Sediment reworking and burrow characteristics***

185 Sediment reworking was first quantified during a 30 days period using luminophores
186 (i.e., inert particle tracers fluorescing under UV light). Previous tests have shown that
187 luminophores stay strictly at the sediment surface in the absence of mud shrimp. Sediment
188 reworking by meiofauna or other small organisms was thus negligible. Fifteen gDW of
189 luminophores (100 - 160 μm size range) were homogeneously spread at the sediment surface
190 of each thin aquarium. Both sides of each aquarium were then photographed with a digital
191 camera (D100, Nikon ®, 3008×2000 pixels) under UV light ($\lambda = 380 \text{ nm}$) immediately
192 following luminophore input (D0) and after 3, 6, 12, 24, 48, 72, 96, 120, 144, 168, 192, 216,
193 240, 288, 336, 408, 480 and 720 h. Two vertically adjacent pictures ($27 \times 18 \text{ cm}$ each) were

194 taken for each side of the aquarium and assembled afterwards as a single image (27×35 cm
 195 in size, $92 \mu\text{m}^2 \text{ pixel}^{-1}$ in resolution). Composite images were saved in JPEG format and
 196 analysed as described in Maire et al. (2006), allowing for the assessment of 1D luminophore
 197 vertical concentration profiles. Vertical biodiffusion (D_{bv}) and bioadvection (V_{bv}) coefficients
 198 were then estimated by fitting a biodiffusion-bioadvection transport model to these vertical
 199 profiles (Gérino et al., 1998; Meysman et al., 2003):

$$\frac{\partial^2 C}{\partial t} = D_{bv} \frac{\partial^2 C}{\partial z^2} - v_{bv} \frac{\partial C}{\partial z} \quad (1)$$

200 where C is the luminophore concentration (%), t is the time (year) and z is the vertical depth
 201 in the sediment column (cm). D_{bv} and V_{bv} were estimated by convergent iterations and
 202 weighted least-squared regressions of model prediction on observed luminophore profiles
 203 (see Maire et al., 2006 for further details).

204 The volume of sediment expelled at the sediment-water interface (V_{ES} , cm^3) was
 205 estimated by measuring the average height of sediment over the original sediment-water
 206 interface (\bar{H} , Fig. 1) and using the following equation:

$$V_{ES} = \bar{H} \times L \times W \quad (2)$$

208 where L and W are the length of and the width of the aquarium, respectively.

209 The average thickness of the reworked layer surrounding burrows (T_{RS} , cm) was
 210 estimated by measuring the distance between the burrow wall and the most distant
 211 luminophore in five different sections randomly distributed within the burrow (Fig. 1). The
 212 average volume of reworked sediment surrounding the burrow within the aquarium (B_{RS} ,
 213 cm^3) was then computed using the following equation:

$$B_{RS} = \frac{[L_b \times \pi(r_b + T_{RS})^2] - [L_b \times \pi r_b^2]}{2} \quad (3)$$

214 where L_b is the total burrow length (cm), r_b is the mean burrow radius (cm) and T_{RS} is the
 215 mean thickness of the reworked sediment layer surrounding the burrow (cm).

216 The diffusion coefficient accounting for the component of sediment reworking
 217 occurring perpendicularly to burrow wall (D_{bw}) was modelled after 4 days of incubation (*i.e.*,
 218 when T_{RS} reaches its maximum value; see discussion for more details) by using a simple
 219 biodiffusive model (Cochran, 1985) to fit the profile of luminophore concentration
 220 perpendicular to burrow wall:

$$221 \quad \frac{\partial^2 C}{\partial t} = D_{bw} \frac{\partial^2 C}{\partial x^2} \quad (4)$$

222 Where C is the luminophore concentration (%), t is the time (year) and x is the orthogonal
 223 distance from the burrow wall (cm). This was achieved on three aquaria per season. Selected
 224 aquaria were those with the longest proportion of visible burrow wall and thus those allowing
 225 for the best assessments of decrease in luminophore concentration with increasing orthogonal
 226 distances from burrow wall.

227 Burrow lengths and maximal depths within the sediment column as well as the
 228 numbers of openings and chambers (*i.e.*, dilatations of the burrow tube that serve mainly as
 229 turning chambers) (Fig. 1) were also measured on thin aquaria pictures at D0, and after 4
 230 (D4) and 30 days (D30) of experiments using ImageJ software.

231 **2.3.Behaviour**

232 Mud shrimp behaviours were recorded within thin aquaria for a 3-day time period starting
 233 one day after luminophore input. Behaviours were recorded using an automated image
 234 acquisition system composed of a video sensor (μ Eye UI-1480SE, IDS Imaging®, 2560 ×
 235 1920 pixels) connected to a microcomputer and driven by the AviExplore software (Romero-
 236 Ramirez et al., 2016). This sensor was positioned in front of the aquarium side displaying the

237 longest visible part of the burrow lumen. Images were acquired in total darkness under
238 infrared light ($\lambda > 700$ nm) during 72 h with an acquisition frequency of 0.1 Hz. Collected
239 images with a surface resolution of $98 \mu\text{m}^2 \text{pixel}^{-1}$ were assembled in a time-lapse AVI video
240 file. Time-lapse sequences were then visually inspected, which allowed for the identification
241 of the main behaviours and the assessments of: (1) the proportion of time allocated to each
242 behaviour, (2) the average bout-duration of each behaviour, and (3) the average time between
243 two bouts of the same behaviour (interval-duration). Despite the small thickness width of our
244 aquaria, mud shrimp could sometimes remain hidden in parts of their burrow, which was
245 covered by a thin layer of sediment. In order not to bias the estimates of the relative
246 proportions of time devoted to the different behaviours (Stamhuis et al., 1996), only records
247 during which mud shrimp were visible more than 90 % of the time were considered for
248 analysis. Accordingly, the behaviours of only 4, 5 and 5 mud shrimps were investigated
249 during winter, spring and summer, respectively. Despite this relatively low replication,
250 interindividual variability in time allocation pattern within a same season was quite low (Fig.
251 2). Overall, this corresponded to 840 h of monitoring.

252 ***2.4. Oxygen dynamics***

253 The O_2 saturation within the burrow was recorded during a 72 h time-period starting
254 immediately after the end of the sediment reworking experiment. By the end of sediment
255 reworking experiments during winter and spring, mud shrimp were not visible enough to
256 allow accurate behavioural observations. Oxygen dynamics study was thus achieved only
257 during summer on the 5 thin aquaria within which mud shrimp were visible more than 90 %
258 of the time. O_2 saturations were measured at a frequency of 1 Hz, simultaneously with a
259 second sequence of behaviour monitoring as described above. A micro-optode (OXF1100,
260 Pyroscience) was positioned using a micromanipulator in the lumen of the “U” part of the

261 burrow (*i.e.*, ~10 cm deep in the sediment column; 2 mm from the burrow wall). A mini-
262 optode (OXROB10, Pyroscience) was placed in the overlying water ~10 cm above the
263 sediment surface to check for the full oxygenation of the water column. Both sensors were
264 connected to a Firesting oxygen meter (Pyroscience) driven by the Firesting logger software
265 (Ver. 2.364). A two-point linear calibration of both sensors was initially achieved between
266 the O₂ concentration of the overlying water measured by Winkler titration (Grasshoff et al.,
267 1999) and a zero O₂ concentration in a sodium ascorbate solution. After 72 h of continuous
268 recording, the micro-optode was carefully removed from the sediment and the aquarium was
269 hermetically sealed with a PVC lid. The mini-optode was then inserted into the lid and
270 repositioned in the overlying water ~10 cm above the sediment surface. The overlying water
271 was continuously stirred with a Teflon-coated magnetic disc at ~100 rpm during incubations.
272 Measurements were stopped as soon as the O₂ level in the overlying water fell below 70 % of
273 its initial value.

274 ***2.5.Porewater exchange***

275 Porewater exchange rates were assessed as a proxy of bioirrigation and were
276 quantified following Pascal et al. (2016b). A fluororimetric probe (Cyclops ©-7, Turner
277 Design, $\lambda_{\text{excitation}}=490\text{nm}$; $\lambda_{\text{measured}}=514\text{nm}$) was positioned in the overlying water of each
278 sediment core. Uranine (sodium fluorescein, C₂₀H₁₀Na₂O₅) was used as transport tracer to
279 quantify the volumetric exchange of water and dissolved solutes across the sediment–water
280 interface (Na et al., 2008). At the start of each experiment a solution of uranine was added in
281 the overlying water to reach an initial concentration of 10 $\mu\text{g L}^{-1}$. Constant aeration and
282 homogenization of the tracer in the overlying water were insured by air bubbling. The
283 decrease in uranine concentration was then continuously (1 Hz) measured during 36 h. The
284 porewater exchange rate (Q in mL h⁻¹) was estimated by fitting a simplified version of the

285 mathematical model developed by Meysman et al. (2007) to the moving average (*i.e.*, over 1
286 min) of the tracer concentration:

$$287 \quad C_{ow}(t) = \frac{A}{B} C_{ow}^0 + \left(1 - \frac{A}{B}\right) C_{ow}^0 e^{-Bt} \quad (5)$$

$$288 \quad A = \frac{Q}{V_{pw} + M_s K_{ad}}, B = \frac{Q}{V_{ow}} \left(1 + \frac{V_{ow}}{V_{pw} + M_s K_{ad}}\right) \quad (6)$$

289 where C_{ow} is the concentration of the dissolved tracer in overlying water ($\mu\text{g L}^{-1}$), V_{ow} and
290 V_{pw} the volumes (mL) of overlying and of porewaters, M_s the sediment wet weight (gWW)
291 and K_{ad} (mL gDW^{-1}) the mean adsorption rate of uranine onto sediment particles (see Pascal
292 et al., 2016b for further details). The first 30 min of the experiments were not considered for
293 the calculation of porewater exchange rate since the decrease during this time period was
294 mostly due to (1) the mixing of overlying and burrow water and (2) the rapid adsorption of
295 uranine onto sediment organic particles (Pascal et al., 2016b).

296 **2.6.Data analysis**

297 All data in the main text are expressed as average \pm standard error. For each
298 behaviour, the significance of between seasons differences in: (1) proportions of allocated
299 time, (2) bout-durations, and (3) interval-durations were assessed using One-Way
300 PERmutation Multivariate ANalyses Of VAriances (PERMANOVAs). Since all records
301 lasted exactly the same time, these analyses were performed on raw durations. The effect of
302 seasons on the component of sediment reworking occurring perpendicularly to the burrow
303 wall (as indicated by D_{bw}) was assessed using a One-Way PERMANOVA. The effects of
304 experiment durations and seasons on burrow characteristics and sediment reworking
305 parameters were assessed using Two-Way PERMANOVA. The design consisted in two fixed
306 factors (Experiment duration and Season) with a third random factor (Replicate) nested
307 within Season. In case of significant interaction between fixed factors, pairwise tests were

308 performed to characterise their modalities. The effect of seasons on porewater exchange rate
309 (Q) was assessed using a Two-Way PERMANOVA. The effects of the tested factors on the
310 dispersion (*i.e.*, among experiment variability) of each variable were checked using the
311 PERMDISP procedure (Anderson, 2006) (same design as described above). All
312 PERMANOVAs and associated tests were performed on untransformed data using Euclidean
313 distance and the PRIMER v6 package with the PERMANOVA+ add-on software (Anderson
314 et al., 2008; Clarke and Warwick, 2001).

315 The relationships between: (1) reworked sediment surrounding the burrow (B_{RS}) and
316 the volume of sediment expelled at the sediment-water interface (V_{ES}), (2) the durations of
317 the time period preceding each ventilation event and the magnitudes of the decrease in O_2
318 concentration in the overlying water column during ventilation (summer experiments), and
319 (3) the O_2 saturations in the burrow at the onset of ventilation and the distances of the mud
320 shrimp from the micro-optode (summer experiments) were tested using simple linear
321 regression models. The relationships between the (1) different types of activity, and (2) total
322 volume of reworked sediment was assessed using a (forward stepwise) multiple linear
323 regression model. All regression analyses were performed using the SIGMAPLOT, v12.5
324 software.

325 **3. Results**

326 ***3.1. Burrow characteristics***

327 Mud shrimp built a complete open-ended burrow within less than 24 hours during
328 winter and less than 12 hours during spring and summer. All initial U-shape burrows
329 progressively evolved into Y-shape burrows during spring and summer *versus* only 30 %
330 during winter. Mud shrimp burrows were on average between 34.5 ± 7.3 and 96.7 ± 27.5 cm

331 long with an average maximal depth between 14.0 ± 3.3 and 26.7 ± 8.9 cm within the
332 sediment column (Table 1). They had 2 to 3 openings and a rather constant diameter close to
333 1.5 cm with on average 2.2 ± 0.5 to 5.1 ± 1.2 chambers located 10 to 20 cm apart (Table 1).
334 Burrow depth and the number of openings significantly differed between experiment
335 durations but not between seasons (Table 2). Both parameters tended to increase with
336 experiment durations (Table 1). Burrow length and the number of chambers significantly
337 differed between seasons and experiment durations with a significant interaction between
338 these two factors (Table 2) due to a more pronounced increase in the values of these two
339 parameters with experiment durations during summer and a less marked one during winter
340 (Table 1).

341 **3.2.Behaviours**

342 Four main behaviours were identified, namely “Walking”, “Ventilating”,
343 “Burrowing” and “Resting” (Table 3). During “Walking”, mud shrimp alternatively walked
344 and turned in their burrow without transporting sediment. During “Ventilating”, mud shrimp
345 generated a unidirectional water flow by beating their four pairs of pleopods. “Ventilating”
346 behaviour was further divided into two subclasses, namely: (1) “Flushing” during which mud
347 shrimp quickly (*i.e.*, < 1 min on average) renewed the water of their burrow, usually
348 immediately following a period of intense burrowing; and (2) “Pumping” which consisted in
349 a regular beating movement of pleopods inducing a constant water flow through the burrow,
350 without sediment transport towards the sediment-water interface. These two behaviours could
351 easily be discriminated based on: (1) the pleopod beating frequency, and (2) the ejection of
352 unconsolidated sediment in the overlying water. “Burrowing” consisted in digging and
353 carrying sediment. During “Resting”, no visible movement was observed, although mud
354 shrimp periodically bended their abdomen under their cephalothorax.

355 For each behaviour, the proportions of allocated time significantly differed between
356 seasons (Fig. 2, One-Way PERMANOVA, $p < 0.001$ in all cases). Mud shrimp significantly
357 spent more time both “Ventilating” and “Burrowing” during summer than during winter (43.0
358 ± 2.5 vs. 14.1 ± 1.3 % and 36.7 ± 0.7 vs. 25.3 ± 2.7 %, respectively) whereas the time
359 allocated to “Resting” was reduced (18.7 ± 1.9 vs. 55.7 ± 2.3 %). Moreover, the way mud
360 shrimp seasonally changed their time allocation differed between behaviours. Changes in the
361 proportion of time allocated to “Ventilating” mainly resulted from changes in the mean
362 interval-duration between successive ventilation bouts, whereas the mean duration of each
363 ventilation bout did not significantly differ between seasons (Table 3). Conversely, changes
364 in the proportions of time allocated to “Burrowing” resulted from significant changes in both
365 bout- and interval-durations (Table 3). Changes in the proportion of time allocated to
366 “Resting” resulted from significant differences between bout-durations whereas interval-
367 durations did not significantly differ between seasons mostly due to a high variability during
368 spring (Table 3).

369 ***3.3.Sediment reworking***

370 The thickness of the reworked sediment layer surrounding the burrow (T_{RS}), the
371 volume of reworked sediment surrounding the burrow (B_{RS}) and the volume of sediment
372 expelled at the sediment-water interface (V_{ES}) all significantly differed between experiment
373 durations and seasons with significant interactions between these two factors (Table 2). T_{RS}
374 sharply increased during the first 4 days of the experiments (*i.e.*, until D4) and then remained
375 relatively constant until the end of the experiment (Fig. 3A). This initial increase was more
376 pronounced during summer than during spring and winter. B_{RS} also sharply increased until
377 D4 but did not stabilize afterward due to continuous increases in burrow lengths (Fig. 3B).
378 Here again the initial increase was more pronounced during summer than during spring and

379 winter. Conversely, V_{ES} tended to increase constantly with experiment durations but at a
 380 higher rate during summer versus an intermediate and a lower one during spring and winter,
 381 respectively (Fig. 3C). At D4, B_{RS} and V_{ES} correlated positively (simple linear regression, $F =$
 382 61.554 , $p < 0.001$; Fig. 3D). B_{RS} then represented 66.0, 56.4 and 56.6 % of total cumulative
 383 reworked sediment (*i.e.*, $B_{RS} + V_{ES}$) during winter, spring and summer, respectively. Overall,
 384 changes in the total volume of reworked sediment were best described by the amount of time
 385 allocated to “Burrowing” (multiple linear regression, $F = 75.372$, $p < 0.001$; supplementary
 386 material Fig. S1). Associated model was:

$$387 \quad y = 0.00617x - 2.433 \quad (5)$$

388 where y represents the total volume of reworked sediment and x the amount of time (min)
 389 allocated to “Burrowing”.

390 Vertical biodiffusion (D_{bv}) and bioadvection (V_{bv}) coefficients significantly differed
 391 between experiment durations and seasons (Table 2) without significant interactions between
 392 these two factors. Changes in D_{bv} with experiment durations showed similar patterns during
 393 all 3 seasons (Fig. 4A). D_{bv} increased during the first days of the experiment to reach
 394 maximal values (90.2 ± 44.0 , 347.7 ± 114.1 and $1181.7 \pm 189.8 \text{ cm}^2 \text{ y}^{-1}$, during winter, spring
 395 and summer, respectively) around D4. D_{bv} then consistently decreased until the end of the
 396 experiment. The lack of interaction between seasons and experimental durations in affecting
 397 V_{bv} likely resulted from the very high variability in V_{bv} during the very first days of the
 398 experiments. Indeed, the relationships between V_{bv} and experiment durations seemed to show
 399 different patterns between seasons (Fig. 4B). During summer, V_{bv} increased during the first
 400 days of the experiment to reach a maximal value of $234.7 \pm 111.8 \text{ cm y}^{-1}$ at D3. V_{bv} then
 401 decreased to $144.5 \pm 10.3 \text{ cm y}^{-1}$ at D17 before remaining almost constant until the end of the
 402 experiment. In spring, V_{bv} reached its maximal value ($101.2 \pm 10.1 \text{ cm y}^{-1}$) only at D17 and
 403 then slightly decreased until the end of the experiment. In winter, V_{bv} remained nil until D10.

404 It then steadily increased to reach its maximal value ($46.6 \pm 18.5 \text{ cm y}^{-1}$) at D30. Overall,
405 mean D_{bv} and V_{bv} were always higher in summer than in spring and in spring than in winter.

406 Biodiffusion coefficients associated with the component of sediment reworking
407 occurring around burrow wall (D_{bw}) significantly differed between seasons (One-Way
408 PERMANOVA, $F = 38.745$, $p = 0.004$). Average D_{bw} were higher during summer,
409 intermediate during spring and lower during winter (7.9 ± 1.4 , 3.6 ± 0.9 and $1.1 \pm 0.0 \text{ cm}^2 \text{ y}^{-1}$,
410 respectively).

411 ***3.4.Porewater exchange***

412 Porewater exchange rates (Q) significantly differed in the presence and the absence of
413 the mud shrimp and between seasons with a significant interaction between these two factors
414 (Two-way PERMANOVA, $p < 0.001$). Porewater exchange rates in the absence of the mud
415 shrimp were low (1.2 ± 0.2 , 1.3 ± 0.2 and $1.4 \pm 0.2 \text{ mL ind.}^{-1} \text{ h}^{-1}$ during winter, spring and
416 summer, respectively) and did not significantly differed between seasons. Porewater
417 exchange rates were significantly higher in the presence than in the absence of the mud
418 shrimp. In the presence of the mud shrimp porewater exchange rates significantly differed
419 between seasons with lower values during winter than during spring and during spring than
420 during summer (5.7 ± 2.3 , 8.1 ± 1.6 and $21.2 \pm 5.6 \text{ mL ind.}^{-1} \text{ h}^{-1}$, respectively).
421 Representative examples of temporal changes in uranine concentration recorded in the
422 overlying water during core incubations in the presence of a mud shrimp are presented in
423 supplementary material Fig. S2. Uranine concentration decreased non-linearly over time with
424 a succession of periods of low and rather constant decrease lasting for 47.3 ± 19.6 , 17.4 ± 5.0
425 and $9.5 \pm 2.0 \text{ min}$ on average during winter, spring and summer, respectively, interspersed by
426 sudden drops in uranine concentration.

427 3.5. Oxygen dynamics

428 In summer, all temporal changes in O₂ saturation in the overlying water column
429 showed a typical pattern in stair-shape (Fig. 5). Stair-shape curves consisted in a succession
430 of periods of relatively low oxygen decline ($-0.08 \pm 0.04 \text{ \% min}^{-1}$) interspersed by periods of
431 relatively rapid oxygen decline ($-0.33 \pm 0.09 \text{ \% min}^{-1}$). Periods of relatively low decline
432 lasted on average $11.8 \pm 5.2 \text{ min}$ during which mud shrimp were either “Burrowing”,
433 “Walking” or “Resting” while periods of rapid decline lasted on average $2.9 \pm 1.3 \text{ min}$ during
434 which mud shrimp were always “Ventilating”. Ventilation bouts sometimes lasted longer
435 than the period of oxygen declines *per se* as can be seen on the third and the sixth steps in
436 Fig. 5.

437 Oxygen saturations in the burrow lumen were between 95 and 10 % (Fig. 6A, B and
438 C). The directions and magnitudes of temporal changes in O₂ saturations were tightly related
439 to the behaviours of mud shrimp (Fig. 6A, B and C). Slow decreases ($-0.9 \pm 0.3 \text{ \% min}^{-1}$) in
440 O₂ saturation were detected when mud shrimp were “Resting” or “Walking” (Fig. 6A, C).
441 Rapid O₂ saturation decreases ($-6.7 \pm 3.4 \text{ \% min}^{-1}$) were detected when mud shrimp were
442 “Burrowing” (Fig. 6B, C). Conversely, sharp increases in O₂ saturation ($27.4 \pm 4.3 \text{ \% min}^{-1}$)
443 were always associated with “Ventilating” (Fig. 6A, B and C). The mean ventilation duration
444 necessary for O₂ saturation to reach its maximum value during a single ventilation event was
445 $2.9 \pm 0.7 \text{ min}$. There was a significant positive linear relationship ($F = 165.364, p < 0.001$)
446 between the distance of the mud shrimp from the sensor and the values of O₂ saturation at the
447 onset of ventilation (Fig. 6D). O₂ saturation inducing the onset of “Ventilating” (*i.e.*,
448 measured when mud shrimp were in the immediate vicinity of the optical sensor) was
449 consistently between 12 and 25 %.

450 4. Discussion

451 4.1. Behaviours and time allocation pattern

452 Previous studies regarding mud shrimp behaviours have mostly been carried out on
453 deposit-feeding species whereas *Upogebia pusilla* is a suspension-feeder (Dworschak,
454 1987b). The four behaviours identified during the present study were nevertheless similar to
455 those described for the deposit feeding mud shrimp *Calocaris templemani* (Gagnon et al.
456 2013) and *Callianassa subterranea* (Stamhuis et al., 1996). The average proportion of time
457 allocated to active behaviours (*i.e.*, “Burrowing”, “Ventilating” and “Walking”) by *U. pusilla*
458 were 43, 60 and 82% during winter, spring and summer, respectively. This is quite similar to
459 the 47 and 66% reported during winter for *C. templemani* (Gagnon et al., 2013) and during
460 spring for *C. subterranea* (Stamhuis et al., 1996), respectively. This tends to suggest that the
461 overall level of activity in mud shrimp is not related to feeding modes. There were however
462 differences in time allocation between *U. pusilla* and the two deposit-feeding mud shrimp.
463 Those differences were mainly associated to “Ventilating” and “Walking”. During winter, *U*
464 *pusilla* spent 14.1 % of its time ventilating *versus* only 5.0 % for *C. Templemani*.
465 Accordingly, during Spring *U. pusilla* spent 26.6% of its time ventilating *versus* only 9.9%
466 for *C. subterranea*. Conversely, and during the same seasons, *U. pusilla* spent only 4.9 % of
467 its time “Walking” *versus* 27.3 % for *C. templemani* and 2.6% *versus* 14.8% for *C.*
468 *subterranea*. These differences probably relate to trophic modes since: (1) “Ventilating” may
469 occur more frequently in suspension feeders because it is related both to respiration and
470 nutrition, and (2) deposit-feeders rely on “Walking” to forage for food within their burrows
471 (Pillay and Branch, 2011).

472 To our knowledge, this study is the first one assessing seasonal changes in between-
473 behaviour time allocation in a mud shrimp. Between winter and summer, the proportion of

474 time allocated by *U. pusilla* to an active behaviour increased by a factor 2.5. More
475 specifically, the proportions of time allocated to “Burrowing” and “Ventilating” increased by
476 a factor 1.4 and 3, respectively. These increases both resulted from marked decreases in
477 interval-durations. In the case of “Burrowing”, a counter effect was however associated with
478 the reduction of bout duration during summer. This is consistent with an indirect control of
479 temperature on time allocation pattern. During summertime, oxygen consumptions by *U.*
480 *pusilla* and associated microbial communities indeed increased by a factor 3.8 (Pascal et al.,
481 2016b). Since our results also suggest that the level of O₂ saturation triggering ventilation in
482 *U. pusilla* is constant (between 12 and 25 %; Fig. 6D) and assuming this level constant over
483 seasons, elevated temperature during summer contributes to: (1) the reduction in the time of
484 “Burrowing” required to reach this threshold and thereby to the diminution of the duration of
485 “Burrowing” bouts, and (2) the increase in the frequency of “Ventilating” bouts. Overall, our
486 results therefore clearly support the major role of temperature in controlling seasonal changes
487 in between-behaviour time allocation pattern by *U. pusilla*. In this sense, they are in good
488 agreement with previous observations by Berkenbusch and Rowden (1999) who reported a
489 strong positive correlation between sediment turnover (*i.e.* the ejection of deep material from
490 the burrow forming mounds at the sediment surface) rate by *Callinassa filholi* and seawater
491 temperature. It should however be stressed that the influence of temperature on between
492 behaviour time allocation is not necessarily direct (*i.e.* acting on mud shrimp metabolism),
493 but may also be indirect (*i.e.*, through enhancement of organic matter mineralization) since
494 both pathways contribute to limit oxygen availability within the burrows.

495 **4.2. Sediment reworking and “Burrowing”**

496 **4.2.1. The different components of sediment reworking and their relative importance**

497 There are three distinct patterns in the sediment reworking induced by *Upogebia*
498 *pusilla* (see Fig. 1 for visual description). Individual of this species rework sediment: (1)
499 outside their burrows by expelling excavated sediment at the sediment-water interface (P1),
500 (2) below the sediment surface by introducing and then moving downward sediment particles
501 within their burrows (P2), and (3) by compacting sediment against the walls of their burrow
502 (P3). P1 and P2 are mostly vertical, whereas P3 occurs perpendicularly to burrow walls (*i.e.*,
503 mostly horizontally due to the general morphology of the burrows, Fig. 1). Previous studies
504 assessing sediment reworking by mud shrimp have only considered P1 through the
505 assessment of sediment turnover rates (*e.g.*, Berkenbusch and Rowden, 1999; Pillay et al.,
506 2012; Rowden et al., 1998; Suchanek, 1983). During the present study, we also assessed: (1)
507 P1 by measuring the volume of sediment expelled at the sediment-water interface (V_{ES}), (2)
508 the resultant of P1 and P2 by using a 1D vertical biodiffusion-bioadvection transport model
509 (characterized by a biodiffusion and a bioadvection coefficient: D_{bv} and V_{bv} , respectively),
510 and (2) P3 by experimentally measuring the volume of reworked sediment surrounding the
511 burrow (B_{RS}) and by using a simple biodiffusion model (characterized by a biodiffusion
512 coefficient: D_{bw}).

513 The relative importance of P1 and P3 can be assessed based on the comparison of
514 sediment reworked volumes (*i.e.*, V_{ES} and B_{RS}). During all three seasons the thickness of the
515 reworked sediment layer surrounding the burrow (T_{RS}) stabilized after *ca.* 4-5 days. We thus
516 decided to limit our comparisons to the periods of initial increases in T_{RS} (*i.e.*, until D4). V_{ES}
517 then accounted on average for about 40 % of the total (*i.e.*, $V_{ES} + B_{RS}$) volume of reworked
518 sediment. By comparing the volumes of the burrows and expelled sediments, Dworschak

519 (1983) estimated this proportion to be 50 % in natural environment. These two values clearly
520 underline the importance of sediment reworking occurring below the sediment surface and
521 the necessity of considering this component when assessing sediment reworking in *U. pusilla*.
522 This statement is likely to hold for other mud shrimp irrespective of their feeding mode and
523 the associated pattern of extension of their burrow (Dworschak, 1983; Nickell and Atkinson,
524 1995). Although less straightforward, due to the interactions between P1, P2 and P3 and the
525 fact that two different models were used, the comparison between D_{bv} and D_{bw} also provides
526 information on the relative intensity of vertical (*i.e.*, mostly P2 and to a lesser extent P1) and
527 horizontal (*i.e.*, mostly P3) sediment reworking intensities, respectively. After four days (*i.e.*,
528 when T_{RS} reached their maximum values), D_{bw} were about 100-folds lower than D_{bv} . This is
529 due to the fact that, although affecting larger volumes of sediment, sediment compaction
530 against the burrow wall (*i.e.*, P3) transports particles over small distances, which results in a
531 thin (typically 5 mm) layer of sediment around burrow wall and thus a low D_{bw} . This is
532 coherent with the fact that in thalassinid the maintenance of the burrow is typically insured by
533 sediment compaction (Dworschak, 1983). P1 and *a fortiori* P2 induce particle displacements
534 over a much larger (typically several tenth of cm) spatial scale in association with upward
535 non-local transport (mostly P1) and enhanced downward biodiffusion (mostly P2). Overall,
536 P1, P2 and P3 all constitute important but highly different components of sediment
537 reworking.

538 4.2.2. *Evidences for the induction of sediment reworking by "Burrowing"*

539 There are several lines of evidence suggesting that the different component of
540 sediment reworking tightly correlate between each other. First, all proxies of the different
541 components (*i.e.*, V_{ES} for P1, D_{bv} for P2, B_{RS} and D_{bw} for P3) of sediment reworking showed
542 a similar seasonal pattern with higher values during summer, intermediate ones during spring

543 and lower ones during winter. Second, at D4 there was a significant correlation between V_{ES}
544 and B_{RS} . Third, during summer (*i.e.*, when sediment reworking was highest), D_{bv} and V_{bv}
545 showed similar temporal changes during the whole experiment duration. This suggests that
546 all three components are probably controlled by the same behaviour of the mud shrimp. Even
547 though cross correlation effects cannot be absolutely excluded, their probability of occurrence
548 can indeed be considered low. Based on the multiple linear regression model linking the total
549 volumes (*i.e.*, $V_{ES} + B_{RS}$) of reworked sediment at D4 and the proportions of time allocated to
550 the 4 different behaviours, our results suggest that “Burrowing” is the behaviour that is
551 mostly inducing sediment reworking. This statement is further supported by the similarity of
552 the seasonal changes in the proportion of time allocated to “Burrowing” and all the proxies of
553 the different components of sediment reworking. This is in good agreement with the
554 mechanisms inducing P1 (*i.e.*, sediment excavation) and P3 (*i.e.*, sediment compaction along
555 burrow walls) but a little less clear for P2 (*i.e.*, sediment introduction within the burrow),
556 which could *a priori* result from a wider set of mechanisms/activities including “Burrowing”.

557 ***4.3. Porewater exchange, oxygen dynamics and behaviours***

558 *4.3.1. Evidences for the direct effect of “Ventilating” on porewater exchange and oxygen* 559 *dynamics*

560 During the present study, porewater exchange rates were assessed based on the
561 monitoring of the temporal dynamics of uranine concentrations in the overlying water. This
562 dynamics clearly presented a cyclical pattern with alternation between relatively long periods
563 of low decrease and short events of sharp decrease in concentration. This is clearly indicative
564 of the discontinuous nature of porewater exchange. The mean time duration of low decrease
565 (*i.e.*, low porewater exchange) periods differed between seasons. They were longer during
566 winter and shorter during summer (47.3 vs. 9.5 min, respectively). Moreover, during all three

567 seasons, they tended to be similar to the time intervals between two consecutive ventilation
568 bouts (47.3 vs. 42.5 min, 17.4 vs. 17.7 min, and 9.5 vs. 9.5 min, during winter, spring and
569 summer, respectively). This suggests that, similarly to the Polychaete *Marenzelleria viridis*
570 (Quintana et al., 2011), in *U. pusilla*, “Ventilating” is the behaviour inducing porewater
571 exchange.

572 This is further supported by the analysis of the dynamics of O₂ saturation in the
573 overlying water of the thin aquaria during summer experiments. Oxygen saturation also
574 showed a cyclical pattern superimposed to an overall decreasing trend quite similar to
575 uranine. The mean time interval between two consecutive drops was 11.8 minutes and the
576 duration of each drop was 2.9 minutes. These values are consistent with those available for *U.*
577 *pusilla* (Dworschak, 1981) and other mud shrimp (Forster and Graf, 1995; Stamhuis et al.,
578 1996; Volkenborn et al., 2012b). During the present study, the average duration of an
579 individual cycle of O₂ saturation in the overlying water was thus 14.7 minutes, which is fully
580 compatible with the mean length of a ventilation cycle (*i.e.*, 16.4 minutes) considering
581 associated variability. Moreover, the direct examination of the two time-series further
582 supports that temporal changes in the O₂ saturation of the overlying water are clearly
583 controlled by the “Ventilating” behaviour of the mud shrimp since drops in O₂ saturation of
584 overlying waters were always associated with ventilation events.

585 4.3.2. Evidences for the effect of “Burrowing” on the onset of “ventilating”

586 During summer experiment, oxygen saturation within the burrow showed a cyclical
587 pattern as already observed for other mud shrimp such as *C. subterranea* (Forster and Graf,
588 1995) and *N. californiensis* (Volkenborn et al., 2012b) and for the polychaete *Allita succinea*
589 (Murphy and Reidenbach, 2016). Temporal changes were clearly related with the behaviour
590 of the mud shrimp. Oxygen decreases were very low when mud shrimp were “Resting” or

591 “Walking”. Since thalassinid mud shrimp show low basal metabolic rates (Atkinson and
592 Taylor, 2005), microbial community respiration and diffusive transport of O₂ through the
593 burrow wall probably account for the main part of oxygen consumption during these time
594 periods. Conversely, O₂ saturation dropped quickly when mud shrimp were “Burrowing” due
595 to: (1) the increase in mud shrimp metabolism and (2) the release of reduced compounds
596 previously trapped within the sediment column, which are quickly re-oxidized through a
597 series of coupled oxidation-reduction reactions that ultimately consume oxygen (Aller et al.,
598 1983; Kristensen, 2000; Kristensen and Kostka, 2005).

599 We also found a significant positive relationship between O₂ saturation measured by
600 the optode within the burrow and the distances of the mud shrimp to this sensor at the onset
601 of ventilation events. Given that mud shrimp initiate a ventilation event at a given O₂
602 saturation, this suggests that the spatial distribution of O₂ saturation within the burrow is not
603 uniform. More specifically, this result supports the fact that O₂ saturation would be minimal
604 close to the mud shrimp and would increase with increasing distance from the mud shrimp.
605 There are some rationales to support this assumption: (1) the mud shrimp is respiring and
606 thus consuming O₂ (Forster and Graf, 1995; Koike and Mukai, 1983), and (2) its activity
607 contribute to release reduced compounds, which are readily oxidized in the oxygenated
608 burrow water (Aller et al., 1983; Kristensen, 2000; Kristensen and Kostka, 2005). According
609 to these hypotheses, the O₂ saturation threshold at which *U. pusilla* initiates ventilation would
610 be between 12 and 25%, which is fully coherent with the minimal O₂ saturation levels
611 observed within the burrow water of *C. japonica* (12 %, Koike and Mukai, 1983), *N.*
612 *californiensis* (20 %, Volkenborn et al., 2012b) and *U. major* (30 %, Koike and Mukai,
613 1983). No data on oxygen dynamics were available for winter and spring. However, the
614 existence of an O₂ saturation threshold triggering burrow ventilation together with
615 behavioural data suggest that the oscillation frequency in oxygen saturation within the burrow

616 would be the lowest during winter and intermediate during spring. Here again there are some
617 rationales supporting this assumption: (1) a lower oxygen consumption by the sediment at
618 low temperature (Epping and Helder, 1997; Hall et al., 1989; Thamdrup et al., 1998), and (2)
619 as observed during this study and similarly to what has been observed for other thalassinids
620 (Stanzel and Finelli, 2004), an increase in ventilation and burrowing event frequencies with
621 temperature.

622 **5. Conclusion**

623 We assessed how different behaviours by the mud shrimp *Upogebia pusilla* affect
624 sediment reworking, bioirrigation and oxygen dynamics at and below the sediment-water
625 interface. Our results show that *U. pusilla* is an efficient bioturbating species causing both
626 high sediment reworking and porewater exchange rates. There were three components of
627 sediment reworking: (1) the expulsion of excavated sediment at the sediment-water interface
628 (2) the introduction and then the downward transport of surface sediment particles within the
629 burrow, and (3) the compaction of sediment around burrow walls. The intensities of all three
630 components correlated positively so that sediment reworking as a whole appeared mainly
631 induced by the “Burrowing” behaviour. In summer, porewater exchange and oxygen
632 dynamics were directly cued by the “Ventilating” which is initiated by an oxygen saturation
633 level between 12 and 25%. “Ventilating” was thus also indirectly cued by “Burrowing”,
634 which, conversely to “Walking” and “Resting” induces marked decreases in O₂ saturation
635 within the burrow. This underlines the importance of taking into account changes in animal
636 behaviour types/intensities at the appropriate temporal scales when assessing the impact of
637 bioturbation on biogeochemical processes taking place at the sediment-water interface.

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892 **Table 1** Seasonal changes in the mean (\pm SE), minimum (Min) and maximum (Max) values of main burrow characteristics (length, depth, number of
893 openings and number of chambers) recorded immediately after luminophore input (D0), at day 4 (D4) and at day 30 (D30).

Time / Season	<i>n</i>	Length (cm)			Depth (cm)			Number of openings			Number of chambers		
		Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
D0													
Winter	10	34.5 \pm 7.3	24.6	49.0	14.0 \pm 3.3	9.6	18.7	2.0 \pm 0.0	2	2	2.2 \pm 0.5	2	3
Spring	10	39.9 \pm 13.4	19.8	61.0	16.5 \pm 5.9	6.5	24.5	2.0 \pm 0.0	2	2	2.9 \pm 0.5	2	4
Summer	10	42.3 \pm 13.1	16.4	58.4	15.7 \pm 4.9	8.4	24.7	2.0 \pm 0.0	2	2	2.8 \pm 0.8	2	4
D4													
Winter	10	35.9 \pm 9.4	24.6	57.1	14.3 \pm 3.3	10.0	18.7	2.0 \pm 0.0	2	2	2.2 \pm 0.5	2	3
Spring	10	44.5 \pm 17.6	21.6	81.3	17.9 \pm 7.3	7.0	26.1	2.0 \pm 0.0	2	2	2.9 \pm 0.5	2	4
Summer	10	52.3 \pm 9.9	35.6	66.1	19.3 \pm 5.4	13.9	27.3	2.0 \pm 0.0	2	2	2.8 \pm 0.8	2	4
D30													
Winter	10	47.1 \pm 16.8	28.3	81.8	15.5 \pm 3.8	12.9	23.5	2.6 \pm 0.6	2	3	3.8 \pm 1.5	2	6
Spring	10	76.8 \pm 26.0	48.3	127.0	22.4 \pm 8.2	14.2	29.8	2.5 \pm 0.5	2	3	4.4 \pm 1.3	3	7
Summer	10	96.7 \pm 27.5	66.6	154.9	26.7 \pm 8.9	16.1	31.0	2.3 \pm 0.5	2	3	5.1 \pm 1.2	4	8

895 **Table 2** Results of the PERMANOVA and PERMDISP analyses for assessing differences in burrow length, burrow depth, number of burrow openings,
 896 number of chambers, mean thickness of the reworked sediment layer surrounding the burrow (T_{RS}), volume of reworked sediment surrounding the burrow
 897 (B_{RS}) and volume of sediment expelled at the sediment-water interface (V_{ES}), between Seasons and (experiment) Durations. p values in bold indicate
 898 significant factor effect. *: PERMDISP, $p < 0.05$

Factors		Burrow length	Burrow depth	Number of burrow openings	Number of chambers	T_{RS}	B_{RS}	V_{ES}	D_{bv}	V_{bv}
<i>Seasons</i>	df	2	2	2	2	2	2	2	2	2
	MS	4478.8	234.63	0.0333	6.7111	0.184	32969	83391	1.618E7	6.832E5
	Pseudo-F	7.047*	2.727*	0.443	4.387	43.979	42.573*	54.447*	78.580	12.052*
	p(perm)	0.005	0.097	0.883	0.023	0.001	0.001	0.001	0.001	0.001
<i>Durations</i>	df	2	2	2	2	15	15	15	15	15
	MS	10595	287.09	0.9	22.411	2.285	121490	410850	2.208E5	24467
	Pseudo-F	82.991*	29.399*	11.951*	42.315*	1192.700*	255.160*	296.570*	2.182	1.942*
	p(perm)	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.013	0.034
<i>Replicate(Seasons)</i>	df	27	27	27	27	27	27	27	27	27
	MS	635.52	86.038	0.0753	1.530	0.004	774.43	1531.6	2.0479E5	56379
	Pseudo-F	4.978*	8.811*	1.000*	2.888*	2.184	1.627	1.106	2.024	4.475
	p(perm)	0.001	0.001	0.483	0.003	0.003	0.046	0.378	0.004	0.001
<i>Season x Durations</i>	df	4	4	4	4	30	30	30	30	30
	MS	1408.2	61.061	0.033	1.478	0.0462	49489	49748	1.115E5	14616
	Pseudo-F	11.030*	6.253*	0.443*	2.790	24.131*	25.985*	35.911*	1.102	1.160
	p(perm)	0.001	0.002	0.8	0.049	0.001	0.001	0.001	0.338	0.274
<i>Residuals</i>	df	54	54	54	54	300	300	300	300	300
	MS	127.7	9.7651	0.0753	0.5296	0.0019	476.14	1385.3	1.012E5	12599

901 **Table 3** Description, average bout-duration (minutes \pm SE and interval-duration (*i.e.*, average time duration between two bouts of the same behaviour;
 902 minutes \pm SD) of each behaviour during winter (n = 4), spring (n = 5) and summer (n = 5) experiments. * indicates significant between seasons differences
 903 (one-way PERMANOVA, p < 0.05)

Behaviour	Description	Bout-duration (minutes)			Interval-duration (minutes)			
		Winter	Spring	Summer	Winter	Spring	Summer	
Walking^a	Walking or turning through the burrow without sediment transport	*	1.8 \pm 0.1	2.0 \pm 0.2	1.0 \pm 0.2	42.5 \pm 9.4	80.4 \pm 11.9	80.4 \pm 16.7
Ventilating^b	Movements of the four pairs of pleopods		5.7 \pm 1.1	7.9 \pm 2.0	6.9 \pm 0.7	* 42.4 \pm 12.2	17.7 \pm 2.3	9.5 \pm 1.0
- Flushing	<i>Strong ventilation causing the ejection of sediment out of the burrow</i>	*	0.7 \pm 0.1	0.8 \pm 0.0	0.9 \pm 0.0	512.6 \pm 222.5	159.4 \pm 64.0	69.8 \pm 14.3
-Pumping	<i>Movement of the pleopods without sediment transport</i>		6.2 \pm 1.1	9.9 \pm 2.7	8.3 \pm 0.7	* 46.9 \pm 12.4	23.1 \pm 3.4	12.1 \pm 1.4
Burrowing^c	Sediment transport	*	12.7 \pm 1.5	9.2 \pm 1.4	7.1 \pm 0.6	* 46.1 \pm 14.3	21.9 \pm 4.3	12.7 \pm 1.3
Resting^d	Stay stationary	*	16.9 \pm 2.6	17.1 \pm 2.5	7.7 \pm 0.8	18.6 \pm 1.9	28.8 \pm 6.0	31.8 \pm 2.6

904 Corresponding terminology in Stamhuis et al. (1996) ^aWander, ^bVentilate, ^cBurrow, ^dRest

905 Corresponding terminology in Gagnon et al. (2013) ^aOther activities, ^bIrrigation of burrow, ^cSediment to surface, Transport and digging + manipulation, ^dIn
 906 sight inactive

1 **Figure captions:**

2
3 **Fig. 1 Burrow:** Schematic view of a representative burrow. Green line: Former sediment-water interface
4 as evidenced by the remaining of the luminophore layer, dotted line: burrow length, T_{RS} : average
5 thickness of the reworked sediment layer surrounding the burrow, \bar{H} : average height of the sediment
6 expelled at the sediment water-interface. Red dotted arrows represent the three identified patterns of
7 sediment reworking (P1, P2 and P3; see text for details).
8

9 **Fig. 2 Behaviour:** Seasonal changes in the proportions of time allocated to the different behaviours.
10 Vertical bars are standard errors. Different letters indicate significant (PERMANOVA and pair-wise
11 test, $p < 0.05$) differences between seasons.
12

13 **Fig. 3 Sediment reworking:** Seasonal changes in the relationships between experiment duration and: (A)
14 the thickness of reworked sediment surrounding the burrow (T_{RS}), (B) the volume of reworked sediment
15 surrounding the burrow (B_{RS}), and (C) the volume of sediment expelled at the sediment-water interface
16 (V_{ES}). Relationship between B_{RS} and V_{ES} at day 4 (D).
17

18 **Fig. 4 Sediment reworking modelling:** Seasonal changes in the relationships between experiment
19 duration and: (A) average vertical biodiffusion (D_{bv}), and (B) vertical bioadvection (V_{bv}) coefficients.
20 Vertical bars are standard errors.
21

22 **Fig. 5 Oxygen dynamics in the overlying water during core incubations:** Representative example of the
23 effect of *Upogebia pusilla* activity on temporal changes of O_2 saturation in the overlying water. Red,
24 blue, green and black colours depict changes during “Burrowing”, “Ventilating”, “Walking” and
25 “Resting”, respectively.
26

27 **Fig. 6 Oxygen dynamics in the burrow water:** Examples of temporal changes in O_2 saturation when the
28 mud shrimp was (A and B) far and (C) close from the micro-optode. Red, blue, green and black colours
29 depict changes during “Burrowing”, “Ventilating”, “Walking” and “Resting”, respectively. Relationship
30 between O_2 saturation at the onset of a ventilation event and the mud shrimp distance from the sensor
31 (D). See text for details.











