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1 **How do food sources drive meiofauna community structure in soft-bottom coastal food webs?**

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14 **Abstract**

15 Meiofauna have a strong role in the functioning of coastal ecosystems but how their food sources
16 affect their community structure remains unclear, likely due to the influence of abiotic parameters and the
17 small size of these organisms. The meiofauna and their potential food sources were sampled in several
18 intertidal habitats (i.e. mudflat, seagrass bed, sandflat) of the Marennes-Oléron Bay, France, and the Sylt-
19 Rømø Bight, Germany, to assess the relationships between habitat characteristics and meiofauna
20 community structure. Biomass and quality (carbon/chlorophyll *a* ratios) of food sources were estimated.
21 Meiofauna community structure based on density and biomass was determined, as well as nematode
22 diversity and feeding types. Meiofauna density and biomass varied highly within habitats and within
23 ecosystems, ranging from $1.7 \cdot 10^5$ ind. m^{-2} to $3.4 \cdot 10^6$ ind. m^{-2} and from 0.057 gC m^{-2} to 1.541 gC m^{-2} ,
24 respectively. Benthic microalgae and sediment organic matter are important drivers in these food webs as
25 the density of two important trophic groups of nematodes, non-selective deposit feeders and epigrowth
26 feeders, varied in accordance with these food sources. No clear relationship was observed between
27 bacterial biomass and selective deposit feeders (i.e. bacterivores) probably due to the high production rate
28 of bacteria. Complementary information about production rates of food source as well as data from
29 trophic markers would provide complimentary information to better understand flows of organic matter in
30 intertidal habitats, particularly for opportunistic species such as non-selective deposit feeders.

31 **Introduction**

32 Soft-bottom intertidal habitats are highly productive (Underwood and Kromkamp 1999; Hemminga
33 and Duarte 2000), fueling complex food webs and providing food resources for a large diversity of top
34 consumers like fish and birds (Day et al. 1989; Duarte and Cebrián 1996) via trophic pathways going
35 through meiofauna (Chardy and Dauvin 1992) and macrofauna (Haubois et al. 2005). Meiofauna, here
36 defined as metazoans associated with sediments with a size range from 40 to 500 μm , are considered as
37 an important trophic component in the functioning of coastal ecosystems. They have an intermediate
38 trophic position (Leguerrier et al. 2003; Giere 2009) and high secondary production (from 4 to 29 gC m^{-2}
39 $year^{-1}$) (Escaravage et al. 1989; Chardy and Dauvin 1992; Danovaro et al. 2002) that often exceeds that of
40 the macrofauna (Giere 2009). Meiofauna are connected to the microorganisms in the food web via the
41 consumption of microalgae and bacteria (Rzeznik-Orignac et al. 2003; Vafeiadou et al. 2014) and to the
42 food webs of macroconsumers especially via their consumption by small benthic fish and predatory
43 invertebrates (Coull 1999). Nematodes are the most dominant group in meiofauna; their food resources
44 can be very specific, or in the contrary, relatively diverse, and their buccal cavity is very distinct based on
45 these feeding types. This morphological trait has been used for decades to define feeding types (Wieser
46 1953; Warwick 1971; Heip et al. 1985) and some more recent methods (i.e. feeding behavior

47 experiments; (Moens and Vincx 1997), trophic markers (Moens et al. 2005)) permitted to revise or
48 precise the feeding types of some genera (e.g. assort of *Metachromadora* from the omnivores/predators to
49 the epigrowth feeders).

50 Both, biotic and abiotic parameters, have been shown to affect meiofauna community structure.
51 Among biotic parameters, food availability in general (Castel et al. 1989; Danovaro 1996), availability of
52 specific food sources such as bacteria and microphytobenthos (Danovaro and Gambi 2002; Fonseca et al.
53 2011), the quality of the food (Danovaro et al. 2002) and the deposition of organic material of pelagic
54 origin (Franco et al. 2008) have been identified as structuring parameters. Abiotic parameters such as
55 sediment grain-size (Steyaert et al. 2003; Dupuy et al. 2015), habitat structure (Fonseca et al. 2011),
56 oxygen gradients (Josefson and Widbom 1988), intertidal water level (Steyaert et al. 2001) as well as
57 anthropogenic impacts (Semprucci et al. 2010) are influencing meiofauna community structure. Studies
58 on meiobenthic communities in intertidal systems have been carried out mainly on single habitats,
59 focusing on effects of abiotic and biotic parameters at the habitat scale (Reise 1985; Rzeznik-Orignac et
60 al. 2003; Lebreton et al. 2012). Factors affecting the community structure of meiofauna at a larger scale
61 (Moens et al. 2013) in intertidal habitats are still poorly known, as few studies have compared several
62 habitats and/or different ecosystems.

63 The present study investigates whether meiobenthic communities, especially free-living nematodes
64 and benthic copepods, differ among habitats with different characteristics (i.e. mudflats, seagrass beds
65 and sandflats; influence of terrestrial organic matter inputs or not) to define which factors are structuring
66 these communities. Particular attention is paid to the role of food sources, as they have been highlighted
67 as important drivers of ecosystem functioning in intertidal habitats (Asmus and Asmus 1985; Underwood
68 and Kromkamp 1999; McLusky and Elliott 2004). Aim of this study is therefore to define if changes in
69 biomass and quality of food sources can affect meiofauna community structure. If yes, the objective is to
70 determine—among all available food sources (i.e. benthic microalgae, sediment organic matter (SOM),
71 suspended particulate organic matter (SPOM) and bacteria)—what food sources play a role and how
72 changes in these food sources influence meiofauna community structure. In this aim, a temporal sampling
73 was done in spring and autumn in several habitats to define the temporal and spatial variations of the
74 food sources and those of meiofauna community structure.

75 **Materials and methods**

76 **Study sites**

77 *Marennes-Oléron Bay*

78 The Marennes-Oléron Bay is a semi-enclosed system, located in the middle of the western Atlantic
79 coast of France, between the Oléron Island and the mainland (Fig. 1). The bay has a surface of 180 km²
80 (Gouleau et al. 2000) and is influenced by both oceanic and continental inputs, mainly from the Charente
81 River (river input ranges from 15 to 500 m³ s⁻¹) (Ravail et al. 1988). Tides are semi-diurnal, with a period
82 of emersion of ca. 6 h per tidal cycle and a tidal range from 0.9 to 6.5 m (Kervella 2009). The system is
83 dominated by intertidal bare mudflats (91 km², i.e. 58%) which have a flat bottom slope (1:1000) and
84 represent a large tidal area (up to 4.5 km wide) (Gouleau et al. 2000).

85 The Brouage mudflat, located on the eastern part of the bay, is the most extensive mudflat (40 km²)
86 (Fig. 1). The sediment consists mainly of silt and clay particles (95%) with a size smaller than 63 µm
87 (Pascal et al. 2009). Seagrass beds, consisting of the species *Zostera noltii* (Lebreton et al. 2009), are
88 located on the western side of the bay, along the coast of the Oléron Island, which is more influenced by
89 offshore waters than the eastern side (Dechambenoy et al. 1977). The seagrass meadow is stretched out
90 over 15 km along the upper part of the flat, with an average width of 1.5 km (Guillaumont 1991).

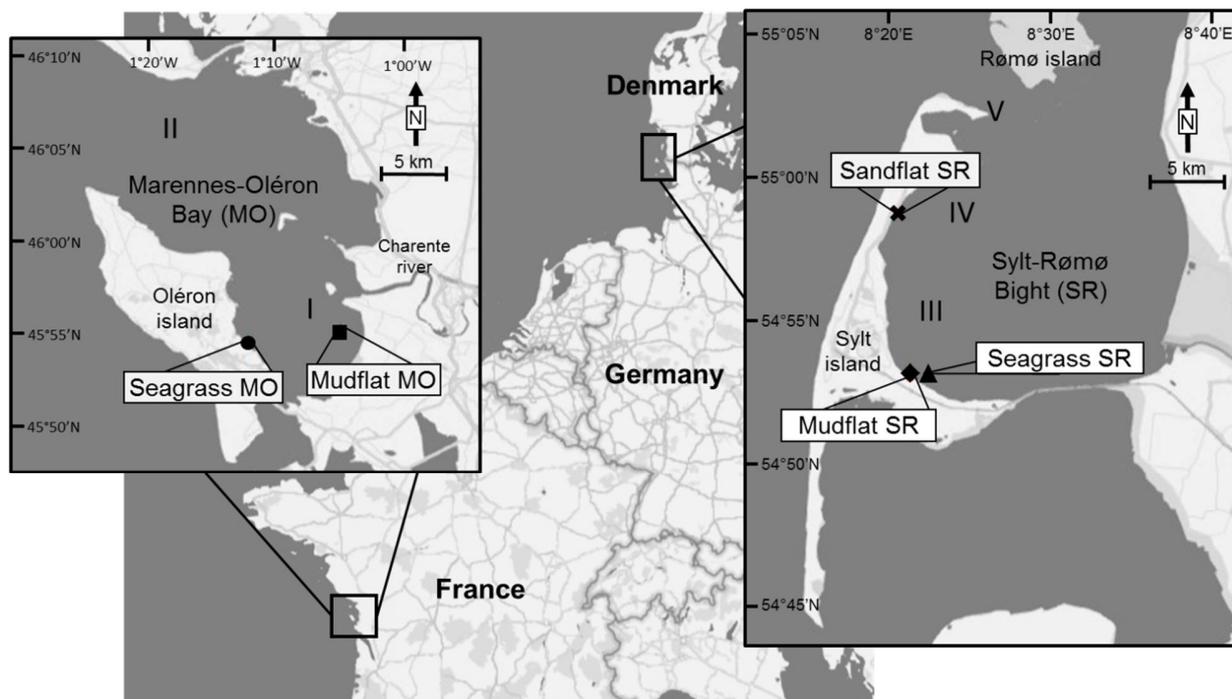
91 *Sylt-Rømø Bight*

92 The Sylt-Rømø Bight is a semi-enclosed basin, located in the north of Germany between the
93 mainland of Germany and Denmark, the islands of Sylt (Germany) and of Rømø (Denmark) (Fig. 1). The
94 bight consists of a mosaic of habitats, mainly intertidal and subtidal sandflats, seagrass beds, and mudflats
95 (Asmus and Asmus 1985). The bight has a coverage of 404 km² of which 135 km² are intertidal (Asmus
96 and Asmus 1985) and the tidal gauge is 1.8 m on average (Asmus and Asmus 1985).

97 The *Arenicola* sandflat is the most represented intertidal habitat in the bay with 91 km² (67%)
98 (Asmus and Asmus 2005). However, *Zostera noltii* seagrass beds expanded over the last years, from 15
99 km² in 1995 to 83 km² (i.e. 21% of the bay surface) in 2010 (Reise and Kohlus 2008). The intertidal bare
100 mudflats are poorly represented in the bight, with an area of 4 km² (Fig. 1).

101 *Field sampling and laboratory processes*

102 Three intertidal habitats were studied in the two bays: a bare mudflat (mudflat MO) and a seagrass
103 bed (seagrass MO) in the Marennes-Oléron Bay, and a bare mudflat (mudflat SR), a seagrass bed
104 (seagrass SR) and a sandflat (sandflat SR) in the Sylt-Rømø Bight (Fig. 1). Based on knowledge already
105 gained about these habitats in each of these five locations (Leguerrier et al. 2003; Baird et al. 2007;
106 Pacella et al. 2013; Saint-Béat et al. 2013) one sampling station that was the most representative for the
107 studied habitat was selected.



108

109 **Figure 1.** Sampling stations of the mudflats, seagrass beds and sandflat in the Marenes-Oléron Bay (MO) and the
 110 Sylt-Rømø Bight (SR) along the European coast. Pelagic sampling stations, where samples for suspended particulate
 111 organic matter were taken, are indicated by roman numbers in both Marenes-Oléron Bay (I-II) and Sylt-Rømø
 112 Bight (III-V).

113 *Sediment grain size*

114 Sediment samples (n = 3) were collected randomly with cores ($\varnothing = 4$ cm) and were split into 0-1 cm
 115 and 1-5 cm depth fractions. Sediment grain size was determined by laser granulometry analyses for the
 116 sediment from the seagrass bed and mudflats (Mastersize 2000, Malvern Instruments Limited, United
 117 Kingdom). The freeze-dried sediment of these habitats was rehydrated before analyses in order to avoid
 118 the use of ultrasound to disaggregate the sediment. Sediment grain size of freeze-dried samples from the
 119 sandflat of the Sylt-Rømø Bight was determined by dry sieving. Samples were classified based on their
 120 median sediment grain size after Wentworth (1922).

121 *Benthic primary producers, composite sources and bacteria*

122 For all stations, sampling was carried out in two seasons, in spring (from May 17 to June 17, 2016)
 123 and in autumn (from November 14 to December 15, 2016), to compare a season with a high primary
 124 production with a season with a high load of detrital matter. Sampling was carried out during low tide,
 125 starting about one hour before lowest water level.

126 Samples for sediment organic matter (SOM), detritus, and seagrass leaves and roots (3 replicates)
127 were taken using cores ($\varnothing = 19$ cm) which were separated in two layers (a surface layer from 0-1 cm, a
128 sub-surface layer from 1-5 cm). The collected material was gently sieved on a 500 μm mesh screen (1
129 mm for sandflat SR samples) after which the upper fraction was sorted in seagrass leaves, roots and
130 detritus (brown to black colored leaves and roots). All samples were freeze-dried, then weighed (± 0.001
131 g). Carbon to dry weight ratios were determined on each sample: A small amount was ground to a fine
132 and homogeneous powder using a ball mill (MM 400, Retsch, Germany) and carbon content was
133 determined using an elemental analyzer (Flash EA 1112, Thermo Scientific, Italy). Subsamples were
134 collected in the lower fraction (SOM), freeze-dried, and ground using a mortar and pestle. Chlorophyll *a*
135 and organic carbon concentrations were determined in sub-samples by fluorimetry (TD-700, Turner
136 Designs, USA) using the method of Lorenzen (1966) and elemental analyses (Flash EA 1112, Thermo
137 Scientific, Italy), respectively. Chlorophyll *a* values were converted into carbon biomass using the
138 conversion ratio (47.63) provided by de Jonge (1980) and used as a proxy of fresh material of microalgae
139 origin (i.e. microphytobenthos and trapped phytoplankton) in sediment, thereafter called “benthic
140 microalgae”. Carbonates were removed prior to elemental analyses by adding HCl at 2 mol.l⁻¹ drop-by-
141 drop on SOM samples until cessation of bubbling. Subsequently samples were dried at 60°C to constant
142 weight, freeze-dried and ground again.

143 Bacterial biomass (3 replicates) was determined using cores ($\varnothing = 4$ cm) which were separated in two
144 layers (0-1 cm and 1-5 cm). These sediment layers were homogenized with a spatula and 2 mL of this
145 material were mixed with 2 mL formalin (4%). Samples were deep frozen in liquid nitrogen and stored at
146 -80°C. The number of bacteria was determined following the protocol of Lavergne et al. (2014). Samples
147 were diluted (1/2000) using sodium pyrophosphate (P-8010, Sigma Aldrich, France) and Tween 80 (P-
148 1754, Sigma Aldrich, France), homogenized and then incubated at 4 °C during 30 minutes. Samples were
149 then sonicated at 60 W during 30 seconds, after which 1 mL of the pre-diluted sample was stained with 20
150 μL of SYBR Green I (Invitrogen-11540746; 1/5000 final concentration) and incubated in the dark at
151 room temperature for 15 minutes. Afterwards, 2 μL of calibration beads (1 μM) were added and the
152 samples were analyzed using a flow cytometer (BD FACSCANTO II, BD Biosciences, USA). Bacterial
153 densities were converted into carbon using the conversion factor (20 fgC cell⁻¹) established by Lee and
154 Fuhrman (1987).

155 *Suspended particulate organic matter*

156 Sampling of the suspended particulate organic matter (SPOM) was conducted by collecting samples
157 of surface water during high tide, in the same timeframe as the benthic samples. Water was sampled at
158 two stations (I and II) in the Marennes-Oléron Bay and three stations (III, IV and V) in the Sylt-Rømø

159 Bight (Fig. 1). Station I, in the north of the Brouage mudflat, represented the water mass covering the
160 mudflat MO station. Station II, near the inlet of the Marennes-Oléron bay, represented the water mass
161 influencing the seagrass MO station. Station II is regularly sampled in the framework of the SOMLIT
162 surveys (data provided by “Service d’Observation en Milieu Littoral, INSU-CNRS, La Rochelle station”).
163 Water samples collected at stations III and IV represented water masses covering the sandflat SR (III),
164 and the mudflat SR and seagrass SR stations (IV), respectively. Station V, near the entrance of the Sylt-
165 Rømø Bight, represented the SPOM originating from the North Sea.

166 SPOM was sampled by collecting 10 to 100 mL of surface seawater which was pre-filtered on a 250-
167 μm mesh screen to eliminate large particles/organisms. Water samples were then filtered on
168 precombusted (4 hours, 450°C) Whatman GF/F glass fiber filters (0.7 μm nominal porosity) under
169 moderate vacuum and these filters were freeze-dried. Chlorophyll *a* content, used as a proxy of
170 phytoplankton biomass, of the freeze-dried GF/F filters was measured by fluorimetry using the method of
171 Lorenzen (1966). Phytoplankton biomass was determined by using the conversion factor (56.4)
172 established by Lü et al. (2009).

173 *Meiofauna*

174 Meiofauna was sampled for taxonomic composition, density (ind. m^{-2}) and biomass (gC m^{-2})
175 estimations at the same time as benthic primary producers and composite sources. Three replicates were
176 collected randomly in a ten square meters area using cores ($\varnothing = 4 \text{ cm}$). Cores were separated in two layers
177 (0-1 cm and 1-5 cm) to study the changes of meiofauna communities related to sediment depth. Samples
178 were sieved with a 500- μm mesh to eliminate macrofauna and large detritus. Meiofauna was extracted
179 from the sediment using Ludox HS-40 (Sigma Aldrich, France) (de Jonge and Bouwman 1977) and
180 retrieved with a 40- μm mesh sieve (Higgins and Thiel 1988). From each replicate, 100 nematodes were
181 haphazardly taken with fine tweezers (#55, Dumont, Switzerland), mounted on slides in anhydrous
182 glycerol to prevent dehydration (Seinhorst 1959) and examined microscopically. The taxonomic
183 composition of the nematode community was determined at least to the genera level based on these 100
184 individuals according to the identification keys of Platt and Warwick (1983, 1988), and Warwick and
185 Clarke (1998). Density was calculated for each genera as number of individuals per m^2 (ind. m^{-2}) and
186 relative abundance as the percent composition of each genera relative to the total number of organisms.
187 Species diversity indices were calculated on 100 individuals for each replicate at the five habitats for the
188 two seasons. Community structure of the other meiofauna groups was not determined due to low
189 densities. Nematodes were allocated into four trophic groups according to Wieser (1953) as follows:
190 selective deposit-feeders (1A), non-selective deposit-feeders (1B), epigrowth feeders (2A), and
191 omnivores/predators (2B). Various nematode genera, including at least one of each from the 4 different

192 feeding groups, were selected for determination of individual dry weight and carbon content. Between 10
193 and 200 nematodes from the same genera were picked for dry weight determination, freeze-dried and
194 weighed ($\pm 1 \mu\text{g}$) using a microbalance (ME 5, Sartorius, Germany). Organic carbon composition was
195 determined using an elemental analyzer (Flash EA 1112, Thermo Scientific, Italy). Mean biomass of
196 species-specific nematodes and benthic copepods were used to convert the density of nematodes into
197 grams of carbon per m^2 and dry weight per m^2 (Supplementary material, Appendix 1).

198 **Data treatment and statistical methods**

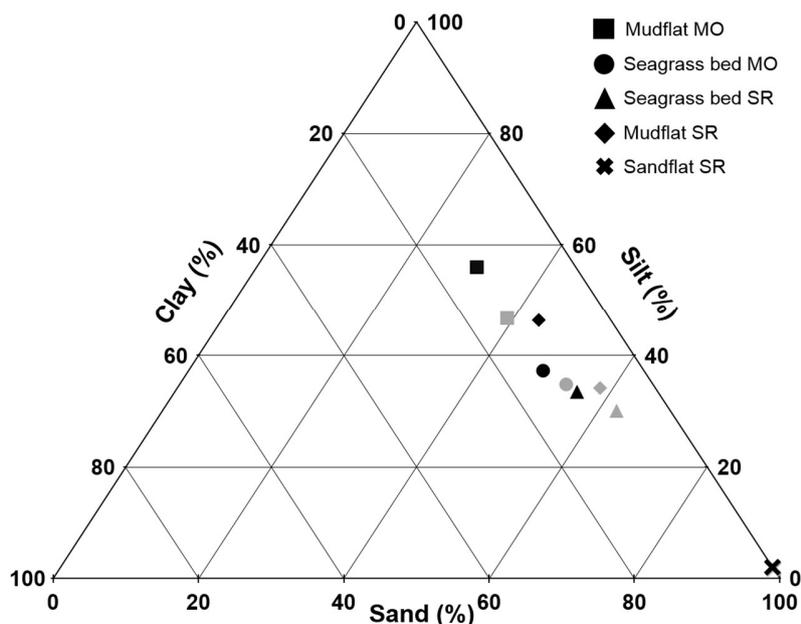
199 All analyses were conducted using the R software (R Core Team, 2016) and all hypotheses were
200 tested at $p < 0.05$ level. Normality of the data was tested using Shapiro-Wilks tests. Homogeneity of
201 variance was checked using Bartlett and Levene tests. Average hierarchical clusters (data dissimilarity,
202 Bray-Curtis distance) were realized to discriminate groups within the food sources and within the
203 meiofauna trophic structure using the *vegan* package (Oksanen et al. 2017) and *pvclust* package (Suzuki
204 and Shimodaira 2015). ANOVA followed by Tukey *post-hoc* test were used to compare sediment
205 characteristics, meiofauna densities, biomass and diversity indices: Hill's diversity N_1 (Hill 1973) and
206 species evenness J' (Formula in supplementary material, Appendix 2). Comparisons between sediment
207 layers were conducted on meiofauna densities (ind. m^{-3}) and biomasses (gC m^{-3}) expressed in volume of
208 sediment. Comparisons between seasons and habitats were done on meiofauna densities, biomasses and
209 diversity indices from combined layers (expressed per surface area). Environmental variables have been
210 analyzed through a preliminary Principal Components Analysis (PCA) to visualize the differences
211 between habitats based on these variables. In a subsequent step copepods, other meiofauna taxa
212 (ostracods, foraminifers and polychaetes) and feeding types of nematodes were compared with Bray-
213 Curtis similarity redundancy relationship analyses (RDA) made with the *vegan* package (Oksanen et al.
214 2017). The relative abundance of copepods, other meiofauna (ostracods, foraminifers and polychaetes)
215 and different feeding types of nematodes (dependent variables) were linked to environmental variables
216 (independent variables) that were selected after stepwise forward procedure. Multicollinearity was tested
217 for the explanatory variables using the *vif.cca* function in the *vegan* package (values over 10 indicated
218 collinearity; Oksanen et al. 2017). The significance of the model was tested using a two-way ANOVA.

219 **Results**

220 **Sediment grain size**

221 Sediment of the mudflats and seagrass beds consisted of a mixture of sand (29 to 64%), silt (29 to
222 58%) and clay (7 to 15%), while the sandflat consisted mainly of sand (98%) (Fig. 2). Sediments were
223 classified as silt for mudflat MO, mudflat SR (autumn) and seagrass MO (autumn), very fine sand for

224 seagrass SR, mudflat SR (spring) and seagrass MO (spring) and medium sand for sandflat SR. The mud
 225 content within the different layers of the same habitat was relatively similar, with a variation lower than
 226 2%. The sediment grain-size of mudflat MO was lower than all other habitats with a median sediment
 227 grain-size of $32 \pm 4.3 \mu\text{m}$, and the grain-size of sandflat SR was higher than all other habitats with a
 228 median sediment grain-size of $407 \pm 16.3 \mu\text{m}$ (Supplementary material, Appendix 3).



229
 230 **Figure 2.** Ternary diagram presenting the sediment composition of the mudflats, seagrass beds and sandflat in the
 231 Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in spring (grey symbols) and autumn (black symbols).
 232 Separation by size for clay ($< 3.9 \mu\text{M}$), silty ($3.9 - 63 \mu\text{M}$), and sandy ($63 - 2000 \mu\text{M}$) sediment. ($n = 3$)

233 Potential food sources

234 The total biomass of benthic food sources ranged from 67.4 (sandflat SR, autumn) to 447.4 gC m^{-2}
 235 (mudflat SR, spring) (Fig 3; C and E). SOM was dominant in all habitats sources with proportions
 236 ranging from 29.3 to 94.5%, representing 19.8 (sandflat SR, autumn) to 290.3 gC m^{-2} (mudflat MO,
 237 autumn). Benthic microalgae were the second most dominant food source, with biomass ranging from 7.1
 238 gC m^{-2} (3.7%, mudflat MO, spring) to 70.3 gC m^{-2} (22.6%, seagrass SR, spring). Detrital matter was
 239 found mainly in the two seagrass beds and mudflat SR with 4.3 (1.0%, mudflat SR, spring) to 45.5 gC m^{-2}
 240 (16.7%, seagrass bed MO, autumn). In the seagrass beds, leaves and roots were occurring with biomass
 241 ranging from 1.6 (0.5%, seagrass SR, autumn) to 15.0 gC m^{-2} (5.1%, seagrass MO, spring) and 0.3 (0.1%,
 242 seagrass SR, autumn) to 24.4 gC m^{-2} (8.2%, seagrass MO, autumn). Bacteria represented the lowest
 243 biomass in all habitats with 0.6 (0.9%, sandflat SR, autumn) to 20.1 gC m^{-2} (4.5%, mudflat SR, spring).
 244 Some differences of food source biomass could be observed between the surface and the sub-surface

245 layers, always with higher biomass in the surface layer when they occurred: detrital matter in mudflat SR
246 in spring and in seagrass MO in autumn, bacteria in mudflat SR in spring, and benthic microalgae in all
247 habitats in all seasons except for mudflat SR and sandflat SR in autumn (two-way ANOVA with Tukey
248 *post-hoc* test, highest p-value 0.032).

249 The average hierarchical cluster of dissimilarities highlighted that food source composition in the
250 sandflat SR was different than in the other habitats (Fig. 3; A), due to the much lower biomass of SOM in
251 sandflat SR (29.2 gC m⁻²) than in mudflats and seagrass beds (256.6 gC m⁻²; two-way ANOVA with
252 Tukey *post-hoc* test, $p < 0.001$, Fig. 3C and E). Benthic microalgae biomass was much higher in sandflat
253 SR (54.2 gC m⁻²) than in mudflat SR (27.8 gC m⁻²), mudflat MO (10.5 gC m⁻²) and seagrass MO (22.6 gC
254 m⁻², two-way ANOVA with Tukey *post-hoc* test, $p < 0.001$). Food source composition in both mudflats
255 and both seagrass beds of the two bays appeared to be similar as highlighted by the clustering but some
256 variations could be pointed out based on two-way ANOVA. Biomass of bacteria in spring was higher in
257 mudflat SR (13.5 gC m⁻²) compared to mudflat MO (3.9 gC m⁻²), seagrass MO (4.2 gC m⁻²), seagrass SR
258 (6.9 gC m⁻²) and sandflat SR (1.8 gC m⁻², two-way ANOVA with Tukey *post-hoc* test, $p < 0.001$). The
259 presence of detrital matter in mudflat SR versus its absence in mudflat MO discriminated both mudflats as
260 well. Lastly, biomass of leaves and roots in spring were higher in the Marennes-Oléron Bay (39.4 gC m⁻²)
261 compared to the Sylt-Rømø Bight (6.4 gC m⁻², two-way ANOVA with Tukey *post-hoc* test, $p < 0.001$).

262 Some differences occurred at the seasonal scale as well, with higher biomass of primary producers in
263 spring when a difference occurred. Such a pattern was observed for benthic microalgae in sandflat SR,
264 seagrass SR and seagrass MO, and for seagrass leaves in seagrass bed MO (two-way ANOVA with
265 Tukey *post-hoc* test, $p < 0.001$). Bacteria biomass of mudflat SR and seagrass SR were also higher in
266 spring compared to autumn (two-way ANOVA followed by Tukey *post-hoc* test, $p < 0.001$). About
267 detrital matter, seasonal changes followed an opposite pattern when they occurred, with an increase in
268 biomass of detritus from spring to autumn in mudflat SR and seagrass MO (two-way ANOVA with
269 Tukey *post-hoc* test, $p < 0.001$). SOM biomass was stable between spring and autumn (two-way ANOVA
270 with Tukey *post-hoc* test, lowest p-value 0.44).

271 Regarding quality of potential food sources in the different habitats, they varied from being partly
272 detrital in sandflat SR (57 to 63%) to being almost completely made out of detrital matter in mudflat MO
273 (from 93 to 99%). Carbon: chlorophyll *a* (C:chl *a*) ratios of SOM were higher in mudflat MO (1201.4),
274 mudflat SR (681.8) and seagrass MO (504.6) compared to seagrass SR (221.4) and sandflat SR (72.3;
275 two-way ANOVA with Tukey *post-hoc* test, $p < 0.001$, Table 1). SOM had much higher C:chl *a* ratios in
276 the sub-surface layer than in the surface layer (two-way ANOVA with Tukey *post-hoc* test, $p < 0.001$).
277 Variation in C:chl *a* ratios between spring and autumn were not observed (two-way ANOVA, lowest p-

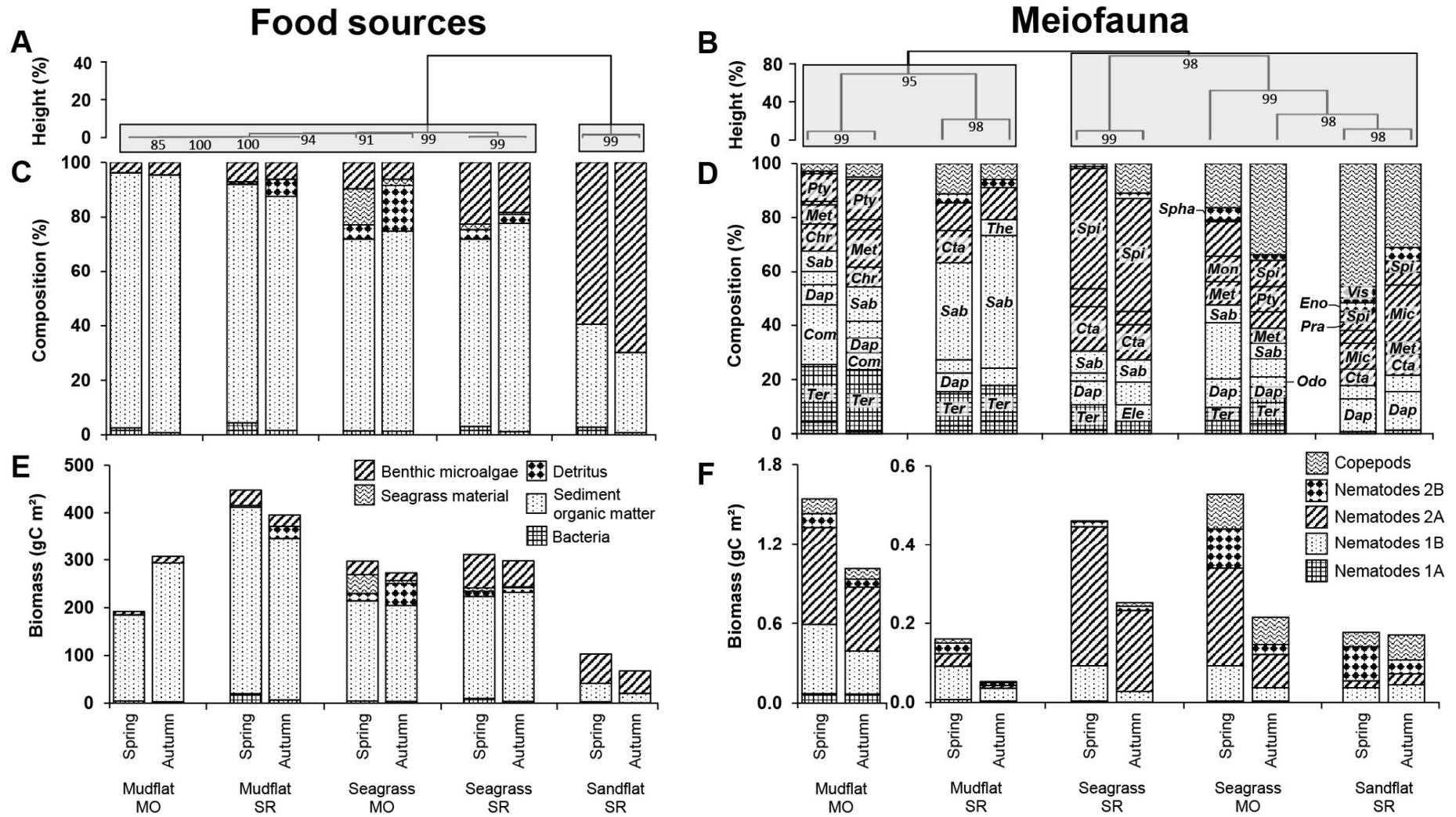
278 value 0.33, Table 1). Proportions of SOM that were originating from fresh microalgae (i.e.
 279 microphytobenthos and trapped phytoplankton) ranged from 3.6 (mudflat MO, spring) to 71.1% (sandflat
 280 SR, autumn, Table 1). These proportions were much higher in sandflat SR (66.6%) and seagrass SR
 281 (22.0%) than in mudflat SR (7.0%) and mudflat MO (4.0%, two-way ANOVA with Tukey *post-hoc* test,
 282 Table 1). Quantities of SPOM ranged between 0.32 and 0.54 gC L⁻¹. Minor variations between habitats
 283 observed within SPOM are reported in the supplementary material (Appendix 4).

284 **Table 1.** Carbon: chlorophyll *a* ratios (mean ± standard deviation, *n* = 3) and percentage of carbon
 285 originating from fresh microalgae (mean ± standard deviation, %, *n* = 3) in sediment organic matter
 286 (SOM) in the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø
 287 Bight (SR) in spring and autumn. Letters displayed after mean values indicated grouping of similar
 288 samples (two-way ANOVA with Tukey *post-hoc* tests, *p* < 0.05).

289

Habitat	Carbon: chlorophyll <i>a</i> ratio		Carbon of SOM originating from fresh microalgae	
	Spring	Autumn	%	
	Spring	Autumn	Spring	Autumn
Mudflat MO	1314.3 ^E ± 35.3	1088.5 ^D ± 166.2	3.6 ^A ± 0.1	4.4 ^A ± 0.7
Mudflat SR	643.9 ^C ± 60.1	719.7 ^C ± 60.6	7.4 ^A ± 0.7	6.6 ^A ± 0.6
Seagrass MO	389.2 ^B ± 47.5	619.9 ^C ± 47.6	12.4 ^{AB} ± 1.4	7.7 ^A ± 0.6
Seagrass SR	193.9 ^A ± 14.3	249.0 ^{AB} ± 29.8	24.6 ^C ± 1.8	19.3 ^{BC} ± 2.4
Sandflat SR	76.8 ^A ± 2.2	67.8 ^A ± 9.1	62.0 ^D ± 1.7	71.1 ^D ± 9.8

290



291

292 **Figure 3.** Composition of potential benthic food sources for meiofauna and of meiofauna in the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the
 293 Sylt-Rømø Bight (SR) in spring and autumn. **A)** Hierarchical average cluster of dissimilarity for the proportional composition of potential food sources. **B)** Hierarchical average
 294 cluster of dissimilarity for proportional composition of meiofauna (nematodes and benthic copepods). Approximately unbiased (AU) probability values (p-values) by multiscale
 295 bootstrap resampling are under each node and clusters (AU \geq 95%) are highlighted with grey rectangles. **C)** Proportional composition of potential food sources. **D)**

296 Proportional composition of benthic copepods and trophic groups of nematodes. Trophic groups of genera with
297 relative abundance > 5% are displayed. **E)** Biomass of potential food sources. **F)** Biomass of benthic copepods and
298 trophic groups of nematodes. Selective deposit feeders = 1A, non-selective deposit feeders = 1B, epigrowth feeders
299 = 2A and omnivores/predators = 2B (Wieser 1953). Abbreviations: Chr = *Chromadora*, Cta = *Chromadorita*, Com =
300 *Comesa*, Dap = *Daptonema*, Ele = *Eleutherolaimus*, Eno = *Enoplolaimus*, Met = *Metachromadora*, Mic =
301 *Microlaimus*, Mon = *Monoposthia*, Odo = *Odontophora*, Pra = *Praeacanthochus*, Pty = *Ptycholaimellus*, Sab =
302 *Sabatieria*, Spha = *Sphaerolaimus*, Spi = *Spirinia*, Ter = *Terschellingia*, The = *Theristus*, Vis = *Viscosia*. ($n = 3$)

303 **Meiofauna community structure**

304 The meiofauna community was dominated by nematodes with relative abundance ranging from
305 41.7% (sandflat SR, surface layer, spring) to 100% (mudflat MO, sub-surface layer, spring), except for
306 the surface layer of sandflat SR where copepods dominated (55.5%, Fig. 4). Four other meiofauna taxa
307 occurred in the different habitats: copepods (0 to 55.5%), foraminifera (0 to 7.4%), polychaetes (0 to
308 5.3%), and ostracods (0 to 0.4%). Total meiofauna density was higher in the surface layer than in the sub-
309 surface layer in all habitats (two-way ANOVA with Tukey *post-hoc* test, highest p -value 0.033). Mean
310 meiofaunal density of both layers combined ranged from $1.7 \cdot 10^5$ ind. m^{-2} (mudflat SR, autumn) to
311 $3.4 \cdot 10^6$ ind. m^{-2} (mudflat MO, autumn, Appendix 5). Meiofauna densities (both layers combined) were
312 similar between spring and autumn, except in seagrass SR where densities were higher in spring (two-way
313 ANOVA with Tukey *post-hoc* test, highest p -value 0.020, Table 2).

314 Total biomass of nematodes (both layers combined) ranged from $0.053 \text{ gC } m^{-2}$ ($1.6 \cdot 10^5$ ind. m^{-2} ,
315 mudflat SR, autumn) to $1.541 \text{ gC } m^{-2}$ ($2.9 \cdot 10^6$ ind. m^{-2} , mudflat MO, spring, Fig. 3F). Nematode density
316 and biomass were higher in surface layers than in the sub-surface layers (two-way ANOVA with Tukey
317 *post-hoc* test, highest p -value 0.042). Nematodes from the surface layers dominated the contribution to
318 the total biomass in all habitats, with lowest proportions in seagrass SR (54.0%) and mudflat SR (55.4%)
319 and higher proportions in sandflat SR (82.3%), mudflat MO (83.3%) and seagrass SR (95.7%). At the
320 habitat scale, nematode density and biomass were much higher in mudflat MO (density: $3.0 \cdot 10^6$ ind. m^{-2} ;
321 biomass: $1.257 \text{ gC } m^{-2}$) than in all other habitats (two-way ANOVA with Tukey *post-hoc* test, $p < 0.001$,
322 Table 2, Appendix 5). Nematode biomass in the seagrass beds ranged from 0.146 (seagrass MO, autumn)
323 to $0.459 \text{ gC } m^{-2}$ (seagrass SR, spring). Nematode biomass of the mudflat SR and sandflat SR ranged from
324 0.054 (mudflat SR, autumn) to $0.150 \text{ gC } m^{-2}$ (mudflat SR, spring). Some temporal variations occurred as
325 well, with higher nematode densities in spring in seagrass SR and higher nematode biomass in spring in
326 mudflat MO (two-way ANOVA with Tukey *post-hoc* test, highest p -value 0.005, Table 2).

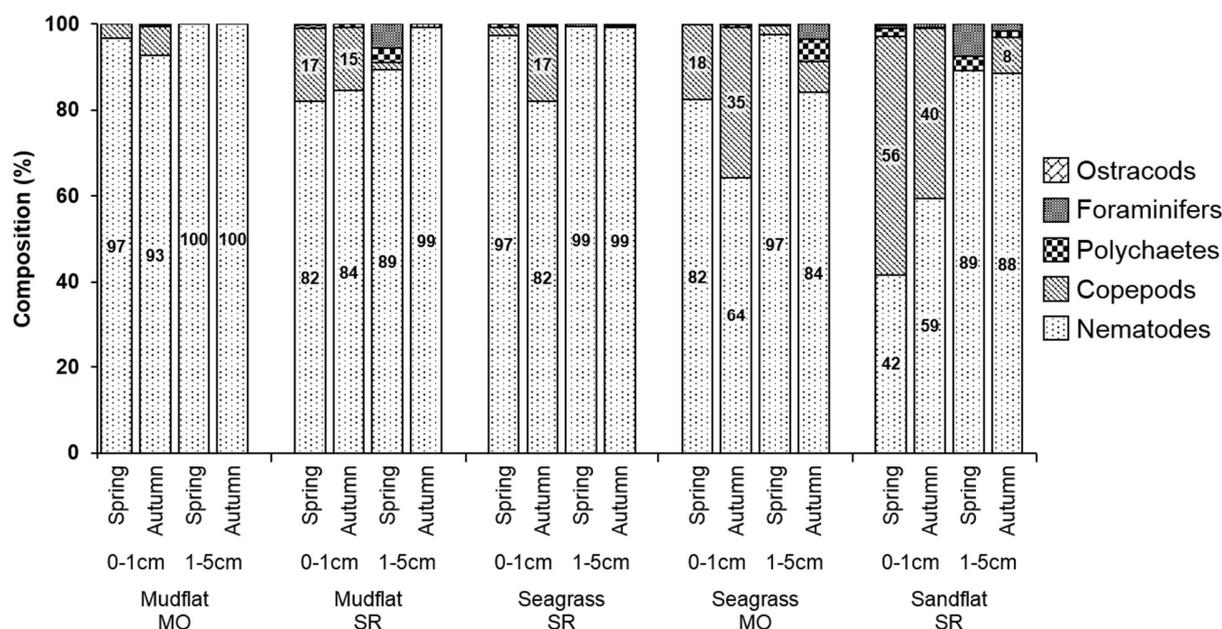
327 Total biomass of benthic copepods, which were merely present in the surface layers, ranged from
328 $0.003 \text{ gC } m^{-2}$ ($1.0 \cdot 10^4$ ind. m^{-2} , mudflat SR, autumn) to $0.110 \text{ gC } m^{-2}$ ($1.7 \cdot 10^5$ ind. m^{-2} , mudflat MO,

329 spring, Fig. 3F). Copepod biomass of the mudflat MO (0.095 gC m⁻²) was much higher than in the
 330 mudflat SR (0.006 gC m⁻²), while copepod density was higher in the seagrass MO than in the seagrass SR
 331 and mudflat SR (two-way ANOVA with Tukey *post-hoc* test, $p < 0.001$). Densities and biomass of
 332 benthic copepods were similar in spring and autumn (two-way ANOVA with Tukey *post-hoc* test, lowest
 333 p -value 0.178, Table 2).

334 **Table 2.** Results of the two-way ANOVA for differences in total meiofauna, nematode, and benthic copepod density
 335 and nematode and benthic copepod biomass across habitats and seasons.

Source	Total meiofauna			Nematodes		Benthic copepods	
	df	F-ratio	<i>P</i> > F	F-ratio	<i>P</i> > F	F-ratio	<i>P</i> > F
Density							
Habitat	4	363.0	< 0.001	385.8	< 0.001	12.7	< 0.001
Season	1	6.3	0.020	9.6	0.005	1.9	0.178
Habitat:season	4	8.8	< 0.001	9.1	< 0.001	2.8	0.052
Error	20						
Biomass							
Habitat	4			216.2	< 0.001	29.01	< 0.001
Season	1			34.5	< 0.001	0.47	0.503
Habitat:season	4			11.7	< 0.001	2.14	0.113
Error	40						

336 df = degree of freedom; F = F statistic; *P* = probability. Values in bold indicate a significant difference ($\alpha \leq 0.05$)



337

338 **Figure 4.** Proportional composition of meiofauna in the mudflats, seagrass beds and sandflat in the Marennes-
 339 Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in spring and autumn and in each sediment layer (0-1cm/1-5cm).
 340 Densities (%) are indicated when > 7.5%. ($n = 3$)

341 **Nematode community structure**

342 Five thousand four hundred nematodes were determined at genus and/or species level. A total of 139
 343 species, belonging to 65 genera and 20 families were found at the five habitats in both the Marennes-
 344 Oléron Bay and the Sylt-Rømø Bight. Eight genera represented 70% of the community in the surface
 345 layer of all habitats combined: *Daptonema* (1B, 18%), *Chromadorita* (2A, 10%), *Metachromadora* (2A,
 346 10%), *Sabatieria* (1B, 10%), *Ptycholaimellus* (2A, 7%), *Spirinia* (2A, 6%), *Terschellingia* (1A, 5%), and
 347 *Praeacanthochus* (2A, 4%). Four genera represented 70% of the community in the sub-surface layer of
 348 all habitats combined: *Terschellingia* (1A, 28%), *Sabatieria* (1B, 25%), *Spirinia* (2A, 13%), and
 349 *Metachromadora* (2A, 6%). The surface layer had a higher number of genera (from 3 to 9 genera, mean:
 350 5.8) that represented 75% of the community compared to the sub-surface layer (from 2 to 9 genera, mean:
 351 3.4) for all habitats. The ten most dominant genera per habitat, season and sediment layer are presented in
 352 the supplementary material (Appendix 6). Species richness varied from 8 to 28, Hill's diversity from 2.3
 353 to 19.1, and species evenness from 0.41 to 0.88 (Table 3). Species richness, diversity and evenness
 354 decreased with depth at all habitats (two-way ANOVA, $p < 0.001$, Table 4). Species richness and
 355 evenness were higher at the seagrass MO than at the mudflat SR and the seagrass SR (two-way ANOVA
 356 with Tukey *post-hoc* test, $p < 0.001$). Hills diversity was higher at the seagrass MO than at all other
 357 habitats (two-way ANOVA with Tukey *post-hoc* test, $p < 0.001$). There was no difference in diversity and
 358 evenness between seasons (two-way ANOVA, lowest p-value 0.126, Table 4).

359 **Table 3.** Number of nematode genera, Hill's diversity (N_I), and species evenness (J') in the mudflats,
 360 seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in spring
 361 and autumn. ($n = 3$)

	Mudflat MO		Mudflat SR		Seagrass SR		Seagrass MO		Sandflat SR											
	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn										
Layer (in cm)	0-1	1-5	0-1	1-5	0-1	1-5	0-1	1-5	0-1	1-5										
Species richness	22	11	21	13	23	12	15	13	16	11	16	12	24	19	23	14	20	12	21	18
Hill's diversity (N_I)	14	5	12	6	13	4	9	5	7	3	6	4	15	12	14	8	11	6	12	7
Species evenness (J')	0.9	0.6	0.8	0.7	0.8	0.6	0.8	0.6	0.7	0.5	0.6	0.6	0.8	0.9	0.8	0.8	0.8	0.7	0.8	0.7

362

363 **Table 4.** Results of the two-way ANOVA for differences in species richness, Hill's diversity (N_i), and
 364 species evenness (J') between habitats, sediment layers and season in the mudflats, seagrass beds and
 365 sandflat in the Marennes-Oléron Bay and the Sylt-Rømø Bight.

Source	Species richness			Hill's diversity		Species evenness	
	df	F-ratio	$P > F$	F-ratio	$P > F$	F-ratio	$P > F$
Layer	1	88.3	< 0.001	149.6	< 0.001	55.9	< 0.001
Site	4	11.0	< 0.001	29.0	< 0.001	16.2	< 0.001
Season	1	0.1	0.802	2.4	0.126	0.0	1.000
Layer:site	4	1.5	0.214	4.75	0.003	4.5	0.005
Layer:season	1	6.4	0.015	3.3	0.078	0.6	0.452
Site:season	4	3.1	0.026	1.9	0.134	0.3	0.878
Layer:site:season	4	2.3	0.079	2.5	0.062	2.3	0.077
Error	38						

366 df = degree of freedom; F = F statistic; P = probability. Values in bold indicate a significant difference ($\alpha \leq 0.05$)

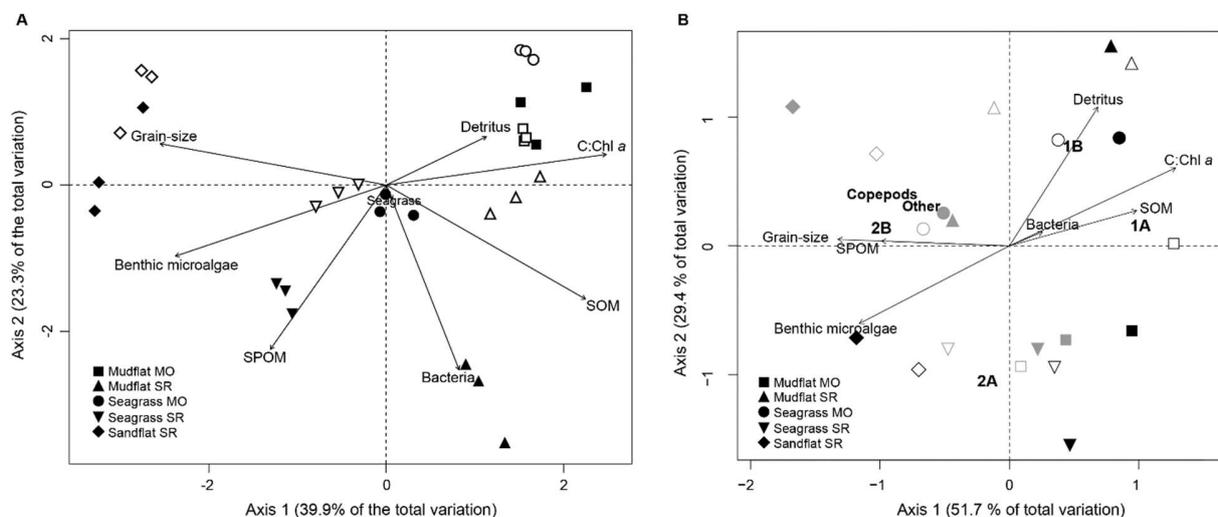
367 Community compositions, based on proportions of benthic copepods and of trophic groups of
 368 nematodes, were similar between the two mudflats (besides the very large difference of biomass), as
 369 highlighted by the average hierarchical cluster analysis ($p < 0.05$, Fig. 3B). The sandflat SR and the two
 370 seagrass beds had similar communities as well. The difference of trophic structures between the mudflats
 371 and the other habitats was related to the higher proportions of selective deposit-feeders (1A) and of non-
 372 selective deposit-feeders (1B) in the mudflats. The mudflat MO was dominated by genera belonging to
 373 non-selective deposit feeders (36%, 0.579 gC m⁻²), epigrowth feeders (34%, 0.525 gC m⁻²), and selective
 374 deposit feeders (25%, 0.071 gC m⁻²) with *Terschellingia* (1A, 22%, 0.055 gC m⁻²), *Comesa* (1B, 14%,
 375 0.082 gC m⁻²) and *Ptycholaimellus* (2A, 13%, 0.048 gC m⁻²) being the most common genera (Fig. 3D). At
 376 the mudflat SR, the non-selective deposit feeders dominated (55%), and the most abundant genera were
 377 *Sabatieria* (1B, 43%, 0.042 gC m⁻²) and *Terschellingia* (1A, 13%, 0.004 gC m⁻²). The seagrass bed SR
 378 was dominated by epigrowth feeders with the genera *Spirinia* (2A, 46%, 0.225 gC m⁻²) and *Chromadorita*
 379 (2A, 16%, 0.026 gC m⁻²). The seagrass bed MO was dominated by various genera belonging to epigrowth
 380 feeders (31%, 0.165 gC m⁻²) and non-selective deposit feeders (29%, 0.061 gC m⁻²). There, the biomass
 381 of nematodes was dominated by the epigrowth feeder genera *Metachromadora* (7%, 0.035 gC m⁻²). The
 382 sandflat SR was dominated by genera belonging to epigrowth feeders (35%, 0.023 gC m⁻²) and non-
 383 selective deposit feeders (19%, 0.040 gC m⁻²), with the genera *Microlaimus* (2A, 15%, 0.006 gC m⁻²) and
 384 *Daptonema* (1B, 13%, 0.028 gC m⁻²) being the most common.

385 Relationships between environmental parameters and meiofauna trophic structure

386 The PCA on the environmental variables explained 63.2% of the total variation (Axis 1: 39.9%, axis
387 2: 23.3%, Fig. 5A). Axis 1 highlights a positive relationship between SPOM, benthic microalgae and
388 sediment grain size. At the opposite, when biomass of benthic microalgae, SPOM and sediment grain size
389 were low, quantities of SOM were higher, as well as bacteria and detritus biomass, and
390 carbon:chlorophyll *a* ratios of SOM. Axis 2 demonstrates that biomass of bacteria increased with biomass
391 of SOM, SPOM, and benthic microalgae. Sandflat SR is defined by larger sediment grain size, higher
392 biomass of benthic microalgae and of SPOM, as highlighted on axis 1. Axis 1 also discriminates seagrass
393 SR from mudflat SR, mudflat MO and seagrass MO (autumn), the later ones being characterized with
394 lower biomass of benthic microalgae and SPOM and/or higher carbon:chlorophyll *a* ratios of SOM, and
395 higher biomass of SOM and detritus. In spring axis 2 discriminates well the mudflat and seagrass bed in
396 the Marennes-Oléron Bay compared to the Sylt-Rømø Bight, which could be due to higher biomass of
397 bacteria (mudflat SR) and/or benthic microalgae (seagrass SR). In terms of temporal variations, axis 1
398 highlights low variation in environmental variables between spring and autumn except for seagrass MO,
399 which could be due to a significant increase in biomass of detritus from spring to autumn in this habitat.
400 Axis 2 highlights a stronger temporal variation (Fig. 5A), especially in seagrass SR, seagrass MO and
401 mudflat SR. For seagrass SR this could be due to a decrease in bacteria, benthic microalgae, SPOM and
402 SOM biomass from spring to autumn, as well as an increase in detrital matter, while changes in seagrass
403 MO may be related to opposite patterns. For mudflat SR variations could be explained by the decrease in
404 biomass of benthic microalgae and bacteria and/or the increase in detritus from spring to autumn.

405 The redundancy analyses (RDA) represented 51.8% of the total variation and 81.1% of the
406 constrained variation (Fig. 5B). Fresh seagrass material was excluded from the RDA due to collinearity
407 after stepwise forward selection of constraints ($vif.cca > 10$). Axis 1 explains 33.0% of the total variation
408 and 51.8% of the constrained variation. Axis 2 explains 18.8% of the total variation and 29.4% of the
409 constrained variation. Both axes significantly explain the model, which highlights relationships between
410 differences of communities and environmental parameters, particularly biomass of benthic microalgae,
411 SPOM, detritus, SOM, carbon:chlorophyll *a* ratios and sediment grain size. Patterns highlighted by axis 1
412 about environmental parameters were similar as those highlighted in the PCA: there was a positive
413 relationship between benthic microalgae and SPOM biomasses, and sediment grain size. At the opposite,
414 when benthic microalgae, SPOM and detritus biomasses were low, the carbon:chlorophyll *a* ratio was
415 higher, as well as biomasses of SOM, bacteria and detritus. Differences of meiofauna trophic structure
416 within habitats are mainly explained by sediment grain-size, carbon:chlorophyll *a* ratio of SOM, and
417 biomasses of SOM, SPOM, detritus, benthic microalgae, and bacteria (Fig. 5). Selective deposit feeders
418 and non-selective deposit feeders occurred mainly within habitats where biomasses of SOM, detritus and
419 bacteria were high (i.e. sub-surface layers of mudflat SR in both seasons, sub-surface layers of seagrass

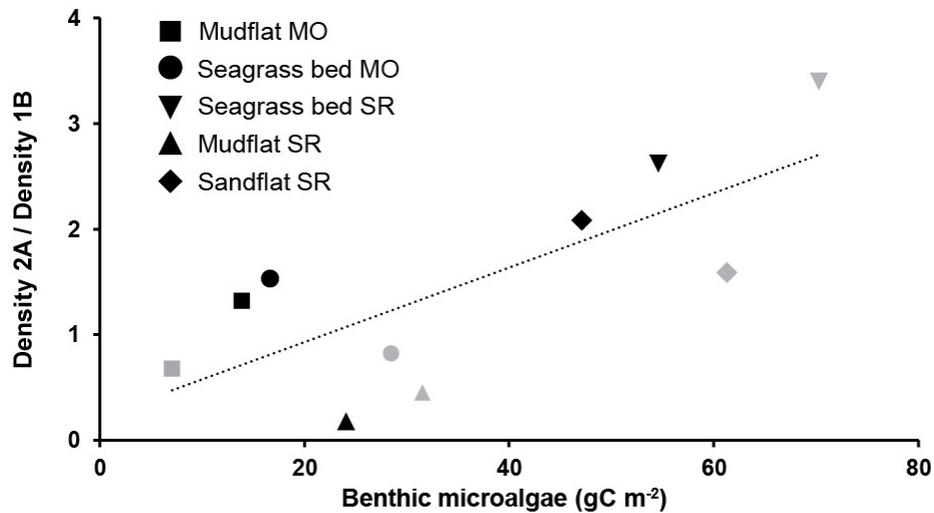
420 MO in both seasons, and sub-surface layers of mudflat MO in autumn). Epigrowth feeders dominated in
 421 habitats where benthic microalgae were an important driving factor (i.e. surface layers of mudflat MO in
 422 both seasons, sub-surface layers of mudflat MO in spring, surface and sub-surface layers of seagrass SR
 423 in both seasons, and sub-surface layers of sandflat SR in both seasons). Omnivore/predatory nematodes,
 424 benthic copepods and other meiofauna taxa occurred in habitats with high biomass of benthic microalgae
 425 and SPOM, as well as large sediment grain-size (i.e. surface and sub-surface layers of sandflat SR in both
 426 seasons and surface layers of seagrass MO in both seasons, and surface layers of mudflat SR in both
 427 seasons).



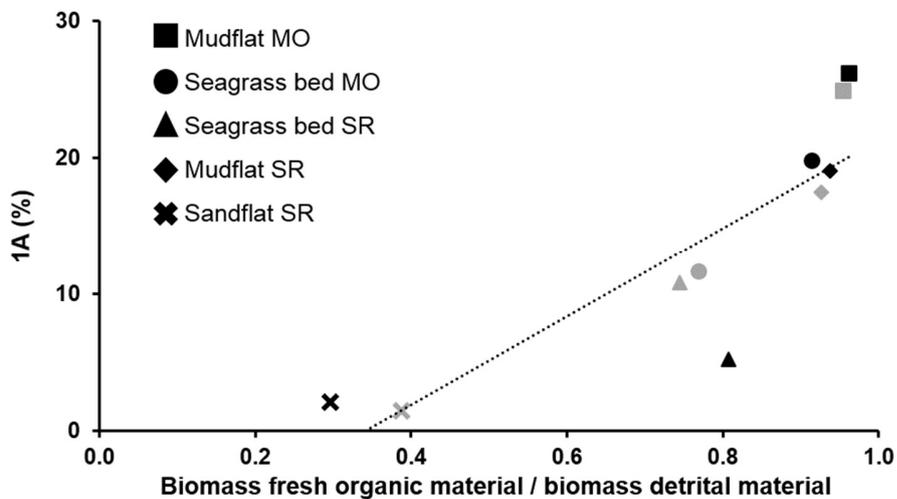
428
 429 **Figure 5. (A)** Principal component analyses for the environmental factors (arrows) plotted for the
 430 mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in
 431 spring (closed symbols) and autumn (open symbols). **(B)** Redundancy relationship analyses of
 432 environmental factors (arrows) selected with stepwise forward procedure plotted against the different
 433 groups of meiofauna (benthic copepods, trophic groups of nematodes and other meiofauna taxa) and the
 434 surface (grey symbols) and sub-surface layers (black symbols) of the mudflats, seagrass beds and sandflat
 435 in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in spring (closed symbols) and autumn
 436 (open symbols). Abbreviations: OTHER = other meiofauna (i.e. polychaetes, foraminifers, and
 437 ostracods); SPOM = suspended particulate organic matter; SOM = sediment organic matter; 1A =
 438 nematodes, selective deposit feeders; 1B = nematodes, non-selective deposit feeders; 2A = nematodes,
 439 epigrowth feeders; 2B = nematodes, omnivores/predators.

440 A regression using nematode feeding type data from all habitats highlighted that the ratios between
 441 densities of epigrowth feeders and densities of non-selective deposit feeders increased when benthic
 442 microalgae biomass increased ($F[1, 8] = 10.4, p = 0.01, r^2 = 0.61$, Fig. 6). The relative abundance of
 443 selective deposit feeders was positively correlated to the ratio between biomass of fresh organic material

444 (i.e. benthic microalgae and seagrass leaves and roots) and biomass of detrital material (i.e. SOM and
 445 detritus) ($F[1, 8] = 23.1, p < 0.01, r^2 = 0.74$, Fig. 7).



446
 447 **Figure 6** Relationship between the biomass of benthic microalgae and the ratio between densities of epigrowth
 448 feeders (2A) and densities of non-selective deposit feeders (1B) in the mudflats, seagrass beds and sandflat in the
 449 Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in spring (grey symbols) and autumn (black symbols).
 450 ($n = 3$)



451
 452 **Figure 7.** Relationship between the ratio of fresh organic material to detrital material and the relative abundance of
 453 selective deposit feeders (1A) in the mudflats, seagrass beds and sandflats in the Marennes-Oléron Bay (MO) and
 454 the Sylt-Rømø Bight (SR) in spring (grey symbols) and autumn (black symbols). ($n = 3$)

455 **Discussion**

456 **Habitat description**

457 The different habitats compared in this study are characterized by a broad range of abiotic and biotic
458 factors. This provides a good framework to determine how changes in these parameters, particularly
459 potential food resources, may influence meiofauna community structure. Biomass of benthic microalgae
460 was much higher in habitats with a larger sediment grain size (sandflat SR and seagrass SR) as already
461 observed in the Marennes-Oléron Bay (Guarini et al. 1998), and benthic microalgae therefore represented
462 a much higher proportion of the SOM in these habitats. This pattern is quite unusual, as habitats with large
463 sediment grain size generally support less microphytobenthos biomass than habitats with small sediment
464 grain size (Cammen 1991; de Jong and de Jonge 1995). Estimations of benthic microalgae biomass were
465 based on chlorophyll *a* measurements and therefore included trapped fresh phytoplankton. Trapped
466 phytoplankton represents a lower proportion of fresh microalgae material than benthic microphytobenthos,
467 although some variations can occur depending on seasons and locations (Asmus 1983; Lebreton et al. 2012).
468 Microphytobenthos community structure and its production may change as well depending on habitats:
469 muddy sediments are usually dominated by large epipellic diatoms (Thornton et al. 2002; Azovsky et al.
470 2004) whereas small epipsammic diatoms are the main taxa in sandy habitats (Asmus and Bauerfeind 1994;
471 Azovsky et al. 2004). Benthic microalgae production can be very high in muddy sediments (i.e. 372 gC m⁻²
472 yr⁻¹ in mudflat MO) (Pinckney and Zingmark 1993; Leguerrier et al. 2003) and, under favorable
473 conditions, epipellic diatoms can double their standing stock on a daily basis (Underwood and Paterson
474 1993). All these changes of biomass, community structure and production rates likely affect the use of this
475 food resource by meiofauna.

476 Biomass of SOM was much lower in sandflat SR than in seagrass beds and mudflats. This is likely
477 related to the high benthic microalgae production in bare mudflats (MacIntyre et al. 1996) and to the smaller
478 sediment grain size in mudflats and seagrass beds (Bergamaschi et al. 1997). A decrease in sediment grain
479 size generally leads to an increase in SOM (Bergamaschi et al. 1997) as fine particles enhance adsorption
480 of organic compounds (Mayer 1994). Decrease of sediment grain size is also associated to lower
481 hydrodynamics which increases sedimentation of organic matter particles (Frontalini et al. 2014) and of
482 finer sediment. The presence of seagrass beds, reducing hydrodynamics and enhancing sedimentation as
483 well (Leduc et al. 2009), also likely increased the load of SOM. As a result, even if SPOM was relatively
484 similar between habitats, the presence of meadows may influence the biomass and the nature of the organic
485 matter available to meiofauna between unvegetated and vegetated habitats (Machás and Santos 1999). The
486 quality of the organic matter available to consumers was also correlated with sediment grain size, with
487 SOM dominated by fresh organic matter in the sandflat and being of much lower quality in habitats made
488 of fine sediments (seagrass bed and mudflats), where loads of detrital matter were higher.

489 Loads of detritus were high in seagrass beds, the largest ones being measured in seagrass MO, probably
490 due to the much higher biomass of seagrass roots in this habitat compared to seagrass SR. The higher load
491 of detrital matter in mudflat SR compared to mudflat MO is much likely related to the proximity between
492 the mudflat and the seagrass bed in the Sylt-Rømø Bight, highlighting that seagrass material can be exported
493 to bare systems. The presence of seagrass in intertidal systems may also indirectly affect the composition
494 of the detrital organic matter available to meiofauna and meiofauna distribution in the sediment (Marbà et
495 al. 2006). The complex root structure of seagrass beds indeed plays a role for the amount of fine particles
496 and detritus associated with the shallow oxic zone in vegetated sediments (Wetzel et al. 2001), as well as
497 in the release of oxygen and dissolved organic matter by the roots (Pedersen et al. 1998). Nevertheless,
498 seagrass material is generally poorly used by most of the consumers as fresh or as detrital material
499 (Danovaro 1996; Vizzini et al. 2002). The presence of seagrass and detritus as well as smaller sediment
500 grain size also affected the abundance of bacteria within the studied habitats. Much lower biomass of
501 bacteria was observed in habitats with lower quantities of detrital matter and SOM and in habitats with
502 coarser sediment (i.e. sandflat), likely due to the reduced surface for bacteria colonization (Dale 1974;
503 Mayer 1994).

504 **Meiofauna community structure: spatial and temporal variations**

505 Meiofauna density and biomass varied highly within habitats and ecosystems, with lowest and
506 highest values observed in mudflat SR (density: $0.17 \cdot 10^6$ ind. m^{-2} , biomass: 0.057 gC m^{-2}) and mudflat
507 MO (density: $3.36 \cdot 10^6$ ind. m^{-2} , biomass: 1.598 gC m^{-2}), respectively. Meiofauna in all habitats were
508 dominated by nematodes, followed by benthic copepods, as typically observed in intertidal habitats
509 (Armonies and Hellwig-Armonies 1987; Rzeznik-Orignac et al. 2003; Leduc and Probert 2011). Data
510 comparisons (Table 5) highlight that density and biomass of nematodes and benthic copepods measured
511 in this study are in the range of those previously measured but, more generally, that these values can be
512 highly variable between different soft-bottom habitats as well as within similar habitats (Heip et al. 1985;
513 Castel et al. 1989; Kotwicki et al. 2005b).

514 In terms of community structure, proportions of benthic copepods increased from habitats with a
515 lower complexity (mudflats: 6.2%) to habitats with a higher complexity caused by a higher seagrass
516 biomass (seagrass beds: 15.5%) or by larger sediment grain size (sandflat: 38.4%). Larger proportions of
517 copepods in the sandflat could be explained by a higher feeding efficiency in sandier sediment, probably
518 due to a better accessibility to benthic microalgae and a better ability of these grazers to move in sand (De
519 Troch et al. 2006). Higher proportions of benthic copepods in seagrass bed MO may be related to a more
520 developed seagrass bed and therefore a more complex habitat, providing a larger diversity of ecological
521 niches (Ndaro and Olafsson 1999; De Troch et al. 2001). The presence and development stage of seagrass

522 beds also affected nematode diversity as species richness was higher in the most dense seagrass bed
 523 (Marennes-Oléron) between the two studied ones. Hill's diversity was also higher in seagrass MO than in
 524 all other habitats, which could be partially linked to habitat complexity as well (Austen et al. 1998;
 525 Steyaert et al. 2003; Giere 2009). Proportions of omnivore/predatory nematodes increased as well when
 526 complexity increased due to larger sediment grain size as previously observed in sandflats of several other
 527 coastal ecosystems (Warwick 1971; Steyaert et al. 2003). This could be explained by the increase of
 528 foraging efficiency of predators with an increase in sediment grain size (Gallucci et al. 2005).

529 If some patterns could be observed between meiofauna community structure and habitat type,
 530 direct relationships between biomass of food sources and density and/or biomass of nematodes and
 531 benthic copepods could not be observed in this study. This is very likely related to the diversity of feeding
 532 types observed in nematodes (Moens et al. 2005b; Vafeiadou et al. 2014) and, to a lower extent, in
 533 benthic copepods (Cnudde et al. 2015), confirming the importance of approaches carried out at the scale
 534 of the feeding type, as this was done for nematodes in this study.

535 Within these different habitats nematode density, biomass and diversity were similar between
 536 spring and autumn, except for higher nematode density in seagrass SR and higher nematode biomass in
 537 mudflat MO in spring. No temporal variation was observed for meiofauna community structure. The lack
 538 of a clear temporal pattern between spring and autumn (Escaravage et al. 1989; Danovaro and Gambi
 539 2002; Rzeznik-Orignac et al. 2003) could be partly explained by low temporal variation in parameters
 540 strongly defining meiofauna community structure (i.e. food sources and sediment grain size; Moens et al.
 541 2013).

542 **Table 5.** Density (ind. m⁻² * 10⁶) and biomass (in gC m⁻² and/or g dry weight m⁻²) of nematodes and
 543 benthic copepods in mudflats, seagrass beds (*Zostera* spp.) and sandflats from this study and from the
 544 available literature about marine soft-bottom intertidal systems. Average conversion factors used to
 545 estimate biomass in gC m⁻² from densities are: nematodes: 2.28*10⁶, benthic copepods: 3.49*10⁶, and
 546 from biomass (in g dry-weight m⁻²) are: nematodes: 3.26, benthic copepods: 3.40. Converted values are in
 547 italic.

Habitat type	Location	Density		Biomass (g dry weight m ⁻²)		Biomass (gC m ⁻²)		Reference
		Nematodes	Copepods	Nematodes	Copepods	Nematodes	Copepods	
Mudflat	Papanui Inlet, New Zealand	2.1–3.2	0.5–1.1	0.163	0.125	<i>0.05</i>	<i>0.04</i>	Leduc and Probert 2011
	Danish Wadden Sea, Denmark	0.22		0.03–0.4		<i>0.01–0.12</i>		Smidt 1951
	Sylt-Rømø Bight, Germany	0.28	0.03	0.233	0.015	0.102	0.006	This study
	Cornwall, U.K.	1.1				<i>0.48</i>		Ellison 1984
	Marennes-Oléron Bay, France	2.1				<i>0.92</i>		Rzeznik-Orignac et al. 2003
	Sylt-Rømø Bight, Germany	2.4	0.07			<i>1.05</i>	<i>0.02</i>	Armonies and Hellwig-Armonies 1987
	Lynher estuary, U.K.	0.8–22.9		1.4–3.4		<i>0.43–1.49</i>		Warwick and Price 1979

	Marenes-Oléron Bay, France					0.2–1.5	< 0.09	Pascal 2008
	Marenes-Oléron Bay, France	3.03	0.13	6.070	0.346	1.257	0.095	This study
	South Carolina, U.S.A.	2.3–4.4				1.01–1.93		Sikora and Sikora 1982
	European estuaries	0.13–14.5				0.06–6.35		Soetaert et al. 1995
	Papanui Inlet, New Zealand	4.9–5.2	< 0.04	0.480	< 0.009	0.15	< 0.003	Leduc and Probert 2011
	Marenes-Oléron Bay, France	0.65	0.21	1.303	0.459	0.294	0.078	This study
	Sylt-Rømø Bight, Germany	0.81	0.04	0.819	0.015	0.351	0.006	This study
Seagrass bed	Sylt-Rømø Bight, Germany	2.0				0.88		Armonies and Hellwig-Armonies 1987
	Arcachon Bay, France	5.5–8.0		2.4–5.3		0.74–2.32		Castel et al. 1989; Escaravage et al. 1989
	Mira estuary, Portugal	1.8–3.3				0.79–1.46		Materatski et al. 2018
	Marenes-Oléron Bay, France					2.75	0.36	Lebreton 2009
	North Sea intertidal sandflats	0.15	0.11			0.07	0.03	Kotwicki et al. 2005a
	Sylt-Rømø Bight, Germany	0.22	0.14	0.303	0.130	0.124	0.050	This study
	Arcachon Bay, France	0.7–1.2		0.8–1.3		0.25–0.57		Castel et al. 1989; Escaravage et al. 1989
Sandflat	Oosterschelde, Netherlands	5.0	0.13	2.0	0.2	0.61	0.06	Smol et al. 1994
	Sylt-Rømø Bight, Germany	2.3	3.5			1.01	1.00	Armonies and Hellwig-Armonies 1987
	European intertidal flats	0.24–4.1	< 0.35			0.11–1.80	< 0.10	Hicks and Coull 1983; Kotwicki et al. 2005b

548

549 **Benthic microalgae and sediment organic matter are important drivers of nematode community**
550 **structure**

551 Changes in benthic microalgae biomass influenced the community structure of nematodes: relative
552 abundance of epigrowth feeders, relying on benthic microalgae, were reduced when biomass of this food
553 source decreased. Such a relationship between biomass of benthic microalgae and density of epigrowth
554 feeders had already been observed in a subtidal seagrass meadow (Danovaro and Gambi 2002) and during
555 grazing experiments (Rzeznik-Orignac and Fichet 2012). A relationship was also observed between
556 biomass of benthic microalgae and relative abundances of benthic copepods and omnivores/predators.
557 However, this relationship may be partly mediated by sediment grain size as benthic microalgae biomass
558 (this study) and relative abundance of benthic copepods increase when sediment get coarser (Hicks and
559 Coull 1983). Nevertheless, the much higher biomass of benthic microalgae in the sandflat compared to
560 SOM suggests that consumers rely—at least partly—directly (i.e. copepods) or indirectly (i.e.
561 omnivores/predators) on benthic microalgae in this habitat. Such a dependence to benthic microalgae as a
562 food source has been demonstrated for benthic copepods (Leduc et al. 2009).

563 At a more global scale (i.e. whole meiofauna, all habitats combined), no general pattern could be
564 observed between benthic microalgae biomass and those of nematodes and benthic copepods. Some other
565 parameters should probably be taken into account to better consider relationships between this food
566 resource and consumers. Benthic microalgae can indeed reach very high production rates and is a food
567 source of high quality (Cebrián 1999). Intense grazing by meiofauna may affect benthic microalgae as well.

568 The high primary production of benthic microalgae in mudflat MO ($372 \text{ gC m}^{-2} \text{ yr}^{-1}$; Leguerrier et al. 2003)
569 and high grazing pressure on this food source by the large biomass of nematodes (Blanchard 1991) could
570 explain the lack of relationship between benthic microalgae and meiofauna biomass within these habitats.
571 Quality is of high importance as well: Moens et al. (1999b) suggested that meiofauna migrates actively
572 towards 'optimal' food sources. In addition to epigrowth feeders, several studies demonstrated that deposit
573 feeders rely on microalgae (Moens and Vincx 1997; Rzeznik-Orignac et al. 2003; Vafeiadou et al. 2014)
574 likely due to the better quality of microalgae. A relationship between density of nematodes belonging to
575 these feeding groups and microalgae has been observed (Moens et al. 1999a). In particular, grazing
576 experiments using ^{14}C labelled diatoms indicated the dependence of a non-selective deposit feeding
577 nematode (*Daptonema*), an epigrowth feeding nematode (*Metachromadora*) and benthic copepods on
578 microalgae (Rzeznik-Orignac and Fichet 2012). Buccal cavities of epigrowth feeders are appropriate for
579 consumption of benthic microalgae, due to the presence of a dorsal tooth which is used to pierce diatoms
580 (Wieser 1953; Moens and Vincx 1997). Vafeiadou et al. (2014), using stable isotopes, confirmed that non-
581 selective deposit feeding nematodes, epigrowth feeding nematodes and benthic copepods can largely rely
582 on benthic microalgae in sparsely covered seagrass beds. The non-selective deposit feeders can therefore
583 be considered as opportunistic feeders, which may change feeding strategies depending on the availability
584 of food sources (Moens and Vincx 1997; Rzeznik-Orignac et al. 2008). As a result, benthic microalgae are
585 often considered as the principal food source for nematodes and benthic copepods (Moens et al. 2005a;
586 Rzeznik-Orignac et al. 2008; Maria et al. 2012).

587 Benthic microalgae followed an opposite pattern than detrital material (SOM and detritus), with
588 decreasing biomass of benthic microalgae when detrital material increased. SOM biomass was stable
589 between spring and autumn, as well as between surface and sub-surface layers, but large variations were
590 observed between the different habitats (i.e. much lower biomass in sandflat SR). Relative abundance of
591 non-selective deposit feeders, closely related to detrital matter based on the RDA, decreased when biomass
592 of SOM was lowered. Higher SOM quality in the surface sediment layers could lead to higher biomass,
593 density and diversity of nematodes in the surface layer compared to the sub-surface layer. As a result, the
594 important role of SOM is very likely related to its very high amount, as well as variations in quality between
595 the studied systems. A relationship between SOM and density of non-selective deposit feeders was also
596 recognized in a subtidal seagrass meadow (Danovaro and Gambi 2002), while a grazing experiment
597 indicated that non-selective and selective deposit feeding nematode species assimilated predominantly
598 SOM and bacteria (Tietjen and Lee 1977).

599 As a result, SOM and benthic microalgae appear to be important biotic factors driving the nematode
600 community structure and, *a fortiori*, the composition of meiofauna assemblages as nematodes represent a

601 large proportion of the meiofauna in coastal ecosystems (Armonies and Hellwig-Armonies 1987; Rzeznik-
602 Orignac et al. 2003; Leduc and Probert 2011).

603 **Role of bacteria as a food source?**

604 Selective deposit feeders had much higher relative abundances in habitats with larger loads of detritus
605 and SOM compared to those dominated by fresh material. In addition, multivariate analyses indicated that
606 biomass of bacteria were higher when loads of SOM increased. These results highlight a probable
607 relationship between bacteria biomass and relative abundance of selective deposit feeders, endorsing that
608 consumers from this trophic group rely on bacteria (Moens and Vincx 1997), which develop on detrital
609 particles (Day et al. 1989; Danovaro 1996), or dissolved organic matter (Moens and Vincx 1997). The use
610 of bacteria as food resources has been confirmed by stable isotope studies demonstrating that selective
611 deposit feeders can rely on sulfide-oxidizing bacteria (Vafeiadou et al. 2014), such specific diets being
612 related to their small buccal cavity (Wieser 1953; Moens and Vincx 1997). The lack of direct relationship
613 between abundances of selective deposit feeders and biomass of bacteria, as in Semprucci et al. (2010),
614 might be due to the influence of additional abiotic parameters (i.e. oxic conditions (Jensen 1983) and
615 sediment grain size (Steyaert et al. 2003)), the reliance of bacteria on a large diversity of substrates
616 (Boschker et al. 2000), and high bacterial production which is only partially grazed (< 28%, Pascal et al.
617 2009).

618 Multivariate analyses demonstrated as well a relationship between relative abundances of non-
619 selective deposit feeders and biomass of detritus and, to a lower extent, those of bacteria and SOM.
620 Nevertheless, no direct relationship was observed between relative abundances of non-selective deposit
621 feeders and bacteria, SOM or detritus biomass, which is likely related to the more opportunistic feeding
622 behavior of these nematodes (Moens and Vincx 1997; Rzeznik-Orignac et al. 2008). The shape of the buccal
623 cavity of non-selective deposit feeders allows them to rely on a much larger diversity of food sources:
624 benthic microalgae, SOM, bacteria and seagrass detritus, as demonstrated by stable isotope studies
625 (Rzeznik-Orignac et al. 2008; Maria et al. 2012; Vafeiadou et al. 2014) and observations of feeding behavior
626 (Moens and Vincx 1997). Biomass of fresh seagrass matter, which varied highly between habitats in this
627 study, could also not be linked to variations in non-selective deposit feeders. However, the lack of relation
628 here is expected since this resource is poorly used by these nematodes, and, to a larger extent, to meiofauna
629 in general, due to its low nutritional value and high lignocellulose content (Vizzini et al. 2002). This was
630 confirmed by Materatski et al. (2015) who observed no changes in nematode density before and after a
631 seagrass collapse.

632 **Effect of sediment depth on meiofauna communities: influence of oxic conditions**

633 Nematode and benthic copepod densities and biomasses decreased from surface to sub-surface layers
634 in all habitats, which is a common pattern in seagrass beds and unvegetated habitats (Castel et al. 1989;
635 Lebreton 2009; Leduc and Probert 2011). Benthic microalgae, which have the highest biomass in the
636 surface layer, might influence the vertical distribution and migration of nematodes and benthic copepods
637 (Moens et al. 2013), particularly nematode epigrowth feeders which specifically rely on benthic microalgae
638 and which were very abundant in all habitats. Differences in abiotic parameters, such as oxygen depletion
639 towards deeper layers, could affect as well the vertical distribution of meiofauna (Steyaert et al. 2003;
640 Vanaverbeke et al. 2004), as anoxic conditions are much less favorable to nematodes and benthic copepods.
641 Besides influencing biomass and densities, anoxic conditions affect diversity and community structure as
642 well. Diversity of nematodes clearly decreased with depth in all the studied habitats, which was observed
643 in other studies (Steyaert et al. 2003; Leduc and Probert 2011). *Terschellingia* spp. and *Sabatieria* spp. had
644 a higher relative abundance in sub-surface layers than in surface layers, related to their higher tolerance
645 regarding hypoxic conditions (Steyaert et al. 2007). *Terschellingia* spp. and *Sabatieria* spp. are also known
646 to feed on sulfide-oxidizing bacteria that occur in these hypoxic zones (Semprucci and Balsamo 2012;
647 Vafeiadou et al. 2014).

648 **Conclusion**

649 Benthic microalgae and SOM are two important drivers in the functioning of soft-bottom coastal food
650 webs as changes in these food resources affect the two most dominant nematode trophic groups (i.e. non-
651 selective deposit feeders, considered as more opportunistic, and epigrowth feeders, more specifically related
652 to benthic microalgae). This is likely related to the high biomass of these food sources, as well as the quality
653 and high production rates of benthic microalgae (MacIntyre et al. 1996; Cebrián 1999). Therefore, this
654 study highlights the existence of some relationships between composition of food sources and the trophic
655 structure of the meiofauna community, when studied at the scale of trophic groups. On the contrary, no
656 clear relationship was observed between bacterial biomass and density of selective deposit feeders
657 (bacterivores; 1A), despite a relationship between SOM biomass and relative abundances of selective
658 deposit feeders. This lack of relationship may be related to the high production rates of bacteria and the
659 influence of abiotic factors, especially oxic conditions. Approaches such as trophic markers (e.g. stable
660 isotope and/or fatty acid analyses) would be very complementary to the determination of feeding types
661 based on the morphology of the buccal cavity. Such tools would provide a more comprehensive picture of
662 food sources really assimilated by meiofauna and highlight how the use of food sources by meiofauna may
663 change depending on availability. Combining trophic marker data with biomass and production data in food
664 web models would then provide a much more complete overview of the functioning of coastal food webs.

665 **Compliance with ethical standards**

666 **Conflict of interest**

667 All authors declare that they have no conflict of interest.

668 **Ethical statement**

669 All applicable international, national and/or institutional guidelines for the sampling, care and use of
670 organisms were followed.

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