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1 **Meiofauna communities' response to an anthropogenic pressure: the case study**
2 **of green macroalgal bloom on sandy beach in Brittany**

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17
18 **Abstract:** Open sandy beaches support key ecological functions and a distinctive biodiversity, but
19 are threatened by an increasing anthropogenic pressure. Among these threats is the occurrence of
20 green tides of *Ulva* spp., expression of the eutrophication phenomenon. Our study aimed at
21 determining the impact of green macroalgal accumulations on benthic meiofauna inhabiting two
22 macrotidal sandy beaches of Brittany: Saint Nic (impacted) and Anse de Dinan (unimpacted). The
23 presence of *Ulva* enhanced total meiofaunal abundance and nematode functional diversity when
24 compared to a state free from macroalgal mats. The stranded *Ulva* supported high values of
25 meiofaunal β -diversity as well. This unexpected response was likely due to the highly dynamic
26 nature of open sandy beaches that prevents O₂ depletion within sediments. Natural seasonal changes
27 in meiofaunal biomass and composition were also evident at both beaches and changes in
28 environmental features, apart from eutrophication alone, do drive the variability in meiofaunal
29 biomass and nematodes diversity.

30 **Keywords:** Meiofauna, macroalgal bloom, sandy beach, nematodes, Brittany, anthropogenic
31 impact, *Ulva* spp.

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35 **Declaration of interest: none**

36

37 **1. Introduction**

38 There is growing scientific evidence that our coastlines are suffering from catastrophic ecological
39 damage as a result of anthropogenic activities (Cloern et al., 2016). Eutrophication is a process of
40 natural or man-made enrichment with inorganic nutrient elements (e.g. nitrogen and phosphorus)
41 beyond the maximum critical level of the self-regulatory capacity of a given system for a balanced
42 flow and cycling of nutrients (Fletcher, 1996). It is a direct consequence of increasing population
43 densities along coastal areas and the use of fertilizers for agriculture (Grall and Chauvaud, 2002).
44 Increased nutrient loading leads to stimulated primary production and, in particular conditions, such
45 as shallow and enclosed areas with low water turnover, eutrophication may induce opportunistic
46 green or brown macroalgal blooms (Liu et al., 2009). The term “Green Tides” (here after GT) or
47 macroalgal blooms covers a heterogeneous set of events that share two characteristics: they are
48 caused predominantly by green macroalgae, and have negative impacts on the environment (Garcia
49 and Johnstone, 2006; Ye et al., 2011). Thus, although macroalgal blooms can be in some cases a
50 natural phenomenon, the global problem of green tides has increased both in extent and in its public
51 perception over the last three decades. GT occur mainly in the North Temperate Zone, with
52 America, Europe and the Asia-Pacific being the most seriously affected (Morand and Merceron,
53 2004). In Brittany (Western France), the first green algal bloom was recorded on the southwestern
54 channel bays in the early 70’s. Nowadays, many coastal areas and beaches around Brittany are
55 affected by green tides. In 2012, green macroalgal blooms were reported from 51 beaches and 33
56 estuaries for a total volume of 40,000 m³ of fresh algae (CGDD 2014). From 1997 to 2015 the
57 number of sites affected by green tides increased from 34 to 63, while the number of Brittany
58 coastal cities affected by GT increased from 60 to 138 ([http://www.ceva.fr/fre/MAREES-](http://www.ceva.fr/fre/MAREES-VERTES)
59 VERTES). In 1986, 25,000 m³ of *Ulva* spp. accumulated in Lannion Bay in a single season
60 (Charlier et al., 2006).

61 Sandy beaches are the most extensive intertidal system worldwide (Wright and Short, 1983) and
62 dominate a majority of temperate and tropical coastlines where they represent both important
63 recreational assets and functions as well as buffer zones against the sea (Sun et al., 2014). Sandy
64 beaches are known to be among the most dynamic soft bottom habitat, with abundant biological
65 resources (McLachlan and Brown, 2010) and act as nurseries and feeding areas for commercially
66 important fishes and bivalves (surf clams) (Schlacher et al., 2008). Sandy beach ecosystems are
67 populated by many organisms that are specialized and adapted to life in mobile substrate and their
68 peculiar harsh environment. These species all play important roles in the ecological functioning of
69 the beach system, e.g. as primary producers (diatoms and algae), decomposers (bacteria),
70 consumers (heterotrophic bacteria, meiobenthos and macrobenthos). From regional to global scales,

71 sandy beaches also highly contribute to β -diversity (Schlacher et al., 2008). As a transition zone
72 between land and sea, sandy beach ecosystems suffer from various anthropogenic disturbances such
73 as coastal development and pollution (Schlacher et al., 2007; Defeo et al., 2009); as well as from
74 green macroalgal blooms mainly caused by nutrient enrichment of coastal waters by human
75 activities (Quillien et al., 2015a, 2016). These macroalgae can form stranded mats along beaches,
76 such as the documented large *Ulva* spp. mats along Brittany beaches (CGDD 2014). The presence
77 of such free-living macroalgal mats affects exchange between sediments and water and modifies
78 local hydrodynamics (Hull, 1987) and primary production (Liu et al., 2009) and affects benthic
79 macro- and meiofauna fauna (e.g. Dolbeth et al., 2007; Carriço et al., 2013; Quillien et al., 2015a,
80 2015b; Sun et al., 2014) and fish populations (Le Luherne et al., 2016).

81 The majority of the studies and monitoring programs dedicated to the evaluation of anthropogenic
82 impacts (e.g. eutrophication, algal blooms) in the marine environment focus on benthic macrofauna,
83 as well as microbial and epiphyte communities; only few included hitherto meiofauna especially in
84 the case of macroalgal bloom impacts (Villano et al., 1995; Neira et al., 1996; Garcia and
85 Jonhstone, 2006; Carriço et al., 2013). Nevertheless, meiofauna has recently started to be
86 recognized as useful biological indicators, since the community may contain information that
87 macrofauna cannot provide (Zeppilli et al., 2015; Bianchelli et al., 2016; Schratzberger and Ingels,
88 2017). Relative to macrofauna, meiofauna exhibits a shorter response time and many perturbations
89 are detectable due to their asynchronous reproduction, rapid turnover rate, and lack of larval
90 dispersal. As a result, the abundance of meiofauna is more sensitive to environmental fluctuations
91 and is therefore useful as indicator of disturbances (Schratzberger et al., 2000; Austen and
92 Widdicombe, 2006). Free-living nematodes, usually the dominant meiobenthic taxon, have been
93 pointed out as potential indicators for the effects of anthropogenic disturbance on biodiversity in
94 aquatic ecosystems (Moreno et al., 2008; Vanaverbeke and Vincx, 2008; Semprucci et al., 2015,
95 2016; Zeppilli et al., 2015). Moreover, nematodes direct development coupled to the one to three
96 months long life-cycle, permit observing changes in the community structure readily observable in
97 short term benthic studies (Moens et al., 2014a).

98 The aim of the present study was to assess the impact of eutrophication by green macroalgae (i.e.
99 *Ulva* spp.) on benthic meiofauna, and particularly nematodes, inhabiting macrotidal sandy beaches
100 of Brittany. To reach this objective, the meiofaunal communities inhabiting two beaches in the bay
101 of Douarnenez (south of Finistère, France) with different impact of GT were investigated. The
102 beach of Saint Nic, is impacted seasonally by GT while the beach of Anse de Dinan was considered
103 as unimpacted since it has never harboured GT. The meiobenthic communities were sampled at
104 different seasons, since meiofauna can show natural seasonal variations in relation to changes in

105 environmental conditions (Liu et al., 2008). Hence, the following hypotheses were studied: (1)
106 meiofaunal and nematode abundance, biomass, structural and functional diversity are affected by
107 the presence of *Ulva* spp.; (2) natural seasonal environmental changes differently affect the
108 meiofauna populations inhabiting impacted and unimpacted sandy beaches. Because an integrated
109 approach considering different benthic components appears to be the most suitable when assessing
110 environmental impacts and ecological status of coastal zones (Patrício et al., 2012), our main results
111 will be discussed in perspective with the macrofaunal results previously published for the same
112 ecosystem (Quillien et al., 2015a, 2015b).

113

114 **2. Material and Methods**

115 *2.1 Study area and sampling strategy*

116 The study was performed in two sandy beaches located in the bay of Douarnenez (Brittany, France):
117 Anse de Dinan and Saint Nic (Fig. 1). The two sandy beaches consist of large areas (up to 500 m
118 from shore during spring tides) that are uncovered at low tide (mean tidal regime = 6.5 ± 0.5 m) and
119 have lengths ranging from 2.1 to 3.0 km (see more detailed description in Quillien et al., 2015a).
120 The unimpacted beach of Anse de Dinan (AD, 48°14.109'N, 4°32.545'W) never harbored green
121 tides and the anthropogenic impact is negligible (a wetland area located just behind the beach filters
122 terrestrial water inputs and has limited urbanization); conversely the impacted beach of Saint Nic
123 (SN, 48° 10.132'N, 4° 17.465'W) is characterized by the presence of spatially heterogeneous GT
124 blooms, mainly *Ulva* sp., since the early 80's (Charlier et al., 2007). In order to characterize the
125 meiofaunal communities, sediment sampling was conducted manually in the intertidal zone during
126 three months - May, July and December 2012 - using Plexiglas corers (10cm²). At each site two
127 separated sediment replicates of 15 cm depth were collected and stored frozen (-20°C) until the
128 laboratory analyses. At both sites a single sediment core (inner diameter: 11.3cm; depth: 15cm;
129 surface: 100cm²) was collected from which grain size and organic matter content characteristics
130 were determined. Seawater temperature, salinity, and dissolved oxygen content were measured at
131 each sampling occasion using an YSI-OMS v2 multi-parameter probe.

132

133 *2.2 Samples processing*

134 **Meiofauna and nematode analyses.** For meiofaunal extraction, sediment samples (0-15 cm) were
135 sieved through a 1000 µm mesh. The fraction remaining on a 40 µm mesh was centrifuged three
136 times with Ludox HS40 (diluted with water to a final density of 1.18 g cm⁻³) and stained with Rose
137 Bengal (0.5 g l⁻¹) (Heip et al., 1985). Meiofauna was counted and classified to higher taxonomic

138 level under a stereomicroscope after which the density (n. of individuals/10 cm⁻²) and taxon
139 richness of the communities were estimated.

140 The determination of meiofaunal biomass was performed using the volumetric method that consists
141 of indirect estimates of biomass extrapolating organism weight from a volume (Danovaro, 2010).
142 From each sample, 100 randomly collected nematodes were mounted on slides after a formalin–
143 ethanol–glycerol treatment to prevent dehydration (Danovaro, 2010) and then identified to the
144 genus level according to Platt and Warwick (1983, 1988), Warwick et al. (1998), and the NeMys
145 database (<http://nemys.ugent.be>). The different nematode morphotypes were reported under the
146 name of the genus and then as putative species sp1, sp2 and so on. The nematode biomass was
147 calculated from the biovolume, which was estimated from all specimens per replicate using the
148 Andrassy formula ($V=L \times W^2 \times 0.063 \times 10^{-5}$, with body length, L, and width, W, expressed in μm ;
149 Andrassy, 1956). The carbon contents was considered as 40 % of the dry weight (Feller and
150 Warwick, 1988).

151 Species richness (SR) was calculated as the total number of species collected at each site. Nematode
152 species diversity (H, using log base e) was measured using the Shannon–Weaver diversity index
153 (Shannon and Weaver, 1949), with the evenness as the Pielou index (J; Pielou, 1975). In order to
154 facilitate comparison among samples, the expected number of nematode species for a theoretical
155 random sample of 51 individuals, $ES_{(51)}$, was calculated. All indices were calculated using PRIMER
156 v6.0+ (Plymouth Marine Laboratory, UK; Clarke and Gorley, 2006).

157 The trophic diversity of the nematodes was determined by analyzing trophic groups, as reported by
158 Wieser (1953). The nematodes were divided into four groups, as follows: no buccal cavity or a fine
159 tubular one, as selective (bacterial) feeders (1A); large, but unarmed, buccal cavity, as non-
160 selective deposit feeders (1B); buccal cavity with scraping tooth or teeth epistrate or epigrowth
161 feeders (2A); and buccal cavity with large jaws, as predators/omnivores (2B). The index of trophic
162 diversity (ITD) was calculated as Θ , where $\Theta=g_1^2+g_2^2+g_3^2\dots+g_n^2$, and g is the relative contribution
163 (in terms of number of specimens) of each trophic group to the total number of individuals, and n is
164 the number of trophic groups (Heip et al., 1985). For n=4, Θ ranges from 0.25 (highest trophic
165 diversity; i.e. each of the four trophic groups accounts for 25 % of the nematode abundance) to 1.0
166 (lowest diversity; i.e., when one trophic group accounts for 100 % of the nematode abundance).
167 Nematode trophic structure was calculated based on the nematode biomass matrix. The maturity
168 index (MI) of nematode populations was calculated from life strategies (r - K) of the nematodes for
169 which these strategies are known (Bongers, 1990; Bongers et al., 1995). In order to identify
170 colonization strategies, nematodes are divided into “colonizers” (comparable to r-strategists,
171 characterized by a short life cycle, high colonization ability, and tolerance to disturbance, e.g.,

172 eutrophication) and “persisters” (K-strategists with a low reproduction rate, long life cycle, and low
173 colonization ability and tolerance to disturbance; the list of species with different life strategies is
174 reported by Bongers et al., 1991). The MI was calculated according to the weighted mean of the
175 individual genus scores: $MI = \sum v(i) \times f(i)$, where v is the c–p value (colonisers–persisters; ranging
176 from 1, i.e. only opportunistic colonizers, to 5, i.e. only persisters) of the genus i (Bongers et al.,
177 1991) and $f(i)$ is the frequency of that genus.

178
179 **Environmental variable analyses.** Grain size was measured by dry-sieving the sediment, using a
180 series of 16 sieves from 63 to 10,000 μm . The sorting index (SI) was calculated based on the first
181 and third quartile ratio ($\sqrt{Q25/Q75}$, where Q25 and Q75 denote the first and the third quartiles of
182 the sediment grain size, respectively), and the median (Q50) was equal to the second quartile of the
183 sediment grain size value (hereafter referred to as ‘median’; Quillien et al., 2015a). Organic matter
184 content was measured by weight loss after combustion at 450°C for 5h. *Ulva* biomass was
185 estimated by CEVA (www.ceva.fr/fre) through monthly aerial surveys (for estimation of surface
186 area covered by mats) and field sampling (for conversion into biomass). Monthly mean values for
187 wave height were taken from the publicly available database PREVIMER. PREVIMER estimates
188 the wave height using the model WW3 (grid = 200 m).

189

190 2.3 Data analyses

191 Principal component analysis (PCA) with Euclidean distance was carried out on environmental
192 data, previously normalized, in order to visualize the comparison of the two sandy beaches based on
193 the main abiotic variables.

194 Uni- and multivariate analyses were carried out in order to assess temporal and spatial differences
195 in meiofauna and nematode assemblage composition. The sampling design included two fixed and
196 orthogonal factors: beach (2 levels: Saint Nic and Anse de Dinan) and month (3 levels: May, July
197 and December). Pair wise tests were carried out to verify the significance of the differences among
198 beaches at different months. The distance-based permutation analysis of variance (PERMANOVA;
199 Anderson, 2001) in either univariate (separately for each meiofauna and nematode diversity index)
200 or multivariate data (for both meiofaunal assemblages and nematode communities) was used for
201 testing for differences in community structure between beaches and seasons. Faunal data (square-
202 root transformed) were analyzed using tests based on Bray-Curtis similarity matrices and on
203 Euclidean-distance similarity matrices for univariate data. PCA analysis was performed to visualize
204 the spatial (i.e. beaches) and temporal (i.e. seasons) patterns in the meiofaunal assemblages and to
205 identify the meiofaunal taxa mainly responsible for the spatio-temporal variability.

206 Afterwards, the relative contribution of each nematode species to the average dissimilarities
207 between beaches and periods (i.e. months) was calculated using SIMPER test (using 90% as cutoff).
208 The β diversity provides indications of any change in community composition and can be expressed
209 as percentages of dissimilarity (e.g. based on a Bray–Curtis similarity matrix; Gray, 2000). The
210 SIMPER analysis was used to determine the contributions of each species to the average Bray–
211 Curtis dissimilarity (Clarke and Warwick, 2001). This analysis of dissimilarities was based on a
212 square-root transformation matrix. Non-metric multidimensional scaling (nMDS) based on Bray–
213 Curtis similarity matrix was used to visualize spatio-temporal patterns on nematode assemblages at
214 the two sandy beaches.

215 Multivariate multiple regression analyses (DistLM forward, Anderson et al., 2008) were performed
216 to test the influence of abiotic variables (wave height, seawater temperature (SWT), salinity, oxygen
217 concentration (O_2), *Ulva* biomass, median grain size (MGS) and organic matter (OM) into the
218 sediment) on meiofaunal standing stock and community composition, nematode species
219 composition, trophic diversity and nematode life strategy. The DistLM forward was carried out
220 using the routine included in the PRIMER v6.0 + software (Clarke and Gorley, 2006). This analysis
221 was based on Bray-Curtis dissimilarities with 4999 permutations of residuals. PERMANOVA, pair
222 wise tests, PCA, SIMPER and nMDS were carried out by means of the software PRIMER v6.0 +
223 (Clarke and Gorley, 2006).

224

225 **3. Results**

226 *3.1 Environmental characterization*

227 Environmental characteristics of the Anse de Dinan (AD, unimpacted) and Saint Nic (SN,
228 impacted) beaches are reported in Table 1. Seawater temperature, salinity, and dissolved oxygen did
229 not show significant differences (see also Quillien et al., 2015a) between the two beaches, but lower
230 seawater temperatures were reported during winter time. The two environments were well
231 oxygenized during all sampling periods. Organic matter content (from 3.19% to 4.90% at SN in
232 December and AD in May, respectively) were comparable between the two sampling sites but a
233 decreasing trend was observed from May to December (Table 1). Higher values of sorting index
234 and median grain size were found at AD compared to SN, particularly in May (Table 1). However,
235 both sampling sites characteristics were part of dissipative sandy beaches definition (Carrigo et al.
236 2013). Actually, the presence (SN, until $1445.8 \cdot 10^3$ kg in July; Table 1) or absence of *Ulva* (AD)
237 was the most important environmental variable that made the difference between the two beaches.

238 The PCA visualized data trends of the multivariate characteristics of the two sandy beaches over
239 different sampling periods (Fig. 2). The two axes, PC1 and PC2, explained 82% of the differences
240 between Saint Nic and Anse de Dinan (Supplementary Material 1). In particular, PC1 axis
241 accounted for 50.3% of differences between beaches and they were separated into two groups
242 according to the season (December and May-July) related to differences in organic matter (OM),
243 oxygen (O₂ %), wave height (WH), salinity (Sal) and seawater temperature (SWT) (Fig. 2). Along
244 the PC2 axis, beaches were ordinated according to the presence/absence of *Ulva* and to the grain
245 size (MGS, SI) and clearly separated impacted (SN) and unimpacted (AD) beaches (Fig.2).

246
247

248 3.2 Spatial and temporal variations in meiofaunal standing stock and composition

249 **Meiofauna standing stock.** Total mean meiofaunal abundance varied from 221.8 ind.10 cm⁻² (AD
250 in July) to 933.9 ind.10 cm⁻² (SN in July; Fig. 3a, Table 2). PERMANOVA tests based on
251 meiofaunal abundance data highlighted significant spatial variation (i.e. significant differences
252 between beaches; Table 3), with higher meiofaunal abundance at SN beach compared to AD beach.
253 Total meiofaunal biomass ranged from 13.8 µg C/10 cm² (AD in December) to 91 µg C/10 cm² (SN
254 in July; Fig. 3b, Table 2).

255 PERMANOVA tests demonstrated significant temporal variation in the meiofaunal biomass (Table
256 3). More specifically, the pairwise tests revealed higher meiofaunal biomass in the “warmer”
257 months May and July compared to the “colder” December month (P< 0.05).

258

259 **Meiofauna community composition.** A total of 14 *taxa* were identified: Amphipoda, Bivalvia
260 Cladocera, Copepoda with their *nauplii*, Cumacea, Gastrotricha, Halacaridae, Isopoda, Nematoda,
261 Oligochaeta, Ostracoda, Platyhelminthes, Polychaeta and Tardigrada. Eight was the highest mean
262 number of taxa, at SN beach during December, while two was the lowest mean number of taxa, at
263 AD in December (Table 2). The results of the PERMANOVA tests reported a major significant
264 effect of the interaction between Beach x Month on the number of meiofaunal higher taxa (Table 3).
265 Overall, a higher mean number of meiofaunal taxa characterized the impacted beach (SN), with the
266 only exception for May during which the number of taxa was comparable between the two beaches
267 (Table 2).

268 Nematoda phylum was always the most represented group, accounting for 91-99% of meiofauna
269 (Fig. 4a; Supplementary Material 2). The second most represented group was Crustacea (i.e.
270 Amphipoda, Copepoda, Cumacea, Isopoda and Ostracoda) in both beaches (accounting for 73-82%
271 of the group of ‘others’), with the only exception for AD in December where Platyhelminthes was
272 more dominant (Fig. 4b). At Saint Nic, Copepoda with their *nauplii* constituted the majority of the

273 crustaceans followed by Ostracoda. Differently, at Anse de Dinan, Copepoda (with their *nauplii*)
274 and Cumacea were the most abundant groups followed by Amphipoda. Other taxa were reported
275 just in one of the two beaches and not at all sampling periods. For instance, a high contribution of
276 Platyhelminthes found at both beaches during winter period; a unique presence of Gastrotricha and
277 Isopoda in May at AD and Bivalvia found only at SN especially during the warmer sampling
278 months. Taxa such as Cumacea, Amphipoda, Isopoda, Polychaeta and Tardigrada were more
279 abundant during warmer seasons; whereas Platyhelminthes (at SN and AD) and Ostracoda (at SN)
280 coped were more abundant during colder month. Three taxa never appeared in SN - Gastrotricha,
281 Tardigrada and Isopoda; four taxa were never detected at AD - Bivalvia, Halacaridae, Oligochaeta
282 and Cladocera (Fig. 4b; Supplementary Material 2). PERMANOVA tests revealed a significant
283 spatial (Beach) and temporal (Month) effect on meiofaunal community structure (Table 3). In
284 particular, the pairwise test demonstrated a significant difference on the meiobenthic community
285 composition between July vs December at AD beach ($P < 0.05$) (Fig. 4b).

286 The PCA visualized the contribution of taxa to the spatial and temporal variability in the meiofauna
287 community structure (Fig. 5). PC axis 1, which explained 33% of the variability, grouped samples
288 related to the beach (AD on right side and SN on the left side of the graph) and was driven by the
289 taxa: Cumacea, Amphipoda, Polychaeta, Copepoda + *nauplii*, Nematoda, Ostracoda and Bivalvia
290 (Fig. 5; Supplementary Material 2). PC axis 2 explained 27% of the variability and samples were
291 grouped according to season ('colder' samples on the upper part and 'warmer' samples on the lower
292 part of the graph). Platyhelminthes, Copepoda, Cumacea and Nematoda contributed the most to the
293 separation of these samples (Fig. 5; Supplementary Material 3).

294

295 3.3 Nematode structural and functional diversity.

296 **Nematode diversity.** A total of 76 putative species, 59 genera and 21 families of nematodes were
297 identified (Supplementary Material 4). Xyalidae was the most diversified family with 10 genera,
298 followed by Desmodoridae (seven genera), Axonolaimidae, Chromadoridae and
299 Thoracostomopsidae (all four genera). Selachinematidae was the most abundant family representing
300 28% of the total nematode fauna (characterized the AD site), followed by Xyalidae (21%),
301 Desmodoridae (12%) and Thoracostomopsidae (11%) characterizing both AD and SN sediments.
302 The diversity indices (SR, H and $ES_{(51)}$) did not show any significant differences between impacted
303 (SN) and unimpacted (AD) beaches and over different sampling periods (Table 2). PERMANOVA
304 tests only revealed significant effects of factor Beach on the equitability values (J; Table 3) with
305 lower mean values in the equitability index at AD (0.7 ± 0.1) compared to SN (0.8 ± 0.0).

306 PERMANOVA results based on nematode species composition revealed spatial and temporal
307 significant differences (Table 3). Saint Nic and Anse de Dinan beaches were characterized by a
308 specific nematode community inhabiting impacted and unimpacted beaches which changed also
309 between warmer and colder months. More specifically, the pairwise tests reported significant
310 differences in nematode species composition between May vs. December ($p < 0.01$) at both beaches
311 and July vs. December ($p < 0.01$) only at AD beach.

312 The results of SIMPER analyses (Table 4) showed a 64.5% of dissimilarity in nematode species
313 composition between the impacted and unimpacted beaches. The dissimilarity between the two
314 beaches was mainly due to the dominance of *Richtersia* spp. at Anse de Dinan and the higher
315 abundance of *Promonhystera* sp1, *Microlaimus* sp1, *Viscosia* sp1 and *Marylynnia* sp1 at Saint Nic.
316 The highest dissimilarity percentage (75.4%) was reported among sampling periods: May vs
317 December and July vs December (Table 4). Differences among sampling periods were due to the
318 presence of some 'warmer' species, such as *Omicronema* sp1; *Daptonema* sp1, *Promonhystera* sp1
319 and *Trileptium* sp2 vs 'colder' species such as *Molgolaimus* spp. and *Endeolophos* sp1. Overall, a
320 total of 24 exclusive species were encountered at Anse de Dinan, whereas 21 exclusive species
321 characterized Saint Nic (Supplementary Material 4). Spatio-temporal dissimilarities in nematode
322 species composition were clearly shown by the nMDS graph (Fig. 6). Along the horizontal axis
323 stations followed a seasonal gradient and they were distributed in the space from 'warmer' to
324 'colder' seasons, whereas along the vertical axis stations were grouped according to the beach from
325 unimpacted to impacted one.

326

327 **Nematode trophic diversity and life strategy.** The results of PERMANOVA highlighted a
328 significant 'beach' effect on the trophic structure of nematodes (Table 3). Predators (2B) and non-
329 selective deposit feeders (1B) were the most represented trophic groups at SN beach (45.2% and
330 26.6%, respectively), where the contribution of epistrate feeders (2A, 21.3%) and selective deposit
331 feeders/bacterivores (1A, 6.8%) should not be neglected (Fig. 7). Differently, at AD beach the 1B
332 (82.8%) group dominated over all the other feeding groups. The contribution of the other groups
333 varied between 1% (1A) and 9 % (2B) (Fig. 7). No seasonal variation in the nematode trophic
334 structure was observed for the beaches of Saint Nic and Anse de Dinan (Fig. 7). The mean ITD
335 value of 0.31 at SN indicated almost equal distribution of nematodes in each trophic group whereas
336 at AD dominance of a single group (i.e. 1B = non-selective deposit feeders) was indicated with a
337 mean ITD value of 0.56.

338 Mean values of nematode maturity index (MI) were very similar between the two beaches
339 (2.06 ± 0.81 and 1.97 ± 0.64 at AD and SN, respectively) and indicated “r-strategy” communities of
340 nematodes. PERMANOVA tests revealed a significant ‘month’ effect on the MI (Table 3), with
341 lower MI values in the winter (Table 2). Indeed, pairwise tests reported significant differences in
342 the nematode maturity index between May-July and December ($P < 0.01$) at both beaches.

343 The results of PERMANOVA tests demonstrated a significant effect on the interaction between
344 Beach x Month on contribution of males, females and juveniles (Table 3). The contribution of
345 males remained quite constant during all the sampling periods in both beaches, while the percentage
346 of females (gravid and non-gravid) was higher during the warmer periods. Instead, the percentage
347 of juveniles increased during winter particularly at AD beach (Table 2).

348

349 *3.4 Meiobenthic community and nematode composition related to environmental features*

350 The results of DistLM forward analyses revealed that total meiofaunal abundance was significantly
351 and highly explained by *Ulva* biomass (65%), while total meiofaunal biomass was significantly
352 explained by seawater temperature (SWT) and salinity (73%; Table 5).

353 Salinity and SWT significantly explained the meiofaunal diversity (n° taxa; 52%); while the
354 variability in meiofaunal community structure was mostly explained by *Ulva* biomass and SWT
355 (61%; Table 5). Nematode trophic structure is explained by median grain size (MGS), salinity and
356 SWT, whereas MI is explained by O_2 , salinity and SWT (Table 5). Nematode assemblages
357 composition were significantly explained by O_2 , salinity, *Ulva* biomass, organic matter (OM) and
358 SWT, cumulatively explaining 82% of the observed variance (Table 5; Fig. 8). The dbRDA graph
359 (Fig. 8) clearly showed a separation of samples according to season (along axis 1; 47% explained)
360 and according to impacted and unimpacted beach (along axis 2; 30 explained). None of the
361 environmental variables considered could explained nematode diversity (SR, H and $ES_{(51)}$).

362

363

364 **4. Discussion**

365

366 Eutrophication in estuaries and coastal waters in the form of green macroalgal blooms occurs all
367 over the world (Liu et al., 2009; Ye et al., 2011). Increasing degradable organic matter may strongly
368 affect biogeochemical cycling and nutrient processes, leading to oxygen depletion and the
369 accumulation of toxic sulphide (Diaz and Rosenberg, 1995). High organic loads usually has
370 negative effects on the abundance and diversity of zoobenthic communities and causes massive

371 benthic fauna mortality and/or disappearance of sensitive taxa (e.g. McLachlan, 1978; Villano and
372 Warwick, 1995; García and Johnstone, 2006; Sun et al., 2014).

373 Most of the studies concerning the effects of eutrophication on meiobenthic communities have been
374 conducted on sheltered coastal systems (McLachlan, 1978; Villano and Warwick, 1995; García and
375 Johnstone, 2006), or by *in situ* (Neira and Rackemann, 1996; Gambi et al., 2009; Bohórquez et al.,
376 2013) or laboratory experiments (Wang et al., 2011). Reduced sediment layers, due to a dramatic
377 fall in oxygen levels following algal blooms, frequently occur in sheltered beaches whereas open
378 sandy beaches generally remain well oxygenated (McLachlan, 1978, 1985). In these cases, the
379 effect of eutrophication on the macrobenthic communities may be subtle although objective
380 (Quillien et al., 2015a, 2015b) while they can cause significant increase in meiofaunal abundance
381 and diversity (Koop and Griffiths, 1982; Giere, 2009).

382

383 *4.1 Effect of Ulva bloom on meiobenthic communities inhabiting open sandy beaches.*

384 In the present study, the impacted beach of Saint Nic demonstrated overall higher values in
385 meiofaunal standing stock (i.e. abundance and biomass) and diversity (i.e. number of major taxa).
386 Total meiofaunal abundance appeared to be positively affected by the presence of *Ulva*, while the
387 total biomass was subjected to the natural seasonality of meiofauna communities with lower values
388 during winter (e.g. Alongi, 1990; Guidi-Guilvard and Buscail, 1995), independently of the
389 presence/absence of *Ulva* mats. A variety of factors are considered to control seasonal oscillations
390 in benthic standing stock and feeding mode such as temperature fluctuation, and food availability
391 (Ólafsson and Elmegren, 1997; García and Johnstone, 2006; Liu et al., 2008). Seasonal fluctuation
392 in algal abundances, for instance, can imply a shift in meiofaunal diets and ingestion of other food
393 sources, such as bacteria (Pascal et al., 2009).

394 Meiofaunal abundance values reported from the Bay of Douarnenez (i.e. SN and AD beaches) were
395 in the range of values documented for other pristine sandy beaches and sandy littoral sites from
396 northern Europe and elsewhere (Gheskiere et al., 2002, 2004a; Kotwicki et al., 2005 and literature
397 therein). Abundance values found in this study were higher when compared to those from sheltered
398 impacted sandy beaches (e.g. García and Johnstone, 2006) by macroalgal blooms. The depletion of
399 oxygen in Moreton Bay (García and Johnstone, 2006), not reported in our case of study could
400 explain the lower values in the meiofaunal abundance when compared to SN and AD.

401 The presence of *Ulva* mats could only partially explained the variability in meiofaunal community
402 structure, which also highlighted a certain seasonality. The significant interaction of the two factors
403 ‘beach’ and ‘month’ explaining the variation of meiofaunal community composition suggests that
404 the effects of the presence of GT (factor sites) depends on the month (factor time). The dominance

405 of nematodes, as the most ubiquitous and tolerant taxon, followed by copepods has been described
406 as a classic feature for meiofauna inhabiting many marine habitats (Gheskiere et al., 2004a, 2004b;
407 Giere, 2009). All the remaining taxa, even if scarcely represented (1-9%), were usually found
408 characterizing sandy beach systems (Gheskiere et al., 2002, 2004a; Kotwicki et al., 2005;
409 Albuquerque et al., 2007) e.g. the high relative abundance of Platyhelminthes particularly during
410 winter time (McLachlan, 1978; Rzeznik-Orignac et al., 2003). Gastrotricha and Tardigrada, the
411 most sensitive taxa which are generally strongly affected by a stressed environment (Zeppilli et al.,
412 2015) never appeared at the impacted beach of SN. Nevertheless, other taxa such as Bivalvia,
413 Halacaridae, Ostracoda, Cumacea and Amphipoda, usually found characterizing not impacted
414 systems (e.g. Kotwicki et al., 2005; Gambi et al., 2009; Wang et al., 2011), were reported from the
415 impacted beach of SN.

416

417 No clear negative effect of *Ulva* mats on meiobenthic community structure was demonstrated.
418 Meiofaunal diversity (i.e. number of major taxa) was highest at SN during December, when *Ulva*
419 biomass showed minimum biomass value. While at AD meiofaunal diversity decreased from
420 warmer to colder months. Carriço et al. (2013) reported a negative effect of stranded *Ulva* on
421 meiofauna composition, with number of higher taxa depressed at the impacted beach of Saint Nic
422 (i.e. only three taxa identified), but authors did not consider the seasonal variability. When
423 considering a longer time scale (present study), such a negative effect was far from evident. As
424 already reported from the macrofaunal community studies (Quillien et al., 2015a), our findings
425 indicated that meiofauna community structure and diversity were dependent both on time of the
426 year and on the beach system considered. Results on meiofaunal standing stock, community
427 composition and diversity supported the hypothesis of an *Ulva* effect on meiobenthic populations.
428 This effect, somehow subtle, may not be regarded as negative, especially from sheltered sandy
429 beach systems (e.g. McLachlan, 1978; Evans, 1993; Villano and Warwick, 1995).

430 Our second hypothesis, regarding the different effect of seasonality on meiobenthic communities at
431 impacted and unimpacted beaches, is also only partially verified. Indeed, the total meiofaunal
432 biomass changed seasonally at both beaches and showed lower values during winter time. For other
433 meiofaunal descriptors, such as meiofaunal community structure and diversity, the seasonality was
434 less evident and the effects of the presence of GT (factor sites) are not the same depending on the
435 month (factor time). A similar subtle response was reported by Quillien et al. (2015a) for
436 macrobenthic communities inhabiting open sandy beaches. They sustained the theory of
437 intermediate disturbance (Connell, 1978), in which benthic communities have a positive response to
438 a moderate disturbance by an increase in abundance and diversity (see for example Pearson and

439 Rosenberg, 1978). It appears that open sandy beach systems would be able to support high stranded
440 biomass of algae while avoiding reduced conditions in the sediments and thus a direct, strong
441 disturbance effect on meiobenthic communities.

442

443 4.2 Nematode structural and functional response to green macroalgal bloom

444 Nematodes, the dominant meiofaunal taxon (from 50 to over 90% of the total meiofauna
445 abundance; Merckx et al., 2009), have been largely utilized as indicators of high organic loads
446 especially when investigating the response of systems subjected to eutrophication phenomena (e.g.
447 Gambi et al., 2009; Moreno et al., 2011; Wang et al., 2011; Sun et al., 2014; Bianchelli et al., 2018).
448 Strong changes in nematode structural and functional diversity, assemblage composition and trophic
449 structure occur under various scenarios of organic enrichment (Mirto et al., 2002; Moreno et al.,
450 2008; Semprucci et al., 2015; Franzo et al., 2018). In some studies (e.g. Villano and Warwick,
451 1995; Gambi et al., 2009), nematode species richness was not affected during algal bloom and
452 under hypoxic-anoxic conditions deriving from high organic loads, while beta-diversity and
453 functional diversity changed drastically. Nematode genera such as *Rhabditis*, *Diplolaimella* and
454 *Diplolaimelloides* were reported in extreme high abundances associated with decaying algae/plant
455 material (Villano and Warwick, 1995; Franzo et al., 2018; Bertocci et al., 2019). Some studies
456 reported an increase in nematode abundances under high-organic enrichment (Wang et al., 2011;
457 Bohórquez et al., 2013), whereas other studies reported a decline in nematode and/or meiofaunal
458 abundance values under such conditions (Neira and Rackemann, 1996; García and Johnstone,
459 2006). Usually, the decline in meiofauna abundance coincided with an oxygen depletion going
460 deeper into the sediments or with formation of black spots indicating reduced oxygen concentration
461 in surface sediments.

462

463 Nematode structural diversity (i.e. SR, H, ES₍₅₁₎) was not affected by *Ulva* mats and nematode
464 species richness was comparable between the impacted (SN) and unimpacted (AD) sites, as
465 reported by Carriço et al. (2013). Nematode diversity indices were in range with values from
466 pristine sandy beach systems (e.g. Rzeznik-Orignac et al., 2003; Liu et al., 2008) and appear to be
467 higher than values reported from highly organic enriched systems (e.g. Villano and Warwick, 1995;
468 Jouili et al., 2017; Bianchelli et al., 2018). The high values in the nematode species evenness (J),
469 especially at the impacted beach of SN, underlined the lack of strongly dominating species, such as
470 tolerant nematode species, as may be expected for stressed environments (Steyaert et al., 2007). All
471 these findings suggest that changes induced by the presence of *Ulva* mats have a minor impact in
472 terms of structural diversity (α -diversity).

473

474 Seasonal changes were evident in nematofauna composition at both beaches, suggesting that these
475 changes were not exclusively linked to *Ulva* cycles as may have been reported in previous studies
476 (Villano and Warwick, 1995). In fact, not only *Ulva* biomass, but most of the environmental
477 variables considered could help to explain the seasonal variability in nematode community
478 composition. The variation of environmental factors such as sediment type, organic matter content,
479 salinity and seawater temperature are fundamental factors that govern species composition
480 inhabiting sandy beaches (Schratzberger and Warwick, 1998, 1999).

481

482 Stranded *Ulva* alone had significant effects on nematode community composition, mainly in
483 promoting a high turnover diversity. Indeed, the presence of a high number of unique species at
484 both sandy beaches (24 at AD and 21 at SN) indicated a high β -diversity in nematode composition,
485 even though α -diversity was comparable between sites (Carriço et al., 2013). The presence vs.
486 absence of *Ulva* mats may generate the spatial heterogeneity between the two sandy beaches
487 necessary to support the high β -diversity in nematode composition. This would not be detected
488 when merely considering the α -diversity, as the α -diversity usually does not reflect the β -diversity
489 (Gambi et al., 2014).

490 *Richtersia* spp., abundant at the unimpacted beach of Anse de Dinan generally inhabits un-impacted
491 systems and is a proxy for good environmental status (Moreno et al., 2011). At the impacted beach,
492 the most represented genera *Microlaimus*, *Viscosia* and *Marylynnia* were reported as less sensitive
493 genera, tolerant to high organic loads and proxy of a moderate quality status of the system (Jouili et
494 al., 2017; Franzo et al., 2018; Bianchelli et al., 2018). Nevertheless, other opportunist and more
495 tolerant genera known to be proxy of a poor environmental quality status were found at both
496 beaches, e.g. *Daptonema*, *Parodontophora* and genera belonging to the family Chromadoridae,
497 Desmodoridae and Xyalidae (Gambi et al., 2009; Moreno et al., 2011; Jouili et al., 2017). Many
498 other genera reported from unimpacted sandy beach systems in the northern Europe (Gheskiere et
499 al., 2000, 2002) characterized Anse de Dinan and/or Saint Nic beaches: *Andoncholaimus*,
500 *Axonolaimus*, *Chromadorita*, *Comesoma*, *Daptonema*, *Leptolaimus*, *Metadesmolaimus*,
501 *Oncholaimellus*, *Theristus* and *Trichotheristus*.

502

503 The presence of stranded *Ulva* sustained higher functional diversity at Saint Nic where all feeding
504 types were represented equally. The presence of all feeding types indicates the input of a broad
505 spectrum of potential food sources, e.g., microbes (involved in decomposition processes; Wang et
506 al., 2011), detritus, freshly stranded *Ulva*, available for nematodes and all other meiofauna taxa

507 (McGwynne and McLachlan, 1988). Nematofauna can use, both directly and indirectly through one
508 or more trophic intermediates, a wide range of food sources in vegetated sediments e.g.,
509 microphytobenthos, seagrass detritus, benthic bacteria and sediment particulate organic matter
510 (Vafeiadou et al., 2014; Moens et al., 2014b; van der Heijden et al., 2019). Riera and Hubas (2003)
511 highlighted that stranded macroalgae is another potential primary food source for meiobenthic
512 populations inhabiting sandy beaches, thereby demonstrating that *Ulva* could directly or indirectly,
513 through microbial loop, fuels the benthic food web. The higher relative abundance of predators at
514 SN could be explained by a higher presence of their potential preys (other meiofauna and small
515 macrofauna) which themselves rely on the organic enrichment associated with stranded *Ulva*
516 (according to Jensen, 1987). Moens et al. (2014b) stated that the guts of predators can sometimes be
517 filled with diatoms from direct grazing or from the gut contents of the nematode's prey. The high
518 amounts of organic material derived from stranded *Ulva* enriched the growth of diatoms and ciliates
519 which in turn contributed significantly as a food source to epistrate feeders (Pascal et al., 2009;
520 Lebreton et al., 2011), a well represented group at SN. At the beach of Anse de Dinan the non-
521 selective deposit feeders dominated and they were mainly represented by *Richtersia* spp; the
522 dominance of deposit feeders is common in open sandy beaches (Gheskiere et al., 2004b) that
523 consist of sediments rich in organic detritus (Jouili et al., 2017 and literature therein). In particular,
524 this feeding behavior coupled with the prompt reaction of *Richtersia* to a pulsed food supply
525 (Vanaverbeke et al., 2004), contribute to the success of the genus (Peters and Wassenberg, 1983;
526 Moens and Vincx, 1997).

527 No seasonal changes were observed for the trophic structure, despite the seasonal turnover in
528 nematode species composition. The presence vs. absence of *Ulva* mats, coupled with seasonal
529 changes in environmental features, affected the nematode structural (species composition) diversity
530 over time but not their functional diversity. Differently from previous studies (Semprucci et al.,
531 2010, 2018), nematode functional diversity did not mirror their taxonomical diversity and thus these
532 parameters provided different information on nematode communities inhabiting sandy beaches.

533 Open macrotidal sandy beaches are highly dynamic systems, physically stressed by waves, tidal
534 currents and mobile sediments (McLachlan and Brown, 2006). Accordingly with Bongers's model,
535 the r-strategists were more abundant when the hydrodynamic stress was strong. At both impacted
536 and un-impacted beaches, c-p values between 2 and 3 were reported indicating 'r-strategy'
537 nematode communities with relatively short life-cycles and high colonization abilities. Such life
538 strategies were in line with the equal repartition of nematodes into juveniles and adults (male and
539 female), suggesting a reproductive-active population of nematodes (Giere, 2009).

540

541 The Pearson-Rosenberg model (Pearson & Rosenberg, 1978) describes three successive steps of the
542 effects of organic enrichment on qualitative characteristics of benthic communities. This depends
543 on the organic input: 1) if organic loading increases only slightly, species abundances and biomass
544 values increase; 2) further increase of organic input favors opportunistic organisms; 3) even more
545 organic loading leads to disappearance of zoobenthic organisms and appearance of 'azoic'
546 sediments. The impacted beach of Saint-Nic could be placed between step 1 and 2 of the Pearson-
547 Rosenberg model, with an overall increase in the meiofauna standing stock, turnover diversity and
548 promoting colonizers (i.e. opportunistic nematofauna communities). McGwynne et al. (1988)
549 reported a similar observation describing the response of meiofaunal community inhabiting
550 Australian exposed sandy beaches impacted by stranded macroalgae. Therefore, the beach of Saint-
551 Nic can be seen as a system in which a balance between food and oxygen availability is reached
552 approaching the 'optimum point' (McGwynne et al., 1988): abundance of food coincides with well
553 oxygenated environment and other favorable features (e.g. grain size). In this case, *Ulva* mats does
554 not disturb meiobenthic populations but rather stimulate species that are able to thrive on these new
555 carbon sources.

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557

558 *4.3 Ulva bloom effect on meio- and macrofauna communities: a comparison*

559

560 Quillien et al. (2015a) investigated the spatio-temporal variation in the distribution of macrofauna
561 standing stock and diversity from open sandy beaches impacted and un-impacted by *Ulva* bloom,
562 where two of those beaches corresponded to the beaches of Saint-Nic and Anse de Dinan.
563 Conditions affecting the meiofauna are somewhat different from those affecting the macrofauna
564 (Wang et al., 2011). Therefore, the response of meio- and macrofauna communities inhabiting open
565 sandy beaches impacted by stranded macroalgae has been reported as different (e.g. McLachlan,
566 1985), or comparable (e.g. Koop and Griffiths, 1982).

567 The spatio-temporal changes detected for both meio- and macrofauna community composition
568 inhabiting the investigated sandy beaches indicated that the community structure of both benthic
569 components was dependent on beach and time (i.e. seasonal variability).

570 For both benthic components the response to dense *Ulva* mats was subtle and not as obvious as it
571 may have been expected, with drastic decrease in diversity or mortality in zoobenthic communities
572 (Neira and Rackemann, 1986; Bolam et al., 2000; Gambi et al., 2009). As reported above, an
573 explanation could be that the highly dynamic nature of open sandy beaches, that somehow prevents
574 the hypoxic-anoxic sediment conditions.

575 Quillien et al. (2015a) invoked the Pearson-Rosenberg model (Pearson & Rosenberg, 1978) to
576 explain the observed macrofauna patterns and the concept of the intermediate disturbance (Connell,
577 1978), which agreed with the meiofauna and nematofauna standing stock and diversity patterns.
578 Shifts in macrobenthic community composition and functional diversity (trophic groups; Quillien et
579 al., 2016) between the impacted and unimpacted sandy beaches were also observed for the
580 meiobenthos, in particular the nematofauna. For the meiofauna we did not detect the decrease in β -
581 diversity in the presence of homogenous coverage of *Ulva*, conversely to macrofaunal community
582 composition. This may be related to the fact that we did not consider a gradient of increasing
583 coverage of stranded *Ulva* in our investigation, as in Quillien et al. (2015a), but a ‘simple’
584 comparison between a state with and without *Ulva*. Moreover, an heterogeneous coverage of *Ulva*
585 in SN, instead of homogeneous *Ulva* mats, probably promoted the spatial heterogeneity and
586 sustained the nematode diversity. The faster turnover rate of the meiobenthic population compared
587 to the macrofauna (Balsamo et al., 2012; Semprucci et al., 2015), coupled with the ability of
588 nematodes to adjust to all kind of environments (Tahseen, 2012), could have enhanced the high
589 spatio- (impacted vs. un-impacted beach) and temporal turnover diversity in nematode
590 communities.

591

592 **5. Conclusions**

593

- 594 • The response of meiobenthic community to macroalgal bloom is strictly linked to the system
595 considered. When eutrophic conditions are not associated with long-lasting O₂
596 depletion/limitation, meiofaunal abundance and diversity may eventually increase. As for
597 macrofaunal communities, a minor response of meiofauna and nematofauna to *Ulva*
598 accumulation is observed and the impact is not evident as previously reported for sheltered
599 systems.
- 600 • As for the macrofauna (Quillien et al., 2015a), the Pearson-Rosenberg model (Pearson &
601 Rosenberg, 1978) and the concept of the intermediate disturbance (Connell, 1978) can be
602 used to explain the meiofauna response to *Ulva* mats affecting open sandy beaches.
- 603 • Overall, the presence of *Ulva* positively affects meiofaunal abundance, structural and
604 functional diversity and supports the high values of β -diversity.
- 605 • Natural seasonal changes in meiofaunal biomass and composition are evident at both
606 beaches. Changes in environmental features partially explain the variability in meiofauna
607 and nematodes structural and functional diversity at the beaches of Saint-Nic and Anse de
608 Dinan.

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923 **Tables**

924

925 **Table 1** Environmental characteristics of the two beaches (Anse de Dinan and Saint Nic) sampled during three different periods:
926 May, July and December 2012 (Quillien et al., 2015a). Abbreviations: SWT= seawater temperature; O₂= dissolved oxygen; WH= wave height; MGS= median
927 grain size; OM= organic matter; SI= sorting index.

Beach	Month	SWT (°C)	Salinity	O ₂ (%)	<i>Ulva</i> biomass (10 ³ kg)	WH (m)	MGS (µm)	OM (%)	SI
Anse de Dinan	May	14.08	35.39	106.55	0.00	0.70	240	4.90	1.31
Anse de Dinan	July	18.92	35.04	105.25	0.00	1.37	195	4.39	1.41
Anse de Dinan	December	8.70	33.93	102.63	0.00	1.61	180	4.01	1.36
Saint Nic	May	13.30	35.56	106.66	1352.31	0.70	170	4.80	1.11
Saint Nic	July	21.43	34.69	108.07	1445.76	1.65	150	4.45	1.07
Saint Nic	December	8.17	34.60	100.06	100.00	1.91	150	3.19	1.18

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940 **Table 2** Meiofaunal abundance, biomass, diversity (as number of higher taxa), nematode maturity index (MI) and sex percentage contribution values at impacted
 941 (Saint Nic) and un-impacted (Anse de Dinan) beaches. Abbreviations: SR = species richness , H = Shannon index of diversity , ES = expected species number, J
 942 = equitability index, M = male, F = female, GF = gravid female , Ju. = juvenile.
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Year	Month	Beach	Replicate	Abundance (ind. 10cm ⁻²)	Biomass (µgC/10cm ²)	n° taxa	SR	H (log _e)	ES ₍₅₁₎	J	MI	M %	F %	GF %	J %
2012	May	AD	1	372.7	53.2	7	18	2.1	14.0	0.7	2.67	23	37	8	32
	May	AD	2	394.8	52.1	5	22	2.3	16.2	0.8	2.49	23	37	8	32
	July	AD	1	196.4	32.0	5	15	2.2	13.2	0.8	2.62	22	48	9	21
	July	AD	2	247.3	40.5	4	18	2.3	14.0	0.8	2.51	22	48	9	21
	December	AD	1	365.0	15.0	2	19	2.0	12.2	0.7	0.89	23	10	1	65
	December	AD	2	284.7	12.5	4	26	2.4	15.6	0.7	1.16	28	20	2	51
2012	May	SN	1	646.9	75.3	4	18	2.5	15.0	0.9	2.20	22	50	5	23
	May	SN	2	633.8	53.9	4	24	2.9	19.5	0.9	2.55	22	50	5	23
	July	SN	1	796.4	62.5	5	16	2.4	13.4	0.8	2.39	27	34	10	29
	July	SN	2	1071.3	119.6	5	18	2.4	14.1	0.8	2.36	27	34	10	29
	December	SN	1	209.8	10.4	9	16	2.2	12.6	0.8	1.01	34	31	4	30
	December	SN	2	627.6	24.9	6	19	2.3	13.5	0.8	1.33	38	30	5	27

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959 **Table 3** Results of PERMANOVA testing variations (A) meiofaunal standing stock (i.e. abundance and biomass), community structure and diversity (i.e. n° taxa)
 960 and (B) nematode diversity indices and species composition. dF = degree of freedom; MS = mean square; F = F statistic; ** = P < 0.01; * = P < 0.05; ns = not
 961 significant. Abbreviations: Be = beach, Mo = month, MI = maturity index, J = equitability index, ES = expected species number, H = Shannon index of diversity,
 962 SR = species richness.
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A)	Source	df	MS	F	P	% explained variance	B)	Source	df	MS	F	P	% explained variance
Meiofauna abundance	Beach	1	5.2	5.2	**	46.6	ES ₍₅₁₎ , H, SR	Beach	1	0.0	0.0	ns	-14.3
	Month	2	1.2	0.6	ns	4.5		Month	2	39.1	19.5	ns	20.6
	Be x Mo	2	2.8	1.4	ns	31.9		Be x Mo	2	21.1	10.6	ns	2.5
	Residual	6	1.8	0.3		17.1		Residual	7	69.9	10.0		91.3
Meiofauna biomass	Beach	1	1.7	1.7	ns	16.1	J	Beach	1	20.0	20.0	*	50.8
	Month	2	5.7	2.9	*	44.5		Month	2	6.7	3.4	ns	3.6
	Be x Mo	2	1.5	0.8	ns	15.1		Be x Mo	2	4.8	2.4	ns	-1.3
	Residual	6	2.1	0.3		24.3		Residual	7	17.7	2.5		46.9
Meiofauna community structure	Beach	1	1654.4	1654.4	**	27.2	MI	Beach	1	0.0	0.0	ns	-0.6
	Month	2	2721.7	1360.9	**	32.6		Month	2	0.7	0.4	**	95.1
	Be x Mo	2	1067.9	533.9	*	19.2		Be x Mo	2	0.0	0.0	ns	0.6
	Residual	6	1133.5	188.9		21.0		Residual	6	0.0	0.0		4.9
n° Taxa	Beach	1	203.3	203.3	*	25.5	ITD	Beach	1	0.1	0.1	**	94.5
	Month	2	10.7	5.3	ns	-2.9		Month	2	0.0	0.0	ns	2.1
	Be x Mo	2	332.8	166.4	*	61.3		Be x Mo	2	0.0	0.0	ns	-2.9
	Residual	6	116.1	19.3		16.1		Residual	6	0.0	0.0		6.3
							Sex % contribution	Beach	1	3.3	3.3	**	9.1
						Month		2	19.1	9.5	**	41.5	
						Be x Mo		2	10.6	5.3	**	44.8	
						Residual		6	1.6	0.3		4.6	
							Species	Beach	1	7033.3	7033.3	**	27.5

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composition	Month	2	12814.0	6407.1	**	37.0
	Be x Mo	2	3792.6	1896.3	**	15.2
	Residual	7	5137.9	734.0		20.3

Table 4 Results of SIMPER tests assessing the dissimilarity levels in the nematode species composition among beaches (Anse de Dinan and Saint Nic) and sampling times. The first ten species that contributed mostly to the dissimilarity are reported.

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Contrast	Dissimilarity %	Responsible species
AD vs SN	64.5	<i>Richtersia sp1, Richtersia sp2, Richtersia sp3</i> <i>Promonhystera sp1, Microlaimus sp1, Viscosia sp1</i> <i>Marylynnia sp1, Onyx sp1, Xyala sp1</i> <i>Parodontophora sp1</i>
May vs July	44.9	<i>Richtersia sp3, Neochromadora sp1, Viscosia sp2</i> <i>Thalassinorus sp1, Chromadorita sp1, Trichotheristus sp2</i> <i>Daptonema sp1, Microlaimus sp2, Paracomesoma sp1</i> <i>Richtersia sp1</i>
May vs December	75.4	<i>Omicronema sp1, Daptonema sp1, Trileptium sp2,</i> <i>Metadesmolaimus sp1, Microlaimus sp3, Molgolaimus sp2,</i> <i>Endeolophos sp1, Molgolaimus sp1, Diodontolaimus sp1,</i> <i>Viscosia sp2</i>
July vs December	75.4	<i>Omicronema sp1, Molgolaimus sp1, Promonhystera sp1</i> <i>Trileptium sp2, Metadesmolaimus sp1, Molgolaimus sp2</i> <i>Endeolophos sp1, Microlaimus sp3, Diodontolaimus sp1</i> <i>Odontophora sp1</i>

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967 **Table 5** Results of DistLM forward to assess the role of environmental variables on meiofauna standing stock, diversity (n° taxa), community structure, nematode species composition, trophic structure, maturity index (MI) and diversity (ES₍₅₁₎, H, SR). SS = mean square; F = F statistic; ** = P < 0.01; * = P < 0.05; ns = not significant. Abbreviations: SWT = seawater temperature; OM = organic matter; MGS = median grain size, ES₍₅₁₎ = expected species number, H = Shannon diversity index, SR = species richness.

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	Variable	SS	F	P	Prop %	Cum. Prop %
Abundance	<i>Ulva</i>	1276.60	18.33	**	64.7	64.7
	SWT	29.03	0.39	ns	1.5	66.2
	O ₂	29.02	0.36	ns	1.5	67.6
	OM	203.15	3.27	ns	10.3	77.9
	Salinity	13.70	0.20	ns	0.7	78.6
Biomass	SWT	1900.60	11.41	**	53.3	53.3
	Salinity	695.28	6.45	*	19.5	72.8
	O ₂	307.77	3.72	ns	8.6	81.4
	<i>Ulva</i>	156.25	2.16	ns	4.4	85.8
	MGS	84.54	1.20	ns	2.4	88.2
	OM	0.00	0.00	ns	0.0	88.2
n° taxa	Salinity	245.93	6.52	*	37.1	37.1
	SWT	100.44	5.19	*	15.2	52.3
	O ₂	81.99	2.55	ns	12.4	64.6
	OM	77.24	1.32	ns	11.7	76.3
	MGS	41.07	1.33	ns	6.2	82.5
Meiofauna community structure	<i>Ulva</i>	1803.90	6.44	**	39.2	39.2
	SWT	993.43	4.95	**	21.6	60.8
	O ₂	366.24	2.03	ns	8.0	68.7
	OM	378.97	2.50	ns	8.2	77.0
	Salinity	299.45	2.36	ns	6.5	83.5
Nematode species	O ₂	10567.00	5.53	**	33.5	33.5
	<i>Ulva</i>	6858.40	4.84	**	21.7	55.2

composition	Salinity	3788.80	3.29	**	12.0	67.2
	OM	2852.80	3.04	**	9.0	76.2
	SWT	1932.80	2.42	**	6.1	82.3
	MGS	0.00	0.00	ns	0.0	82.3
Nematode	MGS	2312.10	10.46	**	51.1	51.1
trophic structure	Salinity	546.94	2.96	*	12.1	63.2
	SWT	609.36	4.62	*	13.5	76.7
	OM	268.24	2.39	ns	5.9	82.6
	O ₂	215.50	2.27	ns	4.8	87.4
MI	O ₂	827.27	24.63	**	71.1	71.1
	Salinity	179.25	10.30	*	15.4	86.5
	SWT	83.63	9.16	*	7.2	93.7
	<i>Ulva</i>	18.52	2.38	ns	1.6	95.3
	OM	0.16	0.02	ns	0.0	95.3
ES ₍₅₁₎ , H, SR	OM	24.61	2.63	ns	19.3	19.3
	SWT	21.89	2.70	ns	17.2	36.4
	MGS	10.01	1.27	ns	7.8	44.3
	O ₂	0.95	0.11	ns	0.7	45.0
	<i>Ulva</i>	0.26	0.03	ns	0.2	45.2
	Salinity	0.00	0.00	ns	0.0	45.2

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980 **Figure Captions**

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982 **Fig. 1.** Location (Brittany, France) of the two sampled sandy beaches: the un-impacted Anse de Dinan beach (control) and the impacted Saint Nic
983 beach.

984 **Fig. 2.** Principal Component Analysis output based on environmental variables characterizing the two beaches, Anse de Dinan (AD) and Saint Nic
985 (SN), over three sampling periods (May, July and December 2012). Abbreviations: WH = wave height; SI = sorting index; MGS = mean grain size;
986 OM = organic matter; Sal = salinity; O₂ = percentage of oxygen; SWT = sea water temperature. Ordination of sampling stations using the first and
987 second Principal Component.

988 **Fig. 3.** Total meiofaunal abundance (ind.10 cm⁻²) (a) and biomass (µg C/10 cm²) (b) at the beaches of Anse de Dinan (AD, light orange bars) and
989 Saint Nic (SN, green bars) at different sampling periods (May, July and December).

990 **Fig. 4.** Meiofaunal community structure characterizing Anse de Dinan (AD) and Saint Nic (SN) beaches over the three sampling periods.
991 Contribution of each taxon (expressed as %) to the community composition with a focus on the contribution of the most abundant taxon of
992 Nematoda (a) and with a focus on the contribution of taxa belonging to the group 'others' (b).

993 **Fig. 5.** Principal Component Analysis output based on meiofauna community structure at Saint Nic (SN) and Anse de Dinan (AD) beaches over
994 three sampling periods (May, July and December). Ordination of sampling stations using the first and second Principal Component (PC).

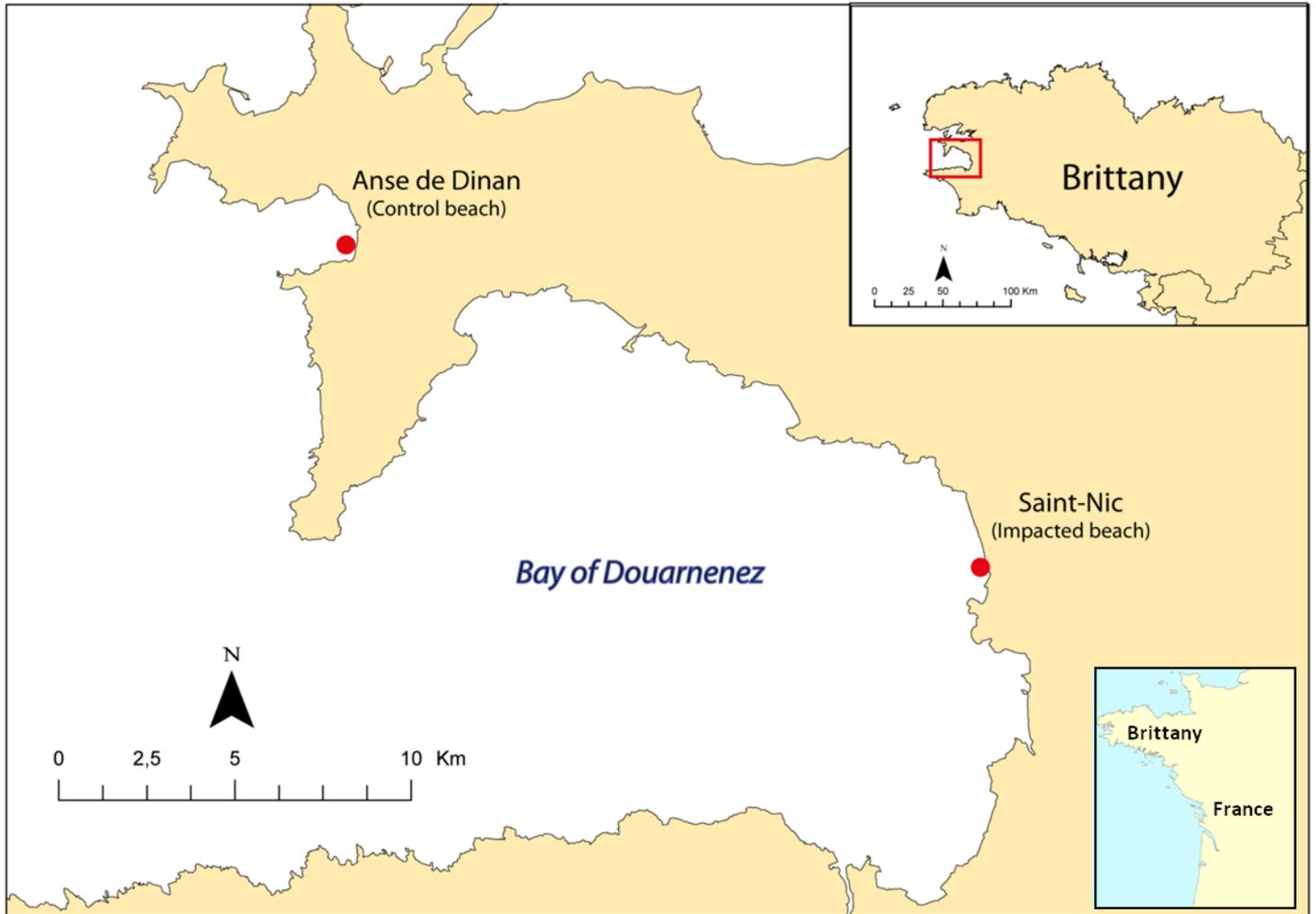
995 **Fig. 6.** nMDS of nematode assemblages characterizing Saint Nic (SN; impacted) and Anse de Dinan (AD; unimpacted) beaches over different
996 sampling periods. All replicates are displayed.

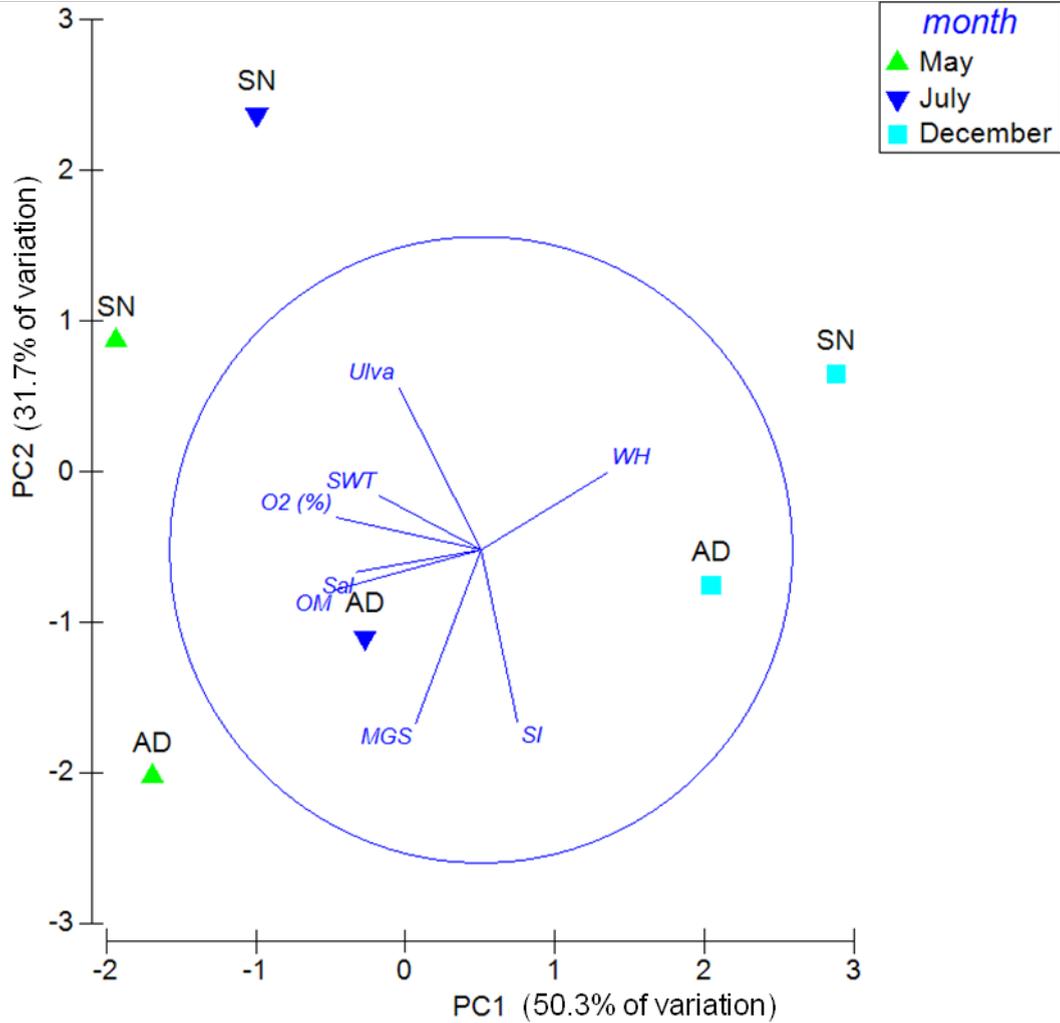
997 **Fig. 7.** Nematode trophic structure at Saint Nic (SN) and Anse de Dinan (AD) beaches over different sampling periods. The ITD (index of trophic
998 diversity) values are reported at the top of the histogram bars. The contribution of each trophic group is expressed as % and based on nematode
999 biomass. Abbreviations: 1A = selective deposit feeders; 1B = non-selective deposit feeders; 2A = epistrate feeders; 2B = predators/omnivores.

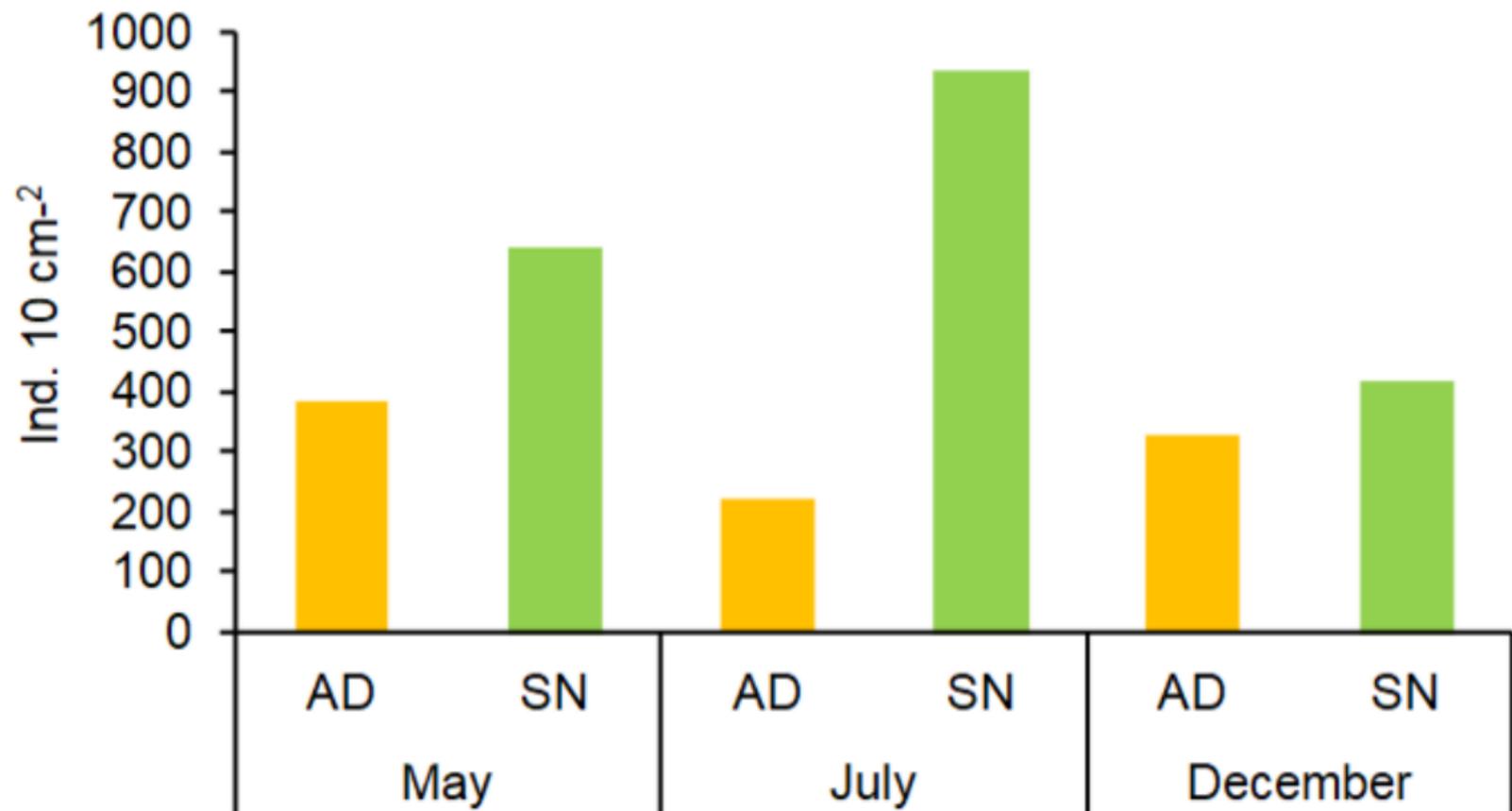
1000 **Fig. 8.** DistLM (distance-based linear model) and dbRDA showing the effect of environmental variables on meiofaunal community structure.
1001 Abbreviations: AD = Anse de Dinan; SN = Saint Nic; dec = December. All replicates are shown.

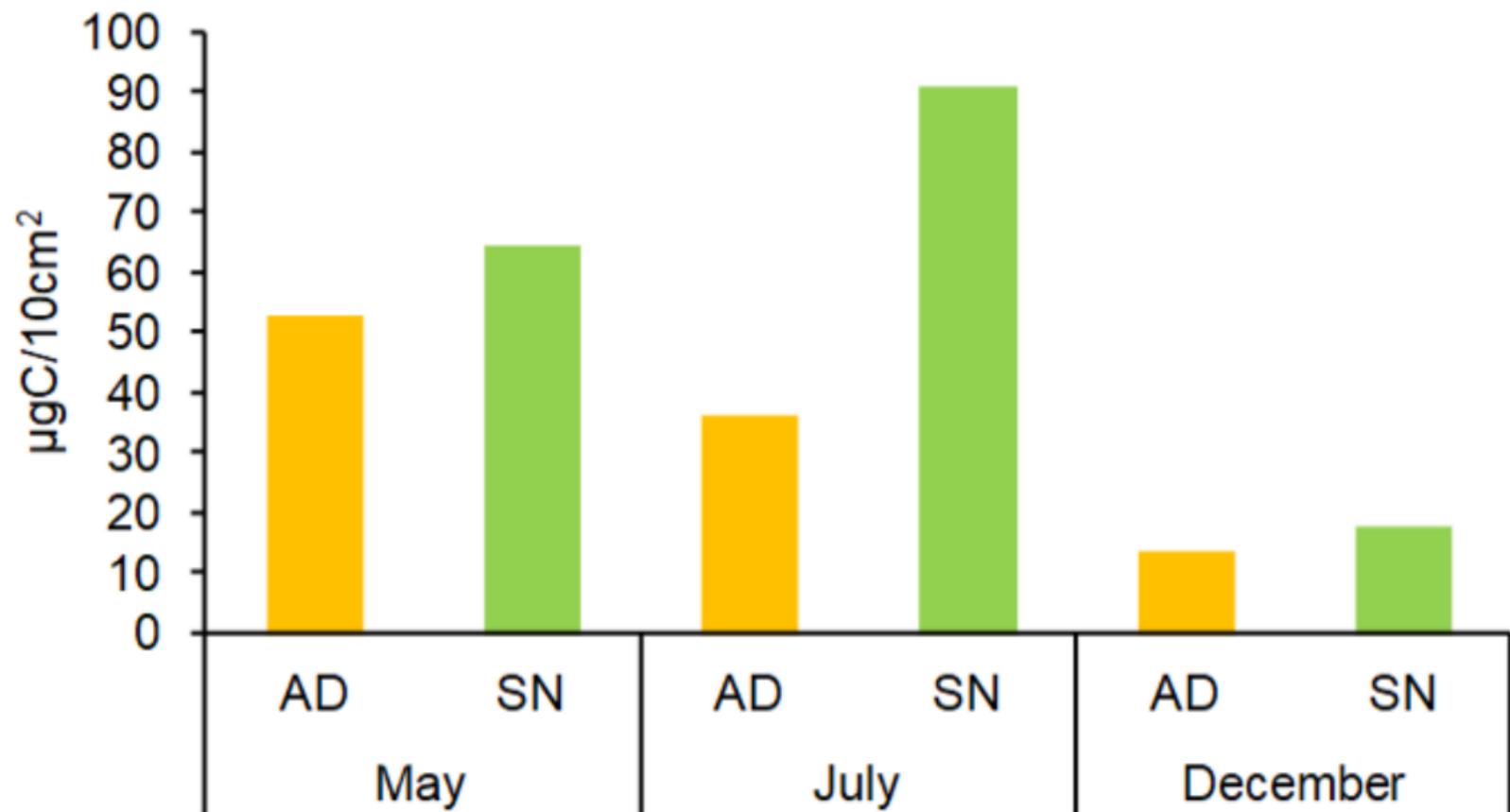
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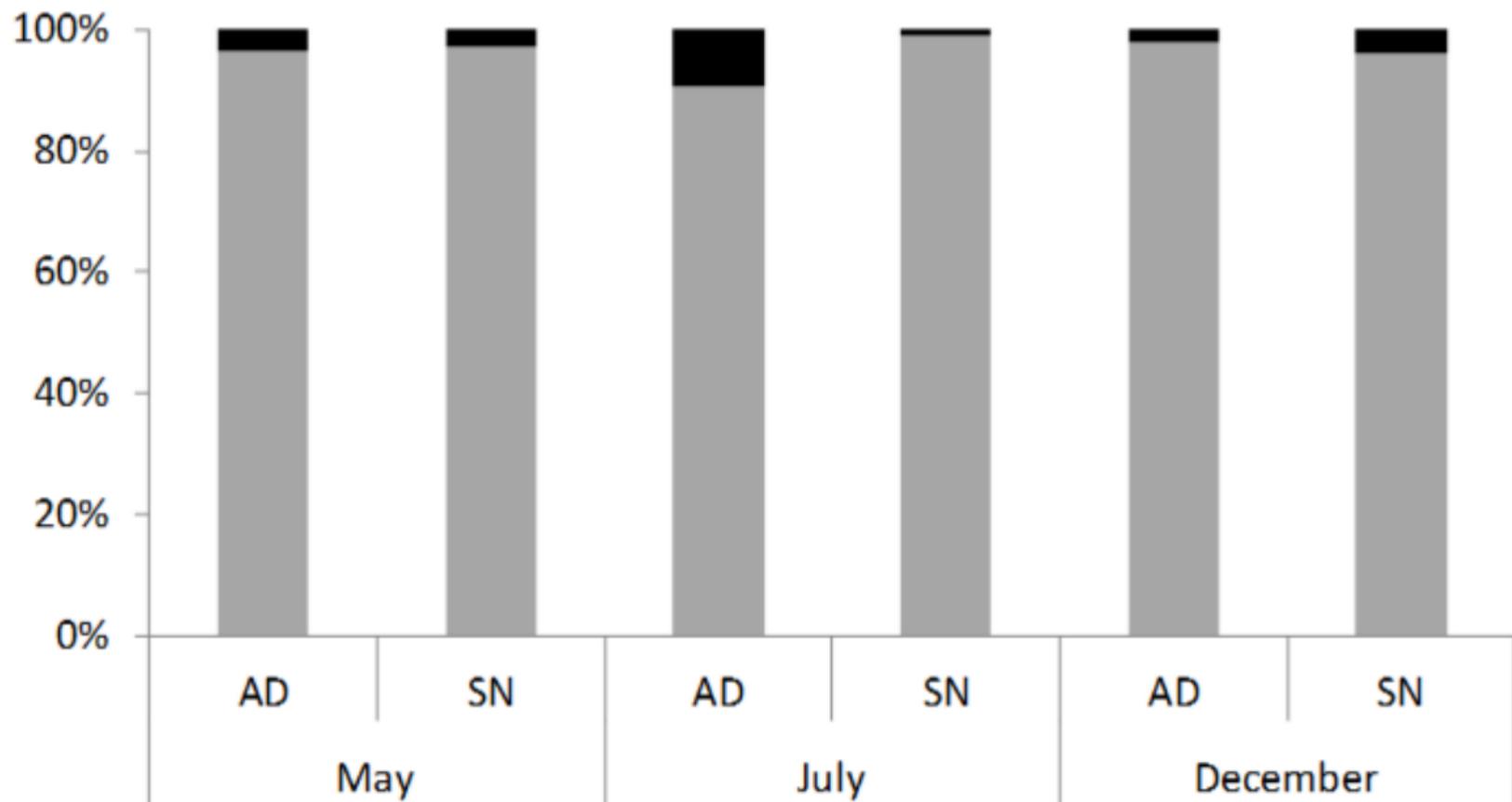


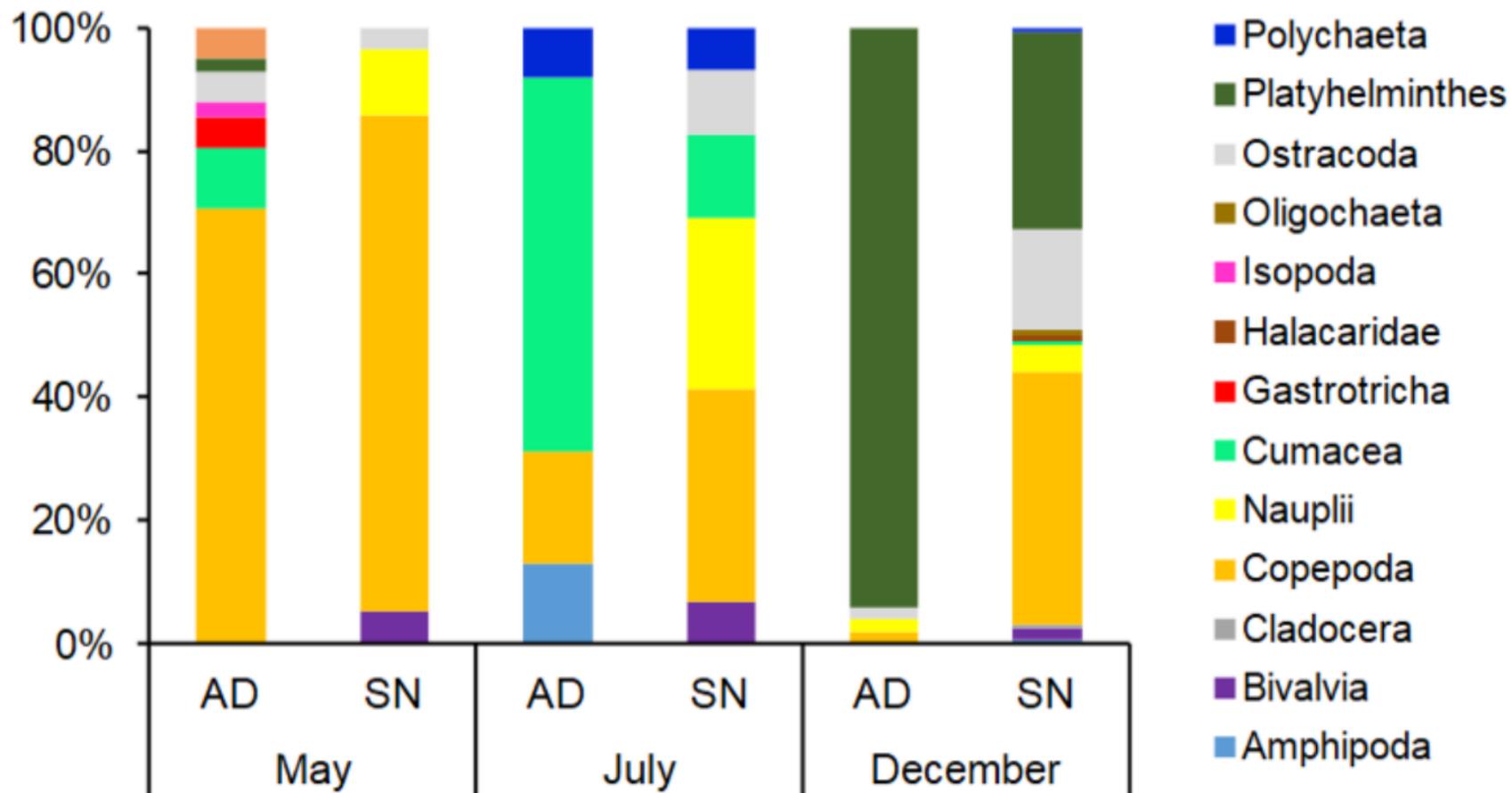
a

b

a

■ Nematoda ■ others



b

■ 1A ■ 1B ■ 2A ■ 2B

