



HAL
open science

Antagonistic impacts of benthic bioturbator species: Interconnected effects on sedimentary properties, biogeochemical variables, and microbial dynamics

Jérôme Morelle, A. Huguet, A. Richard, Anniet M. Laverman, C. Roose-Amsaleg, Edith Parlanti, Mahaut Sourzac, Valérie Mesnage, N. Lecoq, Julien Deloffre, et al.

► To cite this version:

Jérôme Morelle, A. Huguet, A. Richard, Anniet M. Laverman, C. Roose-Amsaleg, et al.. Antagonistic impacts of benthic bioturbator species: Interconnected effects on sedimentary properties, biogeochemical variables, and microbial dynamics. *Journal of Experimental Marine Biology and Ecology*, 2024, 573, pp.152000-152000. 10.1016/j.jembe.2024.152000 . hal-04477915

HAL Id: hal-04477915

<https://hal.science/hal-04477915v1>

Submitted on 29 May 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 **Title:** Antagonistic impacts of benthic bioturbator species: interconnected effects on sedimentary
2 properties, biogeochemical variables, and microbial dynamics

3
4 **Authors:** J. Morelle^{1,7*}, A. Huguet³, A. Richard⁴, A.M. Laverman², C. Roose-Amsaleg², E. Parlanti⁴, M. Sourzac⁴,
5 V. Mesnage⁵, N. Lecoq⁵, J. Deloffre⁵, E. Viollier⁶, O. Maire⁴ and F. Orvain¹

6
7 **Affiliations:**

8 ¹ Univ. Caen, FRE 2030 BOREA, CNRS-7208, IRD-207, MNHN, Sorbonne Université, UCBN, UA. Caen, France

9 ² Univ. Rennes, CNRS, ECOBIO [(Ecosystèmes, biodiversité, évolution)] - UMR 6553, Rennes, France

10 ³ Sorbonne Université, CNRS, EPHE, PSL, UMR 7619 METIS, Paris, France

11 ⁴ Univ. Bordeaux, CNRS, EPOC, EPHE, UMR 5805, F-33600 Pessac, France

12 ⁵ Normandie Univ, UNIROUEN, UNICAEN, CNRS, M2C, 76000 Rouen, France

13 ⁶ IPGP, Paris, France

14 ⁷ Present address: Department of Biology and CESAM – Centre for Environmental and Marine Studies, University
15 of Aveiro, Campus de Santiago, Aveiro, 3810-193, Portugal

16 * Corresponding author: jerome.morelle@ua.pt ; ORCID: 0000-0003-2167-818X

17
18 **Abstract:**

19 Macrofaunal species inhabiting intertidal mudflats and performing intense bioturbation are considered as
20 ecosystem engineers, since they profoundly influence their physical, chemical, and biological environments.
21 Nowadays, to complete our knowledge on the effect of bioturbation processes on the surrounding environment,
22 interdisciplinary approach is essential to unravel their complex intertwined effects on intertidal mudflats. In this
23 study, the effects of bioturbators on sediment properties, biogeochemical variables, and microbial dynamics
24 (microphytobenthos, bacteria and archaea) were investigated. To this end, manipulation experiments were carried
25 out in an intertidal mudflat of the Seine Estuary (France) by revamped the abundance of the two dominant
26 bioturbators, *Scrobicularia plana* and *Hediste diversicolor*, in winter and late summer. Results showed that the
27 presence of *H. diversicolor* in winter had a significant effect, with a significant increase in bed level accretion and
28 microbial nitrate reduction rates. In contrast, the presence of *S. plana* showed no significant impact on sediment
29 properties, most likely due to a reduced bioturbating activity at low temperature. In summer, both ecosystem
30 engineers strongly influenced their surrounding environment but with opposite effects. The intense reworking of
31 the sediment surface by *S. plana* limited microbial growth and enhanced erosion processes. Conversely, the
32 presence of *H. diversicolor* favoured sediment accretion and enhanced microbial growth. Overall, this
33 interdisciplinary study confirms the importance of these two ecosystem engineers in temperate estuarine mudflats
34 by highlighting their simultaneous and intertwined effects on the sedimentary, physicochemical, and biological
35 features. This confirms the importance of actively considering ecosystem engineers when restoring the natural
36 habitats of tidal flats to cope with the different vulnerability risks related to global warming (sandification of
37 estuarine sediments, disappearance of productive mudflats, sea level rise, vulnerability to storms and erosion).

38
39 **Keywords:** biogeochemical cycles; ecosystem engineers; microbial communities; microphytobenthos; organic
40 matter; sediment

41 1. Introduction

42 Intertidal mudflats comprise a diverse range of sedimentary habitats that serve as nursery and refuge areas
43 for various migratory and resident species, and play a crucial role in the biogeochemical processes of estuaries and
44 coastal ecosystems (Paterson et al. 2019). In these systems, microphytobenthic biofilms (MPB) represent the main
45 primary producer, supporting a complex trophic network where benthic invertebrates are the primary food source
46 for valuable consumers, such as fish and shorebirds (Dauwe et al. 1998; Underwood and Kromkamp 1999).
47 Moreover, MPB plays an essential role in biogeochemical dynamics and sediment stabilization through the
48 secretion of extracellular polymeric substances (EPS) (Stal 2010; Hope et al. 2020).

49 The growth and productivity of MPB are influenced by various environmental factors (Underwood and
50 Kromkamp 1999). In nutrient rich ecosystems, MPB productivity is mainly driven by the strong variation in light
51 intensity at the sediment surface (Behrenfeld et al. 2004; Cartaxana et al. 2011) and the substantial seasonal
52 variation in temperature impacting both MPB and biochemical reactions (Raven and Geider 1988; Davison 1991;
53 Claquin et al. 2008). Nevertheless, nutrient concentrations at the water-sediment interface, influenced by water
54 fluxes and organic matter (OM) mineralization through microbial respiration, continue to exert a discernible
55 influence on MPB (Aller and Cochran 2019), along with salinity, pH, oxygen levels, currents, and sediment
56 properties (Underwood and Kromkamp 1999; Juneau et al. 2015; Redzuan and Underwood 2021). Finally,
57 biological disturbances of the sediment-water interface (i.e. especially through macrofaunal bioturbation) may lead
58 to drastic changing in sediment abiotic conditions, and thus indirectly influence MPB biomass and productivity,
59 with far-reaching consequences for the intricate trophic network through bottom-up ecological cascades.

60 Bioturbation by macrofaunal species includes sediment reworking (mixing sediment particles) and
61 bioirrigation (transport of solutes) processes, which are mainly related to behaviours burrowing, locomotion, and
62 feeding activities (Kristensen et al. 2012). The impacts of macrofaunal activities on the MPB and its surrounding
63 environment are linked to both direct (trophic) and indirect interactions (Jones et al. 1994; Bruno and Bertness
64 2001; Crain and Bertness 2006; Ubertini et al. 2012; Van De Koppel et al. 2015). Despite the negative effects of
65 macrofaunal bioturbation related to grazing and sediment surface disruption, bioturbating macrofauna has also
66 been shown to positively influence microbial processes (Swanberg 1991; Orvain et al. 2004; Chennu et al. 2015,
67 2017; Eriksson et al. 2017; D'Hondt et al. 2018). Therefore, by facilitating oxygen and solute exchange at the
68 sediment-water interface, bioturbation activities enhance the influx of dissolved OM (DOM), aerobic OM
69 remineralization, and nutrient cycling. Bioturbation also promotes bacterial growth by accelerating solute and
70 particulate exchanges at the water-sediment interface, (Aller 1988; Boudreau and Jorgensen 2001; He et al. 2019).
71 Oxygenation and sediment surface irrigation by bioturbation may also modify the redox boundary, thus influencing
72 the quantity and quality of sedimentary OM (Fanjul et al. 2015). This, in turn, can be influenced by the structure,
73 metabolic rate, and functioning of benthic communities (Dauwe et al. 1998; Oleszczuk et al. 2019). The chemical
74 composition and dynamics of sedimentary and dissolved OM are thus impacted, especially because the properties
75 of pore-water DOM produced during biodegradation processes have been shown to be mainly dependent on
76 sedimentary OM sources (Burdige and Komada 2015; Derrien et al. 2019). Overall, the influence of bioturbation
77 on the surrounding environment is significant, regulating sediment dynamics, bed erodibility, and biogeochemical
78 processes, with both positive and negative effects on the microbial compartment. Some macrofauna species with
79 high bioirrigation activity can be particularly influential, especially in cohesive sediments, where solute diffusion
80 is limited. These positive and negative effects are expected to exhibit temporal variability as macrofaunal

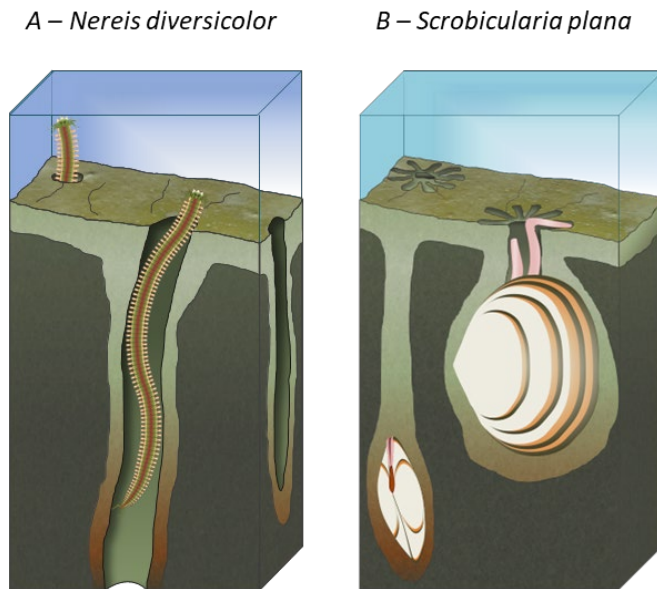
81 bioturbation has been shown to be modulated by temperature, with more pronounced effects in spring, summer,
82 and early autumn (Admiraal and Peletier 1980; Colijn and Dijkema 1981; Underwood 1994; Stal and de Brouwer
83 2003; Orvain et al. 2014; Cozzoli et al. 2018).

84 The impacts of benthic macrofaunal bioturbation and its regulatory effects on various properties of the
85 surrounding environment (e.g., sediment composition, OM, nutrient recycling, recruitment of macrofaunal spats,
86 bacterial and MPB growth, or consumption rates) have been extensively studied. However, complex interactions
87 among all physicochemical and biological components give rise to intricate "bottom-up" and "top-down" forces
88 that are not yet fully understood. Understanding these interactions is essential for maintaining the balance and
89 value of the ecosystem services they provide in intertidal mudflats. Bioturbation by benthic macrofauna and its
90 effects, which are vital drivers of mudflat structure and function, are critical elements to be considered in ecological
91 studies and environmental management strategies. Given the findings of previous studies, it is crucial to investigate
92 the synergistic effects. To achieve this goal, interdisciplinary studies offer a holistic and comprehensive approach
93 that provides insights into the complex and interconnected relationships within trophic networks.

94 In this context, the present study aimed to investigate the effects of two dominant benthic macrofaunal
95 species in intertidal mudflats on different components of the surrounding environment, including bed topography,
96 sediment composition, biogeochemical processes, and microbial and MPB activities. The selected representative
97 site is a temperate intertidal mudflat located downstream the Seine Estuary (northwest France). The selected
98 ecosystem engineers (fig. 1) were the bivalve *Scrobicularia plana*, which is predominantly responsible for surface
99 sediment reworking (Zwarts et al. 1994; Orvain 2005), and the annelid *Hediste diversicolor*, which is primarily
100 involved in gallery bioirrigation (François et al. 2002; Passarelli et al. 2012; Richard et al. 2023). *S. plana* is a
101 widely distributed filter feeder characterized by long siphons that enable it to bury itself in sand or mud. This
102 species thrives at high densities along coastlines and estuaries in northern Europe, the Mediterranean, and West
103 Africa (Santos et al. 2011). *H. diversicolor* is a versatile predator that forms distinctive U-shaped burrows in sand
104 and mud, featuring a mucus net at the entrance. This species creates a water current within its tube to draw particles
105 through the net. Native to the northeast Atlantic, *H. diversicolor* range extends from the Baltic Sea to the
106 Mediterranean and has been introduced to the northwest Atlantic (Einfeldt et al. 2014).

107 Although field observations are typically conducted to study various components of a trophic network
108 simultaneously (Weerman et al. 2011), autocorrelation and confounding factors can complicate the mechanistic
109 understanding of intertwined processes. Therefore, field studies with addition of macrofauna and manipulative
110 experiments are relevant to assess the role of one ecological factor, among others, in bio-mediated sediments
111 (Montserrat et al. 2009; Van Colen et al. 2010; Donadi et al. 2013). As such, a manipulative field experiment was
112 established with enclosures buried in sediments, each containing different densities of macrofauna. Subsequently,
113 a wide range of sedimentary, microbial, and biogeochemical parameters were concurrently measured. This study
114 was conducted during two contrasting periods in terms of biotic and abiotic conditions: late winter (February) and
115 late summer (September). The main hypothesis posited that the two target organisms (*H. diversicolor* and *S.*
116 *plana*), which typically coexist in intertidal mudflats, would have antagonistic effects on bed erodibility (stabilizer
117 vs. destabilizer) and sediment mixing in superficial layers (dissolved exchanges vs. particulate exchanges). The
118 positive influence of the presence of *H. diversicolor* on MPB growth was anticipated because of its impact on
119 sediment stability and bioirrigation activities within its galleries (Morelle et al. 2021; Richard et al. 2023).
120 Conversely, it was expected that the presence of *S. plana* would limit MPB growth owing to disruption of the

121 sediment surface (Richard et al. 2023). Furthermore, the OM quality and quantity are expected to be modified in
122 the presence of ecosystem engineers, particularly in the dissolved phase (DOM), owing to enhanced oxygenation
123 and sediment surface irrigation through bioturbation, especially in the presence of the gallery bioirrigator *H.*
124 *diversicolor*.
125



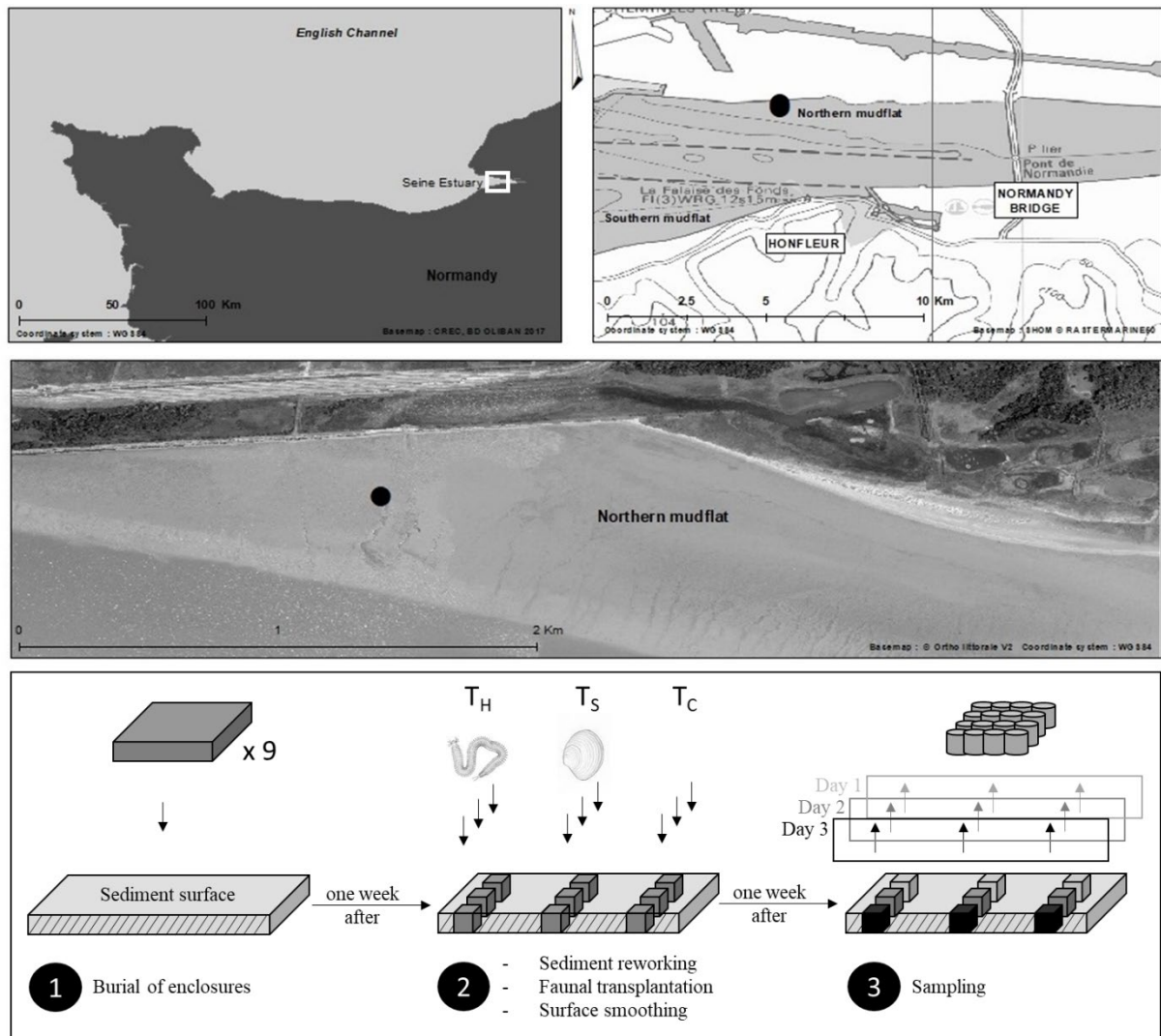
126
127 **Figure 1. Representation of the two species studied in this work.** The annelid *Hediste diversicolor* (A) is
128 primarily involved in gallery bioirrigation while the bivalve *Scrobicularia plana* (B) is predominantly responsible
129 for surface sediment reworking. Copyright: illustrations from Bastien Chouquet for the MELTING POT(ES)
130 project.

131
132 **2. Material and Methods**

133 **2.1. Sampling site and experimental design**

134 Field experiments were conducted in the European temperate macrotidal estuary of the Seine River at an
135 intertidal site (fig. 2). Bivalves (shell length between 40 and 43 mm) and polychaetes (body length of
136 approximately 90 mm) were collected by hand at the same location. Specimens were stored in two distinct tanks,
137 each approximately 100L in capacity, filled with natural seawater and sediment from the sampling site (~10 cm in
138 depth). The water was oxygenated using air pumps, tide conditions were absent, and no supplementary food was
139 provided. The tanks were conserved for one week in a temperature-controlled room at 12°C for winter experiment
140 and at 21°C for late summer experiment with exposure to natural ambient light.

141



142
 143 **Figure 2. Location of the Seine Estuary (Normandy, English Channel, France) with the sampling site located**
 144 **in the northern mudflat (49° 27' 01.6'' N; 0° 12' 20.0'' E).** The experimental design consisted in the burial of
 145 nine enclosures. One week later, sediment inside enclosures were reworked by hand and transplanted with
 146 macrofauna (*Hediste diversicolor*: T_H; *Scrobicularia plana*: T_S; and nothing for control: T_C). After burial of fauna,
 147 sediment surfaces were smoothed and one week later, several cores were sampled over 3 days from each enclosure
 148 (1 replicate for each treatment per day: T_H, T_S or T_C).

149
 150 At the beginning of the experimentation, nine experimental plots (stainless steel enclosures; 50 × 50 ×
 151 20 cm) were buried at the study site so that the top of the enclosures was precisely at the same level than the
 152 sediment surface. To avoid additional topographical variation between replicates, enclosures were placed at a
 153 distance of 1 m from each other in a homogeneous area of the mudflat (fig. 2). Sediment in each plot was then
 154 gently reworked by hand up to a depth of 20 cm and the faunal enrichment was then achieved by direct addition
 155 of the organisms in subsurface (2-3 cm) within the sediment bed. Each specimen was individually added to ensure
 156 vitality and to accurately record the number of individuals in each replicate. In February, the enrichment
 157 represented an addition of 35 individuals per replicate (140 ind m⁻²) while in September, the enrichment
 158 represented an addition of 110 individuals (440 ind m⁻²). The final densities represented the maximum densities
 159 observed at the study site during the sampling periods (comm. pers. Chloé Dancie – “Cellule de Suivi du Littoral

160 Normand | CSLN[®]). In order to have a net monospecific dominance for the two treatments with faunal addition,
161 three replicates were enriched with *S. plana* (treatment T_S) and three others were enriched with *H. diversicolor*
162 (treatment T_H). After animal addition, the sediment surface was flattened in all experimental units, to assess later
163 the effects of bioturbation on bed level. Sediments in control plots were reworked by hand and flattened similarly
164 but without faunal addition (control treatment T_C). The process of the aforementioned steps was completed within
165 one low-tide period. After one week under *in situ* conditions, the samplings were conducted during neap tides,
166 when low-tide coincided with mid-day conditions. The different enclosures were sampled over 3 days due to tidal
167 and safety conditions in intertidal zones. Each day, measurements were performed in successive samplings for one
168 line of enclosure units (fig. 2), including one replicate of each treatment (T_C, T_H, T_S) by following the same
169 sampling method. In addition, the natural state of the mudflat sediment was also sampled each day and assigned
170 as natural treatment (T_N). The experiments were performed in the two most contrasted periods of the year in late
171 winter (February 9th - 26th, 2018) and late summer (September 18th - October 4th, 2018). For that, enclosures were
172 removed after the winter experiment and the whole process was repeated for the summer experiment.

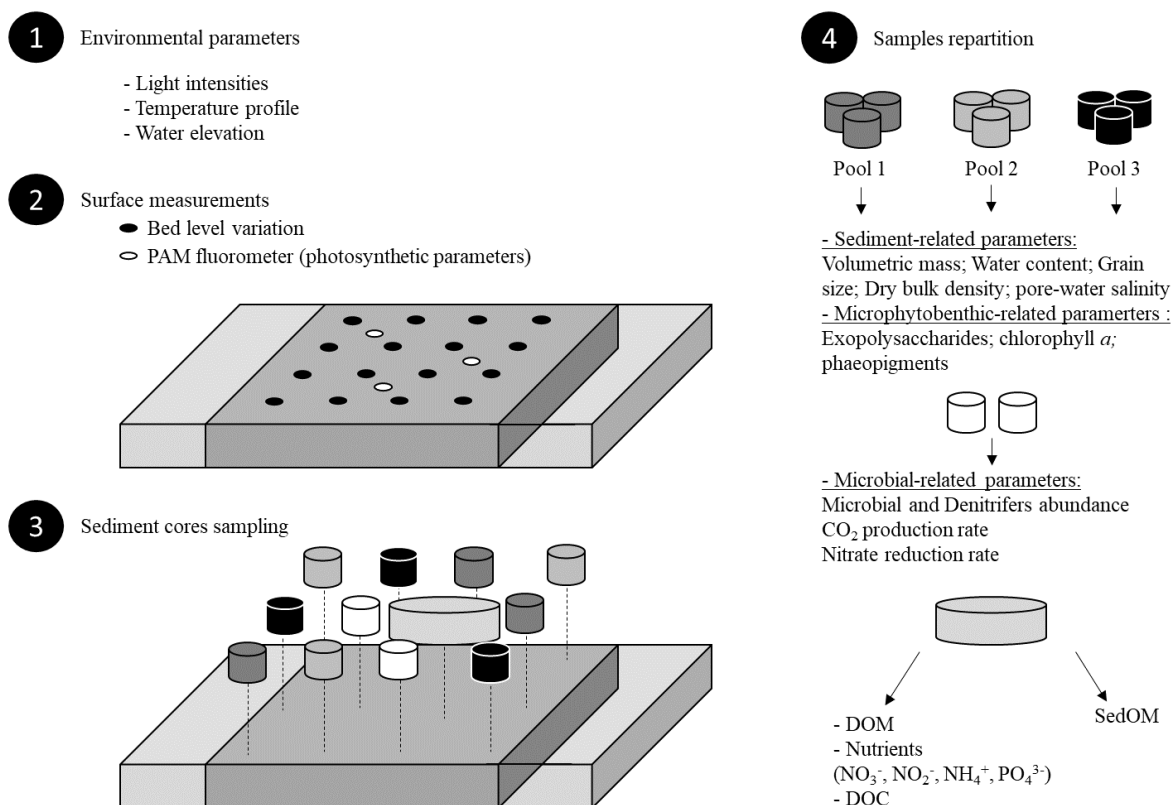
173

174 2.2. Sampling methods

175 The sampling protocol followed was schematically described in figure 3. Due to the interdisciplinary
176 approach and the number of measurements requiring a relatively high quantity of sediment within each enclosure,
177 the sampling strategy followed a precise protocol which was not random but statistically relevant (see 2.4).
178 Throughout each manipulative experiment, environmental parameters (light intensity, temperature profile, water
179 elevation) were recorded *in situ* at the study site, outside the enclosures. Light intensities were recorded every 15
180 min using an Onset Hobo UA-002 Pendant light/temperature data logger placed 15 cm above sediment surface.
181 Vertical temperature profiles were performed every 15 min using five submersible temperature data loggers (Onset
182 Hobo[®] Pendant[®] UA-001) placed at 0, 2, 5, 10 and 15 cm depth using a holder buried in the sediment. Water
183 elevation was measured using a NKE[©] Altus based on a piezo-resistive pressure sensor (accuracy was +/-60 mm
184 while resolution was +/- 8 mm). This instrument was set up to achieve one measurement every 30 seconds.

185 For each treatment with enclosure (T_C, T_H, T_S), the bed level variation was estimated to evaluate the bed
186 accretion or erosion. To this aim, a measurement of the height distance between the enclosure borders (initial
187 sediment surface after flattening) and the sediment surface was performed by using a calliper on 16 fixed points
188 evenly distributed over the surface with a step of 10 cm from each other (fig. 3; total surface of 0.25 m²).

189



190

191 **Figure 3. Schematic representation of the successive actions carried out during each sampling day.** The
 192 environmental parameters (light intensities, temperature profiles and water elevation) were measured
 193 continuously. The first measurements made were the variation of the bed level which was measured at 16 different
 194 points and the PAM fluorometer made at 3 different positions. These two measurements did not disturb the
 195 sediments. Then, the sediment cores were sampled, and the sediment was distributed and conditioned for future
 196 analysis of the parameters considered in this study.

197

198 Immediately after bed level variation measurement, chlorophyll fluorescence was measured in triplicate
 199 ($n=3$) at the sediment surface within each enclosure. This was performed using a Fiber-PAM fluorometer (PAM-
 200 control unit and WATER-EDF-universal emitter detector unit; Walz, Effeltrich, Germany) following the method
 201 fully described in Morelle et al. (2020). Each replicate was exposed to nine actinic irradiance steps from 0 to 168
 202 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in winter and from 0 to 1130 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in summer. These irradiance ranges were
 203 chosen as they match with those of the light environment of each season (Morelle et al. 2018). The treatment of
 204 the fluorescence data using the model of Eilers and Peeters (1988) allowed assessment of photosynthetic
 205 parameters, i.e., the maximum effective quantum yield of the PSII (F_v/F_M), the photosynthetic efficiency (α ;
 206 relative unit), the optimal irradiance for photosynthesis (E_{opt} ; $\mu\text{mol photons. m}^{-2} \text{s}^{-1}$), the relative maximum
 207 electron transport rate ($r\text{ETR}_{\text{max}}$; relative unit), and the saturation coefficient of light (E_k ; $\mu\text{mol photons. m}^{-2} \text{s}^{-1}$).

208 Afterwards, the sediment was sampled through core extraction. Two plexiglass rings (4 cm in diameter
 209 down to a depth of 1 cm) were sampled to study the microbial activity and abundance. A fraction of 3 ml from the
 210 first ring was stored at -80°C for bacterial abundance determination. The remaining sediment from the first ring
 211 and the second ring were kept at 4°C for the microbial activity experiments. Then, nine cores (2.4 cm in diameter

212 down to a depth of 1 cm) were collected and distributed into 3 pools, each representing 13.5 ml of sediment which
213 were cautiously homogenised. For each pool, a fresh sediment aliquot (5 ml) was used for sedimentary analyses.
214 Another sediment aliquot (5 ml) was used to determine exopolysaccharides concentrations. The last sediment
215 aliquot (1.5 ml) was stored at -20 °C for analyses of photopigment concentrations. A last sediment core (9.3 cm in
216 diameter down to a depth of 30 cm) was sampled to analyse the pore-water vertical profiles. Interstitial pore-water
217 samples were extracted using Rhizon samplers (pore size 0.15 µm mean) and polypropylene syringes at a depth
218 interval of 0 – 1 cm (for more information see Seeberg-Elverfeldt et al. (2005)). Each pore water sample was
219 divided into two aliquots and stored in the dark at 4°C. The first aliquot of pore-water was kept for measuring
220 nutrient (Si(OH)₄, PO₄³⁻, NH₄⁺, NO₂⁻, and NO₃⁻) and dissolved organic carbon (DOC) concentrations. The second
221 aliquot was stored for DOM spectroscopic analyses. The 0 – 1 cm depth interval of the core was then sliced and
222 frozen at -20 °C, freeze-dried, ground, and homogenised before sedimentary organic matter (SedOM)
223 characterization.

225 2.3. Analytical methods

226 2.3.1. Sediment-related parameters.

227 To estimate the sediment-related parameters, each aliquot of sediment sampled from the pooled cores (5
228 ml) was weighted to estimate the volumetric mass and was kept at -20°C. After freeze-drying for 24h, the water
229 content (ω ; %) was determined as a percentage of water relative to the total fresh weight. Subsequently, sediment
230 was used for granulometric analysis. For that, sediments were digested in 6% hydrogen peroxide for 48 h to remove
231 OM. The grain size distribution was then measured on subsamples using a LS Coulter particle size analyser. The
232 mud sediment fraction was estimated as the percentage of silt particles < 63 µm (% of fine particles) and the
233 median grain size diameter was estimated from cumulative percentage histogram. The dry bulk density (C_{sed} , kg
234 m⁻³) was then estimated from ω_D (Water weight / Dry weight × 100) and grain density (γ_s ; kg m⁻³) according to
235 the equation $C_{\text{sed}} = (\gamma_s \times 1000) / [(\omega_D/100) \times \gamma_s + 1000]$.

236 Nutrients (NO₃⁻, NO₂⁻, NH₄⁺, PO₄³⁻) and DOC concentrations were obtained from the pore-water samples.
237 Dissolved/reactive silica (Si(OH)₄) concentrations were determined from filtered samples by spectrophotometry
238 (Koroleff, (1983), silico-molybdenum blue method) using a QuAatro (Seal Analytical) continuous segmented
239 flow analyzer. Dissolved nitrates (N-NO₃⁻) and nitrites (N-NO₂) concentrations were analysed using a Gallery™
240 Discrete Analyzer (ThermoFisher scientific, Waltham, Massachusetts, USA). The reactive phosphate P-PO₄³⁻ and
241 the dissolved ammonium N-NH₄⁺ were analysed using a Technicon Auto-analyzer II, with a detection limit of 14
242 µg L⁻¹ and 42 µg L⁻¹, respectively for P-PO₄³⁻ and N-NH₄⁺ and a standard error lower than 5%. DOC was analysed
243 using a “TOC Shimadzu 5050” carbon analyser with two injections or three if the standard error was higher than
244 5%.

246 2.3.2. Microphytobenthos-related parameters.

247 Colloidal and bound fraction of exopolysaccharides were immediately separated from the sediment
248 aliquot (5 ml) using Dowex and conserved at -20°C for analyses following the method fully described in Morelle
249 et al. (2020). The concentrations of high molecular weight (HMW) exopolysaccharides (after separation from
250 Low-MW EPS in 70% Ethanol) were then measured for the colloidal (C-EPS) and bound (B-EPS) fractions.
251 Carbohydrate contents were estimated using sulfuric acid and phenol with glucose as a standard (Dubois et al.

252 1956). Protein contents were estimated using the Bradford assay with bovine serum albumin (BSA) from Sigma-
253 Aldrich as standard (Bradford 1976).

254 After freeze drying, photopigments were extracted from 1g of dry weight (DW) sediment in 90% acetone
255 and the fluorescence of the supernatant was measured using a Turner Trilogy fluorometer (Turner Designs,
256 Sunnyvale, California, USA). Chlorophyll *a* (chl *a*) and phaeopigments concentrations were calculated from the
257 fluorescence values obtained before and after acidification following the method of Lorenzen (1967). The
258 phaeopigment contents were expressed as a percentage of total photopigments.

259

260 **2.3.3. Microbial-related parameters.**

261 Microbial abundances were obtained after DNA extraction from approximately 0.5 g of fresh surface
262 sediment (0-1 cm) according to the protocol detailed in Hellequin et al. (2018) modified from Quaiser et al. (2014).
263 They were determined by quantitative PCR targeting generalist (*16S rRNA* genes of bacteria or archaea) and
264 functional genes as Clade I *nosZ* gene and Clade II *nosZ* gene for N₂O-reducers and calibrated with standard
265 positive DNA. For the *16S rRNA* gene, the standard for Bacteria was DNA of *Pseudomonas fluorescens* SBW25
266 using primers 63f and BU16S4 (Muyzer et al. 1993; Marchesi et al. 1998) and PCR fragment cloned of
267 *Nitrososphaera viennensis* for Archaea with primers Arch806F and Arch915R (Takai and Horikoshi 2000). As in
268 Jones et al. (2013), the standards for *nosZ* genes corresponded to PCR fragment cloned of *Bradyrhizobium*
269 *japonicum* USDA 110 for Clade I and *Gemmatimonas aurantiaca* T-27 for Clade II. No-template controls were
270 performed in duplicate and assays in triplicate. Amplifications were performed in a Lightcycler 480 (LC480,
271 Roche) using Sensyfast Sybr no rox kit (Biotechnofix). Analyses were carried out with LC480 software (release
272 1.5.1) consisting in melting curves and absolute quantification by second derivative maximum analysis method
273 allowing the determination of the crossing points (Cp). We defined the detection limit as fluorescent signals with
274 at least 5 Cp below the signal of the no-template controls.

275 The potential of sedimentary organic carbon degradability was determined in batch incubations by
276 measuring the CO₂ production rate under anoxic conditions. To this end 5 ml of the sediment was placed in a
277 serum bottle with 20 ml of water collected on site (filtered at 0.2 µm). The headspace was replaced by Argon to
278 create anoxic conditions and 500 µM nitrate (NaNO₃) was added. Batches were incubated at 20 °C and agitated
279 (150 g). Samples from the headspace were analysed for CO₂ using a micro-GC Agilent 3000 (SRA Instrument) at
280 the beginning of the incubation, after 2 hours and 4 hours. The CO₂ production was determined over the 4 hours
281 and expressed as CO₂ production in gDW⁻¹ h⁻¹.

282 The potential nitrate reduction rates were estimated from the sediment samples by performing a flow-
283 through reactor experiment. For description of the method see (Laverman et al. 2006, 2012). The reactors were
284 supplied with anoxic saline water (adapted to the onsite salinity) containing 5 mM of NaNO₃ at a flow rate of 3 ml
285 h⁻¹ with a peristaltic pump and incubated at a constant temperature (20°C). The reactors were run for approximately
286 30 hours, allowing determination of nitrate consumption using the *in situ* available carbon present in the sediment.
287 NO₃⁻, NO₂⁻, NH₄⁺ concentrations were determined via a Gallery (ThermoFisher) from outflow samples collected
288 at 2-hour intervals. Samples from the input solution were also collected and analysed for the exact nitrate
289 concentrations. Potential nitrate reduction rates were then calculated and expressed in nmol NO₃⁻ per cm³ of fresh
290 sediment per hour.

291

292 2.3.4. Organic matter-related parameters.

293 DOM spectroscopic analyses were performed on filtered samples. Excitation-emission matrix (EEM)
294 fluorescence spectra were acquired, depending on the pore water volume available, in 1 or 0.5 cm path length
295 quartz SUPRASIL® QS cuvettes (Hellma) regulated at 20 °C, using a Jobin-Yvon Fluorolog FL3-22
296 spectrofluorometer in ratio mode with 4 nm bandwidth for both excitation (250-410 nm, 10 nm intervals) and
297 emission (260-700 nm, 1 nm increments and 0.5 s integration time) (Parlanti et al. 2000). Samples were diluted, if
298 necessary, to avoid inner filter effects, and their spectra, obtained by subtracting an ultrapure water (Milli-Q,
299 Millipore) blank spectrum, were instrumentally corrected as described previously (Huguet et al. 2009). The
300 subsequent fluorescence indices were computed to provide insights into the origin, maturity, and transformation
301 of dissolved organic matter (DOM). The humification index (HIX), indicative of the aromaticity level and maturity
302 of DOM (Zsolnay et al. 1999), was determined based on the position of the emission spectra. Specifically, the
303 upper quarter area (435 - 480 nm) of the usable emission peak was divided by the lower usable quarter area
304 (300 - 445 nm). This calculation facilitated the differentiation between strongly humified organic material,
305 primarily of terrestrial origin ($10 < \text{HIX} < 16$), and autochthonous organic material ($\text{HIX} < 5$). Another key
306 fluorescence index, the fluorescence index (FI), expressed as f_{450}/f_{500} , represents the ratio of fluorescence intensity
307 at the emission wavelength 450 nm to that at 500 nm with an excitation wavelength of 370 nm. This index aids in
308 discriminating between microbial ($\text{FI} = 1.9$) and terrestrial sources ($\text{FI} = 1.3$) of aquatic DOM (McKnight et al.
309 2001). Additionally, the biological index (BIX), serving as a proxy for fresh autochthonous DOM production
310 associated with biological activity (Huguet et al. 2009), was computed at an excitation wavelength of 310 nm. It
311 involves dividing the fluorescence intensity emitted at an emission wavelength of 380 nm by that emitted at 430
312 nm. BIX values exceeding 0.8 indicate a predominantly autochthonous origin of DOM and the presence of freshly
313 released organic matter into the water, while lower BIX values (0.6 – 0.7) suggest moderated DOM production in
314 natural waters.

315 The elemental (organic carbon, nitrogen) and isotopic ($\delta^{13}\text{C}$) analyses of the SedOM were performed on
316 sediment samples after being decarbonated as previously described (Thibault et al. 2019).

317 Lipid extractions were performed using on average 20 g of sediment. Samples were ultrasonically
318 extracted at room temperature with a dichloromethane (DCM)/ methanol (MeOH) mixture (5:1) for 10 minutes (3
319 times). Each extraction was followed by centrifugation (3500 rpm, 10 minutes) and pooling of all extracts. The
320 total lipid extract was rotary evaporated and separated into three fractions of increasing polarity on a column of
321 activated silica: (i) 30 ml of heptane; (ii) 30 ml of heptane:DCM (1: 4, v:v); (iii) 30 ml of DCM:MeOH (1:1, v:v).
322 Each fraction was then rotary evaporated.

323 The *n*-alkanes, contained in the first fraction, were analysed by gas chromatography coupled to a mass
324 spectrometer (GC–MS) using an Agilent Network 6890 GC System coupled with a 5973 Mass Selective Detector,
325 as previously described by Coffinet et al. (2017). 1.1 µg of internal standard (*n*-tetracosane- d_{50} ; Sigma-Aldrich)
326 was added just before injection. The different *n*-alkanes were semi-quantified based on their retention time, after
327 extraction of the characteristic *m/z* 57 fragment.

328 The *n*-alcohols were analysed in the third fraction containing the polar compounds. Before GC-MS
329 analysis, the fraction was dissolved in DCM and derivatized by adding 10% in volume a solution of
330 N,O- bis(trimethylsilyl)trifluoroacetamide – Trimethylchlorosilane 99:1 (Grace Davison Discovery Science,
331 USA). The separation was achieved with the same equipment as above. The GC oven initial temperature was set

332 to 70 °C (maintained for 1 min), increased to 130 °C at 20°C min⁻¹ and then to 320 °C at 4 °C min⁻¹ (maintained
333 for 25 min). Samples were injected in split mode (ratio 30:1), the injector being at 280 °C. 1.5 µg of internal
334 standard (5 α -cholestane; Sigma-Aldrich) was added just before injection. The silylated *n*-alcohols were semi-
335 quantified based on their retention time, after extraction of the characteristic *m/z* 75 fragment.

336 The relative abundances of *n*-alkanes and *n*-alcohols were used to discriminate OM sources in natural
337 environments. Thus, terrestrial vascular plants are dominated by odd long-chain *n*-alkanes (C₂₃-C₃₅), with C₂₇, C₂₉
338 and C₃₁ being the dominant homologues (Bianchi and Canuel (2011) and references therein), and by long-chain *n*-
339 alcohol (\geq C₂₀) (Eglinton and Hamilton 1967). In contrast, algae and bacteria are dominated by short-chain *n*-
340 alkanes, with C₁₅, C₁₇, or C₁₉ predominance, and short-chain *n*-alcohols (C₁₂-C₁₈). Submerged macrophytes have
341 an intermediate composition, with a predominance of mid-chain *n*-alkanes (C₂₁, C₂₃ or C₂₅; Bianchi and Canuel
342 (2011)). In the following, the relative abundance of C₂₇ + C₂₉ + C₃₁ *n*-alkanes *vs.* odd *n*-alkanes in the range C₁₅-
343 C₃₁ will be considered as a proxy of terrestrial OM. Similarly, the relative abundance of long-chain *n*-alcohol (\geq
344 C₂₀) *vs.* total *n*-alcohols (i.e., short (C₁₂₋₁₈) + long-chain homologues) will be used to estimate the proportion of
345 terrestrial *vs.* aquatic (algal/bacterial) OM (e.g., Vonk et al. (2008)).

346

347 **2.4. Statistical analyses**

348 In terms of statistical analyses, it was impossible to include the “season factor” since the fauna treatment
349 was not the same at the two seasons. The densities were chosen to be representative of the observed maximum at
350 each specific season in historical surveys of macrozoobenthic communities. The experiments achieved in winter
351 end and summer end must be therefore considered as 2 independent experiments in contrasted conditions to better
352 unravel the effect of the bioturbators on other properties.

353 For each season, all samples were taken one week after faunal treatments, in a whole 10 × 10 m square
354 experimental study area (one per season) delimited by two perpendicular lines spaced 2 meters apart. The sampling
355 period lasted 3 days. Each day, one replicated square of the 4 treatments was randomly chosen according to the
356 sampling design described in a previous field study (Orvain et al. 2012, 2014), so that day effect cannot bias the
357 analysis. In these squares, surficial sediment was systematically sampled in 1 hour at mid-tide condition to avoid
358 any difference related to the inundation time. No difference was detected between sampling days for all variables.

359 Concerning spatial independence, a preliminary analysis of spatial autocorrelation was performed to
360 evaluate the independence requirements on the site regarding the two main variables (i.e., sediment composition
361 and chlorophyll content). This allowed to guarantee that the condition of spatial independence was not
362 compromised in the analysis since, at 2 meters of distance between each subunit plot, the hypotheses of null
363 autocorrelation was not rejected. A Durbin-Watson test allowed us to confirm the absence of spatial autocorrelation
364 between sub-units, when applying a regression test between sediment composition and chl *a* content.

365 After that Shapiro-Wilk normality tests and Bartlett equal variance tests were applied on each parameter
366 of the dataset, statistical analyses were performed by using a one-way ANOVA to compare the 4 treatments (T_C,
367 T_H, T_S, and T_N) using the R software (version 4.0.2). In the case of significant differences in the ANOVA ($p <$
368 $.05$), Tukey comparison tests were performed with the considered factor to discriminate differences. The non-
369 parametric test of Kruskal-Wallis followed by pairwise-t-tests was used when conditions were invalid. Correlations
370 between parameters were tested using Pearson correlation tests.

371

372 3. Results

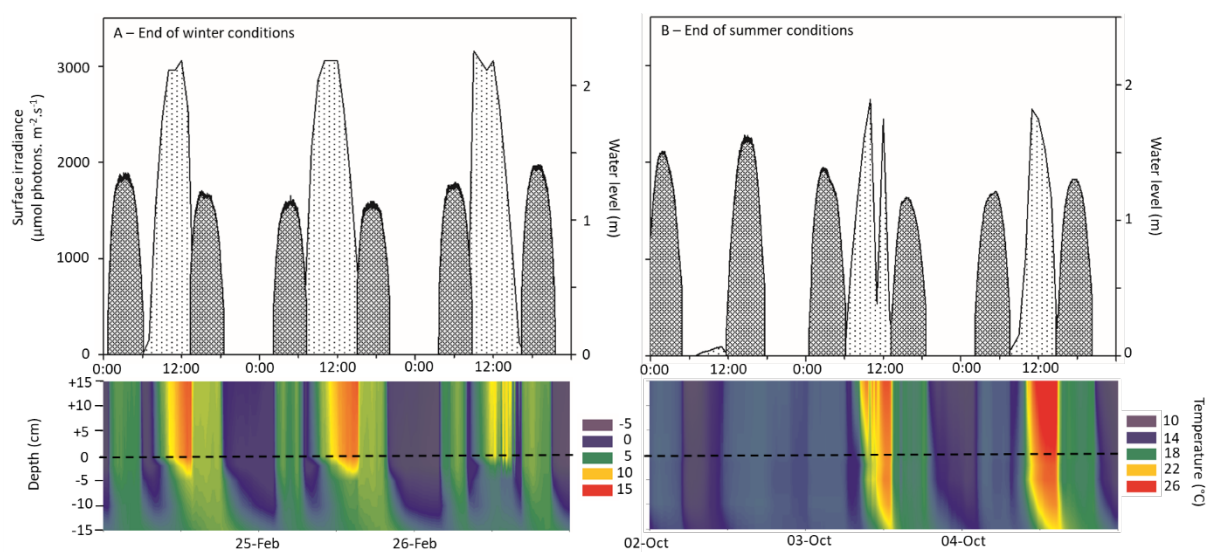
373 3.1. Meteorological conditions during sampling and impact of experimental design

374 Irradiance level varied following the daily cycle with a maximum of $3000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ for
375 winter and $2600 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ for late summer period except during the 1st day of the survey, where
376 irradiance values reached a maximum of $95 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (fig. 4). During the low-tide period (lasting
377 $\sim 5.5\text{h}$), the average values were $1650 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ in winter and $657 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ for late
378 summer period.

379 A diurnal cycle was also observed for temperature values (fig. 4), which varied between -5.5 and $+13.8$
380 $^{\circ}\text{C}$ for winter and between $+9.7$ and $+35.1$ $^{\circ}\text{C}$ for late summer period. Maximal values were observed during zenith,
381 while minimal values were observed during the nocturnal low tide. During the winter sampling period, the
382 temperature values in the sediment surface were lower than 0°C , leading to frost events. At 2 cm depth, the range
383 of temperature variation was lower than on the surface with values between -1.3 and $+7.2$ $^{\circ}\text{C}$ for winter and
384 between $+11.3$ and $+25.1$ $^{\circ}\text{C}$ for late summer period (fig. 4).

385 The impact of the deployment of experimental enclosures was estimated by considering the differences
386 between the control treatment (T_C) and the natural state around enclosures (T_N). A significant difference was
387 observed between T_C and T_N on DOM index and phaeopigments in winter (table 1). For the other parameters and
388 in summer, it was assumed that differences between T_H , T_S , and T_C revealed treatment-related effects and did not
389 result from an experimental artifact.

390



391
392 **Figure 4. Variation of environmental parameters during the monitoring periods under (A) winter and (B)**
393 **late summer conditions.** With the depth profile of temperature in sediment ($^{\circ}\text{C}$), surface irradiance ($\mu\text{mol photons}$
394 $\text{m}^{-2} \text{s}^{-1}$) in pale grey, and water level (m) in dark grey.

395

396 3.2. Winter conditions

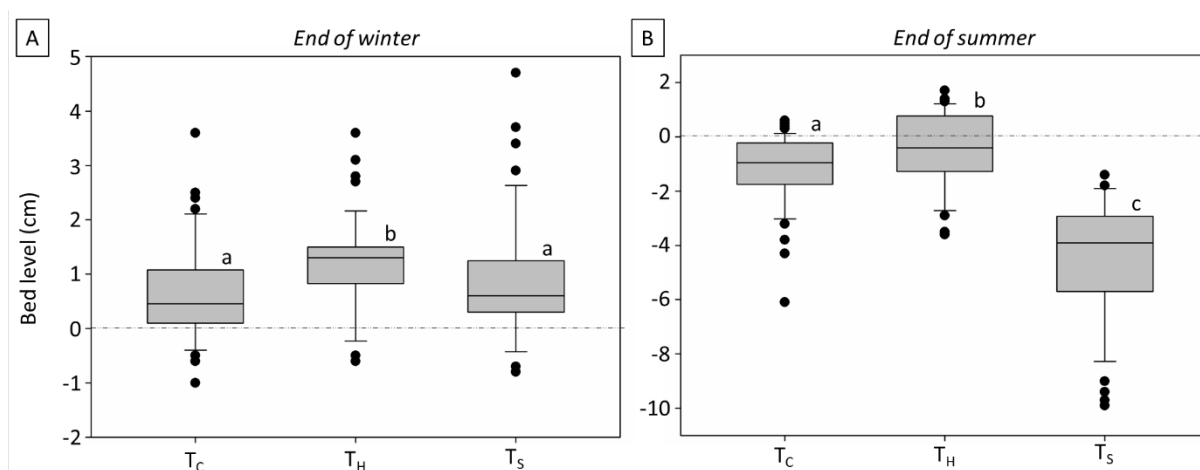
397 3.2.1. Sedimentary parameters

398 In each treatment (T_C , T_H , T_S), the bed level variation showed an increase in sediment height (Table 1;
399 Figure 5-A). This sediment accumulation was significantly higher in the presence of *H. diversicolor* with 1.2 ± 0.6
400 cm compared to the control (0.7 ± 0.7 cm) or in the presence of *S. plana* (0.9 ± 0.8 cm). No other significant

401 differences were recorded between the treatments for sedimentary parameters, with an average of $14.2 \pm 5.3\%$ fine
 402 particles (median of 155.7 ± 9.8), a volumetric mass of 1.9 ± 0.1 kg/L, a dry bulk density of 1633.1 ± 47.8 kg/m³,
 403 and a water content of $23.6 \pm 1.8\%$ (supp. table 1).

404 The parameters related to the SedOM also showed no differences between treatments (supp. table 1).
 405 Total organic carbon (TOC) ranged between 0.07 and 0.37 % while total nitrogen (T_N) was very low between 0.01
 406 and 0.05%. The $\delta^{13}\text{C}$ showed values between -24.44 to -29.44‰. The relative abundance of odd long chain *n*-
 407 alkanes vs. total odd *n*-alkanes was higher than 50 % in most of the samples (on average $61.0 \pm 9.3\%$). Similarly,
 408 long chain *n*-alcohols were largely predominant among total *n*-alcohols in all samples (on average $86.1 \pm 5.0\%$)
 409 without any difference related to the treatment.

410



411
 412 **Figure 5. Bed level variation** with averaged and quartile distribution by gathering all treatments (control: T_C,
 413 *H. diversicolor*: T_H, and *S. plana*: T_S) for the cold season (A) and at the end of the hot season (B). The lower-case
 414 letters on box plot correspond to the statistical groups, the groups being separated by a significant difference after
 415 a Tukey comparison tests.

416

417 **Table 1. Significant differences observed between the values measured in the control treatment (T_C) and**
 418 **each of the others (T_N, T_H, and T_S) during the winter season.** With average and standard deviation values as a
 419 function of *n* (given in the corresponding column). The stars given to values correspond to the significant
 420 difference with T_C ($p < 0.05$: *; $p < 0.01$: **; $p < 0.001$: ***) obtained using a Tukey comparison test or a non-
 421 parametric pairwise t-test.

Treatment	n	T _N	T _C	T _H	T _S
Bed level (cm)	48	n.d.	+ 0.66 ± 0.67	+ 1.20 ± 0.58 ***	+ 0.95 ± 0.83
Biological index (BIX)	3	0.69 ± 0.00*	0.80 ± 0.00	0.72 ± 0.03	0.74 ± 0.02
Fluorescence index (FI)	3	1.25 ± 0.01***	1.43 ± 0.01	1.24 ± 0.01***	1.26 ± 0.02***
Nitrate reduction rates (nmolNO ₃ ⁻ cm ⁻³ h ⁻¹)	15	32.4 ± 8.3	32.0 ± 8.7	42.6 ± 3.7 *	32.9 ± 7.4
Phaeopigments (%)	9	54.7 ± 5.3*	45.1 ± 8.6	48.6 ± 8.5	47.7 ± 5.7
Colloidal carbohydrates EPS (µgEPS gDSW ⁻¹)	9	14.6 ± 12.7	36.9 ± 10.5	18.8 ± 9.2	13.9 ± 3.9**

422

423 3.2.2. Interstitial water parameters

424 In interstitial water samples, the DOC showed high values with on average $7.7 \pm 1.9 \text{ mgC L}^{-1}$ (supp. table
425 1). The DOM optical properties (illustrated from the fluorescence indices HIX, BIX and FI) highlighted a
426 significant treatment effect for BIX and FI (table 1). The HIX index showed values lower than 5 for T_C while
427 higher values were observed for T_N , T_H and T_S , reaching a maximum of about 8 for T_S (supp. table 1). The BIX
428 values ranged between 0.69 and 0.80, with significant higher values for T_C (0.8) than other treatments (0.69 for
429 T_N , 0.72 for T_H and 0.74 for T_S). The FI index showed similar trends as the BIX, with a significant difference
430 between T_C (1.43) and the other treatments (around 1.25). In contrast, the different nutrient concentrations in pore
431 water showed no significant differences between treatments (supp. table 1).

432

433 3.2.3. Biological related parameters

434 Overall, the microbial density in the sediment (bacteria and archaea) showed low values with no
435 significant differences between treatment (on average $22.7 \times 10^4 \pm 9.7 \times 10^4$ microbial (*16S rRNA*) gene copy
436 number per ng of extracted DNA; supp. table 1). Archaea made up 40.5 % of this total microbial community.
437 Despite the differences observed in optical DOM properties, the microbial degradation activity illustrated through
438 the CO_2 production rate showed no differences between treatments with on average $73.3 \pm 10.8 \text{ nmol CO}_2 \text{ gDSW}^{-1} \text{ h}^{-1}$.
439 In contrast, the potential nitrate reduction rates showed significantly higher values in presence of *H.*
440 *diversicolor* than in other treatments (on average $42.6 \pm 3.7 \text{ nmol cm}^{-3} \text{ h}^{-1}$ for T_H vs. $32.1 \pm 7.7 \text{ nmol NO}_3^- \text{ cm}^{-3} \text{ h}^{-1}$
441 for the other ones; table 1). However, the density of denitrifiers in the sediment showed no significant differences
442 with $4.1 \times 10^4 \pm 1.9 \times 10^4 \text{ nosZ}$ gene copy number per ng of extracted DNA. Despite the absence of significant
443 differences, the treatment T_H showed the highest measured microbial activity and some of the highest values of
444 microbial abundance (supp. table 1).

445 Regarding the parameters related to MPB, the chl *a* contents were low at this period with the highest
446 values for T_N ($3.5 \pm 0.5 \text{ } \mu\text{g chl } a \text{ gDW}^{-1}$) but without any significant differences with T_C , T_H and T_S which
447 presented on average $2.7 \pm 0.5 \text{ } \mu\text{g chl } a \text{ gDW}^{-1}$. The colloidal carbohydrate EPS concentrations showed the highest
448 values for T_C ($36.9 \pm 10.5 \text{ } \mu\text{gEPS gDSW}^{-1}$) and significant lower values for the macrofauna treatments with 13.9
449 $\pm 3.9 \text{ } \mu\text{g gDSW}^{-1}$ for T_S and $18.8 \pm 9.2 \text{ } \mu\text{gEPS gDSW}^{-1}$ for T_H (table 1). The other EPS fractions showed no
450 significant difference between treatments with on average a concentration of $45.6 \pm 11.5 \text{ } \mu\text{g gDW}^{-1}$ for bound
451 carbohydrate EPS, and concentrations of 3.15 ± 0.6 and $7.12 \pm 0.4 \text{ } \mu\text{g gDW}^{-1}$ respectively for the colloidal and
452 bound fractions of protein EPS. The percentage of phaeopigments relative to total photopigments showed a
453 significant higher value in T_N ($54.7 \pm 5.3\%$) in comparison to T_C but no significant differences between control
454 and macrofauna treatments was recorded with an average of $49.0 \pm 7.7\%$. Photosynthetic parameters were constant
455 between treatment with on average a F_V/F_M of 0.49 ± 0.07 , an α of 0.37 ± 0.06 and a rETR_{max} of 156 ± 49 . The
456 optimal irradiance (E_{opt}) was on average of $391 \pm 239 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and the saturation coefficient of light
457 (E_k) of $57 \pm 17 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$.

458

459 3.3. Late summer conditions

460 3.3.1. Sedimentary parameters

461 For each treatment (T_C , T_H , T_S), the bed level analysis revealed a global net erosion of the sediment (table
462 2; fig. 5-B). This erosion pattern was significantly stronger for T_S ($-4.5 \pm 1.8 \text{ cm}$) compared to other treatments

463 and significantly weaker for T_H (-0.5 ± 1.0 cm). In the presence of *S. plana*, the silt particles appeared in lower
 464 proportion than with other treatments (on average $22.9 \pm 2.9\%$ for T_S vs. in mean $30.4 \pm 4.1\%$ for T_H , T_C , and T_N).
 465 The other sedimentary parameters highlighted the same significant difference for T_S which showed a higher
 466 volumetric mass (1.95 ± 0.1 kg L^{-1}) and dry bulk density (1349.4 ± 30.3 kg m^{-3}), as well as a lower water content
 467 ($36.4 \pm 1.6\%$) than other treatments (table 2). The three other treatments showed on average a volumetric mass of
 468 1.88 ± 0.1 kg L^{-1} , a dry bulk density of 1257.0 ± 43.8 kg m^{-3} , and a water content of $42.0 \pm 2.8\%$.

469 Parameters related to the SedOM showed no significant differences between treatment with on average a
 470 TOC of $1.49 \pm 0.43\%$, a TN of $0.18 \pm 0.04\%$, and a $\delta^{13}C$ of -26.34% . Sediment samples contained $63.6 \pm 3.5\%$ of
 471 odd long chain *n*-alkanes relative to total odd *n*-alkanes and $87.8 \pm 2.3\%$ of long chain *n*-alcohols among total *n*-
 472 alcohols (supp. table 2).

473
 474 **Table 2. Significant differences observed between the values measured in the control treatment (T_C) and**
 475 **each of the others (T_N , T_H , and T_S) during the late summer period.** With average and standard deviation values
 476 as a function of *n* (given in the corresponding column). The stars given to values correspond to the significant
 477 difference with T_C ($p < 0.05$: *, $p < 0.01$: **, $p < 0.001$: ***) obtained using a Tukey comparison test or a non-
 478 parametric pairwise t-test.

Treatment	n	T_N	T_C	T_H	T_S
Bed level (cm)	48	n.d.	-1.18 ± 0.95	$-0.53 \pm 1.05^*$	$-4.49 \pm 1.78^{***}$
Silt particles content (%)	9	30.7 ± 4.2	29.7 ± 4.5	30.7 ± 3.5	$22.9 \pm 2.9^*$
Water content (%)	9	43.2 ± 2.5	41.42 ± 3.1	41.4 ± 2.6	$36.4 \pm 1.6^*$
Dry bulk density (Csed: kg m^{-3})	9	1237.9 ± 39.0	1266.1 ± 49.0	1266.8 ± 42.8	$1349.4 \pm 30.3^*$
Humification index (HIX)	3	7.30 ± 0.21	5.49 ± 0.16	6.97 ± 0.62	$7.76 \pm 0.69^*$
Nitrate reduction rates (nmolNO ₃ ⁻ cm ⁻³ h ⁻¹)	15	100.9 ± 13.0	95.4 ± 7.3	$77.2 \pm 9.7^*$	$72.6 \pm 8.7^{***}$

479
 480 **3.3.2. Interstitial water parameters**
 481 In interstitial water samples, the DOC showed low values, with on average 4.2 ± 1.3 mgC L^{-1} without any
 482 differences between treatments (supp. table 2). The BIX and FI indices showed higher values for T_C (0.8 and 1.45,
 483 respectively) than for the other treatments (around 0.7 for BIX and 1.26 for FI). The HIX index showed a lower
 484 value, around 6, for T_C and values around 7 for T_H and above 7 for T_S and T_N . The different nutrient concentrations
 485 in pore water showed a high variability between replicates resulting in an absence of significance between
 486 treatments (supp. table 2).

487
 488 **3.3.3. Biological related parameters**
 489 The microbial density in the sediments (bacteria and archaea) showed lower *16S rRNA* gene copy numbers
 490 per ng of extracted DNA in T_S ($22.7 \times 10^4 \pm 1.2 \times 10^4$) compared to T_C , T_H , and T_N ($53.2 \times 10^4 \pm 26.2 \times 10^4$; supp.
 491 table 2). Archaea made up 49.8 % of the total microbial communities. This difference between treatment was also
 492 observed for the *nosZ* genes which showed a lower abundance in T_S ($6.0 \times 10^4 \pm 2.4 \times 10^4$) than in T_H and T_N
 493 ($8.3 \times 10^4 \pm 2.8 \times 10^4$). In terms of microbial activity, the potential nitrate reduction rates were significantly lower

494 in presence of macrofauna (T_S and T_H) than without (T_N and T_C) with respectively 74.9 ± 9.9 and 98.2 ± 10.8
495 $\text{nmol cm}^{-3} \text{ h}^{-1}$ (table 2). The CO_2 production rate showed no differences between treatments with on average
496 $171.0 \pm 24.2 \text{ nmol CO}_2 \text{ gDW}^{-1} \text{ h}^{-1}$.

497 Regarding the MPB related parameters, the chlorophyll *a* content showed a lower content for T_S with
498 $4.2 \pm 1.4 \text{ } \mu\text{g chl } a \text{ gDSW}^{-1}$ while higher values were observed for T_C , T_H and T_N (in mean $6.4 \pm 0.8 \text{ } \mu\text{g chl } a \text{ gDSW}^{-1}$;
499 sup. table 2). The same trend was observed when analysing chl *a* concentration in $\text{mg chl } a \cdot \text{m}^{-2}$. The colloidal
500 carbohydrate EPS concentrations showed a significant difference between T_S ($90.9 \pm 6.6 \text{ } \mu\text{gEPS gDSW}^{-1}$) and T_H
501 ($77.5 \pm 3.7 \text{ } \mu\text{gEPS gDSW}^{-1}$). The other EPS fractions showed no significant difference between treatments with
502 on average a concentration of $171.4 \pm 13.8 \text{ } \mu\text{g gDW}^{-1}$ for bound carbohydrate EPS, and concentrations of 2.5 ± 0.8
503 and $3.2 \pm 0.7 \text{ } \mu\text{g gDW}^{-1}$ respectively for the colloidal and bound fractions of protein EPS. The percentage of
504 phaeopigments relative to total photopigments also showed no significant differences with an average of 68.0
505 $\pm 4.7\%$. Regarding photosynthetic parameters, only the F_v/F_m showed significant lower values for T_S (0.42 ± 0.13)
506 while the other treatments showed a mean value of 0.55 ± 0.07 . The other photosynthetic parameters were similar
507 between treatments with a mean value of 0.37 ± 0.11 and a mean $rETR_{\text{max}}$ of 97.1 ± 33.5 . The optimal irradiance
508 (E_{opt}) was on average of $530.6 \pm 210 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and the saturation coefficient of light (E_k) of 305.4
509 $\pm 118.4 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (sup. table 2).

510

511 4. Discussion

512

513 The central hypothesis of this study posited that coexisting organisms, *Hediste diversicolor* and
514 *Scrobicularia plana*, would exert antagonistic effects on sedimentary properties, biogeochemical processes, and
515 microbial dynamics. Our results shed light on the more intricate dynamics governing intertidal mudflats. During
516 winter conditions, the physical parameters, especially temperature and particles deposition, exert a more significant
517 influence, overshadowing the role played by the presence of ecosystem engineers. No significant effects were
518 observed with the presence of *Scrobicularia plana*. However, in an unexpected way, the presence of *Hediste*
519 *diversicolor* slightly mitigated the impacts of the physical parameters. In late summer conditions, in line with our
520 hypothesis, our results reveal that the presence of each bioturbator strongly exert a strong influence on both biotic
521 and abiotic parameters, with opposite effects. The presence and activity of *S. plana* led to a complete disruption of
522 the sediment matrix, resulting in negative impacts on associated biological and especially microbial processes. In
523 contrast, the presence and activity of *H. diversicolor* contributed to maintaining the sediment matrix and enhanced
524 the studied biogeochemical processes. Although more in-depth measurements of bioturbation processes and the
525 use of more precise methods will be necessary to deepen the findings on specific processes, this interdisciplinary
526 study confirms the significant influence of ecosystem engineers in mudflats and underscores the interconnected
527 and cumulative nature of the consequences arising from their presence on all processes simultaneously.

528

529 4.1. Combined effects of temperature and presence of macrofauna in winter conditions.

530

531 In February, the sediment accretion in all treatments during the experiment revealed that deposition rates
532 were stronger than erosion rates on the site. This is intricately linked to the dynamics of the estuary where currents
533 induce erosion on the southern mudflats, and subsequently transport sediment particles towards the northern
mudflats, leading predominantly to sediment accretion. This pattern being accentuated in winter by the higher

534 currents and the maximum turbidity zone located in the downstream estuary, reinforcing the amount of suspended
535 particles (turbidity up to > 500 NTU; source: SYNAPSES network) that can settle on the upper mudflats of the
536 estuary, especially during neap-tide periods (Le Hir et al. 2001). Thereby, it appears that the abiotic environment
537 exerts a larger impact on the studied parameters variation than the macrofauna activities. This can be explain by
538 the decrease of biological activities at low temperature (Georlette et al. 2004). The low temperatures that varied
539 between -5.5 and 13.8 °C with frost events on the surface, are most likely responsible for the low measured
540 microbial biomass, including bacteria, archaea, and MPB. For MPB, temperature is the most important factor
541 explaining the seasonal variation of biomass and production rates (Blanchard et al. 1996). At low temperature, a
542 decrease in the activity or deactivation of the enzymes involved in photosynthesis limits enzymatic activity by
543 following the rules of the Arrhenius laws, consequently reducing MPB growth and primary production rates
544 (Morgan-Kiss et al. 2006). For bacteria and archaea, frost and low temperatures on the sediment surface also play
545 an important role in the biogeochemical process rates (Shen et al. 2020), the average microbial activity decreasing
546 with the low temperatures, far from the optimum temperature of 15°C for production rates (Shen et al. 2015). The
547 low temperatures also most likely resulted in a reduced activity for *S. plana* in T_S regarding motility, grazing, and
548 respiration rates, which might explain the low influence of their presence. This ecosystem engineer is known to
549 generate an intense sediment reworking (Wiesebron et al. 2021) that was not observed through the bed level
550 variations under the low temperature of the present study. Moreover, no active siphons were visible on the site
551 even in the bivalve-enriched units. This is supported by previous results showing that the fauna-mediation of the
552 sediment matrix is regulated by temperature for bivalves with an optimal value between 24 and 30 °C for *S. plana*
553 (Hughes 1969; Brey 2001; Cozzoli et al. 2018).

554 The observed significant differences between the treatment with the addition of *H. diversicolor* and the
555 control, especially regarding bed accretion, suggest that the influence of this species on the surrounding
556 environment was not inhibited by environmental factors. This resulted in cumulative effects of both winter
557 conditions and bio-irrigation by this gallery-diffuser on the measured parameters. *H. diversicolor* can tolerate wide
558 temperature fluctuations (Wolff 1973) with reduced food-searching activity only occurring below 8°C (Scaps
559 2002). Furthermore, its bioirrigation rates are not temperature-dependent (Sanz-Lázaro et al. 2011). This species
560 inhabits burrows lined with mucus-filled galleries that extend over 10 cm into the sediment (Davey 1994).
561 Temperature fluctuations at this depth tend to be more moderate, consistent with our observed temperature profiles,
562 and explaining their tolerance to low environmental temperature. Therefore, it can be asserted that temperature
563 during the winter manipulative experiment doesn't significantly decrease the activity of *H. diversicolor*, especially
564 considering the insulating effect of their mucus secretions, known to confer resistance to cold conditions (Hawes
565 et al. 2010). In addition to constructing mucus-lined galleries, *H. diversicolor* releases mucus during its feeding
566 activities by using a mucous trapping-net even at a temperature of 5°C (Riisgård et al. 1992). This mucus secretion
567 were shown to trap particles as much as during high tide where they behave as filter-feeders and at low tide where
568 they switch to deposit-feeding (Esselink and Zwarts 1989; Esnault et al. 1990; Riisgard 1991a; Scaps 2002). These
569 mucus secretions, functioning as sediment traps, most likely explain the significantly higher sediment
570 accumulation observed in the T_H treatment. However, the mucus released by *H. diversicolor* at the sediment
571 surface was not detected in our study, as no significant differences in EPS concentrations were observed between
572 T_H and T_C (supp. table 1). Nonetheless, this multidisciplinary study revealed a notable impact of *H. diversicolor*
573 on the microbial community. T_H treatments exhibited higher values for microbial-related parameters compared to

574 T_C and T_S (supp. table 1), indicating enhanced microbial growth and activity. The preference of microbes for EPS
575 as a carbon source (Bouillon and Boschker 2006; Bellinger et al. 2009; Taylor et al. 2013; Morelle et al. 2022)
576 likely led to rapid EPS consumption in the presence of *H. diversicolor*, resulting in non-detectable EPS levels.
577 This assumption is further supported by the slightly higher average DOC values in T_H treatment compared to T_C
578 (+7.7%) and T_S (+28.8%; supp. table 1), suggesting a higher degradation of labile OM (Perkins et al. 2022).
579 Although not statistically significant, this aligns with slightly higher average NH₄⁺ concentrations in pore water
580 samples from T_H compared to T_C (+9%) and T_S (+5.6%; supp. table 1). Microbes involved in nitrate reduction
581 appeared to benefit from the presence of *H. diversicolor*, as evidenced by the significantly higher nitrate reduction
582 rates and, although not reaching statistical significance (p = 0.13), the slightly higher abundance of *nosZ* genes in
583 T_H, respectively 48% and 42% higher than in T_S and T_C (supp. Table 1). This also aligns with the lower, though
584 not statistically significant (p = 0.7), average in NO₃⁻ concentrations measured in the pore water samples from T_H
585 with an average 15% lower than T_C (supp. table 1). This difference between T_H and the other treatments may be
586 attributed to bioirrigation activities. As demonstrated in various sediment dwellers (e.g., bivalves, worms,
587 crustaceans, echinids), bioturbation directly stimulates nutrient release at the sediment-water interface (Eriksson
588 et al. 2017). Nematodes have also been shown to enhance bacterial activity and nutrient fluxes by frequently
589 ventilating galleries across the sediment-water interface (D'Hondt et al. 2018). In our case, the bioirrigation
590 performed by *H. diversicolor* (Kristensen and Hansen 1999) is known to enhance oxygen penetration, thereby
591 promoting aerobic and anaerobic organic matter remineralization, which likely stimulated bacterial productivity
592 and nutrient release (Richard et al. 2023). Even in winter conditions, when ventilation rates of *H. diversicolor* may
593 decrease (Kristensen 1983; Riisgård et al. 1992; Vedel 1998), our results showed that their presence still exerts an
594 influence on the surrounding environment.

595 Significantly higher values of EPS concentrations were observed in the control treatment (T_C) in
596 concomitance with lower values of the humification index HIX and higher values of the fluorescence indices BIX
597 and FI (table 1). The reworking, reshaping, and flattening of the sediments may have disturbed the sediment matrix
598 and MPB biofilm. This hypothesis is confirmed by the significantly lower values of chl *a* measured in T_C, T_H, and
599 T_S, in comparison to T_N (Table 1). In those conditions, MPB cells would have to build new pioneering biofilms by
600 performing migration, this process occurring during a lag phase of several days (Yallop et al. 2000; Orvain et al.
601 2014). In T_C, the high values of carbohydrate EPS must have played a role in the migrating movement of epipellic
602 benthic diatoms and contributed to the adhesion of microalgae at the sediment surfaces by forming biofilms. This
603 was supported by the values of the fluorescence indices, suggesting the presence of a more freshly and microbially
604 produced less aromatic DOM (McKnight et al. 2001) which could be attributed to a higher EPS production by
605 MPB. This assumption was support by Li et al. (2023) showing that microbial EPS showed higher BIX and FI
606 concomitant with lower HIX than more aromatic products with values in the range of our results. The absence of
607 such trends in the treatments with macrofaunal addition (T_S and T_H) could be attributed to the feeding activity of
608 the ecosystem engineers which, despite an apparent reduced activity for *S. plana*, must continue to feed on the OM
609 pool.

610

611 **4.2. Intense top-down impact of macrofauna in late summer conditions**

612 In late summer, the addition of *S. plana* individuals led to a coarser sediment structure (table 2),
613 suggesting that the reworking activity of the bivalves led to the bioresuspension of fine sediment particles. This is

614 confirmed by the temporal changes of the bed topography, which showed a significant loss by erosion in this
615 treatment (fig. 5). In addition to particle size, the sediment reworking performed by *S. plana* also significantly
616 affected most of the sedimentary parameters (volumetric mass, dry bulk density, and water content; table 2). These
617 results highlight the considerable effects of the *S. plana* activities on the sedimentary matrix at this season. This is
618 in line with the literature showing that the biological activity for bivalves and the related impacts on the
619 sedimentary matrix are important and dependent on temperature (Brown et al. 2004; Cozzoli et al. 2020, 2021;
620 Wiesebron et al. 2021). The modelled sediment loss resulting from *S. plana* activities was estimated at 50 cm year⁻¹
621 in the Marennes-Oléron Bay (Orvain et al. 2012). Considering the seasonal changes and the optima of this species
622 for temperature, our results were in accordance with this estimation, showing an impact of *S. plana* on the
623 sedimentary matrix corresponding to a sediment loss of 3 cm in 1 week. These effects were likely mainly due to
624 the biological activities of *S. plana* related to burrowing and/or nutrition activities, which consist in siphoning the
625 sediment surface that surrounds its semi-permanent burrow (Orvain 2005), continuously consuming the MPB
626 during the low tide (Hughes 1969). The low chl *a* content measured in T_S could thereby most likely be due to an
627 elevated foraging activity. However, in our study, the phaeopigment percentages, which represent the degraded
628 compounds of chl *a*, were not different in T_S compared to other treatments (supp. table 2). Such a difference would
629 have been expected as the result of a more intense predation pressure. The absence of effects on phaeopigments
630 might be due to the rapid diffusion and/or resuspension of these pigments due to a high hydrodynamic stress as
631 already suggested by Anand et al. (2014). This could also include resuspension of benthic diatoms, which in this
632 case would apply to all treatments. In addition, the low chl *a* content could be an indirect effect of *S. plana* due to
633 the strong disruption of the sediment matrix, which might limit the formation of structured MPB biofilms and in
634 turn reduce photosynthesis and biomass production (Morelle et al. 2020). This assumption is supported by the
635 lower values of the maximum effective quantum yield of the PSII (F_v/F_M) measured in T_S than in other treatments.
636 Indeed, this result suggests that MPB was not in optimal conditions for photosynthesis since this rate depends on
637 the physiological status of the biofilm (Serôdio et al. 2007). Such indirect negative impact of *S. plana* on the
638 biological compartment was also observed in the microbial abundances and activity. Indeed, the T_S showed low
639 microbial abundance both for bacteria and archaea (*16S rRNA* copy numbers) and the lowest activity in terms of
640 nitrate reduction rates. This suggests that the presence of *S. plana* at such density (440 ind m⁻²) in summer resulted
641 in an intense sediment reworking almost completely inhibiting the biological components at the basis of the benthic
642 trophic network of the intertidal mudflats. However, the present densities tested were the highest found for this
643 species in the studied mudflat, and the activity of *S. plana* was somewhat slowed down by temperature (as seen in
644 our winter results). Thereby, it's likely that this destructive impact is usually less pronounced compared to what
645 we observed during our late-summer experiment. In addition, this effect must also be lower by the intense predation
646 pressure that this bivalve receives from the upper compartment of the trophic network which can result in a strong
647 reduction of siphon extension and feeding activity for bivalves (Maire et al. 2010).

648 In contrast, the treatment with *H. diversicolor* showed the lowest bed level erosion (fig. 5), thereby
649 suggesting that the presence of polychaetes limit particle resuspension due to biostabilisation effects by mucus
650 secretion which can result in a relative bed accretion (Riisgard 1991b; Passarelli et al. 2012). In this survey, since
651 the sediment parameters were not significantly different compared to T_N and T_C, we suggest that the activity of *H.*
652 *diversicolor* improved the stability of the sediments and, thus, attenuated the erosion, rather than promoting
653 sediment accumulation. The fact that the presence of *H. diversicolor* reduced sediment erosion rates must also

654 have limited the MPB biofilm resuspension (Andersen et al. 2010; Donadi et al. 2013) and played a role in the
655 high level of MPB biomass that was observed (table 2). Despite the predation pressure exerted by *H. diversicolor*
656 (Scaps 2002), the chl *a* concentrations were similar to the natural and control treatments (T_N and T_C). This could
657 be explained by a balance existing between the decrease in MPB biomass related to the feeding activity of
658 *H. diversicolor* and the increase in the biomass related to their bioirrigation activities (Asmus and Bauerfeind 1994;
659 Fernandes et al. 2006; Morelle et al. 2021; Richard et al. 2023). In the present case, enhancement of nutrients
660 fluxes through bioirrigation of *H. diversicolor* (Kristensen and Hansen 1999) may have promoted bacterial
661 productivity and MPB growth, which in turn may have decreased the vulnerability to erosion and promoted
662 sediment accumulation through additional EPS production (Widdows et al. 2004; Andersen et al. 2010). Indeed, a
663 higher abundance of both *16S rRNA* genes (bacteria, archaea) and *nosZ* genes (denitrifiers) was observed in the
664 T_H treatments compared to T_C and T_N, suggesting a stimulation process of microbial growth by *H. diversicolor*.
665 This might be due to a higher degradation rate of OM in the presence of *H. diversicolor* related to the higher
666 oxygen penetration with bioirrigation activities (Pischedda et al. 2012). However, this potential increase in
667 degradation activity was not observed in the microbial activity measured at the end of the experiment (CO₂
668 production and nitrate reduction rates) which showed higher values in T_C. Moreover, higher values of HIX as well
669 as lower values of BIX and FI in T_H than in T_C suggest an increase in DOM aromaticity related to the presence of
670 *H. diversicolor* and/or to the use, consumption, or transformation of components of lower aromaticity (Aller 1980;
671 Zhang et al. 2022). Indeed, such an increase could be explained by the transfer of more degraded organic material
672 from deeper sediment to the surface (also significant and pertinent for the T_S treatment). This is in line with the
673 observations made by He et al. (2019), who showed that bioturbation activities accelerated the DOM release,
674 mainly composed of aromatic/mature material (higher HIX), from sediment to overlying water with bioturbation.
675 He et al. (2019) also reported changes in DOM composition over time, with an increase of microbially-produced
676 DOM resulting from bacterial growth and propagation by bioturbation. In the present study, microbial production
677 of DOM was not observed through the fluorescence indices, as the FI values corroborate a more terrestrial/mature
678 character of DOM in the enriched treatments, in line with the HIX variations (table 2). Overall, the HIX and FI
679 values were low and BIX values high, reflecting a mixture of organic material of low aromaticity and moderate to
680 strong autochthonous sources with more mature and hydrophobic DOM components (Huguet et al. 2009). These
681 results are consistent with those reported by Bowen et al. (2017) in the pore waters of California intertidal wetlands
682 and by Burdige et al. (2004) in marine surface sediments, with autochthonous aquatic DOM predominant in surface
683 waters and more terrestrial/refractory material in deeper pore waters. Nevertheless, the nature of sedimentary OM
684 remains the same whatever the season and the treatment, with a strong terrestrial imprint. This is shown by both
685 bulk and molecular analyses, with depleted δ¹³C values of sedimentary OM and the predominance of long-chain
686 *n*-alkanes and *n*-alcohols derived from terrestrial plants vs. short-chain homologues (Bianchi and Canuel 2011).
687 Such results converge with the general view that terrestrial OM is refractory and well-preserved in sediments, in
688 contrast with OM components produced *in situ*, considered as labile and less abundant in sediments (e.g., Burdige
689 2007). Nevertheless, the lower BIX values in T_H than in T_C suggested that the freshly produced DOM was
690 used/consumed, degraded, or released in surficial water. Thereby, we assumed that, during the experiment, the
691 presence of *H. diversicolor* stimulated the degradation of low aromatic compounds, as the latter are, by nature,
692 more rapidly and easily degraded (Hansen et al. 2016). This is in line with the increase in microbial abundance
693 and the decrease in DOM aromaticity (lower HIX) observed in T_H. The rapid depletion of easily degradable

694 compounds in pore waters, and the release of such compounds in surficial water favoured by bioirrigation of *H.*
695 *diversicolor*, thus explain that the microbial production of DOM was not observed through the fluorescence
696 analyses. Thereby, our results suggested that the activity of *H. diversicolor* had positive effects on both the
697 sedimentary matrix and on microbial carbon fluxes, despite its high density and consequent predatory activity.

698

699 **5. Conclusions**

700 The influence of two intertidal bioturbators, *H. diversicolor* and *S. plana*, on the sedimentary,
701 biogeochemical, and microbial dynamics was evaluated through field manipulative experiments during the two
702 most contrasted seasons in a temperate estuarine mudflat. The present study confirmed the importance of
703 temperature and water flow regimes both on macrofauna activity and microbial dynamics in intertidal mudflat. In
704 the two different situations (either high sediment deposition and low temperature in winter, or high erosion and
705 temperature under late summer conditions), the presence or absence of the bioturbators was shown to modify the
706 sediment particle grain size composition and bed topography, with the erosion/accretion of the sediment partly
707 related to the nutrition and burrowing activities of the species. The bioturbators were also observed to have a
708 simultaneous influence on most of the studied parameters in the surficial sediment layer – with a direct or indirect
709 impact on the pore water DOM quality, the growth, and activities of microorganisms (i.e., bacteria, archaea, and
710 MPB). This study showed that some links between the different compartments are difficult to highlight without
711 studying all components reinforcing the interest of conducting interdisciplinary studies to consider a maximum of
712 biological and physicochemical variables to improve the understanding of ecosystem functioning. This study also
713 highlights the importance of biological control of sedimentary systems on tidal flats, even in macrotidal estuaries.
714 This is critical to improve management and conservation policies of estuarine ecosystems by better integrating the
715 functional roles and bioturbation of dominating macrofauna, to restore the productivity of the intertidal zones, and
716 to develop new models coupling biogeochemistry and benthic processes to sediment dynamics able to produce
717 more realistic scenarios in the context of the global warming.

718

719 **Acknowledgments:**

720 This study was funded by the PHARESEE[©] project (Program GIP Seine-Aval 6) which aims to better
721 understand, for modelling and restoration purposes, the links existing between hydrosedimentary, biogeochemical
722 and microbial dynamics on mudflats ecosystems. The authors want to thank the GIP Seine-Aval agency, especially
723 N. Bacq. Thank you to Jean Paul Lehodey (CREC) & Jean-Marc Paint (IUT Grand Ouest Normandie) for their
724 help in the field systems conception and to the people who actively participated in sampling and/or analyses,
725 especially Thomas Lecarpentier (Maison de l'Estuaire), Mathieu Chauveau, Guillaume Izabel, Guillaume Bouger,
726 Amelie Gaigaerd, Cedric Fouillet, Véronique Vaury, Johanne Lebrun-Thauront, Kéline Judith, Jessica Maubert,
727 Sarah Adeline, Théo Chiron, Camille Duchemin, Enora Logodin, Clémence Paucis, Amaury Tuon, Michel Simon
728 and Romain Levailant. We are also thankful to Virginie Daburon who performed genetic analyses of microbial
729 DNA from sediment at the molecular ecology platform (UMR 6553 Ecobio, Rennes, CNRS/UR1), Marion Chorin
730 for the nutrient analyses at the EcoChimie Platform (EcoChim) from UMS OSUR 3343, and David Moussa,
731 chemical engineer at Rouen University (M2C-Rouen) for providing nutrients and TOC chemical analysis. Authors
732 thank the support of CESAM (UIDP/50017/2020 + UIDB/50017/2020 + LA/P/0094/2020).

733

734 **References**

- 735 Admiraal, W., and H. Peletier. 1980. Influence of Seasonal Variations of Temperature and Light on the Growth
736 Rate of Cultures and Natural Populations of Intertidal Diatoms *. **2**: 35–43.
- 737 Aller, R. C. 1980. Diagenetic Processes Near the Sediment-Water Interface of Long Island Sound. I.:
738 Decomposition and Nutrient Element Geochemistry (S, N, P), p. 237–350. *In* B.B.T.-A. in G. Saltzman [ed.],
739 Estuarine Physics and Chemistry: Studies in Long Island Sound. Elsevier.
- 740 Aller, R. C. 1988. Benthic fauna and biogeochemical processes in marine sediments: The role of burrow structures.
741 Nitrogen Cycl. Coast. Mar. Environ. 301–341.
- 742 Aller, R. C., and J. K. Cochran. 2019. The critical role of bioturbation for particle dynamics, priming potential,
743 and organic c remineralization in marine sediments: Local and basin scales. *Front. Earth Sci.* **7**: 1–14.
744 doi:10.3389/feart.2019.00157
- 745 Anand, S. S., K. J. Anju, D. Mathew, and M. D. Kumar. 2014. Sub-hourly changes in biogeochemical properties
746 in surface waters of Zuari estuary, Goa. *Environ. Monit. Assess.* **186**: 719–724. doi:10.1007/s10661-013-
747 3410-1
- 748 Andersen, T. J., M. Lanuru, C. Van Bernem, M. Pejrup, and R. Riethmueller. 2010. Erodibility of a mixed mudflat
749 dominated by microphytobenthos and *Cerastoderma edule*, East Frisian Wadden Sea, Germany. *Estuar.*
750 *Coast. Shelf Sci.* **87**: 197–206. doi:10.1016/j.ecss.2009.10.014
- 751 Asmus, R. M., and E. Bauerfeind. 1994. The microphytobenthos of Königshafen - spatial and seasonal distribution
752 on a sandy tidal flat. *Helgolander Meeresuntersuchungen* **48**: 257–276.
- 753 Behrenfeld, M. J., O. Prasil, M. Babin, and F. Bruyant. 2004. in Search of a Physiological Basis for Covariations
754 in Light-Limited and Light-Saturated Photosynthesis1. *J. Phycol.* **40**: 4–25. doi:10.1046/j.1529-
755 8817.2004.03083.x
- 756 Bellinger, B. J., G. J. C. Underwood, S. E. Ziegler, and M. R. Gretz. 2009. Significance of diatom-derived polymers
757 in carbon flow dynamics within estuarine biofilms determined through isotopic enrichment. *Aquat. Microb.*
758 *Ecol.* **55**: 169–187. doi:10.3354/ame01287
- 759 Bianchi, T. S., and E. A. Canuel. 2011. Chemical biomarkers in aquatic ecosystems, Princeton University Press.
- 760 Blanchard, G. F., J.-M. Guarini, P. Richard, P. Gros, and F. Mornet. 1996. Quantifying the short-term temperature
761 effect on light-saturated photosynthesis of intertidal microphytobenthos. *Mar Ecol Prog Ser* **134**: 309–313.
762 doi:10.3354/meps134309
- 763 Boudreau, B. P., and B. B. Jorgensen. 2001. The benthic boundary layer: Transport processes and biogeochemistry,
764 Oxford Uni. Oxford University Press.
- 765 Bouillon, S., and H. T. S. Boschker. 2006. Bacterial carbon sources in coastal sediments: a review based on stable
766 isotope data of biomarkers. *Biogeosciences* **3**: 175–185. doi:10.5194/bgd-2-1617-2005
- 767 Bowen, J. C., C. D. Clark, J. K. Keller, and W. J. De Bruyn. 2017. Optical properties of chromophoric dissolved
768 organic matter (CDOM) in surface and pore waters adjacent to an oil well in a southern California salt marsh.
769 *Mar. Pollut. Bull.* **114**: 157–168. doi:10.1016/j.marpolbul.2016.08.071
- 770 Bradford, M. M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein
771 utilizing the principle of protein-dye binding. *Anal. Biochem.* **72**: 248–254.
- 772 Brey, T. 2001. Population dynamics in benthic invertebrates. A virtual handbook. [http://www. awi-bremerhaven.](http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html)
773 [de/Benthic/Ecosystem/FoodWeb/Handbook/main. html.](http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html) Alfred Wegener Inst. Polar Mar. Res. Ger.

- 774 Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Response to Forum Commentary
775 on " Toward a Metabolic Theory of Ecology ". *Ecology* **85**: 1818–1821.
- 776 Bruno, J. F., and M. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. *Mar.*
777 *community Ecol.*
- 778 Burdige, D. J. 2007. Preservation of organic matter in marine sediments: Controls, mechanisms, and an imbalance
779 in sediment organic carbon budgets? *Chem. Rev.* **107**: 467–485. doi:10.1021/cr050347q
- 780 Burdige, D. J., S. W. Kline, and W. Chen. 2004. Fluorescent dissolved organic matter in marine sediment pore
781 waters. *Mar. Chem.* **89**: 289–311. doi:10.1016/j.marchem.2004.02.015
- 782 Burdige, D. J., and T. Komada. 2015. Sediment Pore Waters, p. 535–577. *In* D.A. Hansell and C.A. Carlson [eds.],
783 *Biogeochemistry of marine dissolved organic matter*. Burlington: Academic Press.
- 784 Cartaxana, P., M. Ruivo, C. Hubas, I. Davidson, J. Serôdio, and B. Jesus. 2011. Physiological versus behavioral
785 photoprotection in intertidal epipelagic and epipsammic benthic diatom communities. *J. Exp. Mar. Bio. Ecol.*
786 **405**: 120–127. doi:10.1016/j.jembe.2011.05.027
- 787 Chennu, A., P. Färber, G. De'ath, D. De Beer, and K. E. Fabricius. 2017. A diver-operated hyperspectral imaging
788 and topographic surveying system for automated mapping of benthic habitats. *Sci. Rep.* **7**: 1–12.
789 doi:10.1038/s41598-017-07337-y
- 790 Chennu, A., N. Volkenborn, D. De Beer, D. S. Wetthey, S. A. Woodin, and L. Polerecky. 2015. Effects of
791 bioadvection by *Arenicola marina* on microphytobenthos in permeable sediments. *PLoS One* **10**: 1–16.
792 doi:10.1371/journal.pone.0134236
- 793 Claquin, P., I. Probert, S. Lefebvre, and B. Veron. 2008. Effects of temperature on photosynthetic parameters and
794 TEP production in eight species of marine microalgae. *Aquat. Microb. Ecol.* **51**: 1–11.
795 doi:10.3354/ame01187
- 796 Coffinet, S., A. Huguet, C. Anquetil, and others. 2017. Evaluation of branched GDGTs and leaf wax n-alkane $\delta^{2}H$
797 as (paleo) environmental proxies in East Africa. *Geochim. Cosmochim. Acta* **198**: 182–193.
798 doi:10.1016/j.gca.2016.11.020
- 799 Van Colen, C., F. Montserrat, M. Vincx, P. M. J. Herman, T. Ysebaert, and S. Degraer. 2010. Macrobenthos
800 recruitment success in a tidal flat: Feeding trait dependent effects of disturbance history. *J. Exp. Mar. Bio.*
801 *Ecol.* **385**: 79–84. doi:10.1016/j.jembe.2010.01.009
- 802 Colijn, F., and K. S. Dijkema. 1981. Species Composition of Benthic Diatoms and Distribution of Chlorophyll a
803 on an Intertidal Flat in the Dutch Wadden Sea. *Mar. Ecol. Prog. Ser.* **4**: 9–21.
- 804 Cozzoli, F., T. J. Bouma, P. Ottolander, M. S. Lluch, T. Ysebaert, and P. M. J. Herman. 2018. The combined
805 influence of body size and density on cohesive sediment resuspension by bioturbators. *Sci. Rep.* **8**: 1–12.
806 doi:10.1038/s41598-018-22190-3
- 807 Cozzoli, F., T. Gomes da Conceição, J. Van Dalen, and others. 2020. Biological and physical drivers of bio-
808 mediated sediment resuspension: A flume study on *Cerastoderma edule*. *Estuar. Coast. Shelf Sci.* **241**.
809 doi:10.1016/j.ecss.2020.106824
- 810 Cozzoli, F., M. Shokri, T. Gomes da Conceição, and others. 2021. Modelling spatial and temporal patterns in
811 bioturbator effects on sediment resuspension: A biophysical metabolic approach. *Sci. Total Environ.* **792**:
812 148215. doi:10.1016/j.scitotenv.2021.148215
- 813 Crain, C. M., and M. D. Bertness. 2006. *Ecosystem Engineering across Environmental Gradients : Implications*

814 for Conservation and Management. *Bioscience* **56**: 211–218.

815 D'Hondt, A. S., W. Stock, L. Blommaert, T. Moens, and K. Sabbe. 2018. Nematodes stimulate biomass
816 accumulation in a multispecies diatom biofilm. *Mar. Environ. Res.* **140**: 78–89.
817 doi:10.1016/j.marenvres.2018.06.005

818 Dauwe, B., P. M. J. Herman, and C. H. R. Heip. 1998. Community structure and bioturbation potential of
819 macrofauna at four North Sea stations with contrasting food supply. *Mar. Ecol. Prog. Ser.* **173**: 67–83.
820 doi:10.3354/meps173067

821 Davey, J. T. 1994. The architecture of the burrow of *Nereis diversicolor* and its quantification in relation to
822 sediment-water exchange. *J. Exp. Mar. Bio. Ecol.* **179**: 115–129. doi:10.1016/0022-0981(94)90020-5

823 Davison, I. R. 1991. Environmental Effects on Algal Photosynthesis: Temperature. *J. Phycol.* **27**: 2–8.
824 doi:10.1111/1529-8817.ep10868724

825 Derrien, M., K. H. Shin, and J. Hur. 2019. Biodegradation-induced signatures in sediment pore water dissolved
826 organic matter: Implications from artificial sediments composed of two contrasting sources. *Sci. Total*
827 *Environ.* **694**: 133714. doi:10.1016/j.scitotenv.2019.133714

828 Donadi, S., J. Westra, E. J. Weerman, and others. 2013. Non-trophic Interactions Control Benthic Producers on
829 Intertidal Flats. *Ecosystems* **16**: 1325–1335. doi:10.1007/s10021-013-9686-8

830 Dubois, M., K. A. Gilles, J. K. Hamilton, Pa. Rebers, and F. Smith. 1956. Colorimetric method for determination
831 of sugars and related substances. *Anal. Chem.* **28**: 350–356.

832 Eglinton, G., and R. J. Hamilton. 1967. Leaf epicuticular waxes. *Science* (80-.). **156**: 1322–1335.

833 Einfeldt, A. L., J. R. Doucet, and J. A. Addison. 2014. Phylogeography and cryptic introduction of the ragworm
834 *Hediste diversicolor* (Annelida, Nereididae) in the Northwest Atlantic. *Invertebr. Biol.* **133**: 232–241.
835 doi:10.1111/ivb.12060

836 Eriksson, B. K., J. Westra, I. Van Gerwen, and others. 2017. Facilitation by ecosystem engineers enhances nutrient
837 effects in an intertidal system. *Ecosphere* **8**. doi:10.1002/ecs2.2051

838 Esnault, G., C. Retiere, and R. Lambert. 1990. Food resource partitioning in a population of *Nereis diversicolor*
839 (Annelida, Polychaeta) under experimental conditions. *Trophic Relationships Mar. Environ.* **453467**: 453–
840 467.

841 Esselink, P., and L. Zwarts. 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis*
842 *diversicolor*. *Mar. Ecol. Prog. Ser.* **56**: 243–254.

843 Fanjul, E., M. Escapa, D. Montemayor, M. Addino, M. F. Alvarez, M. A. Grela, and O. Iribarne. 2015. Effect of
844 crab bioturbation on organic matter processing in South West Atlantic intertidal sediments. *J. Sea Res.* **95**:
845 206–216. doi:10.1016/j.seares.2014.05.005

846 Fernandes, S., P. Sobral, and M. H. Costa. 2006. *Nereis diversicolor* effect on the stability of cohesive intertidal
847 sediments. *Aquat. Ecol.* **40**: 567–579. doi:10.1007/s10452-005-8000-z

848 François, F., M. Gerino, G. Stora, J. P. Durbec, and J. C. Poggiale. 2002. Functional approach to sediment
849 reworking by gallery-forming macrobenthic organisms: Modeling and application with the polychaete
850 *Nereis diversicolor*. *Mar. Ecol. Prog. Ser.* **229**: 127–136. doi:10.3354/meps229127

851 Georgette, D., V. Blaise, T. Collins, and others. 2004. Some like it cold: Biocatalysis at low temperatures. *FEMS*
852 *Microbiol. Rev.* **28**: 25–42. doi:10.1016/j.femsre.2003.07.003

853 Hansen, A. M., T. E. C. Kraus, B. A. Pellerin, J. A. Fleck, B. D. Downing, and B. A. Bergamaschi. 2016. Optical

854 properties of dissolved organic matter (DOM): Effects of biological and photolytic degradation. *Limnol.*
855 *Oceanogr.* **61**: 1015–1032. doi:10.1002/lno.10270

856 Hawes, T. C., M. R. Worland, and J. S. Bale. 2010. Freezing in the Antarctic limpet, *Nacella concinna*.
857 *Cryobiology* **61**: 128–132. doi:10.1016/j.cryobiol.2010.06.006

858 He, Y., B. Men, X. Yang, Y. Li, H. Xu, and D. Wang. 2019. Relationship between heavy metals and dissolved
859 organic matter released from sediment by bioturbation/bioirrigation. *J. Environ. Sci. (China)* **75**: 216–223.
860 doi:10.1016/j.jes.2018.03.031

861 Hellequin, E., C. Monard, A. Quaiser, M. Henriot, O. Klarzynski, and F. Binet. 2018. Specific recruitment of soil
862 bacteria and fungi decomposers following a biostimulant application increased crop residues mineralization.
863 *PLoS One* **13**: 1–19. doi:10.1371/journal.pone.0209089

864 Le Hir, P., A. Ficht, R. S. Jacinto, and others. 2001. Fine Sediment Transport and Accumulations at the Mouth of
865 the Seine Estuary (France). *Estuaries* **24**: 950. doi:10.2307/1353009

866 Hope, J. A., D. M. Paterson, and S. F. Thrush. 2020. The role of microphytobenthos in soft-sediment ecological
867 networks and their contribution to the delivery of multiple ecosystem services. *J. Ecol.* **108**: 815–830.
868 doi:10.1111/1365-2745.13322

869 Hughes, R. N. 1969. A study of feeding in *Scrobicularia plana*. *J. Mar. Biol. Assoc. United Kingdom* **49**: 805–823.

870 Huguet, A., L. Vacher, S. Relexans, S. Saubusse, J. M. Froidefond, and E. Parlanti. 2009. Properties of fluorescent
871 dissolved organic matter in the Gironde Estuary. *Org. Geochem.* **40**: 706–719.
872 doi:10.1016/j.orggeochem.2009.03.002

873 Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *OIKOS* **69**: 373–386.

874 Jones, C. M., D. R. H. Graf, D. Bru, L. Philippot, and S. Hallin. 2013. The unaccounted yet abundant nitrous oxide-
875 reducing microbial community: A potential nitrous oxide sink. *ISME J.* **7**: 417–426.
876 doi:10.1038/ismej.2012.125

877 Juneau, P., A. Barnett, V. Méléder, C. Dupuy, and J. Lavaud. 2015. Combined effect of high light and high salinity
878 on the regulation of photosynthesis in three diatom species belonging to the main growth forms of intertidal
879 flat inhabiting microphytobenthos. *J. Exp. Mar. Bio. Ecol.* **463**: 95–104. doi:10.1016/j.jembe.2014.11.003

880 Van De Koppel, J., T. Van Der Heide, A. H. Altieri, B. K. Eriksson, T. J. Bouma, H. Oloff, and B. R. Silliman.
881 2015. Long-Distance Interactions Regulate the Structure and Resilience of Coastal Ecosystems. *Ann. Rev.*
882 *Mar. Sci.* **7**: 139–158. doi:10.1146/annurev-marine-010814-015805

883 Kristensen, E. 1983. Ventilation and oxygen uptake by three species of. *Mar. Ecol. Prog. Ser.* **12**: 299–305.

884 Kristensen, E., G. Penha-lobes, M. Delefosse, T. Valdemarsen, C. O. Quintana, and G. T. Banta. 2012. What is
885 bioturbation? The need for a precise definition for fauna in aquatic sciences. **446**: 285–302.
886 doi:10.3354/meps09506

887 Kristensen, K., and K. Hansen. 1999. Transport of carbon dioxide and ammonium in bioturbated (*Nereis*
888 *diversicolor*) coastal, marine sediments. *Biogeochemistry* **45**: 147–168.

889 Laverman, A. M., P. Van Cappellen, D. Van Rotterdam-Los, C. Pallud, and J. Abell. 2006. Potential rates and
890 pathways of microbial nitrate reduction in coastal sediments. *FEMS Microbiol. Ecol.* **58**: 179–192.
891 doi:10.1111/j.1574-6941.2006.00155.x

892 Laverman, A. M., C. Pallud, J. Abell, and P. Van Cappellen. 2012. Comparative survey of potential nitrate and
893 sulfate reduction rates in aquatic sediments. *Geochim. Cosmochim. Acta* **77**: 474–488.

894 doi:10.1016/j.gca.2011.10.033
895 Li, W., X. Li, C. Han, L. Gao, H. Wu, and M. Li. 2023. A new view into three-dimensional excitation-emission
896 matrix fluorescence spectroscopy for dissolved organic matter. *Sci. Total Environ.* **855**: 158963.
897 doi:10.1016/j.scitotenv.2022.158963
898 Lorenzen, C. J. 1967. Determination of Chlorophyll and Pheo-Pigments : Spectrophotometric Equations. *Limnol.*
899 *Oceanogr.* **12**: 343–346. doi:10.4319/lo.1967.12.2.0343
900 Maire, O., J. N. Merchant, M. Bulling, L. R. Teal, A. Grémare, J. C. Duchêne, and M. Solan. 2010. Indirect effects
901 of non-lethal predation on bivalve activity and sediment reworking. *J. Exp. Mar. Bio. Ecol.* **395**: 30–36.
902 doi:10.1016/j.jembe.2010.08.004
903 Marchesi, J. R., T. Sato, A. J. Weightman, T. A. Martin, J. C. Fry, S. J. Hiom, and W. G. Wade. 1998. Design and
904 evaluation of useful bacterium-specific PCR primers that amplify genes coding for bacterial 16S rRNA.
905 *Appl. Environ. Microbiol.* **64**: 795–799. doi:10.1128/aem.64.2.795-799.1998
906 McKnight, D. M., E. W. Boyer, P. K. Westerhoff, P. T. Doran, T. Kulbe, and D. T. Andersen. 2001.
907 Spectrofluorometric characterization of dissolved organic matter for indication of precursor organic material
908 and aromaticity. *Limnol. Oceanogr.* **46**: 38–48. doi:10.4319/lo.2001.46.1.0038
909 Montserrat, F., C. Van Colen, P. Provoost, M. Milla, M. Ponti, K. Van den Meersche, T. Ysebaert, and P. M. J.
910 Herman. 2009. Sediment segregation by biodiffusing bivalves. *Estuar. Coast. Shelf Sci.* **83**: 379–391.
911 doi:10.1016/j.ecss.2009.04.010
912 Morelle, J., P. Claquin, and F. Orvain. 2020. Evidence for better microphytobenthos dynamics in mixed sand/mud
913 zones than in pure sand or mud intertidal flats (Seine estuary, Normandy, France). *PLoS One* **15**: e0237211.
914 doi:10.1371/journal.pone.0237211
915 Morelle, J., O. Maire, A. Richard, A. Slimani, and F. Orvain. 2021. Contrasted impact of two macrofaunal species
916 (*Hediste diversicolor* and *Scrobicularia plana*) on microphytobenthos spatial distribution and photosynthetic
917 activity at microscale. *Mar. Environ. Res.* **163**. doi:10.1016/j.marenvres.2020.105228
918 Morelle, J., C. Roose-Amsaleg, and A. M. Laverman. 2022. Microphytobenthos as a source of labile organic matter
919 for denitrifying microbes. *Estuar. Coast. Shelf Sci.* **275**. doi:10.1016/j.ecss.2022.108006
920 Morelle, J., M. Schapira, F. Orvain, and others. 2018. Annual Phytoplankton Primary Production Estimation in a
921 Temperate Estuary by Coupling PAM and Carbon Incorporation Methods. *Estuaries and Coasts* 1–19.
922 doi:10.1007/s12237-018-0369-8
923 Morgan-Kiss, R. M., J. C. Priscu, T. Pockock, L. Gudynaite-Savitch, and N. P. A. Huner. 2006. Adaptation and
924 Acclimation of Photosynthetic Microorganisms to Permanently Cold Environments. *Microbiol. Mol. Biol.*
925 *Rev.* **70**: 222–252. doi:10.1128/MMBR.70.1.222-252.2006
926 Muyzer, G., E. C. De Waal, and A. G. Uitterlinden. 1993. Profiling of complex microbial populations by
927 denaturing gradient gel electrophoresis analysis of polymerase chain reaction-amplified genes coding for
928 16S rRNA. *Appl. Environ. Microbiol.* **59**: 695–700. doi:10.1128/aem.59.3.695-700.1993
929 Oleszczuk, B., E. Michaud, N. Morata, P. E. Renaud, and M. Kędra. 2019. Benthic macrofaunal bioturbation
930 activities from shelf to deep basin in spring to summer transition in the Arctic Ocean. *Mar. Environ. Res.*
931 **150**: 104746. doi:10.1016/j.marenvres.2019.06.008
932 Orvain, F. 2005. A model of sediment transport under the influence of surface bioturbation: Generalisation to the
933 facultative suspension-feeder *Scrobicularia plana*. *Mar. Ecol. Prog. Ser.* **286**: 43–56.

934 doi:10.3354/meps286043

935 Orvain, F., M. De Crignis, K. Guizien, S. Lefebvre, C. Mallet, E. Takahashi, and C. Dupuy. 2014. Tidal and
936 seasonal effects on the short-term temporal patterns of bacteria, microphytobenthos and exopolymers in
937 natural intertidal biofilms (Brouage, France). *J. Sea Res.*

938 Orvain, F., S. Lefebvre, J. Montepini, M. Sébire, A. Gangnery, and B. Sylvand. 2012. Spatial and temporal
939 interaction between sediment and microphytobenthos in a temperate estuarine macro-intertidal bay. *Mar.*
940 *Ecol. Prog. Ser.* **458**: 53–68.

941 Orvain, F., P. G. Sauriau, A. Sygut, L. Joassard, and P. Le Hir. 2004. Interacting effects of *Hydrobia ulvae*
942 bioturbation and microphytobenthos on the erodibility of mudflat sediments. *Mar. Ecol. Prog. Ser.* **278**: 205–
943 223. doi:10.3354/meps278205

944 Parlanti, E., K. Wörz, L. Geoffroy, and M. Lamotte. 2000. Dissolved organic matter fluorescence spectroscopy as
945 a tool to estimate biological activity in a coastal zone submitted to anthropogenic inputs. *Org. Geochem.* **31**:
946 1765–1781. doi:10.1016/S0146-6380(00)00124-8

947 Passarelli, C., C. Hubas, A. N. Segui, J. Grange, and T. Meziane. 2012. Surface adhesion of microphytobenthic
948 biofilms is enhanced under *Hediste diversicolor* (O.F. Müller) trophic pressure. *J. Exp. Mar. Bio. Ecol.* **438**:
949 52–60. doi:10.1016/j.jembe.2012.10.005

950 Paterson, D. M., I. Fortune, R. J. Aspden, and K. S. Black. 2019. Intertidal Flats: Form and Function, p. 383–406.
951 *In Coastal Wetlands*. Elsevier.

952 Perkins, A. K., I. R. Santos, A. L. Rose, K. G. Schulz, H. P. Grossart, B. D. Eyre, B. P. Kelaher, and J. M. Oakes.
953 2022. Production of dissolved carbon and alkalinity during macroalgal wrack degradation on beaches: a
954 mesocosm experiment with implications for blue carbon. *Biogeochemistry* **160**: 159–175.
955 doi:10.1007/s10533-022-00946-4

956 Pischedda, L., P. Cuny, J. L. Esteves, J. C. Poggiale, and F. Gilbert. 2012. Spatial oxygen heterogeneity in a
957 *Hediste diversicolor* irrigated burrow. *Hydrobiologia* **680**: 109–124. doi:10.1007/s10750-011-0907-x

958 Quaiser, A., X. Bodi, A. Dufresne, and others. 2014. Unraveling the stratification of an iron-oxidizing microbial
959 mat by metatranscriptomics. *PLoS One* **9**: 1–9. doi:10.1371/journal.pone.0102561

960 Raven, J., and R. J. Geider. 1988. Temperature and algal growth. *New Phytol.* **110**: 441–461. doi:10.1111/j.1469-
961 8137.1988.tb00282.x

962 Redzuan, N. S., and G. J. C. Underwood. 2021. The importance of weather and tides on the resuspension and
963 deposition of microphytobenthos (MPB) on intertidal mudflats. *Estuar. Coast. Shelf Sci.* **251**.
964 doi:10.1016/j.ecss.2021.107190

965 Richard, A., F. Orvain, J. Morelle, and others. 2023. Impact of Sediment Bioturbation on Microphytobenthic
966 Primary Producers: Importance of Macrobenthic Functional Traits. *Ecosystems* **26**: 1077–1094.
967 doi:10.1007/s10021-022-00817-x

968 Riisgard, H. U. 1991a. Suspension feeding in the polychaete *Nereis diversicolor*. *Mar. Ecol. Prog. Ser.* **70**: 29–37.
969 doi:10.3354/meps070029

970 Riisgard, H. U. 1991b. Suspension feeding in the polychaete *Nereis diversicolor*. *Mar. Ecol. Prog. Ser.* **70**: 29–37.
971 doi:10.3354/meps070029

972 Riisgård, H., A. Vedel, H. Boye, and P. Larsen. 1992. Filter-net structure and pumping activity in the polychaete
973 *Nereis diversicolor*: effects of temperature and pump-modelling. *Mar. Ecol. Prog. Ser.* **83**: 79–89.

974 doi:10.3354/meps083079

975 Santos, S., P. C. Luttikhuisen, J. Campos, C. H. R. Heip, and H. W. van der Veer. 2011. Spatial distribution
976 patterns of the peppery furrow shell *Scrobicularia plana* (da Costa, 1778) along the European coast: A
977 review. *J. Sea Res.* **66**: 238–247. doi:10.1016/j.seares.2011.07.001

978 Sanz-Lázaro, C., T. Valdemarsen, A. Marín, and M. Holmer. 2011. Effect of temperature on biogeochemistry of
979 marine organic-enriched systems: Implications in a global warming scenario. *Ecol. Appl.* **21**: 2664–2677.
980 doi:10.1890/10-2219.1

981 Scaps, P. 2002. A review of the biology, ecology and potential use of the common ragworm *Hediste diversicolor*
982 (O.F. Müller) (Annelida: Polychaeta). *Hydrobiologia* **470**: 203–218.

983 Seeberg-Elverfeldt, J., M. Schlüter, T. Feseker, and M. Kölling. 2005. Rhizon sampling of porewaters near the
984 sediment-water interface of aquatic systems. *Limnol. Oceanogr. Methods* **3**: 361–371.
985 doi:10.4319/lom.2005.3.361

986 Serôdio, J., S. Vieira, and F. Barroso. 2007. Relationship of variable chlorophyll fluorescence indices to
987 photosynthetic rates in microphytobenthos. *Aquat. Microb. Ecol.* **49**: 71–85. doi:10.3354/ame01129

988 Shen, Q., F. Ji, J. Wei, D. Fang, Q. Zhang, L. Jiang, A. Cai, and L. Kuang. 2020. The influence mechanism of
989 temperature on solid phase denitrification based on denitrification performance, carbon balance, and
990 microbial analysis. *Sci. Total Environ.* **732**. doi:10.1016/j.scitotenv.2020.139333

991 Shen, Z., J. Hu, J. Wang, and Y. Zhou. 2015. Biological denitrification using starch/polycaprolactone blends as
992 carbon source and biofilm support. *Desalin. Water Treat.* **54**: 609–615. doi:10.1080/19443994.2014.885395

993 Stal, L. J. 2010. Microphytobenthos as a biogeomorphological force in intertidal sediment stabilization. *Ecol. Eng.*
994 **36**: 236–245. doi:10.1016/j.ecoleng.2008.12.032

995 Stal, L. J., and J. F. C. de Brouwer. 2003. Biofilm formation by benthic diatoms and their influence on the
996 stabilization of intertidal mudflats. *Berichte – Forschungszentrum Terramare* **12**: 109–111.

997 Swanberg, I. L. 1991. The influence of the filter-feeding bivalve *Cerastoderma edule* L. on microphytobenthos :
998 a laboratory study. *J. Exp. Mar. Bio. Ecol.* **151**: 93–111.

999 Takai, K., and K. Horikoshi. 2000. Rapid detection and quantification of members of the archaeal community by
1000 quantitative PCR using fluorogenic probes. *Appl. Environ. Microbiol.* **66**: 5066–5072.
1001 doi:10.1128/AEM.66.11.5066-5072.2000

1002 Taylor, J. D., B. A. McKew, A. Kuhl, T. J. McGenity, and G. J. C. Underwood. 2013. Microphytobenthic
1003 extracellular polymeric substances (EPS) in intertidal sediments fuel both generalist specialist EPS-
1004 degrading bacteria. *Limnol. Oceanogr.* **58**: 1463–1480. doi:10.4319/lo.2013.58.4.1463

1005 Thibault, A., S. Derenne, E. Parlanti, and others. 2019. Dynamics of organic matter in the Seine Estuary (France):
1006 Bulk and structural approaches. *Mar. Chem.* **212**: 108–119. doi:10.1016/j.marchem.2019.04.007

1007 Ubertini, M., S. Lefebvre, A. Gangnery, K. Grangeré, R. Le Gendre, and F. Orvain. 2012. Spatial variability of
1008 benthic-pelagic coupling in an estuary ecosystem: consequences for microphytobenthos resuspension
1009 phenomenon. *PLoS One* **7**: e44155. doi:10.1371/journal.pone.0044155

1010 Underwood, G. J. C. 1994. Seasonal and spatial variation in epipellic diatom assemblages in the severn estuary.
1011 *Diatom Res.* **9**: 451–472. doi:10.1080/0269249X.1994.9705319

1012 Underwood, G. J. C., and J. C. Kromkamp. 1999. Primary Production by Phytoplankton and Microphytobenthos
1013 in Estuaries. *Adv. Ecol. Res.* **29**: 93–153. doi:10.1016/S0065-2504(08)60192-0

- 1014 Vedel, A. 1998. Phytoplankton depletion in the benthic boundary layer caused by suspension-feeding *Nereis*
1015 *diversicolor* (Polychaeta): grazing impact and effect of temperature. *Mar. Ecol. Prog. Ser.* **171**: 125–132.
1016 doi:10.3354/meps171125
- 1017 Vonk, J. E., B. E. van Dongen, and Ö. Gustafsson. 2008. Lipid biomarker investigation of the origin and diagenetic
1018 state of sub-arctic terrestrial organic matter presently exported into the northern Bothnian Bay. *Mar. Chem.*
1019 **112**: 1–10. doi:10.1016/j.marchem.2008.07.001
- 1020 Weerman, E. J., P. M. J. Herman, and J. Van De Koppel. 2011. Macrobenthos abundance and distribution on a
1021 spatially patterned intertidal flat. *Mar. Ecol. Prog. Ser.* **440**: 95–103. doi:10.3354/meps09332
- 1022 Widdows, J., A. Blauw, C. H. R. Heip, and others. 2004. Role of physical and biological processes in sediment
1023 dynamics of a tidal flat in Westerschelde Estuary, SW Netherlands. *Mar. Ecol. Prog. Ser.* **274**: 41–56.
- 1024 Wiesebron, L. E., N. Steiner, C. Morys, T. Ysebaert, and T. J. Bouma. 2021. Sediment Bulk Density Effects on
1025 Benthic Macrofauna Burrowing and Bioturbation Behavior. *Front. Mar. Sci.* **8**: 1–16.
1026 doi:10.3389/fmars.2021.707785
- 1027 Wolff, W. J. 1973. The estuary as a habitat: an analysis of data on the soft-bottom macrofauna of the estuarine
1028 area of the rivers Rhine, Meuse and Scheldt. *Zool. Verkan.* **126**: 1–242.
- 1029 Yallop, M. L., D. M. Paterson, and P. Wellsbury. 2000. Interrelationships between rates of microbial production,
1030 exopolymer production, microbial biomass, and sediment stability in biofilms of intertidal sediments.
1031 *Microb. Ecol.* **39**: 116–127. doi:10.1007/s002489900186
- 1032 Zhang, Y., J. Wang, J. Tao, and others. 2022. Concentrations of dissolved organic matter and methane in lakes in
1033 Southwest China: Different roles of external factors and in-lake biota. *Water Res.* **225**: 119190.
1034 doi:10.1016/j.watres.2022.119190
- 1035 Zsolnay, A., E. Baigar, M. Jimenez, B. Steinweg, and F. Saccomandi. 1999. Differentiating with fluorescence
1036 spectroscopy the sources of dissolved organic matter in soils subjected to drying. *Chemosphere* **38**: 45–50.
1037 doi:10.1016/S0045-6535(98)00166-0
- 1038 Zwarts, L., A.-M. Blomert, P. Spaak, and B. De Vriers. 1994. Feeding radius, burying depth and siphon size of
1039 *Macoma balthica* and *Scrobicularia plana*. *J. Exp. Bot.* **183**: 193–212.
- 1040