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Cécile Massé, Frédéric Garabetian, Bruno Deflandre, Olivier Maire, Laurence Costes, et al.. Feeding ethology and surface sediment reworking by the ampharetid polychaete *Melinna palmata* Grube, 1870: Effects on sediment characteristics and aerobic bacterial community composition. *Journal of Experimental Marine Biology and Ecology*, 2019, 512, pp.63-77. 10.1016/j.jembe.2018.12.009 . hal-02409099

HAL Id: hal-02409099

<https://hal.science/hal-02409099v1>

Submitted on 21 Oct 2021

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1 **Feeding ethology and surface sediment reworking by the ampharetid polychaete *Melinna***
2 ***palmata* Grube, 1870: effects on sediment characteristics and aerobic bacterial community**
3 **composition**

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11

12 **ABSTRACT**

13 The present study was aiming at describing the feeding ethology and assessing surface
14 sediment reworking together with associated effects on sediment characteristics and aerobic bacterial
15 community composition by the ampharetid polychaete *Melinna palmata*, which exhibits very dense
16 populations in the Arcachon Bay (French Atlantic coast). There was a plasticity in the main aspects
17 (i.e., positioning of the tube at the sediment-water interface, stretching of the worms outside their
18 tubes while feeding, location and mechanism of faeces production) constitutive of the current
19 knowledge regarding feeding ethology in ampharetids. On average, worms dedicated 84.6% of their
20 time to the prospection of surface sediments and produced faeces exclusively at the water sediment
21 interface, which resulted in surface sediment reworking and induced the zonation of surface sediment
22 in three distinct areas, namely: undisturbed sediment, prospected and faecal mound areas. Average
23 individual surface prospected area and surface sediment reworking rate were 28 cm² and 6.8 mm³.h⁻¹,
24 respectively. Surface sediments were coarser and their bulk organic contents were lower in prospected
25 areas, intermediate in faecal mound areas and higher in undisturbed sediments. Oxygen penetrated
26 deeper in the sediment column in faecal mound areas. Aerobic bacterial community composition
27 associated with surface oxygenated sediments within these three areas also significantly differed,
28 which suggests that sediment reworking *per se* (i.e., irrespective of changes in redox conditions) do
29 have an effect on those compositions. These results are discussed in terms of potential food limitation
30 in the very dense populations of *M. palmata* present in the Arcachon Bay. It is suggested that the high

31 densities of these populations result from both hydrosedimentary fluxes due to tidal currents and from
32 the enhancement of particle sedimentation in *Zostera noltei* meadows.

33

34 Key words: Ampharetids, *Melinna palmata*, Feeding ethology, Surface sediment reworking, Sediment
35 characteristics, Aerobic bacterial community composition.

36

37 1. INTRODUCTION

38 Once sedimented, particulate organic matter undergoes early diagenesis (i.e., a sequence of
39 mineralization reactions taking place in the top sediment column). This process is mainly achieved by
40 bacterial communities featuring different metabolic capacities in relation with the availability of a
41 series of final electron acceptors. In the absence of benthic macrofauna, these receptors show a typical
42 vertical zonation (Froelich et al., 1979). By modifying this redox sequence and by creating
43 microenvironments submitted to oscillatory conditions, bioturbation by benthic macrofauna disturbs
44 oxidation processes taking place in the top sediment column (Burdige, 1993). Bioturbation activities
45 include the mixing and spatial redistribution of both sediment particles (i.e., sediment reworking), and
46 pore-water solutes (i.e., bioirrigation; Rhoads, 1974; Kristensen et al., 2012). They directly affect the
47 three components cuing the efficiency of mineralization processes taking place in the top sediment
48 column, namely the spatial distributions of: (1) particulate organic matter; (2) final electron acceptors;
49 and (3) bacterial community biomass (Aller and Yingst, 1985; Reichardt, 1988), composition (Bertics
50 and Ziebis, 2009; Laverock et al., 2010) and biogeochemical functions (Bertics et al., 2010; Gilbertson
51 et al., 2012; Yazdani Foshtoni et al., 2015). By doing so, bioturbation strongly influences the
52 biogeochemical processes taking place at the sediment-water interface (Aller, 1994; Aller and Aller,
53 1998; Lohrer et al., 2005; Furukawa, 2005; Aller, 2014; Braeckman et al., 2014).

54 Sediment reworking is typically a 3D process (Rosenberg et al., 2008). Its quantification is
55 however usually achieved based on a reduced number of dimensions due to the difficulty in
56 penetrating the sediment matrix. Because of the interaction with the vertical zonation of
57 biogeochemical processes (see above) and due to the importance of the problematic of carbon burial,
58 most attention has been devoted to the vertical dimension (see for example Maire et al., 2008).
59 Classically, the assessment of sediment reworking is based on the coupling between: (1) the
60 assessment of a vertical profile of tracer concentrations, and (2) the modelling of this profile. This
61 whole process usually results in the computation of a vertical biodiffusion coefficient (D_b) and/or non-
62 local exchange functions, which account for the intensity of vertical sediment reworking through
63 biodiffusion and non-local transport. Conversely, the quantification of horizontal sediment reworking

64 has received much less attention although some early modelling studies have suggested that this
65 component may be quantitatively as important as the vertical one (Wheatcroft et al., 1990; Wheatcroft,
66 1991) and that surface mixing is often considered as an ecological trait in studies assessing the
67 relationship between species diversity and ecosystem functioning (e.g. Hewitt et al., 2008). The use of
68 thin aquaria and luminophores (i.e., sediment particles coated with a fluorescent paint) coupled with
69 sophisticated image acquisition and analysis techniques has only been recently introduced allowing for
70 the 2D (i.e., vertical and horizontal) assessments of sediment reworking (e.g. Gilbert et al., 2003;
71 Maire et al., 2007b, 2007c, 2010; Bernard et al., 2012).

72 The analysis of the effects of bioturbation on bacterial community composition and function has
73 also favored the assessment of the vertical component due to the tight interactions between these
74 communities and available final electron acceptors. Gallery biodiffusers (*sensu* Kristensen et al.,
75 2012) have been mostly used to tackle this question. Through the ventilation of their burrow, these
76 organisms enhance oxygen penetration deep in the sediment column (e.g. Papaspyrou et al., 2006;
77 Laverock et al., 2010; Pischedda et al., 2011) and thereby induce a patchy distribution of bacterial
78 assemblages (e.g. Laverock et al., 2010). Moreover, and because their activity is often discontinuous,
79 they induce short-term temporal changes in bacterial assemblage functionalities, which results in a
80 non-equilibrium dynamics of mineralization processes (e.g. Wenzhöfer and Glud, 2004; Pischedda et
81 al., 2008). One difficulty when studying the effect of sediment reworking on bacterial assemblages
82 and functions is the unraveling between the effect of sediment reworking *per se* and those related with
83 changes in redox conditions (e.g. Laverock et al., 2010). A possibility to tackle this difficulty is to
84 focus on benthic macrofauna performing sediment reworking without altering the oxygenation of the
85 sediment. This is potentially the case of “Surface deposit feeding Sessile Tentaculate” worms (SST,
86 Fauchald and Jumars, 1979), which collect a very thin layer of particles at the sediment-water
87 interface. Sediment reworking by these organisms typically creates distinct areas at the sediment
88 surface with a clear distinction between undisturbed sediments, and prospected and faecal mound
89 areas (e.g. Nowell et al., 1984). This allows for the establishment of a stratified sampling strategy of
90 surface oxygenated sediment to assess the effect of sediment reworking on sediment characteristics

91 and associated aerobic bacterial community composition (see Warwick et al. (1986) and Olafsson et
92 al. (1990) for a similar approach regarding meiofauna composition).

93 During the present study, we used the ampharetid polychaete *Melinna palmata* as a biological
94 model. This species is abundant in the *Zostera noltei* meadows and the bare intertidal mudflats of the
95 Arcachon Bay (France) where it has been suggested that its dense populations inhibit vertical sediment
96 reworking (Bernard et al., 2014). Although, *M. palmata* clearly belongs to SST (Fauchald and Jumars,
97 1979; Jumars et al., 2015), its feeding ethology has not been deeply investigated yet. The present study
98 therefore aimed at: (1) describing the anatomy of feeding organs; (2) establishing a typology of the
99 different behaviors and assessing the time allocation pattern between these behaviors; (3) quantifying
100 surface sediment reworking, and (4) assessing the effects of sediment reworking on surface sediment
101 main characteristics, oxygen penetration and bacterial community composition. These objectives were
102 tackled using an *ex situ* experimental approach. Due to the practical/technical difficulties in achieving
103 replication (e.g. Maire et al., 2007a), this resulted in three series of experiments dedicated to one or
104 combinations of the above mentioned specific aspects.

105

106 **2. MATERIAL AND METHODS**

107 **2.1. Worm collection and maintenance**

108 *Melinna palmata* is an ampharetid worm with a large boreo-mediterranean distribution
109 (Grehan, 1991). It is abundant along the Atlantic coasts from Norway to Morocco (Guillou and Hily,
110 1983; Grehan, 1991; Cacabelos et al., 2011), in the Black Sea, the Sea of Azov, the Persian Gulf and
111 the Mediterranean Sea (Holthe, 1986; Zaabi and Alfi, 2006). It has been recorded all along the
112 metropolitan French coast (<http://resomar.cnrs.fr/bases/index.php>; Dauvin et al., 2003). Individual
113 worms are typically between 15 and 50 mm in length and between 2 and 3 mm in width. They bear 16
114 thoracic and about 60 abdominal segments. The base of their two sets of four gills is implanted on the
115 dorsal part of their first segment (Fauvel, 1927; Rouse and Pleijel, 2001). The life span is between 2

116 and 2.5 years in inner Galway Bay (Grehan, 1991) and secondary production in Southampton waters is
117 $0.42 \text{ g C}^{-2}\text{yr}^{-1}$ (Oyeneke, 1988).

118 For the present study, adult worms were collected during April 2012 (anatomy of feeding
119 organs, 1st and 2nd series of experiments) and December 2013 (3rd series of experiments and tentacles
120 number) in the Arcachon Bay (French Atlantic Coast) at the “Germanan” site ($44^{\circ}42'726''\text{N}$,
121 $1^{\circ}07'940''\text{W}$) where extremely dense populations of *M. palmata* have been reported in *Zostera noltei*
122 intertidal seagrass meadows (Blanchet et al., 2004; Bernard et al., 2014). Back at the laboratory, tubes
123 were isolated from the sediment by gently sieving on a 1 mm square mesh, and collected by hand.
124 Worms were then acclimatized (>10 days) in aquaria containing sieved (1 mm mesh to discard other
125 macrofauna; e.g. Queiros et al., 2015) sediment from the collection site and fuelled with a continuous
126 flow of filtered seawater from the Arcachon Bay before any subsequent
127 manipulations/experimentations.

128

129 **2.2. Anatomy of feeding organs**

130 The tentacles of 10 worms collected in December 2013 were counted under a Nikon® SMZ25
131 stereomicroscope. The anatomy of the feeding organs was investigated using Scanning Electron
132 Microscopy (SEM). Fifteen worms collected in April 2012 were left for one hour in filtered ($0.22 \mu\text{m}$)
133 and sterilized seawater to ensure that their tentacles were deployed. Heads and tentacles were then
134 dissected and fixed in 2.5 % glutaraldehyde with 0.4 M cacodylate buffer and 7 % NaCl for 24 h.
135 Samples were rinsed 3×30 min in 0.4 M cacodylate and 4 % NaCl before being post-fixed with 2 %
136 osmium tetroxide in 0.4 M cacodylate and 10 % NaCl. They were then dehydrated through a series of
137 incubations in increasing alcohol concentrations (10 min in 50 %, 10 min in 70 %, 10 min in 90 %, 10
138 min in 95 %, 2×10 min in absolute and 15 min in propylene oxide). After critical-point-drying,
139 samples were coated with gold and observed using a Quanta 200 SEM (FEI Company) at the
140 Bordeaux Imaging Centre (University of Bordeaux, France).

141

142 **2.3. Experiments**

143 Three series of experiments were carried out during April 2012, November 2012 and February
144 2014 (Fig. 1). Before each experiment, worms were carefully removed from their tube and examined
145 under a binocular microscope to check for physical integrity. All experiments were achieved on single
146 individual worms, which were introduced at the center of a parallelepiped (11.5×17.5×6.5 cm,
147 corresponding to a density of 50 ind.m⁻²) aquarium filled with a 6 cm layer of sediment from the
148 collection site (sieved on 1 mm-mesh to remove other macrofauna and previously stabilized for 10
149 days) and placed under a continuous flow of filtered seawater from the Arcachon Bay for 10 days.
150 This time period proved sufficient for worms to build a new tube and to efficiently burrow in the
151 sediment.

152

153 *2.3.1. First series of experiments*

154 The aims of the first series of experiments (Fig. 1A) were to: (1) describe feeding ethology, (2)
155 characterize worm behaviors, (3) assess time allocation pattern, (4) quantify the surface of sediment
156 reworked areas, and (5) assess the effect of surface sediment reworking on main sediment
157 characteristics and aerobic bacterial community composition. Thirteen worms were studied during this
158 experiment series (temperature: 15.9 ± 2.0 °C; salinity: 30.5 ± 1.7).

159

160 *2.3.1.1. Feeding ethology, typology of behaviors and time allocation pattern*

161 A computer piloted IDS µeye UI-1580SE-C-HQ video sensor (Stemmer Imaging) was
162 positioned 30 cm straight above the aquarium sediment surface, which was illuminated with infrared
163 light. This system allowed for the collection of images of the sediment surface during 24 hours at a
164 frequency of 0.1 Hz. Collected images were assembled in an AVI film, which was then visually
165 analyzed to assess: (1) feeding ethology, (2) different types of behavior, and (3) time allocation
166 patterns between these behaviors.

167

168 2.3.1.2. *Surface sediment reworked areas*

169 Additional images of the sediment surface were collected under ambient light on days 10, 15,
170 20, 25 and 30 (starting from the beginning of the acclimation period) using a Nikon ® D7000 Reflex
171 16.2 Mpixels camera fitted with a 18-105 mm lens. A special care was taken to insure that the image
172 plan was strictly parallel to the sediment surface. For all worms, a zonation of the sediment surface
173 became rapidly visible. This included: (1) a faecal mound area near the tube opening, (2) a prospected
174 area devoid of surface particles, and (3) undisturbed sediment (Fig. 2A and B). The faecal mound and
175 the total affected areas were manually drawn on each collected image and their surface was assessed
176 using the Image J® software (USA National Institutes of Health) after appropriate calibration. The
177 surfaces of prospected areas were computed as the difference between the surfaces of total affected
178 and faecal mound areas.

179

180 2.3.1.3. *Surface sediment sampling*

181 At the end of the 20 d experiment period, the surface sediments of: (1) faecal mound areas, (2)
182 prospected areas, and (3) undisturbed sediments were sampled using a truncated (to allow the passage
183 of the largest particles) pipette tip fitted to the needle port of a 10 mL syringe. All the surface sediment
184 of each three areas was sucked by gently pulling the syringe plunger while the truncated tip was
185 moved to sample the very top (i.e., about 2 mm) surface sediment layer. Each sample was
186 homogenized and divided in two for the assessments of: (1) main sediment characteristics, and (2)
187 aerobic bacterial community composition.

188

189 2.3.1.4. *Main sediment characteristics*

190 Sediment granulometry was assessed using a Malvern® Master Sizer laser microgranulometer
191 and expressed as median diameter (D50) and mud content (i.e., the volume % of particles less than 63
192 µm in size). Particulate organic carbon (POC) and nitrogen (PON) were measured on 10 mgDW (dry
193 weight) freeze dried decarbonated (with 0.2N HCl according to Kennedy et al., 2005) sediment

194 samples using a ThermoFinnigan® Flash Elemental Analyser Series 1112. Chlorophyll *a* and
195 phaeophytin *a* were assessed on a 6 mL 90 % acetone extracts of 400 mg WW (wet weight) sediment
196 samples using a Perkin Elmer® spectrofluorometer (Neveux and Lantoiné, 1993). Depending on the
197 amount of available sediment, these measurements were achieved on 1 to 3 replicates.

198

199 2.3.1.5. *Aerobic bacterial community composition*

200 Aerobic bacterial community composition was characterized by Automated Ribosomal
201 Intergenic Spacer Analysis (ARISA), a PCR-based whole-community fingerprinting method (Fisher
202 and Triplett, 1999). Within two hours after collection, 0.465 ± 0.003 g WW (Wet Weight) of sediment
203 from each zone was placed in preservative buffer (100 mM Tris-HCl [pH 8.0], 10.0 mM EDTA [pH
204 8.0], 1.5 NaCl and 1 % [wt/vol] cetyltrimethylammonium bromide) (Zhou et al. 1996). Samples were
205 stored at -80°C until analysis. DNA extraction was achieved using 700 μL of homogenized thawed
206 sediment sample. DNA was extracted and purified coupling a bead beating method (Lysing matrix E
207 tubes) and Fast Prep (MP Biomedicals): two runs at 5.5 m s^{-1} during 30 s with the use of an extraction
208 kit UltraClean® Soil DNA Isolation Kits (MO BIO Laboratories Inc.). The amount of extracted and
209 purified DNA was quantified by spectrophotometry with 2 μL of DNA solution, using an Epoch
210 microplate spectrophotometer (Biotek instruments). PCR amplification of the 16S-23S rDNA
211 intergenic spacer was carried out using 5'FAM labelled S-D-Bact-1522-B-S-20 (5'-TGC GGC TGG
212 ATC CCC TCC TT-3') and L-D-Bact-132-a-A-18 primers (5'-CCG GGT TTC CCC ATT CGG-3')
213 (Normand et al., 1996). The final reaction mix (25 μL) consisted of 1X PCR buffer (Promega),
214 1.5 mM MgCl_2 , 0.3 mg mL^{-1} bovine serum albumin (BSA), 5 % Dimethyl sulfoxide (DMSO),
215 200 μM of each deoxynucleoside triphosphate (Invitrogen), 0.5 μM of each primer (Invitrogen),
216 0.25 U of Taq polymerase (Promega) and 10 ng of template DNA at about $1 \text{ ng } \mu\text{L}^{-1}$. Amplification
217 was performed with a Thermocycler (Eppendorf AG). After an initial denaturation at 94°C for 5 min,
218 35 cycles of denaturation (94°C , 1 min), annealing (55°C , 1 min) and extension (72°C , 1 min) were
219 performed, followed by a final extension (72°C , 10 min). For each extracted DNA sample, triplicate
220 PCR assays were performed using 3 x 10 ng of template DNA. Amplification products of the three

221 assays were pooled and purified using QIAquick PCR Purification Kit (QIAGEN). Purified
222 amplification products were then quantified using the spectrophotometric method previously
223 described. Finally, 1.5 μL of amplification product adjusted by dilution to about $10 \text{ ng } \mu\text{L}^{-1}$ were
224 mixed with 0.1 μL GeneScan 1200 LIZ internal size standard (Applied Biosystems) and 10 μL Hi-Di
225 formamide (Applied Biosystems). The mixture was denatured at 94°C for 4 min and fragments were
226 discriminated using an ABI 3730XL automated sequencer (Applied Biosystems®) operated by the
227 *Plateforme Genome-Transcriptome Pierroton* (a joined facility of INRA and University of Bordeaux).
228 Resulting electrophoregrams were analysed using the Applied Biosystems® Peak Scanner software.
229 Peak sizes inferior to 200 bp and superior to 1200 bp were considered as background noise and
230 eliminated. Then, an “optimal divisor” (Od) was determined to remove fluorescence background
231 within remaining peaks (Osborne et al., 2006). Peaks contributing less than 0.1% (i.e. Od value) of the
232 total amplified DNA (as determined by relative fluorescence intensity) were indistinguishable from
233 baseline noise and eliminated. Binning was carried out under the R software (available on [http://cran.r-](http://cran.r-project.org)
234 [project.org](http://cran.r-project.org)) using the algorithm “Interactive binner” (available on <http://www.ecology-research.com> –
235 Ramette, 2009). This allowed for the assessment of the relative abundance of each Operational
236 Taxonomic Unit (OTU) in each sediment replicate. The ARISA fingerprinting method is based on
237 16S–23S ITS size. Since bacterial species have various numbers and types of ribosomic operons, there
238 is no simple relationship between the occurrences of a bacterial species and the number and types of
239 retrieved OTU (Hill et al., 2003). Moreover, PCR biases may distort OTU relative abundances
240 (Wintzingerode et al., 1997). It is nevertheless assumed that OTU richness and composition
241 realistically reflect bacterial taxonomic diversity (Forney et al. 2004) and support diversity pattern
242 analyses (Ramette, 2007). It is important to underline that ARISA only account for changes in OTU
243 relative abundances.

244

245 *2.3.2. Second series of experiments*

246 The aim of the second series of experiments (Fig. 1B) was to assess the effect of surface
247 sediment reworking on oxygen penetration within the sediment column. Oxygen microprofiles were
248 achieved on five aquaria containing individual worms after an incubation period of 20 days
249 (temperature: 16.0 ± 1.6 °C; salinity: 32.5 ± 0.8).

250 Four Unisense® A/S Clark-type microelectrodes (Revsbech, 1989; 100 µm sensor-tip
251 diameter, 90 % response time < 7 s, stirring sensitivity < 1) were positioned on a common holder
252 (forming a 2.5 cm side square) fixed on a MC-232, Unisense® motorized micromanipulator. These
253 microelectrodes were connected to a high-sensitivity Unisense® picoammeter. The whole system was
254 connected to a portable computer and controlled by the SensorTrace® PRO v3.0 software. Oxygen
255 profiles were performed with a vertical resolution of 100 µm and an equilibration time of 7 s down to
256 a 1 cm depth in the sediment column. Two to four sets of 4 profiles were achieved in each aquarium.
257 Overall, 13 micro-profiles were located in faecal mound areas, 18 in prospected areas and 21 in
258 undisturbed areas. Oxygen micro profiles were processed using the PRO2FLUX software (Deflandre
259 and Duchêne, 2010) to assess oxygen penetration depths.

260

261 *2.3.3. Third series of experiments*

262 The aims of the third series of experiments (Fig. 1C) were to further assess worm behaviors,
263 feeding ethology and time allocation patterns, and to quantify surface sediment reworking. Thirteen
264 worms were studied during this series (temperature: 13.5 ± 0.9 °C; salinity: 28.9 ± 1.8).

265 Methodologies for the assessments of feeding ethology, worm behaviors and time allocation patterns
266 were strictly similar to those used during the first series of experiments.

267

268 Surface sediment reworking rates were assessed for 5 individual worms (15.2 ± 5.0 mgWW)
269 through laser telemetry (Maire et al., 2008). This technique allowed for successive microtopography
270 mapping of the sediment surface, which were later compared to assess the volume of reworked

271 sediment during the time interval between two consecutive scans. Experimental aquaria were placed
272 under a set of motorized cross tables (401XR Parker® Hannifin precision linear positioners with 5 mm
273 ball screw) connected to Vix500 Microstepper Indexer Drives with XL-PSU power supplies. These
274 tables were computer controlled, which allowed for precise (i.e., $\pm 1.5 \mu\text{m}$) positioning (Duchêne,
275 2012). A laser telemeter (Sick OD80) was attached to the lower Y table. The raw data (in volts)
276 generated by the telemeter were converted in linear distances using an appropriate calibration (Maire
277 et al., 2007b). The whole system was used for assessing the microtopography of 5 cm side square
278 surfaces centered on tube openings and including faecal mound areas. Each scan was achieved within
279 a 20 min time period and with a $15 \mu\text{m}$ vertical resolution. Surface sediment reworking rates were
280 assessed by summing the differences in microtopography between two consecutive scans of the faecal
281 mound area divided by the time duration between the beginnings of these two scans. Positive
282 differences corresponded to an elevation, whereas negative ones corresponded to a digging of the
283 sediment-water interface. Overall, nine couples (1-3 for each worm) of consecutive (time interval
284 between 15 and 74.5 h) scans were achieved during this experiment.

285

286 *2.4. Data processing*

287 *2.4.1. Time allocation patterns.*

288 Time periods allocated to the different types of behaviors were assessed during the first and the
289 third series of experiments. A Kolmogorov-Smirnov test was performed to check for possible
290 differences in time allocation patterns between these two series.

291 *2.4.2. Main sediment characteristics.*

292 Changes in main sediment characteristics within undisturbed sediment, faecal mound and
293 prospected areas were described using a non-metric Multi Dimensional Scaling (nMDS; Clarke and
294 Warwick, 2001) based on untransformed data (i.e., median grain size, POC, PON, chlorophyll *a* and
295 phaeophytin *a*) and using Euclidean distance. Mud content was not used for this analysis because of its

296 strong redundancy with D50. The sediment characteristics mainly responsible for the difference
 297 between areas were identified using the SIMilarity PERcentage analysis (SIMPER) procedure (Clarke
 298 and Warwick, 2001). Differences in the values of each characteristic between areas were looked for
 299 using univariate Friedman ANOVAs for paired samples.

300 2.4.3. *Aerobic bacterial community composition.*

301 Aerobic bacterial community composition was described using nMDS (Clarke and Warwick,
 302 2001) based on untransformed data and Bray-Curtis dissimilarities. Significant differences between
 303 community composition were looked for using a multivariate One-Way PERMANOVA (Anderson,
 304 2001; McArdle and Anderson, 2001) with the three above-mentioned “sediment areas” as fixed factor.
 305 Bacterial diversity was assessed using the complementary of the Simpson index (1-D) and associated
 306 equitability ($E_{1/D}$) with:

$$307 \quad D = \sum_{i=1}^S p_i^2$$

$$308 \quad E_{1/D} = \frac{1/D}{S}$$

309 where p_i is the relative abundance of OTU i and S is OTU richness

310 Differences in the values of D and $E_{1/D}$ between areas were looked for using univariate
 311 Friedman ANOVAs for paired samples.

312 2.4.4. *Oxygen*

313 Significant differences between oxygen penetration depths between the three considered areas
 314 were looked for using a Friedman ANOVA for paired samples.

315 All statistics, except for Friedman ANOVAs (Excel®), were performed using the PRIMER® 6
 316 package (Clarke and Warwick, 2001) and its PERMANOVA add on (Anderson, 2001).

317

318 **3. RESULTS**319 *3.1. Anatomy of feeding organs and feeding ethology*

320 Examined worms bore from 11 to 15 tentacles (12.6 ± 1.3 mean \pm sd). Tentacles were
321 implanted side by side around the upper lip of the mouth (Fig. 3A and B). On the inner side of each
322 tentacle, a groove was densely covered with cilia (Fig. 3C and D). Tentacle outer side consisted in an
323 accordion shaped structure with only a few dispersed clumps of cilia (Fig. 3E). A particular structure
324 without cilia was present at the tip of each tentacle (Fig. 3F).

325 The position and the elevation of the anterior part of the tube varied between worms. On some
326 occasions, the anterior part of the tube was vertical and only slightly emerging from the sediment
327 surface. On some others, the anterior part of the tube was lying horizontal at the sediment surface.
328 None of the observed worms left their tube during our experiments. Moreover, worms did not always
329 stretch their anterior part out of the tube while feeding (Fig. 4A and B) but they occasionally did (Fig
330 4C). While feeding tentacle tips prospected the sediment surface. For worms 2.0 ± 0.2 cm in length,
331 everted tentacles stretched up to 3.9 ± 0.2 cm over the sediment surface and active tentacles could be
332 almost four times longer than resting ones. We did not notice any evidence of particle-size selection
333 on tentacles. Conversely, we observed that worms were able to detach mineral fragments of several
334 millimeters in size from the sediment and to transport them along the ciliary grooves of their tentacles
335 to their mouth. We only occasionally observed active tentacle retractions toward tube openings. We
336 also observed the presence of an area where large mineral particles were deposited near tube openings
337 (see the tip of the red arrow on Fig. 2B). In spite of numerous attempts using thin aquaria and/or
338 transparent substrates, we never observed the production of faeces within the sediment column (CM
339 personal observation). Faeces were violently expelled from the tube and catapulted on the sediment
340 surface ca 1 cm away from tube openings (Fig. 4D-F). This defecation mode resulted in the creation of
341 ca 1 cm high faecal mounds where we never observed prospection by tentacles while worms were
342 feeding.

343

344 *3.2. Typology of behaviors and time allocation pattern*

345 Seven types of behaviors were identified: (1) *Prospection* when tentacles explored the
346 sediment surface to collect particles and gills are visible outside the tube; (2) *Gill movements* when gill
347 waving could be seen outside the tube opening and when no tentacle is stretched; (3) *Head movements*
348 when head could be seen quickly entering or exiting the tube; (4) *Maintenance* when worms
349 agglomerated particles at the opening of the tube using their tentacles; (5) *Immobility* when gills were
350 visible outside the tube but remained immobile; (6) *Hidden in the tube* when worms were not visible at
351 all at the sediment surface; and (7) *Faeces egestion* which occurred concomitantly with the six above-
352 mentioned behaviors.

353 Time allocation patterns between behaviors did not significantly differ between the first and
354 the third series of experiments (Kolmogorov-Smirnov test, $p > 0.05$) allowing for the pooling of the
355 results of these two series. Overall, monitored individuals were active (i.e., all behavior types but
356 *Immobility* and *Hidden in the tube*) 89.5 ± 2.4 % of the time (Fig. 5). Otherwise, they were either
357 immobile (7.0 ± 8.9 % of the time) or hidden in their tube (3.5 ± 3.6 % of the time). During activity
358 phases, *Prospection* was by far the most dominant behavior (84.6 ± 10.1 % of the time); followed by
359 *Gill movements* (3.3 ± 3.8 % of the time); *Maintenance* (1.2 ± 1.2 % of the time); and *Head*
360 *movements* (0.4 ± 0.8 % of the time). *Faeces egestion* occurred on average every 45.4 ± 3.9 min.

361 *3.3. Surface sediment reworking*

362 During the first series of experiments, average total surface sediment reworked area increased
363 from 37 to 49 cm² between the beginning and the end of the “experiment periods” (Friedman ANOVA
364 for paired samples, $p < 0.01$). During the same time, average faecal mound surface increased from 9 to
365 22 cm² (Friedman ANOVA for paired samples, $p < 0.01$). Conversely, the average surface of the
366 prospected area remained stable at 28 cm² (Friedman ANOVA for paired samples $p > 0.10$). Changes
367 recorded for individual worms globally showed the same pattern with one exception characterized by a
368 transitory decline in total and prospected areas (Fig. 6).

369 An example of a microtopography scan taken during the third series of experiments is shown
370 in Fig.7. One can distinguish the faecal mound, which reaches 11 mm in height and a prospected area,
371 which extends down to 4 mm in depth relative to the undisturbed area. The average surface sediment
372 reworking rate ($+4.9 \cdot 10^{-6} \pm 1.3 \cdot 10^{-5} \text{ mm}^3 \text{ h}^{-1}$) and the mean change in the height of the undisturbed area
373 ($3.3 \cdot 10^{-7} \text{ mm}$) were negligible. Average surface sediment reworking rates were $-4.6 \pm 7.1 \text{ mm}^3 \text{ h}^{-1}$ and
374 $6.8 \pm 5.1 \text{ mm}^3 \text{ h}^{-1}$ in the prospected and the faecal mound areas, respectively. In the prospected area,
375 surface sediment reworking induced a sediment excavation of $1.9 \pm 0.2 \text{ mm}$ in average. Conversely, it
376 resulted in a mean elevation of the faecal mound area of $10.5 \pm 1.9 \text{ mm}$. Considering a simple surface
377 sediment transport between the prospected and the faecal mound areas, and the fact that the whole
378 prospected areas may not have been covered in totality by our scans, the average surface sediment
379 reworking rate of *M. palmata* was estimated to be $6.8 \text{ mm}^3 \cdot \text{h}^{-1}$.
380

381 3.4. Sediment characteristics and oxygen penetration depths

382 Overall, the granulometrical and main biochemical characteristics of surface sediments
383 significantly differed between the undisturbed sediment and the prospected and faecal mound areas
384 (multivariate One-Way PERMANOVA, $p < 0.05$; Fig. 8). The SIMPER analysis showed that POC
385 accounted for 59.2 % of the dissimilarity between faecal mound and prospected areas, to 62.8 % of the
386 dissimilarity between faecal mound areas and undisturbed sediments, and to 64.3 % of the
387 dissimilarity between prospected areas and undisturbed sediments. However, all characteristics
388 significantly differed between areas (Friedman ANOVA for paired samples, $p < 0.01$; Table 1).
389 Undisturbed sediments showed the finest mean D50 ($13.8 \pm 2.0 \mu\text{m}$), the second highest mud content
390 ($83.8 \pm 4.8 \%$), the highest mean POC and PON contents ($33.5 \pm 4.0 \text{ mg g}^{-1} \text{ DW}$ and $3.2 \pm 0.8 \text{ mg g}^{-1}$
391 DW , respectively) and the highest mean pigments contents ($1.4 \pm 0.5 \mu\text{g g}^{-1} \text{ DW}$ in chlorophyll *a* and
392 $6.8 \pm 2.3 \text{ mg g}^{-1} \text{ DW}$ in phaeophytin *a*). Conversely, prospected areas were characterized by the
393 coarsest sediment particles (D50 = $17.1 \pm 2.2 \mu\text{m}$, mud content = $76.6 \pm 3.9 \%$) the lowest mean POC
394 and PON contents ($27.0 \pm 5.4 \text{ mg g}^{-1} \text{ DW}$ and $2.2 \pm 0.7 \text{ mg g}^{-1} \text{ DW}$, respectively) and the lowest mean
395 pigment contents ($1.2 \pm 0.8 \mu\text{g g}^{-1} \text{ DW}$ of chlorophyll *a* (not significantly different from the faecal

396 mound area) and $4.0 \pm 2.3 \mu\text{g g}^{-1}\text{DW}$ of phaeophytin *a*, respectively). Faecal mound areas showed
397 intermediate D50 ($14.5 \pm 2.3 \mu\text{m}$), highest mud content ($84.3 \pm 4.6 \%$), mean POC and PON contents
398 ($30.0 \pm 3.6 \text{ mg g}^{-1} \text{ DW}$ and $2.7 \pm 0.6 \text{ mg g}^{-1} \text{ DW}$, respectively), and mean pigment contents
399 ($1.0 \pm 0.4 \mu\text{g g}^{-1}\text{DW}$ of chlorophyll *a* and $6.7 \pm 1.4 \mu\text{g g}^{-1}\text{DW}$ of phaeophytin *a*). Overall, there was a
400 clear opposition between D50 on one-side and POC and PON contents on the other side. This
401 opposition segregated most the three considered spatial areas. Changes in pigment contents were
402 largely independent and did not clearly differentiate these areas (Fig. 8).

403 Oxygen penetration depths significantly differed between areas (Friedman ANOVA for paired
404 samples, $p < 0.01$). Mean oxygen penetration depths were shallower in prospected areas ($4.0 \pm 0.1 \text{ mm}$)
405 than in undisturbed sediments ($4.9 \pm 0.2 \text{ mm}$) and in faecal mound areas ($7.2 \pm 0.4 \text{ mm}$).

406 3.5. *Aerobic bacterial community composition*

407 Overall, 296 OTUs were found, ranging from 200 to 1166 bp. In undisturbed sediments, we
408 recorded 209 OTUs ranging from 200 to 1032 bp, versus 218 ranging from 200 to 1032 bp in faecal
409 mound areas and, 238 ranging from 200 to 1166 bp in prospected areas. Mean values of 1-D
410 significantly differed between areas (Friedman ANOVA for paired samples, $p < 0.01$). They were lower
411 in undisturbed sediments (0.909 ± 0.043) than in faecal mound (0.938 ± 0.012) and prospected
412 (0.948 ± 0.012) areas. $E_{1/D}$ also significantly differed between areas (Friedman ANOVA for paired
413 samples, $p < 0.05$) with lower values in undisturbed sediments (0.177 ± 0.049) than in prospected
414 (0.220 ± 0.078) and faecal mound (0.234 ± 0.041) areas. Aerobic bacterial community composition
415 significantly differed between the three areas (multivariate One-Way PERMANOVA, $p < 0.05$ – Fig.
416 9). Within-group average Bray-Curtis similarity was 61.2 % in undisturbed sediments, 66.2 % in
417 faecal mound and 66.0 % in prospected areas. These values were clearly higher than between-groups
418 average similarities (i.e., 48.9 % between undisturbed sediments and faecal mound areas, 48.3 %
419 between undisturbed sediments and prospected areas, and 52.9 % between faecal mounds and
420 prospected areas).

421 4. Discussion

422 4.1. Anatomy of feeding organs and feeding ethology

423 The observations achieved during the present study allow refining the current knowledge
424 regarding the anatomy of the feeding organs and the feeding ethology in ampharetid polychaetes. Our
425 morphological observations confirm that the upper lip of *Melinna palmata*, which bears the tentacles
426 is eversible as already described in *Melinna pacifica* (Zhadan and Tzetlin, 2002). Conversely to what
427 had been previously observed for the terebellid *Eupolymnia nebulosa* (Grémare 1988), they showed:
428 (1) the accordion structure of the tentacle, and (2) the existence of a particular structure near the tip of
429 each tentacle that could possibly play the role of an adhesive cup.

430 Bacescu (1972) pictured the positioning of *M. palmata* while feeding. He described a tube, with a
431 posterior part vertically penetrating within the sediment column and an anterior part largely emerging
432 from the sediment surface, which is fastened obliquely by the worm when feeding at the sediment-
433 water interface. Jumars et al. (2015) described a more general pattern for tube positioning in
434 ampharetids with the posterior part of the tube curving down in the sediment and the anterior part
435 usually lying parallel to the sediment surface allowing for a horizontal posture of the worm with its
436 ventral side down. According to Bacescu (1972), while feeding, *M. palmata* “stretches out of the tube
437 spreading the tentaculate palate over the substratum”. Our own observations clearly show that there is
438 not a unique pattern of tube positioning. Most often, tube openings remained vertical only slightly
439 emerging from the sediment surface with worms positioned head up. On some occasions, however, we
440 observed anterior parts of the tube lying on the sediment surface. Interestingly, Buchanan (1963)
441 already reported vertical positioning of tube openings in dense populations of *Melinna cristata* and
442 Fauchald and Jumars (1979) related this positioning with the scarcity of available food. The lack of a
443 unique general pattern is true as well for the extension of worm outside of their tubes while feeding
444 since most of the time, only a few tentacles and the very extremities of the gills were visible at the
445 sediment surface. When everted, tentacles stretched up to ca 4 cm (for 2 cm long worms), which is
446 rather limited as is the case in ampharetids compared to terebellids (Warwick et al., 1986; Grémare,
447 1988; Jumars et al., 2015). While extended, tentacle tips prospected the sediment surface to collect

448 particles, which fully supports that ampharetids use their retractable and ciliated tentacles to pick up
449 food particles on the sediment surface (Fauchald and Jumars, 1979). Overall, and besides differences
450 in their number and extension, the functioning of the tentacles appeared very similar to the one
451 described for *Eupolyornia nebulosa* (Grémare, 1988; Maire et al., 2007a). However, an important
452 difference is that on some occasions we observed a combination of ciliary entrainments along and
453 muscular contractions of the tentacles to convey particles to the mouth as already reported for
454 *Hobsonia florida* (Taghon, 1982). Conversely to this author, we were, however, not able to observe
455 the retraction of mucous coated tentacles into the mouth. During our experiments, worms only
456 produced faeces at the water sediment interface, which has already been observed for several other
457 ampharetids (e.g. Nowell et al., 1984), including *M. palmata* (Olafsson et al., 1990). Faeces were
458 violently expelled from tubes, which resulted in the deposition of fresh faeces ca one centimeter away
459 from tube openings. Nowell et al. (1984) observed a similar pattern in the deep-sea ampharetid
460 *Amphicteis scaphobranchiata*. These authors described the expulsion mechanism, which includes
461 gills, mucous and body binding, and takes much less than 10 s (i.e., the time lag between the
462 acquisitions of two consecutive images during our own experiments). We were not able to depict this
463 process for *M. palmata* based on the experiments described in the present paper. However, other video
464 recordings show that worms bind their body prior egestion so that their pygidia are located close to
465 tube openings and directly expelled faeces (CM personal observation). According to Nowell et al.
466 (1984), faeces expulsion constitutes an adaptation to maintain a feeding pit, which enhances new
467 particle deposition within feeding area of individual *A. scaphobranchiata* living in the deep sea (see
468 also Taghon, 1982). This hypothesis is not necessarily appropriate for shallower ampharetids due to
469 stronger hydrodynamism. Moreover, in *M. Palmata* faecal pellets were expelled within the ca 4 cm
470 radius of prospected areas even though worms never actively transported particles from their faecal
471 mound area (see also below).

472

473 4.2. Evidence for and quantification of surface sediment reworking

474 Queiros et al. (2015) stated that *M. palmata* “is a tube-dweller exhibiting conveyor-belt transport
475 of particulates”. During our own experiments, we observed that faeces egestion only occurred at the
476 sediment-water interface. Together with the collection of surface particles by the tentacles, and the
477 lack of motility in ampharetids (Jumars et al., 2015; confirmed in the case of *M. palmata* by our own
478 observations), this is likely to result in mostly horizontal particle displacements at the sediment-water
479 interface and thus in surface sediment reworking.

480 To our knowledge, vertical sediment reworking by *M. palmata* has only been experimentally
481 quantified once through *ex situ* luminophore experiments and associated image analysis techniques
482 (Queiros et al., 2015). These authors reported vertical biodiffusion coefficients (DBs) less than $1\text{cm}^2\cdot\text{y}^{-1}$
483 ¹ with maximal penetration depth typically less than 2cm. Among the 4 species studied by Queiros et
484 al. (2015), *M. palmata* was clearly the one with the lowest DBs. Moreover, *M. palmata* was also the
485 only species not featuring any marked seasonal changes in DBs, thereby suggesting that its vertical
486 sediment reworking intensity is not cued by seasonally changing parameters but rather limited in itself.
487 Although caution should be taken when comparing DBs derived from different studies since their
488 assessments can be greatly affected both by technological (e.g. incubation duration, vertical
489 resolution...) and environmental parameters (e.g. temperature, food availability, animal density...),
490 this interpretation is further supported by the analysis of literature data regarding DBs derived from
491 luminophore experiments (see for example Maire et al., 2007c). The DBs found for *M. palmata*
492 (Queiros et al., 2015) are clearly among the lowest ever reported. They are for example much lower
493 than those reported for the deposit-feeding bivalve *Abra ovata* during summertime (i.e., up to ca
494 $31\text{cm}^2\cdot\text{y}^{-1}$ in the absence of food addition) and equivalent to those reported during wintertime when
495 this bivalve is considered almost totally inactive due to low temperature (Maire et al., 2007c; Fig.7).
496 Bernard et al. (2014) carried out a series of *in situ* luminophore experiments in both seagrass beds and
497 adjacent bare sediments within the Arcachon Bay where *M. palmata* is present. They reported a
498 significant negative correlation between *M. palmata* abundances and DBs and attributed this effect to
499 the stabilization of the sediment induced by dense populations of this species (Brenchley, 1982). Here

500 again, this supports weak vertical sediment reworking by *M. palmata*. Moreover, while running out
501 these experiments, Bernard (personal communication) observed the penetration of luminophores 2 to
502 4 cm deep in the sediment immediately following their introduction at the sediment surface. This was
503 attributed to passive transfers within the tubes of *M. palmata*. Similar transfers also likely occurred
504 within siphonal galleries during the *A. ovata* experiments mentioned above and probably partly
505 accounted for the decrease in Dbs with incubation duration reported by Maire et al. (2007c) during
506 their wintertime experiments. Anyhow, this type of potential artefactual luminophore penetration may
507 clearly contribute to an overestimation of (already weak) Dbs in *M. palmata*. Based on all this set of
508 rationale and our own observations, our conclusion is that *M. palmata* does not belong to any existing
509 functional group of sediment reworking. Indeed, the unique characteristics of the particle mixing of *M.*
510 *palmata*, conveying particles only on the sediment surface, led us to propose a new functional group of
511 sediment reworking: the surface conveyors. Further studies would validate this hypothesis.

512 Such a sediment reworking mode results in the zonation of the surface sediment in three distinct
513 areas: (1) faecal mounds resulting from faeces accumulation, (2) prospected areas that may be
514 conversely depressed relative to the general sediment surface (Nowell et al., 1984), and (3)
515 undisturbed sediments. Such a zonation has already been observed for several surface tentaculate
516 deposit-feeders (eg Nowell et al., 1984; Warwick et al., 1986) including *M. palmata* (Olafsson et al.,
517 1990). During the present study, we observed a radius of ca 4 cm (for 2 cm long worms) for
518 prospected areas, which is much higher than the 2 cm reported by Gibbs et al. (1981) for 25-35 mm
519 long worms. Conversely, the distances between tube openings and the areas of faeces deposition were
520 smaller during our experiments (i.e., typically close to 1cm) than the 4-5 cm reported by Olafsson et
521 al. (1990, Fig. 1) based on *in situ* observations of a Scottish *M. palmata* population. To our
522 knowledge, the only assessment of surface sediment excavation by an ampharetid is qualitative (i.e.,
523 several mm) for *Amphicteis scaphobranchiata* (Taghon, 1982), which is fully compatible with the 1.9
524 mm reported during the present study for time-limited experiments.

525 The use of laser telemetry to infer surface sediment reworking rates has only been introduced
526 recently (Maire et al., 2007b; Duchêne, 2012), and to our knowledge the only comparable surface
527 sediment reworking rates to ours are therefore those measured by Maire et al. (2007b) in the deposit-

528 feeding bivalve *Abra ovata*. These authors reported major short-term temporal changes in surface
529 sediment reworking rates in relation with the intensity of inhalant siphon activity. Nevertheless,
530 average values over 27 h time periods were equal or superior to $50 \text{ mm}^3 \cdot \text{h}^{-1}$, which is about 8 times the
531 average value (i.e., $6.8 \text{ mm}^3 \cdot \text{h}^{-1}$) found during the present study. Irrespective of differences in
532 experimental conditions that we did not control for, this suggests that the aspiration by sediment
533 siphons is a more efficient mechanism of surface deposit feeding than the use of tentacles. This is
534 supported by the comparison of the average proportions of time allocated to feeding in: (1) *M. palmata*
535 (84.6%, present study), (2) another surface tentaculate feeder the terebellidae *Eupolyornia nebulosa*
536 (74.2 %, Maire et al., 2007a), (3) *Abra ovata* (40.5 %, Grémare et al., 2004), and (4) *Abra nitida*
537 (54.6 %, Grémare et al., 2004). Duchêne and Rosenberg (2001) quantified the activity of *Melinna*
538 *cristata* at the surface of a large sediment core incubated *ex situ*. They also concluded to the
539 investment of a large proportion of time in (feeding) activity at the sediment-water interface by this
540 species. All these results/observations suggest that the meeting of nutritional requirements required
541 less time allocation in siphon than in tentaculate surface deposit-feeders although additional studies
542 are clearly required to further tackle this point.

543

544 4.3. Effect on surface sediment granulometry biochemical characteristics and oxygen penetration 545 depth

546 Sediment reworking by *Melinna palmata* induced an increase in the median size diameter (D50)
547 of surface sediment in prospected areas. It is not fully clear, however, whether this resulted from a
548 selection for finer particles or from the simple depletion of finer surface particles and then the
549 ingestion of coarser particles initially located slightly deeper in the sediment column. Positive
550 selection for finer particles by deposit-feeders has classically been put in relation with the optimal
551 foraging strategy (Taghon et al., 1978) and the fact that these particles are the one featuring the highest
552 organic matter content due to their higher surface/volume ratio (Mayer et al., 2004). Although, this
553 paradigm is currently under debate for deposit-feeders as a whole (see Jumars et al., 2015 for a
554 review), it is still generally accepted that surface tentaculate deposit feeders do indeed tend to

555 preferentially feed on particles smaller than the available median grain size (Jumars et al., 2015).
556 Moreover, it has been suggested that in this feeding guild, particle size selection is mostly mechanical
557 and results from three opposite processes taking place at the tips and along the tentacles (Jumars et al.,
558 1982), namely: (1) particle encounter by the tentacles, which would lead to a positive selection toward
559 larger particles according to the De Lesse's principle; (2) detachment of particles from the sediment,
560 which would result in a selection toward smaller particles because of their higher surface/volume ratio,
561 which better counteracts gravity forces; and (3) differential loss during the transfer of particles within
562 the ciliary groove to the mouth, which here again favors the selection of finer particles due to their
563 higher surface/volume ratio (Jumars et al., 1982) and to their quicker speed of displacement along the
564 tentacles (Maire et al., 2007a). This theoretical mechanical model of particle selection has been tested
565 on the terebellid *Eupolyornia nebulosa* (Grémare, 1988; Maire et al., 2007a). Based on: (1) direct
566 observations of natural particles transiting along the tentacles, and (2) comparison of particle size-
567 selection during feeding (with a positive selection for smaller particles) and tube building (with a
568 positive selection for larger particles), these authors concluded that tentacles are likely not the only
569 organs involved in particle-size selection and that another selection process probably occurs at the
570 level of the mouth as already observed in the spionid *Streblospio benedicti* (Kihlslinger and Woodin,
571 2000). During our own experiments, we did not notice any direct evidence of particle-size selection on
572 the tentacles, which proved able to transport particles several millimeters in size. Conversely, (1) the
573 presence of a structure that may potentially constitute an adhesive cup near the tip of each tentacle
574 may contribute to reduce the mechanical positive selection for finer particles during their detachment
575 from the sediment surface, (2) the limited maximal extension of the tentacles may also contribute to
576 limit the preferential loss of larger particles during their transit along the tentacles so as occasional
577 retraction of tentacles toward the mouth. Moreover, the occurrence of intermediate (i.e., between the
578 unaffected sediment and the prospected area) D50 in faecal mound areas suggests that the size of the
579 particles ingested by *M. palmata* may more rely on their availability at the sediment surface than on
580 their size. Conversely, the observation of the deposition of large mineral particles at the immediate
581 vicinity of tube openings supports the occurrence of a selection process after the transit of particles
582 along the tentacles. Indeed such accumulation probably does not result from the preferential egestion

583 of large inorganic particles (Jumars et al., 2015) since, during our experiments, faecal pellets were
584 catapulted away from tube openings (see above).

585 During the present study, we assessed two bulk characteristics of sedimentary organics, namely
586 POC and PON. Both parameters correlated negatively with D50, which at least partly reflects the
587 general negative relationship linking sediment grain size and associated organic matter concentrations
588 (Mayer et al., 2004; see above). Chlorophyll *a* and phaeophytin *a* are derived from (fresh or degraded,
589 respectively) plant materials and are therefore not representative of bulk sedimentary organics. During
590 the present study, changes in their concentrations were largely independent of those of D50, POC and
591 PON, which may reflect the fact that these concentrations result largely from the presence of
592 individual particles (e.g. diatoms and or plant-derived detritus) rather than from the coating of organic
593 matter to the surface of sediment grains. We identified POC as the parameter contributing most to
594 differences between undisturbed sediments, prospected and faecal mound areas. Chlorophyll *a* and
595 phaeophytin *a* concentrations contributed much less to these differences. Our conclusion is thus that
596 the main effect of *M. palmata* on the biochemical characteristics of surface sediment is quantitative
597 and probably mainly result from changes in sediment granulometry.

598 During the present study, mean oxygen penetration depths were between 4.0 (prospected areas)
599 and 7.2 mm (faecal mound areas). These values are slightly higher than those (i.e., typically between 2
600 and 4 mm) measured both *ex* and *in situ* at the Germanan site (Delgard, 2013; Rigaud et al., 2018).
601 Besides biological activity, the two main factors affecting oxygen penetration within the sediment
602 column are: (1) sediment granulometry, which largely controls sediment porosity and sediment
603 organic content, and (2) organic mineralization processes, which largely control oxygen consumption
604 in the sediment column. During the present study, deeper oxygen penetration were recorded in faecal
605 mound areas despite the fact that they presented intermediate D50 and bulk (i.e., POC and PON)
606 organic content. This may partly result from the fact that faecal mound areas are the ones showing the
607 lowest concentrations of chlorophyll *a*, which is representative of a highly labile component of
608 sedimented POM. Moreover, faecal mound areas are indeed basically constituted by large particle
609 aggregates (i.e., faecal pellets at different stages of dislocation; see Fig. 2 and 4), which are destroyed
610 during microgranulometrical analyses. Sediment microgranulometry measurements therefore probably

611 not constitute a sound proxy of sediment porosity in this particular case. Unfortunately, sediment
612 porosity was not directly assessed during the present study. A clear possibility is thus that sediment
613 porosity is especially high in faecal mound areas, which would also contribute to enhance oxygen
614 penetration within the sediment column.

615

616 4.4. Potential intraspecific interactions and food limitation in field populations

617 In the English Channel and the Celtic sea, the density of subtidal *Melinna palmata* populations
618 is typically only several hundred of individuals per meter square or less (Gage, 1972; Oyeneke, 1988;
619 Olafsson et al., 1990; Grehan, 1991; Dauvin et al., 2007). To our knowledge, the highest recorded
620 density was 1613 ind.m⁻² in the Bay of Morlaix (Ibanez and Dauvin, 1988). As for the Bay of Biscay,
621 the highest recorded density, except for the Arcachon Bay, is apparently 1000 ind.m⁻² (Cacabelos et
622 al., 2011). Several studies suggest that *M. palmata* populations positively respond to an enrichment in
623 fine particles and/or organic matter. Some populations have apparently benefited from the vicinity of a
624 local sewage output in the Bay of Brest (Guillou and Hily, 1983) and from an enrichment of the Bay
625 of Seine in fine particles (Dauvin et al., 2007). At a larger scale, the spread and the increase of *M.*
626 *palmata* during the 1970s in Romanian waters was attributed to an increase in the frequency of
627 phytoplanktonic blooms due to eutrophication (Gomoiu, 1982 cited by Grehan, 1991).

628 During the present study, worms were collected from a very dense (i.e., up to 6745 ind.m⁻²
629 during spring; Bernard et al., 2014) intertidal population associated with a *Zotera noltei* meadow.
630 These authors also reported high (i.e., up to 2000 ind.m⁻² during spring) densities in adjacent bare
631 sediments. To our knowledge, these densities are the highest ever reported for *M. palmata*. They
632 respectively correspond ca 1.5 and 5.0 cm² surfaces available per individual worm, respectively. These
633 values are much smaller than those of individual prospected areas measured during the present study
634 (i.e., mean value of 28 cm²), which suggests the occurrence of intraspecific interactions in the
635 populations of the Arcachon Bay. Massé (2014) assessed the effects of worm density on the feeding
636 ethology and time allocation patterns of *M. palmata* using the same methodologies as in the present
637 study. She reported that at high (i.e., >1184 ind.m⁻²) densities, worms did not only forage in

638 prospected areas but also in neighboring faecal mound areas. Together with the occurrence of lower
639 bulk sedimentary organics in prospected areas (see above), this change in feeding behavior tends to
640 suggest that food limitation may occur in field populations. Ampharetids are classified as discretely
641 motile by Jumars et al. (2015). However, the main mechanism involved in motility is tube elongation,
642 which apparently cannot take place in dense populations when tube anterior parts are vertical
643 (Fauchald and Jumars, 1979) as was most often the case during the present study and in the Germanan
644 *Z. noltei* meadow (Bernard, personal observations). In such cases, taking into account sediment
645 transport to feeding (i.e., prospected) areas is essential when elaborating foraging theories (Nowell et
646 al., 1984). In this context, it is worthwhile to notice that the two populations of the Arcachon Bay are
647 both intertidal, and that tidal currents probably contribute to sedimentary movements between
648 undisturbed sediments, prospected and faecal mounds areas thereby allowing for the continuous
649 renewal of the food resources available for *M. palmata*. Along the same line, the difference in
650 densities between the *Z. noltei* and the bare sediment populations may result from the enhancement of
651 particle trapping by seagrass meadows (Gacia et al., 1999; Gacia and Duarte, 2001; Hendricks et al.,
652 2008).

653 4.5. *Effect on aerobic bacterial community composition*

654 Many studies have assessed the effect of macrobenthic bioturbators on sediment bacteria (see
655 review in Table 2). These studies have concerned a large variety of macrobenthic species belonging to
656 different phyla. They have been carried out either *ex* or *in situ* and for some of them have involved
657 experimental incubations. They also differ by the parameters used to assess bacterial responses. Most
658 studies have dealt with abundance, biomass or viability assessments. As far as ampharetids are
659 concerned, the only available study is the one by Aller and Aller (1986) on *Amphicteis* sp. It has been
660 achieved *in situ* by sampling surface sediments around a single worm at a 4827m depth and has shown
661 an increase in surface sediment bacterial abundances from the prospected area to the tube insertion at
662 the sediment-water interface.

663 Studies assessing bacterial community composition have been mostly carried out *in situ* and
664 have involved samplings at different depths within the sediment column. Observed differences in

665 bacterial community composition thus potentially resulted from changes in oxygen and other electron
666 acceptors availabilities. Only several studies have tackled the effect of macrobenthic bioturbators on
667 bacterial community composition in surface oxygenated sediments. Most of them were however based
668 on the comparison of bacterial community composition in field stations (Bertics and Ziebis, 2009) or
669 experimental enclosures (Laverock et al., 2010) with different bioturbator densities but not from the
670 direct sampling of reworked and non-reworked surface sediments. Wilde and Plante (2002) directly
671 compared bacterial community composition in the faecal mounds of *Balaglonossus aurantiacus* and
672 ambient surface sediments. Based on functional parameters, they reported qualitative differences that
673 were transitory since microbial assemblage composition of degrading faeces rapidly converged with
674 those of ambient surface sediments. These patterns were interpreted as resulting from: (1) the
675 differential digestion of ingested bacteria, and (2) the stimulation/injection of non culturable bacteria
676 during gut passage.

677 Our own results also show that aerobic bacterial community composition differ in undisturbed
678 sediments, faecal mound and prospected areas by *Melinna palmata*. In this sense, they are in good
679 agreement with previous works based on spatial assessments of biogeochemical processes (Reichardt,
680 1988; Bertics and Ziebis, 2010; Bertics et al., 2010, 2012). As mentioned above, changes in sediment
681 bacterial community composition are often related to changes in oxygenation. Sediment reworking is
682 not the only activity of benthic macrofauna that can produce such changes. Hydraulic activities (i.e.,
683 the induction of water transports within biogenic structures and sediment interstices by benthic
684 macrofauna) could as well be involved (Woodin et al., 2010, 2016; Volkenborn et al., 2010).
685 However, several rationale suggest that this is probably not the case in *Melinna palmata*. As stated
686 above, the gills are most of the time out of the tube, and no ventilation behavior of the tube was
687 observed during the present experiments. Second, dedicated experiments using fluoresceine (Pascal et
688 al., 2016) have shown that bioirrigation rates are negligible (Massé, 2014). Third, the transfers of
689 water and inorganic solutes across the mucous lining of the tubes of *Melinna cristata* are clearly
690 inhibited (Hannides et al., 2005). Overall, our interpretation is that surface sediment reworking is thus
691 indeed responsible of the differences in aerobic bacterial community composition recorded during the
692 present study.

693 During our experiments, aerobic bacterial community composition seemed to differ most
694 between undisturbed sediments and prospected areas and were intermediate in faecal mound areas.
695 Diversity and equitability also tended to be lower in undisturbed sediments than in prospected and
696 faecal mound areas. This last result is in contradiction with those of Wilde and Plante (2002) who
697 reported a lower diversity in faecal mounds than in ambient sediments. Discrepancies between the two
698 studies may clearly result from differences in the methodological approaches used to assess bacterial
699 community composition. As far as the present study is concerned, higher bacterial diversity in faecal
700 mounds may result from: (1) the egestion of resident (i.e., enteric) bacteria (Harris, 1993), (2) quick
701 changes in faeces bacterial community composition in faeces as suggested by Wilde and Plante
702 (2002), which would result in the presence of different bacterial communities in faecal mounds, and
703 (3) the possible ingestion (and then the further egestion) of bacteria associated with the surface
704 sediment of prospected areas after excavation (see also the section of the discussion regarding the
705 effect on sediment granulometry). The occurrence of higher diversity in prospected areas than in
706 undisturbed sediments may result from the continuous disturbance experienced by the former due to
707 feeding by *M. palmata*. The intermediate disturbance hypothesis (IDH; Grime, 1973; Connell, 1978)
708 indeed predicts higher biodiversity in areas submitted to intermediate frequency of discrete disturbing
709 events. In prospected areas, the periodic removal of bacteria attached to organic particles from the
710 sediment surface might constitute such events. In the theoretical framework of IDH, the species
711 richness peak results from co-occurrence of K- and r-strategists (Mac Arthur and Wilson, 1967). These
712 concepts are still in debate for micro-organisms (Sousa, 1979), with special respect to general trends in
713 bacterial carbon use in ready biodegradability tests (Vásquez-Rodríguez et al., 2007) or soil
714 community (Fierer et al., 2007). For bacteria, K-strategist species might be slow growing, specialized,
715 exoenzyme producing so-called oligotrophic bacteria while r-strategist species might be fast growing,
716 generalist, opportunist so-called copiotrophic bacteria (Fierer et al., 2007). Accordingly, by removing
717 part of the bacterial biomass, *M. palmata* would promote an optimal degradation of the sediment
718 organic matter in the oxic layer. Further studies could take advantage in testing this hypothesis by
719 addressing community level substrate utilization in prospected areas.

720

721 **AKNOWLEDGMENTS**

722 Cécile Massé was supported by a doctoral fellowship from French *Ministère de*
723 *l'Enseignement Supérieur et de la Recherche*. We thank Isabelle Svahn from the Bordeaux Imaging
724 Center (BIC) – Electronic Microscopy Pole of the University of Bordeaux. We also thank Franck
725 Salin, head of *Plateforme Genome-Transcriptome Pierroton* (INRA, Bordeaux, France) for ARISA
726 analyses.
727

728 **REFERENCES**

- 729 Aller, R.C. 1994. Bioturbation and remineralization of sedimentary organic matter: effects of redox
730 oscillation. *Chem. Geol.* 114: 331-345
- 731 Aller, R.C., 2014. Sedimentary diagenesis, depositional environments, and benthic fluxes. In: Holland,
732 H.D. and Turekian K.K. (eds.) *Treatise on Geochemistry*, Second edition, vol. 8, pp. 293-334
- 733 Aller, J.Y., Aller, R.C., 1986. Evidence for localized enhancement of biological activity associated
734 with tube and burrow structures in deep-sea sediments at the HEBBLE site, western North Atlantic.
735 *Deep-sea res.* 33(6): 755:790
- 736 Aller, R.C., Aller, J.Y., 1998. The effect of biogenic irrigation intensity and solute exchange on
737 diagenetic reaction rates in marine sediments. *J. Mar. Res.* 56: 905-936
- 738 Aller, R.C., Yingst, J.Y., 1985. Effects of marine deposit feeders *Heteromastus filiformis* (Polychaeta),
739 *Macoma balthica* (Bivalvia) and *Tellina texana* (Bivalvia) on averaged sedimentary solute transport,
740 reaction rates, and microbial distributions. *J. Mar. Res.* 43: 615-645
- 741 Alongi, D.M., 1985. Microbes, meiofauna, and bacterial productivity on tubes constructed by the
742 polychaete *Capitella capitata*. *Mar. Ecol. Prog. Ser.* 23: 207-208
- 743 Andresen, M., Kristensen, E., 2002. The importance of bacteria and microalgae in the diet of the
744 deposit-feeding polychaete *Arenicola marina*. *Ophelia.* 56 (3): 179-196
- 745 Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral.*
746 *Ecol.* 26: 32-46
- 747 Bacescu, M.C., 1972. Substratum-Animals. In *Marine Ecology*, Vol. 1, part 3, edited by O. Kinne,
748 Wiley Interscience, New-York, 1291-1322
- 749 Bernard, G., Grémare, A., Maire, O., Lecroart, P., Meysman, F.J.R., Ciutat, A., Deflandre, B.,
750 Duchêne, J.C., 2012. Experimental assessment of particle mixing fingerprints in the deposit-feeding
751 bivalve *Abra alba* (Wood). *J. Mar. Res.* 70 : 689-718
- 752 Bernard, G., Delgard, M.L., Maire, O., Ciutat, A., Lecroart, P. Deflandre, B., Duchêne, J.C., Grémare,
753 A., 2014. A comparative study of sediment particles mixing in a *Zostera noltei* meadow and a bare
754 sediment mudflat. *Mar. Ecol. Prog. Ser.* 514: 71-86
- 755 Bertics, V.J., Ziebis, W., 2009. Biodiversity of benthic microbial communities in bioturbated coastal
756 sediments is controlled by geochemical microniches. *ISME J.* 3: 1269-1285
- 757 Bertics, V.J., Ziebis, W., 2010. Bioturbation and the role of microniches for sulfate reduction in
758 coastal marine sediments. *Environ. Microbiol.* 12(11): 3022-3034

- 759 Bertics, V.J., Sohm, J.A., Treude, T., Chow, C.E.T., Capone, D.G., Fuhrman, J.A., Ziebis, W., 2010.
760 Burrowing deeper into benthic nitrogen cycling: the impact of bioturbation on nitrogen fixation
761 coupled to sulfate reduction. *Mar. Ecol. Prog. Ser.* 409: 1-15
- 762 Bertics, V.J., Sohm, J.A., Magnabosco, C., Ziebis, W., 2012. Denitrification and nitrogen fixation
763 dynamics in the area surrounding an individual ghost shrimp (*Neotrypaea californiensis*) burrow
764 system. *Appl. Environ. Microbiol.* 78(11): 3864-3872
- 765 Bird, F.L., Boon, P.I., Nichols, P.D., 2000. Physicochemical and microbial properties of burrows of
766 the deposit-feeding Thalassinidean ghost shrimp *Biffarius arenosus* (Decapoda: Callinassidae).
767 *Estuar. Coastal Shelf S.* 51: 279-291
- 768 Blanchet, H., de Montaudouin, X., Lucas, A., Chardy, P., 2004. Heterogeneity of macrozoobenthic
769 assemblages within a *Zostera noltii* seagrass bed: diversity, abundance, biomass and structuring
770 factors. *Estuar. Coastal Shelf S.* 61: 111-123
- 771 Braeckman, U., Yazdani Foshtomi, M., Van Gansbeke, D., Meysman, F., Soetaert, K., Vincx, M.,
772 Vanaverbeke, J., 2014. Variable importance of macrofaunal functional biodiversity for
773 biogeochemical cycling in temperate coastal sediments. *Ecosystems.* 17: 720-737
- 774 Branch, G.M., Pringle, A., 1987. The impact of the sand prawn *Callinassa kraussi* Stebbing on
775 sediment turnover and on bacteria, meiofauna, and benthic microflora. *J. Exp. Mar. Biol. Ecol.* 107:
776 219-235
- 777 Brenchley, G.A., 1982. Mechanisms of spatial competition in marine soft-bottom communities. *J. Exp.*
778 *Mar. Biol. Ecol.* 60: 17-33
- 779 Buchanan, J.B., 1963. The bottom fauna communities and their sediment relationship off the coast of
780 Northumberland. *Oikos.* 14: 154-175
- 781 Burdige, D.J., 1993. The biogeochemistry of manganese and iron reduction in marine sediments.
782 *Earth-Sci. Rev.* 35: 249-284
- 783 Bussmann, I., Reichardt, W., 1991. Sulfate-reducing bacteria in temporarily oxic sediments with
784 bivalves. *Mar. Ecol. Prog. Ser.* 78: 97-102
- 785 Cacabelos, E., Moreira, J., Lourido, A., Troncoso, J.S., 2011. Ecological features of Terebellida fauna
786 (Annelida, Polychaeta) from Ensenada de San Simon (NW Spain). *Animal biodiversity and*
787 *conservation.* 34(1): 141-150
- 788 Clarke, K.R., Warwick, R.M., 2001. Change in marine communities: An approach to statistical
789 analysis and interpretation, 2nd edition, PRIMER-E, Plymouth
- 790 Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science.* 4355(199): 1302-1310

- 791 Cuny, P., Mirailles, G., Cornet-Barthaux, V., Acquaviva, M., Stora, G., Grossi, V., Gilbert, F., 2007.
792 Influence of bioturbation by the polychaete *Nereis diversicolor* on the structure of bacterial
793 communities in oil contaminated coastal sediments. Mar. Pollut. Bull. 54: 452-459
- 794 Dauvin, J.C., Dewarumez, J.M., Gentil, F., 2003. An up to date list of polychaetous annelids from the
795 English Channel. Cah. Biol. Mar. 44: 67-95
- 796 Dauvin, J.C., Ruellet, T., Thiebaut, E., Gentil, F., Desroy, N., Janson, A.L., Duhamel, S., Jourde, J.,
797 Simon, S., 2007. The presence of *Melinna palmata* (Annelida: Polychaeta) and *Ensis directus*
798 (Mollusca: Bivalvia) related to sedimentary changes in the Bay of Seine (English Channel, France).
799 Cah. Biol. Mar. 48: 391-401
- 800 Deflandre, B., Duchêne, J.C., 2010. PRO2FLUX - A software program for profile quantification and
801 diffusive O2 flux calculations. Environ. Modell. Softw. 25: 1059-1061
- 802 Delgard, M.L., 2013. Etude des effets et du rôle des herbiers à *Zostera noltii* sur la biogéochimie des
803 sédiments intertidaux. Thèse de Doctorat, Université de Bordeaux 213pp
- 804 Dobbs, F.C., Guckert, J.B., 1988a. *Callianassa trilobata* (Crustacea: Thalassinidea) influences
805 abundance of meiofauna and biomass, composition, and physiologic state of microbial communities
806 within its burrow. Mar. Ecol. Prog. Ser. 45: 69-79
- 807 Dobbs, F.C., Guckert, J.B., 1988b. Microbial food resources of the macrofaunal deposit feeder
808 *Ptychodera bahamensis* (Hemichordata: Enteropneusta). Mar. Ecol. Prog. Ser. 45: 127-136
- 809 Duchêne, J.C., 2012. Hydroid and serpulid recruitment patterns using a new laser microtopography
810 technique. J. Exp. Mar. Biol. Ecol. 412: 27-36
- 811 Duchêne, J.C., Rosenberg, R., 2001. Marine benthic faunal activity patterns on a sediment surface
812 assessed by video numerical tracking. Mar. Ecol. Prog. Ser. 223: 113-119
- 813 Fauchald, K., Jumars, P.A. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr.
814 Mar. Biol. Ann. Rev. 17: 193-284
- 815 Fauvel, P., 1927. Polychètes sédentaires, Faune de France, ed. Lechevalier, Paris, 494p
- 816 Fierer, N., Bradford, M., Jackson, R., 2007. Toward an ecological classification of soil bacteria.
817 Ecology. 88: 1354-1364
- 818 Fisher, M.M., Triplett, E.W., 1999. Automated approach for ribosomal intergenic spacer analysis of
819 microbial diversity and its application to freshwater bacterial communities. Appl. Environ.
820 Microbiol. 65: 4630-4636
- 821 Forney, L.J., Zhou, X., Brown, C.J., 2004. Molecular microbial ecology: land of the one-eyed king.
822 Curr. Opin. Microbiol. 7(3): 210-220

- 823 Froelich, P.N., Klinkhammer, G.P., Bender, M.L., Luedtke, N.A., Heath, G.R., Cullen, D., Dauphin,
824 P., Hammond, D., Hartman, B., Maynard, V., 1979. Early oxydation of organic matter in pelagic
825 sediments of the eastern equatorial Atlantic: suboxic diagenesis. *Geochim. Cosmochim. Ac.* 43:
826 1075-1090
- 827 Furukawa, Y., 2005. Biogeochemical consequences of infaunal activities. In *Interactions between*
828 *macro-and microorganisms in marine sediment*, Coastal and Estuarine Studies 60. American
829 Geophysical Union, Washington DC. 390p
- 830 Gacia, E., Granata, T.C., Duarte, C.M., 1999. An approach to measurement of particle flux and
831 sediment retention within seagrass (*Posidonia oceanica*) meadows. *Aquat. Bot.* 35: 255-268
- 832 Gacia, E., Duarte, C.M., 2001. Sediment retention by a Mediterranean *Posidonia oceanica* meadow:
833 the balance between deposition and resuspension. *Estuar. Coast. Shelf Sci.* 52: 505-514
- 834 Gage, J., 1972. Community structure of the benthos in Scottish sea-lochs. I. Introduction and species
835 diversity. *Mar. Biol.* 14: 281-297
- 836 Gibbs, P.E., Bryan, G.W., Ryan, K.P., 1981. Copper accumulation by the polychaete *Melinna*
837 *palmata*: an antipredation mechanism? *J. Mar. Biol. Assoc. UK.* 61: 707-722
- 838 Gilbert, F., Hulth, S., Strömberg, N., Ringdahl, K., Poggiale, J.C., 2003. 2-D optical quantification of
839 particle reworking activities in marine surface sediments. *J. Exp. Mar. Biol. Ecol.* 285-286: 251-263
- 840 Gilbertson, W.W., Solan, M., Prosser, J.I., 2012. Differential effects of microorganism-invertebrate
841 interactions on benthic nitrogen cycling. *FEMS Microbio. Ecol.* 82: 11-22
- 842 Gomoiu, M.T., 1982. On the populations of *Melinna palmata* Grube at the Romanian littoral of the
843 Black Sea. *Cercetari mar.* 15: 115-131
- 844 Goñi-Urriza, M., de Montaudouin, X., Guyoneaud, R., Bachelet, G., de Wit, R., 1999. Effect of
845 macrofaunal bioturbation on bacterial distribution in marine sandy sediments, with special reference
846 to sulphur-oxidising bacteria. *J. Sea. Res.* 41: 269-279
- 847 Grehan, A.J., 1991. Demography and reproductive biology of *Melinna palmata* (Ampharetidae:
848 Polychaeta) in inner Galway Bay on the west coast of Ireland. *Mar. Biol.* 109: 459-467
- 849 Grémare, A., 1988. Feeding, Tube-building and particle-size selection in the terebellid *Eupolyornia*
850 *nebulosa*. *Mar. Biol.* 97: 243-252
- 851 Grémare, A., Duchêne, J.C., Rosenberg, R., David, E., Desmalades, M., 2004. Feeding behavior and
852 functional response of *Abra ovata* and *A. nitida* compared by image analysis. *Mar. Ecol. Prog. Ser.*
853 267: 195-208
- 854 Grime, J.P., 1973. Competitive exclusion in Herbaceous vegetation. *Nature.* 242(5396): 344-347

- 855 Grossman, S., Reichardt, W., 1991. Impact of *Arenicola marina* on bacteria in intertidal sediments.
856 Mar. Ecol. Prog. Ser. 77: 85-93
- 857 Guillou, M., Hilly, C., 1983. Dynamics and biological cycle of *Melinna palmata* (Ampharetidae)
858 population during the recolonisation of a dredged area in the vicinity of the harbour of Brest
859 (France). Mar. Biol. 73: 43-50
- 860 Hannides, A.K., Dunn, S.M., Aller, R.C., 2005. Diffusion of organic and inorganic solutes through
861 macrofaunal mucus secretions and tube linings in marine sediments. J. Mar. Res. 63: 975-981
- 862 Hansen, K., King, G.M., Kristensen, E., 1996. Impact of the soft-shell clam *Mya arenaria* on sulfate
863 reduction in an intertidal sediment. Aquat. Microb. Ecol. 10: 181-194
- 864 Harris, J.M., 1993. The presence, nature, and role of gut microflora in aquatic invertebrates: a
865 synthesis. Microb. Ecol. 25: 195-231
- 866 Hendricks, I.E., Sintes, T., Bouma, T.J., Duarte, C.M., 2008. Experimental assessment and modeling
867 evaluation of the effects of the seagrass *Posidonia oceanica* on flow and particle trapping. Mar. Ecol.
868 Prog. Ser. 356: 163-173
- 869 Hewitt, J.E., Trush, S.F., Dayton, P.D., 2008. Habitat variation, species diversity and ecological
870 functioning in a marine system. J. Exp. Mar. Biol. Ecol. 366: 116-122.
- 871 Hill, T.C., Walsh, K.A., Harris, J.A., Moffett, B.F., 2003. Using ecological diversity measures with
872 bacterial communities. FEMS. Microbiol. Ecol. 43: 1-11
- 873 Holthe, T., 1986. Polychaeta Terebellomorpha. Marine invertebrates of Scandinavia 7.
874 Universitetsforlaget, Oslo. 194p
- 875 Ibanez, F., Dauvin, J.C., 1988. Long-term changes (1977 to 1987) in a muddy fine sand *Abra alba* –
876 *Melinna palmata* community from the Western English Channel: multivariate time series analysis.
877 Mar. Ecol. Prog. Ser. 49: 65-81
- 878 Jumars, P.A., Self, R.F.L., Nowell, A.R.M., 1982. Mechanics of particle selection by tentaculate
879 deposit feeders. J. Exp. Mar. Biol. Ecol. 64: 47-70
- 880 Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of worms emended: an update of Polychaete
881 feeding guilds. Annu. Rev. Mar. Sci. 7: 497-520
- 882 Kennedy, P., Kennedy, H., Papadimitriou, S., 2005. The effects of acidification on the determination
883 of organic carbon, total nitrogen and their stable isotopic composition in algae and marine sediment.
884 Rapid Commun. Mass. Spectrom. 19: 1063-1068
- 885 Kinoshita, K., Wada, M., Kogure, K., Furota, T., 2008. Microbial activity and accumulation of organic
886 matter in the burrow of the mud shrimp, *Upogebia major* (Crustacea: Thalassinidea). Mar. Biol.
887 153:277-283

- 888 Kihlsinger, R.L., Woodin, S.A., 2000. Food patches and a surface deposit feeding spionid polychaete.
889 Mar. Ecol. Prog. Ser. 201: 233-239
- 890 Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O., Banta G.T., 2012.
891 What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar. Ecol.
892 Prog. Ser. 446: 285-302
- 893 Laverock, B., Smith, C.J., Tait, K., Osborn, A.M., Widdicombe S., Gilbert, J.A., 2010. Bioturbating
894 shrimp alter the structure and diversity of bacterial communities in coastal marine sediments. ISME
895 J. 4: 1531-1544
- 896 Laverock, B., Kitidis, V., Tait, K., Gilbert, J.A., Osborn, A.M., Widdicombe, S., 2013. Bioturbation
897 determines the response of benthic ammonia-oxidizing microorganisms to ocean acidification. Phil.
898 Trans. R. Soc. B. 368: 20120441
- 899 Laverock, B., Tait, K., Gilbert, J.A., Osborn, A.M., Widdicombe, S. 2014. Impacts of bioturbation on
900 temporal variation in bacterial and archaeal nitrogen-cycling gene abundance in coastal sediments.
901 Environ. Microb. Rep. 6(1): 113-121
- 902 Lohrer, A.M., Trush, S.F., Hunt, L., Hancock, N., Lundquist, C., 2005. Rapid reworking of subtidal
903 sediments by burrowing spatangoid urchins. J. Exp. Mar. Biol. Ecol. 321: 155-169
- 904 Mac Arthur, R., Wilson, E.O., 1967. The theory of Island biogeography. Princeton University press.
- 905 Maire, O., Duchêne, J.C., Amouroux, J.M., Grémare, A., 2007a. Activity patterns in the terebellid
906 polychaete *Eupolyornia nebulosa* assessed using a new image analysis system. Mar. Biol. 151: 737-
907 749
- 908 Maire, O., Duchêne, J.C., Bigot, L., Grémare, A., 2007b. Linking feeding activity and sediment
909 reworking in the deposit-feeding bivalve *Abra ovata* with image analysis, laser telemetry and
910 luminophore tracers. Mar. Ecol. Prog. Ser. 351: 139-150
- 911 Maire, O., Duchêne, J.C., Grémare, A., Malyuga, V.S., Meysman, F.J.R., 2007c. A comparison of
912 sediment reworking rates by the surface deposit-feeding bivalve *Abra ovata* during summertime and
913 wintertime, with a comparison between two models of sediment reworking. J. Exp. Mar. Biol. Ecol.
914 343: 21-36
- 915 Maire, O., Lecroart, P., Meysman, F., Rosenberg, R., Duchêne, J.C., Grémare, A., 2008.
916 Quantification of sediment reworking rates in bioturbation research: a review. Aquat. Biol. 2: 219-
917 238
- 918 Maire, O., Merchant, J.N., Bulling, M., Teal, L.R., Grémare, A., Duchêne, J.C., Solan, M., 2010.
919 Indirect effects of non-lethal predation on bivalve activity and sediment reworking. J. Exp. Mar.
920 Biol. Ecol. 395: 30-36

- 921 Massé, C., 2014. Effets de la bioturbation sur la diversité des communautés bactériennes du sédiment.
922 Approches expérimentales et *in-situ*. De *Melinna palmata* aux communautés de la vasière Ouest-
923 Gironde. PhD thesis, university of Bordeaux, 268pp
- 924 Matsui, G.Y., Ringelberg, D.B., Lovell, C.R., 2004. Sulfate-reducing bacteria in tubes constructed by
925 the marine infaunal polychaete *Diopatra cuprea*. Appl. Environ. Microb. 70(12): 7053-7065
- 926 Mayer, L.M., Schick, L.L., Hardy, K.R., Wagai, R., McCarthy, J., 2004. Organic matter in small
927 mesopores in sediments and soils. Geochim. Cosmochim. Ac. 68(19): 3863-3872
- 928 McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on
929 distance-based redundancy analysis. Ecology. 82(1): 290-297
- 930 Mermillod-Blondin, F., Rosenberg, R., François-Carcaillet, F., Norling, K., Mauclaire, L., 2004.
931 Influence of bioturbation by three benthic infaunal species on microbial communities and
932 biogeochemical processes in marine sediment. Aquat. Microb. Ecol. 36: 271-284
- 933 Mermillod-Blondin, F., François-Carcaillet, F., Rosenberg, R., 2005. Biodiversity of benthic
934 invertebrates and organic matter processing in shallow marine sediments: an experimental study. J.
935 Exp. Mar. Biol. Ecol. 315: 187-209
- 936 Michaud, E., Desrosiers, G., Aller, R.C., Mermillod-Blondin, F., Sundby, B., Stora, G., 2009. Spatial
937 interactions in the *Macoma balthica* community control biogeochemical fluxes at the sediment
938 surface and microbial abundances. J. Mar. Res. 67: 43-70
- 939 Neveux, J., Lantoiné, F., 1993. Spectrofluorimetric assay of chlorophylls and phaeopigments using the
940 least squares approximation technique. Deep sea research 40(1): 1747-1765
- 941 Normand, P., Ponsonnet, C., Nesme, X., Neyra, M., Simonet, P., 1996. ITS analysis of prokaryotes. In
942 Molecular Microbial Ecology Manual. Section 3.4.5, pp1-12. Edited by Akkermans, A.D.L., van
943 Elsas, J.D., and De Bruijn, F.J. Dordrecht: Kluwer.
- 944 Nowell, A.R.M., Jumars, P.A., Fauchald, K., 1984. The foraging strategy of a subtidal and deep-sea
945 deposit feeder. Limnol. Oceanogr. 29(3): 645-649
- 946 Olafsson, E., Moore, C.G., Bett, B.J. 1990. The impact of *Melinna palmata* Grube, a tube-building
947 polychaete, on meiofaunal community structure in a soft-bottom subtidal habitat. Estuar. Coast.
948 Shelf. Sci. 31: 883-893
- 949 Osborne, C.A., Rees, G.N., Bernstein, Y., Janssen, P.H., 2006. New threshold and confidence
950 estimates for terminal restriction length polymorphism analysis of complex bacterial communities.
951 Appl. Environ. Microbiol. 72(2): 1270-1278
- 952 Oyekan, J.A., 1988. Population dynamics and secondary production in *Melinna palmata*
953 (Polychaeta: Ampharetidae). Mar. Biol. 98: 247-251

- 954 Papaspyrou, S., Gregersen, T., Cox, R.P., Thessalou-Legaki, M., Kristensen E., 2005. Sediment
955 properties and bacterial community in burrows of the ghost shrimp *Pestarella tyrrhena* (Decapoda:
956 Thalassinidea). *Aquat. Microb. Ecol.* 38: 181-190
- 957 Papaspyrou, S., Gregersen, T., Kristensen, E., Christensen, B., Cox, R.P., 2006. Microbial reaction
958 rates and bacterial communities in sediment surrounding burrows of two nereidid polychaetes
959 (*Nereis diversicolor* and *N. virens*). *Mar. Biol.* 148: 541-550
- 960 Pascal, L., Maire, O., Volkenborn, N., Lecroart, P., Bichon, S., de Montaudouin, X., Grémare A.,
961 Deflandre, B., 2016. Influence of the mud shrimp *Upogebia pusilla* (Decapoda: Gebiidea) on solute
962 and porewater exchanges in an intertidal seagrass (*Zostera noltei*) meadow of Arcachon Bay: an
963 experimental assessment. *J. Exp. Mar. Biol. Ecol.* 477: 69-79
- 964 Pischedda, L., Poggiale, J.C., Cuny, P., Gilbert, F., 2008. Imaging oxygen distribution in marine
965 sediments. The importance of bioturbation and sediment heterogeneity. *Acta Biotheor.* 56: 123-135
- 966 Pischedda, L., Militon, C., Gilbert, F., Cuny, P., 2011. Characterization of specificity of bacterial
967 community structure within the burrow environment of the marine polychaete *Hediste (Nereis)*
968 *diversicolor*. *Res. Microbiol.* 162: 1033-1042
- 969 Queiros, A.M., Stephens, N., Cook, R., Ravaglioli, C., Nunes, J., Dashfield, S., Harris, C., Tilstone,
970 G.H., Fishwick, J., Braeckman, U., Somerfield, P.J., Widdicombe, S., 2015. Can benthic community
971 structure be used to predict process of bioturbation in real ecosystems? *Prog. Oceanogr.* 137: 559-569
- 972 Ramette, A., 2007. Multivariate analyses in microbial ecology. *FEMS. Microbiol. Ecol.* 62(2): 142-
973 160
- 974 Ramette, A., 2009. Quantitative community fingerprinting methods for estimating the abundance of
975 operational taxonomic units in natural microbial communities. *Appl. Environ. Microb.* 75: 2495-2505
- 976 Reichardt, W., 1988. Impact of bioturbation by *Arenicola marina* on microbiological parameters in
977 intertidal sediments. *Mar. Ecol. Prog. Ser.* 44: 149-158
- 978 Revsbech, N.P., 1989. An oxygen microsensor with a guard cathode. *Limnol. Oceanogr.* 34(2): 474-
979 478
- 980 Rhoads, D.C., 1974. Organism-sediment relations on the muddy sea floor. *Oceanogr. Mar. Biol. Annu.*
981 *Rev.* 12: 263-300
- 982 Rigaud, S., Deflandre, B., Maire, O., Bernard, G., Duchêne, J.C., Poirier, D., Anschutz, P., 2018.
983 Transient biogeochemistry in intertidal sediments: New insights from tidal pools in *Zostera noltei*
984 meadows of Arcachon Bay (France). *Mar. Chem.* 200: 1-13

- 985 Rosenberg, R., Grémare, A., Duchêne, J.C., Davey, E., Franck, M., 2008. 3D visualization and
986 quantification of marine benthic biogenic structures and particle transport utilizing computer-aided
987 tomography. *Mar. Ecol. Prog. Ser.* 363: 171-182
- 988 Rouse, G., Pleijel, F., 2001. *Polychaetes*. Oxford University Press, Oxford. 354p
- 989 Shen, H., Jiang, G., Wan, X., Li, H., Qiao, Y., Trush, S., He, P., 2017. Response of the microbial
990 community to bioturbation by benthic macrofauna on intertidal flats. *J. Exp. Mar. Biol. Ecol.* 488:
991 44-55
- 992 Sousa, W.P., 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of
993 species diversity. *Ecology*. 60: 1225-1239
- 994 Steward, C.C., Nold, S.C., Ringelberg, D.B., White, D.C., Lovell, C.R., 1996. Microbial biomass and
995 community structures in the burrows of bromophenol producing and non-producing marine worms
996 and surrounding sediments. *Mar. Ecol. Prog. Ser.* 133: 149-165
- 997 Taghon, G.L., Self, R.F.L., Jumars, P.A., 1978. Predicting particle selection by deposit feeders: a
998 model and its implications. *Limnol. Oceanogr.* 23(4): 752-759
- 999 Taghon, G.L., 1982. Optimal foraging by deposit-feeding invertebrates: roles of particle size and
1000 organic coating. *Oecologia*. 52: 295-304
- 1001 Vázquez-Rodríguez, G.A., Garabetian, F., Rols, J.L., 2007. Inocula from activated sludge for ready
1002 biodegradability testing: homogenization by preconditioning. *Chemosphere*. 68(8): 1447-1454
- 1003 Volkenborn, N., Polerecky, L., Wetthey, D.S., Woodin, S.A., 2010. Oscillatory porewater bioadvection
1004 in marine sediments induced by hydraulic activities of *Arenicola marina*. *Limnol. Oceanogr.* 55(3):
1005 1231-1247
- 1006 Wada, M., Urakawa, T., Tamaki, A., 2016. Dynamics of bacterial community structure on intertidal
1007 sandflat inhabited by the ghost shrimp *Nihonotrypaea harmandi* (Decapoda: Axiidae:
1008 Callianassidae) in Tomioka Bay, Amakusa, Japan. *Gene* 576: 657-666
- 1009 Warwick, R.M., Gee, J.M., Berge, J.A., Ambrose, W.J., 1986. Effects of the feeding activity of the
1010 polychaete *Streblosoma bairdi* (Malmgren) on meiofaunal abundance and community structure.
1011 *Sarsia* 71(1): 11-16
- 1012 Wenzhöfer, F., Glud, R.N., 2004. Small-scale spatial and temporal variability in coastal benthic O₂
1013 dynamics: Effects of fauna activity. *Limnol. Oceanogr.* 49(5): 1471-1481
- 1014 Wheatcroft, R.A., Jumars, P.A., Smith, C.R., Nowell, A.R.M., 1990. A mechanistic view of the
1015 particulate biodiffusion coefficient: Step lengths, rest periods and transport directions. *J. Mar. Res.*
1016 48: 177-207

- 1017 Wheatcroft, R.A., 1991. Conservative tracer study of horizontal sediment mixing rates in a bathyal
1018 basin, California borderland. *J. Mar. Res.* 49: 565-588
- 1019 Wilde, S.B., Plante, C.J., 2002. Spatial heterogeneity of bacterial assemblages in marine sediments:
1020 the influence of deposit feeding by *Balaglonossus aurantiacus*. *Estuar. Coast Shelf S.* 55: 97-107
- 1021 Wintzingerode von F., Göbel, U.B., Stackebrandt, E., 1997. Determination of microbial diversity in
1022 environmental samples: pitfalls of PCR-based rRNA analysis. *FEMS. Microbiol. Rev.* 21(3): 213-
1023 229
- 1024 Woodin, S.A., Wethey, D.S., Volkenborn, N., 2010. Infaunal hydraulic ecosystem engineers: cast of
1025 characters and impacts. *Integr. Comp. Biol.* 50(2): 176-187
- 1026 Woodin, S.A., Volkenborn, N., Pilditch, C.A., Lohrer, A.M., Wethey, D.S., Hewitt, J.E., Trush, S.F.,
1027 2016. Same pattern, different mechanism: locking onto the role of key species in seafloor ecosystem
1028 process. *Sci. Rep.* 6:26678
- 1029 Yazdani Foshtomi, M., Braeckman, U., Derycke, S., Sapp, M., Van Gansbeke, D., Sabbe, K.,
1030 Willems, A., Vincx, M., Vanaverbeke, J., 2015. The link between microbial diversity and nitrogen
1031 cycling in marine sediments is modulated by macrofaunal bioturbation. *PLOS One* 10(6): e0130116.
1032 doi:10.1371/journal.pone.0130116
- 1033 Zaabi, S., Alfi, A., 2006. Significations écologiques de la variabilité des polychaetes dans le golfe de
1034 Tunis. *Bull. Inst. Natu. Scien. Tech. Mer de Salammbô.* 33: 29-36
- 1035 Zhadan, A.E., Tzetlin, A.B., 2002. Comparative morphology of the feeding apparatus in the
1036 Terebellida (Annelida: Polychaeta). *Cah. Biol. Mar.* 43: 149-164
- 1037 Zhou, S., Bruns, M.A., Tiedje, J.M., 1996. DNA recovery from soils of diverse composition. *Appl.*
1038 *Environ. Microbiol.* 62: 316-322
- 1039

1040 **Figure legends:**

1041 Fig. 1: General flowcharts of the three series of experiments carried out during the present study.

1042 Fig. 2: *First series of experiments*. Top views of the sediment surface after reworking by *Melinna*
1043 *palmata*; A & B differ by the location of the faecal mound relative to the tube opening. FM: Faecal
1044 Mound area; PA: Prospected Area; TO: Tube Opening; US: Undisturbed Sediment. The red arrow
1045 shows large the accumulation of large mineral particles near the tube opening.

1046 Fig. 3: Picture of the buccal cavity and the tentacles of *Melinna palmata* obtained by stereomicroscopy
1047 (A) and scanning electron microscopy (B - F). Gi: gills; T: tentacles; L: lip; Bc: buccal cavity; As:
1048 Accordion structure; Gr: ciliary groove; Tip: tip of the tentacle; Ci: cilia.

1049 Fig. 4: *First and third series of experiments*. Examples of images showing the different positions of
1050 the tube and the tentacles at the sediment-water interface (A-C) and sequence of 3 consecutive images
1051 picturing defaecation (D-F). A: The tube is vertical and only the tube opening can be seen; B-C: The
1052 anterior part of the tube is lying on the sediment surface, the gills of the worm are visible outside the
1053 tube in C; D: Positioning of the worm just before defecation; E: Expulsion of the faeces (yellow
1054 arrow) from the tube; F: Location of the newly deposited faeces (yellow arrow) away from the tube
1055 opening. CF: Catapulted Faeces, F: Faeces, G: Gills, NDF: Newly Deposited Faeces, T: Tube, TO:
1056 Tube Opening. Red dots indicate the particle movements detected along the tentacles.

1057 Fig. 5: *First and third series of experiments*. Time allocation pattern of *Melinna palmata* between its
1058 different behaviors. Vertical bars are standard deviations.

1059 Fig. 6: *First series of experiments*. Temporal changes in the: (A) total surface of reworked sediment,
1060 (B) surface of the faecal mound area, and (C) surface of the prospected area by individual worms(see
1061 text for details). Each symbol corresponds to an individual worm.

1062 Fig. 7: *Third series of experiments*. Example of a microtopography scan. FM: Faecal Mound, PA:
1063 Prospected Area.

1064 Fig. 8: *First series of experiments*. nMDS plot based the granulometrical and biogeochemical
1065 characteristics of surface sediments (see text for details).

1066 Fig. 9: *First series of experiments*. nMDS plot based on aerobic bacterial community composition (see
1067 text for details).

1068

Fig. 1

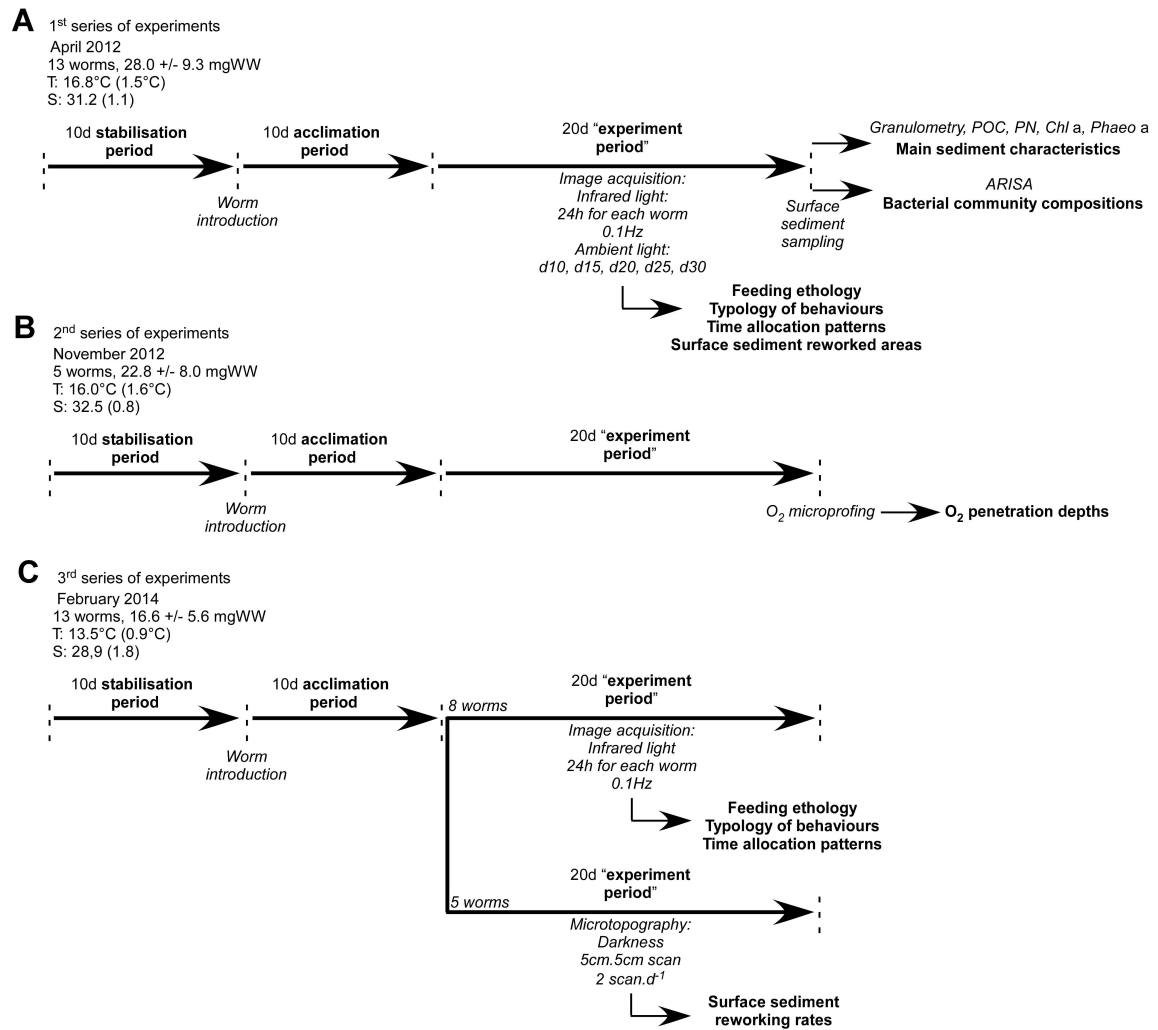


Fig. 2

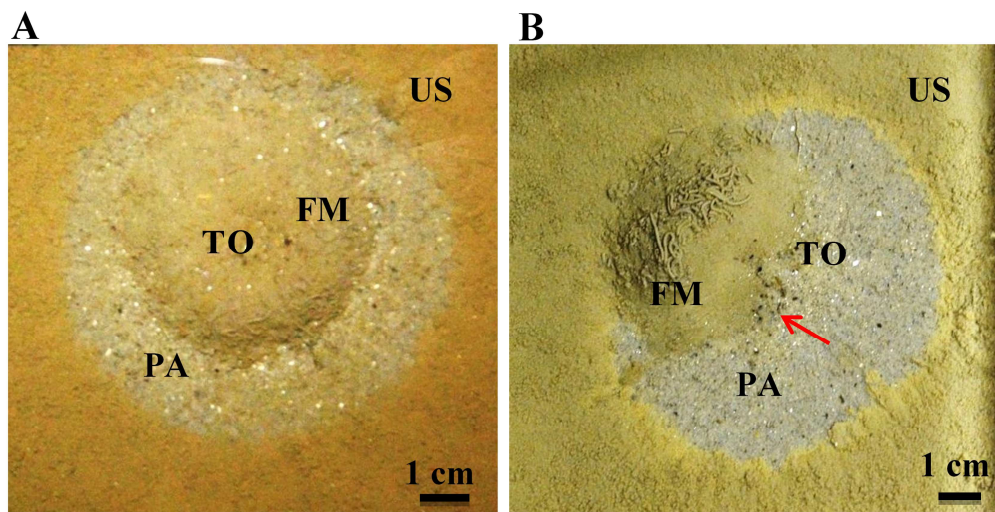
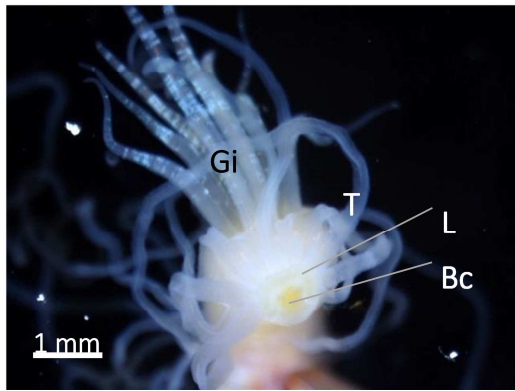
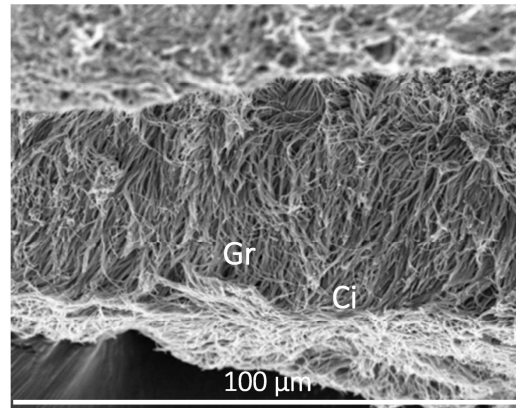


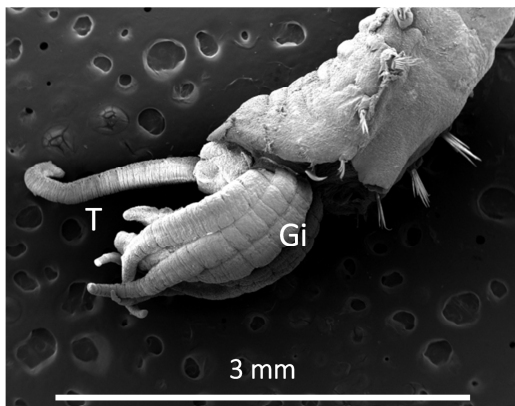
Fig. 3



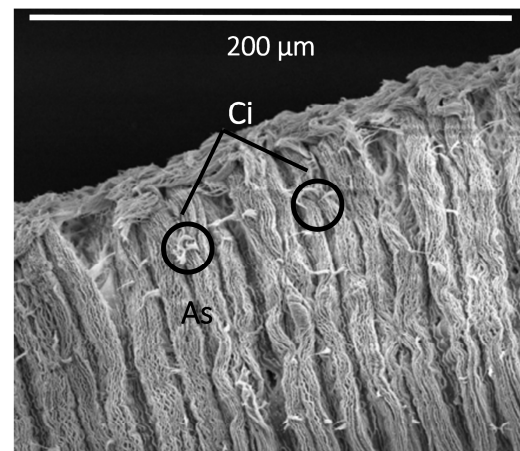
A: Mouth with tentacles and gill crown in background



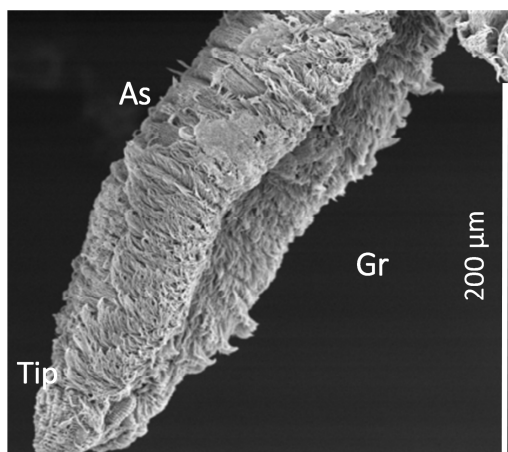
D: Ciliary groove on the inner side of a tentacle



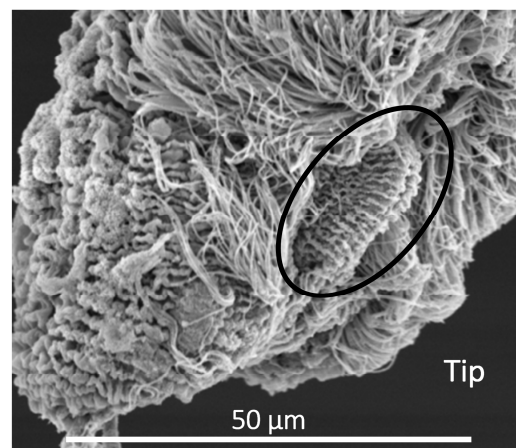
B: Head on lateral view with gills and a tentacle



E: Accordion structure on the outer side of a tentacle



C: Tip of a tentacle showing the ciliary groove and the accordion structure



F: Particular structure close to the tip of a tentacle

Fig. 4

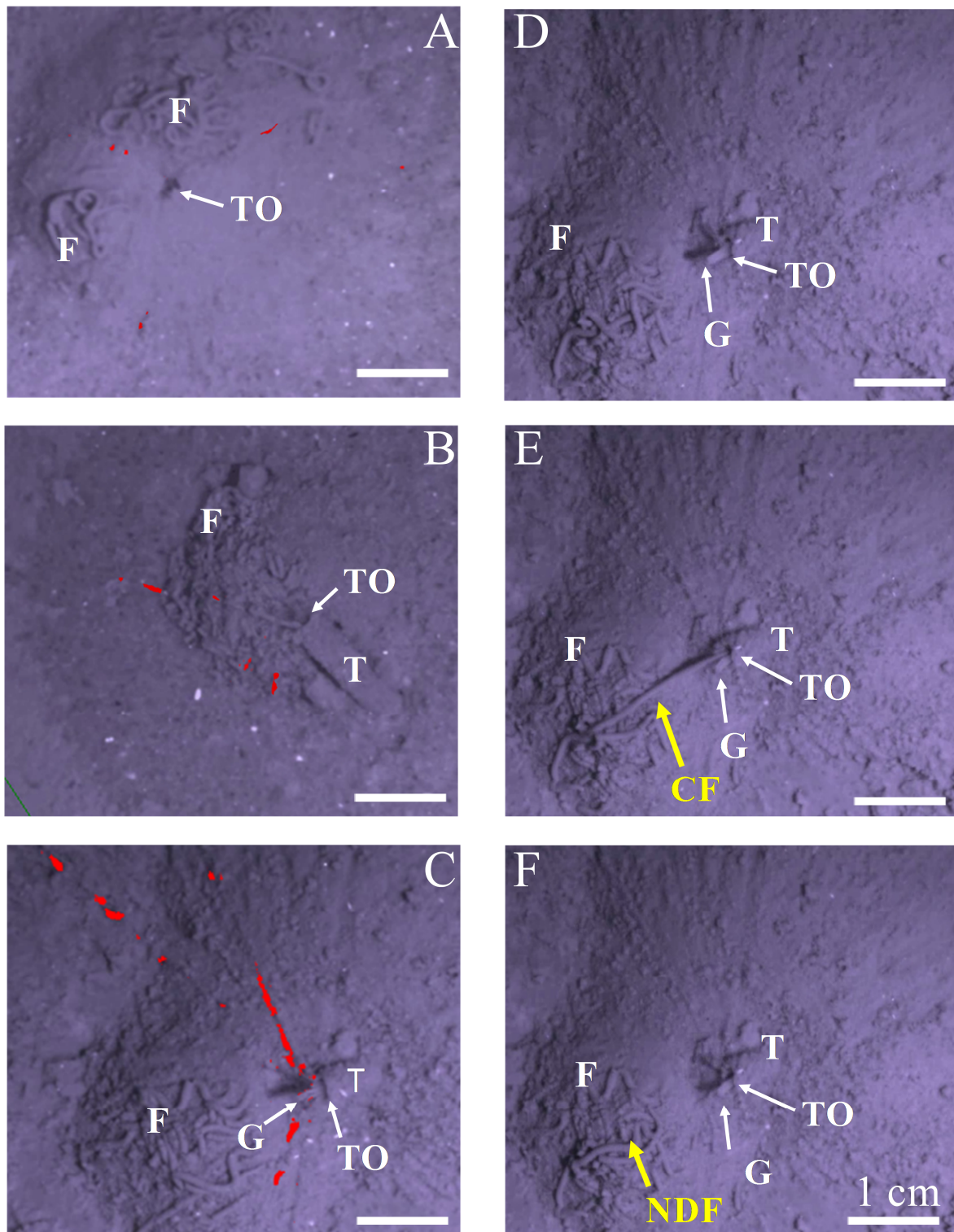


Fig. 5

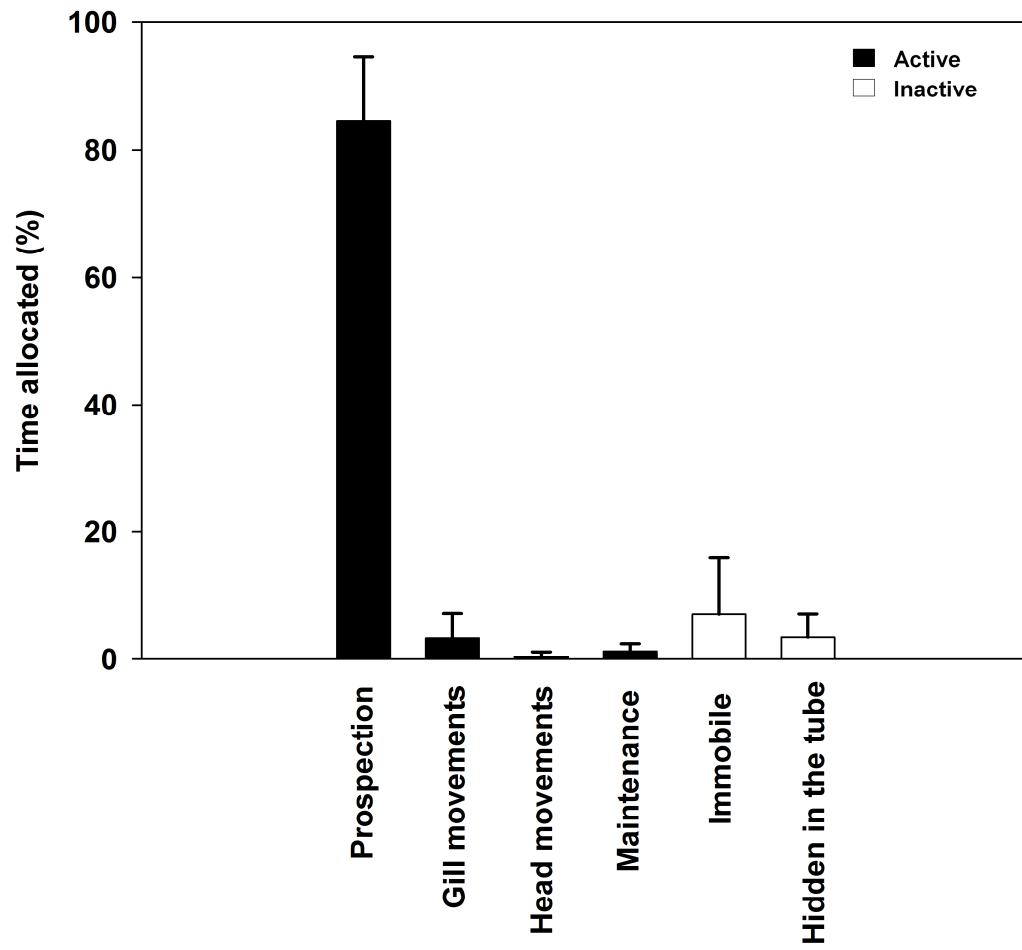


Fig. 6

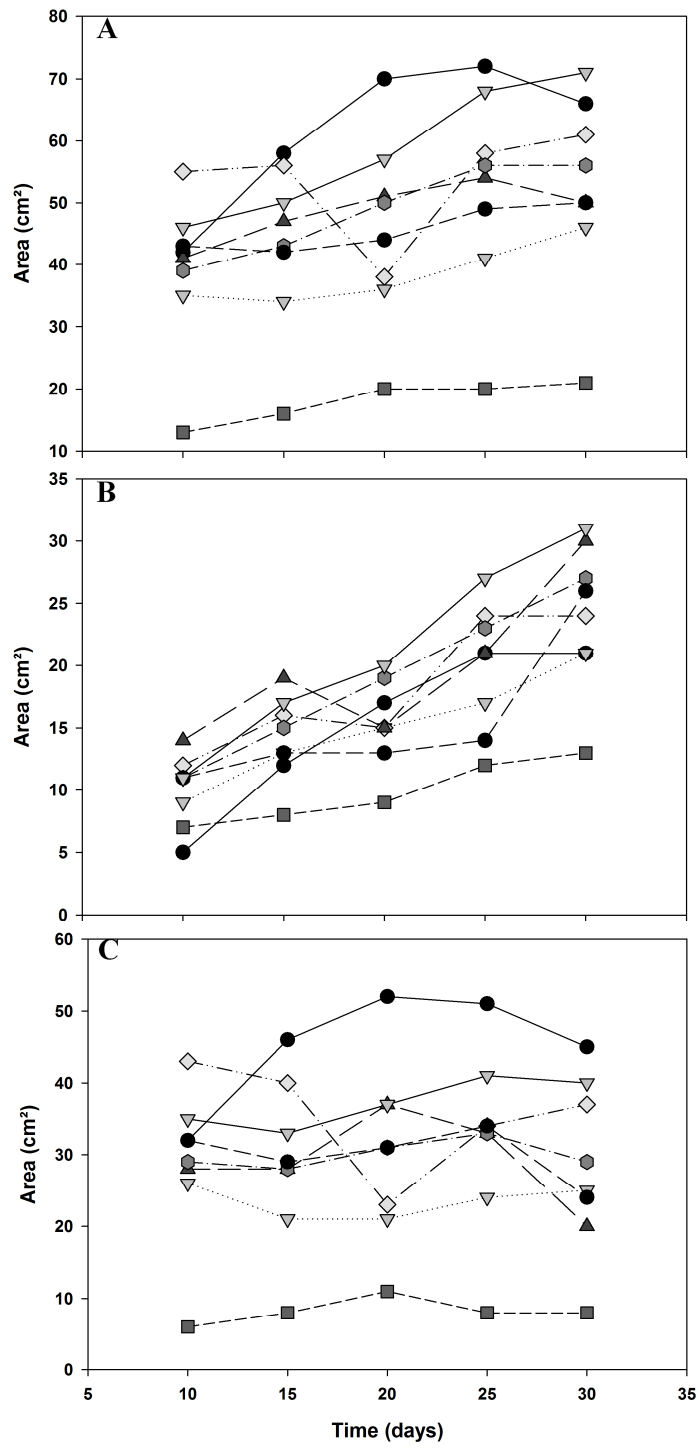


Fig. 7

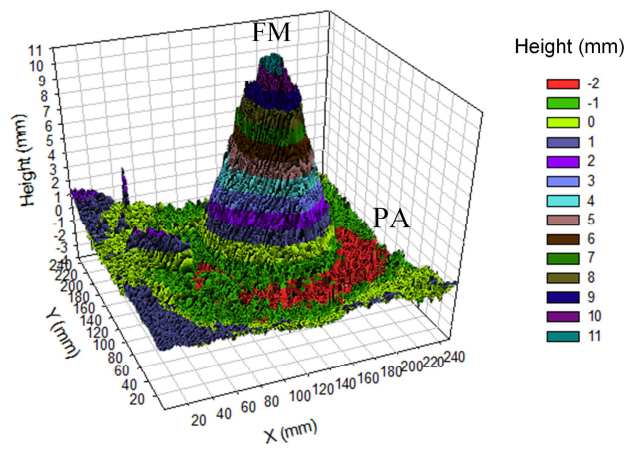


Fig. 8

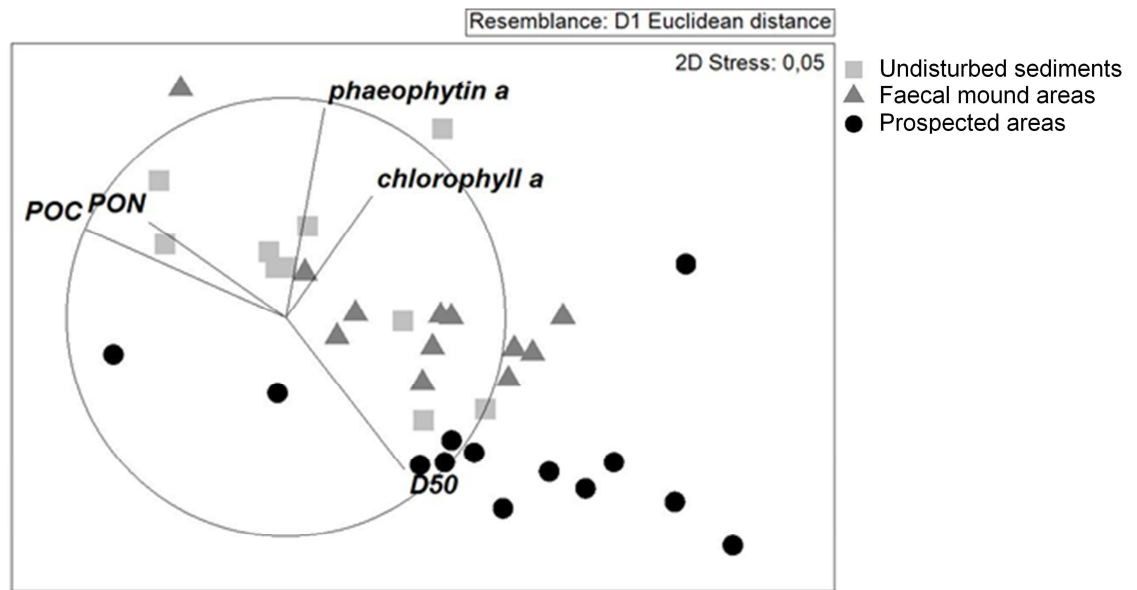


Fig.9

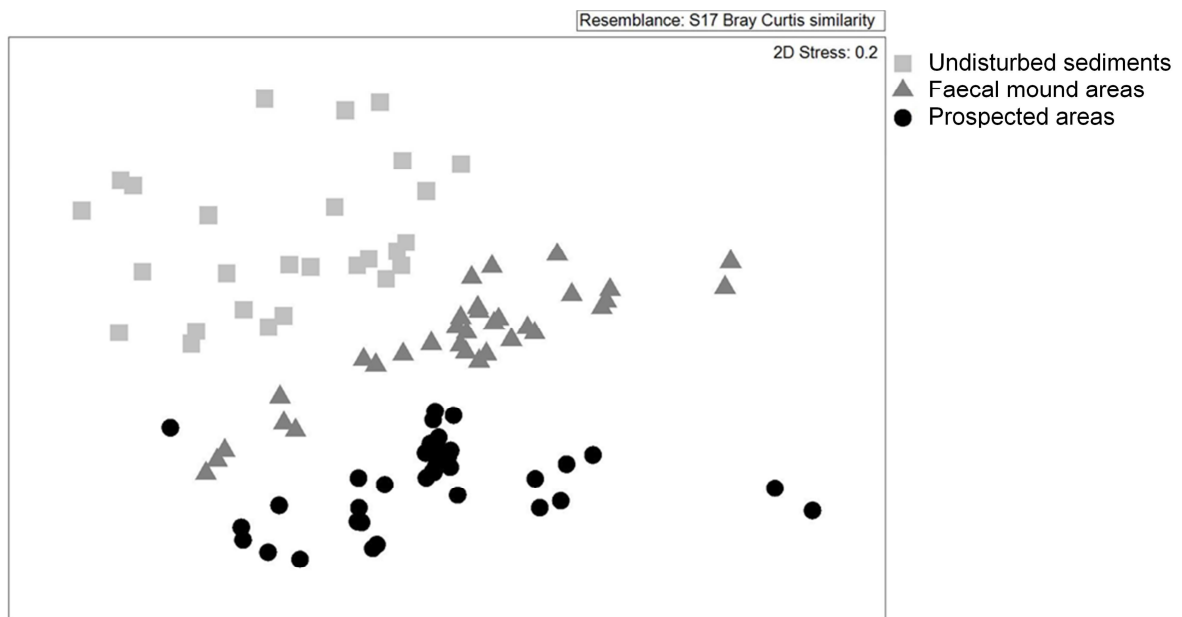


Table legends:

Table 1: Mean \pm Standard deviation of several parameters measured in the three areas defined by the sediment reworking of *Melinna palmata*: median grain size (D50), mud content, chlorophyll and phaeophytin *a*, particulate organic carbon (POC) and nitrogen (PON) and oxygen penetration depth

Table 2: Review of studies on effects of macrofaunal bioturbation on bacterial abundance, biomass, activity or composition with the bioturbator used and the study type. Each number refers to a reference

TABLE 1

	Series of experiments	Mean \pm Std. Dev.		
		Undisturbed sediments	Prospected areas	Faecal mound areas
D50 (μm)	1	13.8 \pm 2.0	17.1 \pm 2.2	14.5 \pm 2.3
Mud content (% volume)	1	83.8 \pm 4.8	76.6 \pm 3.9	84.3 \pm 4.6
Chlorophyll <i>a</i> ($\mu\text{g/g}$ DW)	1	1.4 \pm 0.5	1.2 \pm 0.8	1.0 \pm 0.4
Phaeophytin <i>a</i> ($\mu\text{g/g}$ DW)	1	6.8 \pm 2.3	4.0 \pm 2.3	6.7 \pm 1.4
POC (mg/g DW)	1	33.5 \pm 4.0	27.0 \pm 5.4	30.0 \pm 3.6
PON (mg/g DW)	1	3.2 \pm 0.8	2.2 \pm 0.7	2.7 \pm 0.6
Oxygen penetration depth (mm)	2	4.9 \pm 0.2	4.0 \pm 0.1	7.2 \pm 0.4

1 TABLE 2

Bioturbators	Study type		Effect on bacteria				Studied layers	
	<i>Ex-situ</i> (Experimental)	<i>In-situ</i>	Abundance Biomass Viability	Production	Activity	Composition	Depth (gradient, burrow vs ambient)	Surface (horizontal gradient)
Polychaeta								
<i>Alitta virens</i>	14	12	12, 14			12	12, 14	
<i>Amphicteis</i> sp.		3	3				3	3
<i>Arenicola marina</i>		4, 5, 7, 11	4, 5, 7, 11		4		4, 5, 7, 11	4, 11
<i>Branchioasiscus americana</i>		6	6			6	6	
<i>Capitella capitata</i>	2		2	2			Tubes (2)	
<i>Diopatra cuprea</i>		9	9			9	Tubes (9)	
<i>Hediste diversicolor</i>	8, 10, 13	12, 15	8,10, 12		8, 10	12, 13, 15	8, 10, 12, 13, 15	
<i>Heteromastus filiformis</i>	1		1				1	
<i>Notomastus lobatus</i>		6	6			6	6	
<i>Perinereis aibuhitensis</i>		33	33			33	33	
Bivalvia								
<i>Arctica atlantica</i>	16		16				16	
<i>Cerastoderma edule</i>	8, 10	7	7, 8, 10		8, 10		7, 8, 10	
<i>Macoma balthica</i>	1, 14		1, 14				1, 14	
<i>Meretrix meretrix</i>		33	33			33	33	
<i>Mya arenaria</i>	14	17	14, 17		17		14, 17	
<i>Tellina texana</i>	1		1				1	
Crustacea								
<i>Biffarius arenosus</i>		26	26		26	26	26	
<i>Callianassa kraussi</i>								
<i>Callianassa subterranea</i>	19					19	19	19
<i>Callianassa trilobata</i>		28	28			28	28	
<i>Corophium volutator</i>	8, 10		8, 10		8, 10		8, 10	
<i>Neotrypaea californiensis</i>	23, 24, 25	22, 24, 25	22		23, 24, 25	22, 24	22	22, 23, 24, 25
<i>Nihonotrypaea harmandi</i>		32	32			32	32	
<i>Pestarella tyrrhena</i>		18	18			18	18	
<i>Uca crenulata</i>		22	22			22	22	22
<i>Upogebia deltaura</i>	21	20	20, 21		21	19	20, 21	19
<i>Upogebia major</i>	28	28	28		28		28	
Hemichordata								
<i>Balaglonossus aurantiacus</i>		6, 30	6, 30		30	6	6	30
<i>Ptychodera bahamensis</i>		31	31			31		31

2 1: Aller and Yingst, 1985; 2: Alongi, 1985; 3: Aller and Aller, 1986; 4: Reichardt, 1988; 5: Grossman and Reichardt, 1991; 6: Steward et al., 1996; 7: Goñi-Urriza et
3 al., 1999; 8: Mermillod-Blondin et al., 2004; 9: Matsui et al., 2004; 10: Mermillod-Blondin et al., 2005; 11: Andresen and Kristensen, 2002; 12: Papaspyrou et al.,
4 2006; 13: Cuny et al., 2007; 14: Michaud et al., 2009; 15: Pischedda et al., 2011; 16: Busmann and Reichardt, 1991; 17: Hansen et al., 1996; 19: Papaspyrou et al.,
5 2005; 19: Laverock et al., 2010; 20: Laverock et al., 2014; 21: Laverock et al., 2013; 22: Bertics and Ziebis, 2009; 23: Bertics and Ziebis 2010; 24: Bertics et al.,
6 2010; 25: Bertics et al., 2012; 26: Bird et al., 2000; 27: Dobbs and Guckert 1988a; 28: Kinoshita et al., 2003; 29: Branch and Pringle, 1987; 30: Wilde and Plante,
7 2002; 31: Dobbs and Guckert, 1988b; 32: Wada et al., 2016; 33: Shen et al., 2017

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