

# Quantitative food web modeling unravels the importance of the microphytobenthos-meiofauna pathway for a high trophic transfer by meiofauna in soft-bottom intertidal food webs

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- 33 ABSTRACT
- 34

35 Meiofauna are known to have an important role on many ecological processes, although, their 36 role in food web dynamics is often poorly understood, partially as they have been an overlooked and 37 under sampled organism group. Here, we used quantitative food web modeling to evaluate the trophic 38 relationship between meiofauna and their food sources and how meiofauna can mediate the carbon flow 39 to higher trophic levels in five contrasting soft-bottom intertidal habitats (including seagrass beds, 40 mudflats and sandflats). Carbon flow networks were constructed using the linear inverse model-Markov chain Monte Carlo technique, with increased resolution of the meiofauna compartments (i.e. biomass 41 42 and feeding ecology of the different trophic groups of meiofauna) compared to most previous modeling studies. These models highlighted that the flows between the highly productive microphytobenthos and 43 44 the meiofauna compartments play an important role in transferring carbon to the higher trophic levels, typically more efficiently so than macrofauna. The pathway from microphytobenthos to meiofauna 45 represented the largest flow in all habitats and resulted in high production of meiofauna independent of 46 47 habitat. All trophic groups of meiofauna, except for selective deposit feeders, had a very high dependency on microphytobenthos. Selective deposit feeders relied instead on a wider range of food 48 49 sources, with varying contributions of bacteria, microphytobenthos and sediment organic matter. 50 Ecological network analyses (e.g. cycling, throughput and ascendency) of the modeled systems 51 highlighted the close positive relationship between the food web efficiency and the assimilation of 52 high-quality food sources by primary consumers, e.g. meiofauna and macrofauna. Large proportions of 53 these flows can be attributed to trophic groups of meiofauna. The sensitivity of the network properties 54 to the representation of meiofauna in the models leads to recommending a greater attention in ecological 55 data monitoring and integrating meiofauna into food web models. 56

57 **Keywords:** food web model; linear inverse model; meiofauna; microphytobenthos; stable isotope

58 mixing models; intertidal habitats

#### 59 1. Introduction

60 Meiofauna have been poorly considered in the last decades when assessing functioning of coastal and marine ecosystems (Moens et al., 2011; Schratzberger and Ingels, 2018), e.g. roles in trophic 61 62 processes, energy flows (Leguerrier et al., 2003; Moens et al., 2013). This lack of interest is likely related to the belief that meiofauna were a "trophic dead end" (Heip and Smol, 1975; McIntyre and 63 64 Murison, 1973), and to the methodological issues when studying them, due to their small size (Carman 65 and Fry, 2002; Moens et al., 2005). Methodological improvements (Leduc et al., 2009; Vafeiadou et 66 al., 2014) led to a better perception of meiofauna in the functioning of ecosystems (Coull, 1990; Leguerrier et al., 2003), weakening the "trophic dead end" hypothesis. For example, in intertidal and 67 68 deep-sea ecosystems, the metabolic importance of meiofauna can sometimes overtake that of 69 macrofauna—a compartment which has been highly studied unlike meiofauna—(Giere, 2009; 70 Schwinghamer et al., 1986) with meiofauna's metabolic rate being reported 21 times higher than that 71 of macrofauna in a tidal flat (Kuipers et al., 1981). Nowadays meiofauna are known to take part in many 72 ecological functions, e.g., sediment stabilization, biochemical cycling and food web dynamics 73 (Schratzberger and Ingels, 2018). A better comprehension of ecological functions of meiofauna in 74 coastal food webs requires considering meiofauna at the ecosystem scale, following a holistic approach. 75 Indeed, because meiofauna mediates flows of organic matter between primary producers and higher 76 trophic level consumers (Leguerrier et al., 2003; Pascal et al., 2019), assessments about the role of 77 meiofauna should consider two aspects: (1) the interaction between meiofauna and their food sources 78 and (2) the fate of meiofauna.

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80 Interactions between meiofauna and their resources are complex due to the large variety of potential food sources (e.g. microalgae, detrital matter, bacteria; Lebreton et al., 2012; Moens et al., 81 2005; Vafeiadou et al., 2014) and quantifications of carbon fluxes from lower trophic levels to 82 83 meiofauna are scarce (Danovaro et al., 2002; van Oevelen et al., 2006). In bare sediment systems, 84 meiofauna have been reported to feed mainly on microphytobenthos (Moens et al., 2014; Rzeznik-85 Orignac et al., 2008), whereas their range of food sources is much larger in vegetated sediments (Lebreton et al., 2012; Leduc et al., 2009; Vafeiadou et al., 2014). Nematodes, generally the most 86 abundant taxon of meiofauna, have a very diverse feeding behavior, i.e., herbivory, bacterivory, or 87 88 omnivory/carnivory (Wieser, 1953), and can be classified into various trophic groups. Feeding behavior 89 and abundances of nematodes from these trophic groups might change depending on availability, 90 quantity and quality of food sources (Giere, 2009; Moens et al., 2013). Non-selective deposit feeders 91 for example feed on various food sources such as microphytobenthos, bacteria and detritus, and their 92 diet changes depending on the availability of these food sources (Moens and Vincx, 1997a; 93 Rzeznik-Orignac et al., 2008). It has also been demonstrated that meiofauna, especially benthic 94 copepods, may control microphytobenthos biomass (Blanchard, 1991; Montagna et al., 1995) as well

95 as transfer carbon from bacterial communities towards higher trophic levels (Pascal et al., 2008;
96 Vafeiadou et al., 2014).

97

Many unknowns remain about the fate of meiofauna in benthic food webs. For a long time there 98 99 was a controversy about the fate of meiofauna in benthic food webs (Heip et al., 1992), whether meiofauna was a dead end in the food web (Heip and Smol, 1975; McIntyre and Murison, 1973), or an 100 101 important link between primary producers and higher trophic levels (Coull, 1990; Schückel and Kröncke, 2013). Meiofauna production is high (from 4 to 29 gC m<sup>-2</sup> year<sup>-1</sup>; Chardy and Dauvin, 1992; 102 103 Danovaro et al., 2002) due to their elevated turnover rate (Kuipers et al., 1981), despite their general 104 relatively low biomass. Their nutritional quality, i.e. calories (Sikora et al., 1977), low carbon/nitrogen ratios (Couch, 1989), high levels of amino acids (Vilela, 1992; Watanabe et al., 1978) and essential 105 fatty acids (Watanabe et al., 1983), are sufficient to fulfill a predator's needs (Coull, 1999), explaining 106 107 their preference as prey for higher trophic levels (Danovaro et al., 2007). However, knowledge about 108 carbon fluxes from meiofauna to higher trophic levels and determination of their transfer efficiency 109 remain scarce (Danovaro et al., 2002; Schratzberger and Ingels, 2018). Danovaro et al. (2007) estimated 110 that more than 75% of the total meiofauna production is channeled to higher trophic levels in 111 soft-bottom habitats. However, meiofauna consists of a diversity of organisms which have different 112 feeding strategies (i.e. trophic groups; Wieser, 1953). The fate of these trophic groups in food webs 113 most likely varies due to their relative biomasses among meiofauna, which can differ a lot between 114 habitats (van der Heijden et al., 2018), and due to high variability and selective feeding on this meiofauna by higher trophic levels (Magnhagen et al., 2007; Schückel et al., 2013). Therefore, there is 115 a need to consider meiofauna trophic groups in food web assessments, and inter-habitat comparison can 116 help at understanding how changes in trophic groups' biomass affect the role of meiofauna in coastal 117 food webs. 118

119

120 Linear inverse modeling is a useful tool to describe the functioning of a food web at the habitat or the ecosystem scale (Baird et al., 2007; Leguerrier et al., 2007). It generates a static, mass-balanced, 121 temporally integrated snapshot of the complete food web and its flows using a combination of field and 122 relevant literature data (Niquil et al., 2011; Vézina and Platt, 1988) and it is a powerful method in 123 124 estimating unmeasured flows within an ecosystem (Degré et al., 2006; Leguerrier et al., 2003; Pacella 125 et al., 2013). Combined with the Markov chain Monte Carlo method, it provides the probability 126 distribution of flows in underdetermined systems and avoids underestimations in both the size and complexity of the modeled food web (Johnson et al., 2009; Kones et al., 2006). Based on the estimated 127 128 flow-networks, several food web characteristics can be defined, such as efficiencies, recycling and dependencies (Niquil et al., 2011), which can in turn be useful in ecosystem management and policy 129 130 making (de la Vega et al., 2018; Schückel et al., 2018). One of these food web characteristics, the 131 efficiency with which carbon energy is transferred and assimilated, can be linked to the quality and

132 quantity of primary food sources (Marcarelli et al., 2011). The lower trophic levels of food webs 133 (e.g. meiofauna and macrofauna) have the strongest response to changes in food quality whereas the 134 highest trophic levels (i.e. omnivores/carnivores) seem more dependent on the food quantity (Campanyà-Llovet et al., 2017), highlighting different responses for various trophic groups. However, 135 136 species are often aggregated in lower trophic levels of the food web due to difficulties in taxonomic identification and in segregating the energetics of smaller individuals (Baird et al., 2009). This has 137 typically been the case for meiofauna as they are described as a single compartment in most recent 138 steady-state mass-balanced food web models, or at best are split into nematodes and benthic copepods 139 140 (Baird et al., 2007; Leguerrier et al., 2007, 2003; Pacella et al., 2013). Model input data (i.e. constraints) for meiofauna trophic groups are indeed scarce (Baird et al., 2009) and often derived from experimental 141 studies on single specimens (Herman and Vranken, 1988; Vranken and Heip, 1986). Therefore, 142 separating meiofauna into major trophic groups is necessary if a better understanding of their 143 144 relationships with specific food sources and the role of these organisms in food webs is wanted. Trophic marker based approaches (e.g. stable isotopes), however, has shown successful to better constrain 145 146 consumption flows of meiofauna trophic groups in food web models (Pacella et al., 2013; van Oevelen 147 et al., 2010).

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149 Using food web models, the general aim of this study was to determine how the roles of 150 meiofauna and the food web efficiency can differ in coastal ecosystems depending on the composition 151 of food sources (i.e. availability, quality and quantity). We focus on (1) the trophic relationship between meiofauna and their food sources, (2) production and transfer efficiency of meiofauna, and how these 152 relate to those of macrofauna, and (3) the relationship between the food web efficiency and the 153 composition of food sources. Finally, we provide recommendations on including meiofauna in future 154 food web modeling studies. In this aim, five contrasting different intertidal habitats in terms of food 155 sources and meiofauna group composition—providing several food web scenarios—were compared: 156 habitats influenced by inputs of continental organic matter vs. habitats mostly influenced by marine 157 inputs, habitats characterized by high loads of detrital matter vs. habitats with low loads of detrital 158 matter, habitats with different communities of benthic microalgae. The food web models of these 159 intertidal habitats of the Marennes-Oléron Bay and of the Sylt-Rømø Bight were compared using 160 161 quantitative flow values and food web properties.

162

#### 163 2. Material and methods

Study sites and carbon flow networks

164 *2.1*.

Five benthic-pelagic coupled carbon flow networks were built, characterized by different food source compositions and different meiofauna communities. Model outputs from these five networks 167 were compared to determine how the role of meiofauna differs depending on the composition of food 168 sources. Both autochthonous and allochthonous food sources were considered. To consider autochthonous food sources, three types of habitats were studied: one characterized by high loads of 169 detrital matter (i.e. seagrass bed), one characterized by a lower load of detrital matter and by a 170 171 community of microphytobenthos dominated by epipelic diatoms (i.e. mudflat), and one characterized 172 by a low load of detrital matter and by a community of microphytobenthos dominated by epipsammic diatoms (i.e. sandflat). To consider the role of allochthonous food sources, we studied the functioning 173 of these habitats in two different ecosystems: one influenced by continental inputs of organic matter, 174 175 i.e. the Marennes-Oléron Bay in France, into which the Charente river flows (Gouleau et al., 2000), and one with little direct continental inputs, hence influenced mainly by marine inputs, i.e. the Sylt-Rømø 176 Bight in Germany (Asmus and Asmus, 2005, 1985). As sandflats are not a typical habitat in the 177 Marennes-Oléron Bay, this habitat could not be considered in this ecosystem. As a result, seagrass beds 178 179 and mudflats were studied in both the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR), while 180 the sandflat could only be studied in the Sylt-Rømø Bight, leading to five steady-state mass-balanced flow networks (i.e. one per habitat: mudflat MO, mudflat SR, seagrass MO, seagrass SR, and sandflat 181 182 SR) (Fig. 1). These different habitats are characterized by different plant and animal communities that 183 were previously described: seagrass MO (Lebreton, 2009; Lebreton et al., 2009), mudflat MO (Haubois 184 et al., 2005; Rzeznik-Orignac et al., 2003), Sylt-Rømø Bight habitats (Asmus and Asmus, 2000, 2005, 185 1998, 1993; Asmus and Bauerfeind, 1994; Gätje and Reise, 1998), and additional information can be 186 found in van der Heijden et al. (2018).



#### 187

188 Figure 1. Study sites in the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-

189 Rømø Bight (SR) along the European Atlantic coast. Pelagic sampling stations, where samples for suspended

190 particulate organic matter were taken, are indicated with roman numbers in Marennes-Oléron Bay (I-II) and 191 Sylt-Rømø Bight (III-V).

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#### 2.2. Linear inverse model construction

Linear inverse ecosystem models with Markov chain Monte Carlo (LIM-MCMC) were built to 194 determine carbon flows in the five habitats on a daily basis (mgC m<sup>-2</sup> d<sup>-1</sup>) using the R software (R Core 195 Team, 2019). The flow estimations originated from annual averages but are expressed as daily averages 196 197 here. Annual averages were chosen in order to smoothen the daily and seasonal fluctuations that occur 198 in these habitats, which can affect the network indices and prevent a clear comparison (Baird et al., 2004b; Baird and Ulanowicz, 1989). Most constraints, except for meiofauna constraints, that were used 199 to construct the flow networks of these habitats originated from established models (Baird et al., 2007; 200 201 Leguerrier et al., 2003; Pacella et al., 2013; Saint-Béat et al., 2014, 2013). New models focused on 202 meiofauna and thus represented the diversity of this group at a higher resolution. Consequently, 203 meiofauna was partitioned into five compartments according to their trophic group: selective deposit 204 feeding nematodes, non-selective deposit feeding nematodes, epigrowth feeding nematodes, 205 omnivorous/predating nematodes and benthic copepods. Recent in situ data on biomass (Table 1; van 206 der Heijden et al., 2018) and on diets (used in stable isotope mixing models; van der Heijden et al., 207 2019) were used to constrain food web models. The prior established models aggregated meiofauna 208 into two compartments, allowing us to compare the effects of this two-compartment partitioning versus 209 the trophic group partitioning presented here. Macrofauna were aggregated based on feeding types (i.e. benthic deposit feeders, benthic grazers, suspension feeders and benthic omnivores/predators) in 210 211 order to have a homogeneous topology of food web models (i.e. number of compartments), required 212 when comparing different systems (Table 1; Baird and Ulanowicz, 1993).

213

214 Table 1. Abbreviations (Abbr.) and biomass of compartments used in the food web models of the mudflats,

- 215 seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). NA = no data
- 216 available; - = compartment absent.

SR
20
108
417.3
71.7
120.0
0890.0
625.0
2.0
58.2
3

Nematodes – epigrowth feeders	NEF	607.5	165.5	23.2	19.4	279.4
Nematodes – omnivores/predators	NOM	82.5	63.2	60.2	19.1	11.0
Benthic copepods	COP	94.8	78.3	50.1	6.0	6.1
Macrofauna – benthic deposit feeders	BDF	3.5	98.8	6797.6	3997.6	12841.2
Macrofauna – benthic grazers	BGR	695.6	4076.6	406.0	8004.0	7174.6
Macrofauna – benthic suspension feeders	SUS	42.7	1704.8	19204.6	6275.6	12048.1
Macrofauna – benthic omnivores/carnivores	BOM	597.4	50.8	729.6	2939.8	1097.9
Sediment organic matter	SOM	NA	27560.0	19000.0	19000.0	19000.0
Pelagic						
Phytoplankton	PHY	254.5	254.5	1040.0	1040.0	1040.0
Pelagic bacteria	PBA	157.2	157.2	9.0	9.0	9.0
Mesozooplankton	ZOO	160.0	160.0	11.2	-	-
Microzooplankton	MZO	110.0	-	-	-	-
Benthic fish	BFI	195.0	195.0	2.9	1.5	14.9
Suspended particulate organic matter	SPOM	NA	1044.2	500.0	500.0	500.0
Dissolved organic matter	DOC	-	1850.3	-	-	62.0

#### 218 2.2.1. Established model constraints

The model of mudflat MO was based on data provided by Leguerrier et al. (2003), Degré et al. (2006), Saint-Béat et al. (2014) (Appendices A.1 and A.2). Original compartments of this previous model were used as a basis for the other food web models and therefore no aggregations were conducted.

223 The seagrass MO model was based on data provided by Pacella et al. (2013) (Appendix A.3). 224 Biomass of bacteria for the whole Marennes-Oléron Bay was obtained from Leguerrier et al. (2003). 225 Macrofauna constraints used in Pacella et al. (2013) were aggregated based on feeding types. Trophic 226 groups were: benthic deposit feeders (Abra spp., Arenicola marina, and Notomastus latericeus), benthic 227 grazers (Peringia ulvae and gastropod grazers), benthic omnivores/predators (Carcinus maenas, Crangon crangon, and Cerebratulus marginatus), and suspension feeders (Cerastoderma edule, 228 229 Limecola balthica, Mytilus galloprovincialis, Scrobicularia plana, and Tapes spp.). Consumption rates 230 of these feeding groups were estimated using aggregated stable isotope values (Pacella et al., 2013). 231 Aggregation was done based on weighted averages using biomass and flows of the different genera. 232

The models of habitats from the Sylt-Rømø Bight (i.e. mudflat SR, seagrass SR and sandflat 233 234 SR) were based on data provided by Baird et al. (2007) and modified by Saint-Béat et al. (2013) (Appendices A.4 to A.6). For these models fewer minimum and maximum values of flow constraints 235 236 (mainly production and consumption constraints) were known compared to models of the Marennes-Oléron Bay. Equalities, provided by Saint-Béat et al. (2013), were therefore converted to 237 238 inequalities by increasing or reducing the equality value with 30%. These ranges correspond with 239 seasonal fluctuations observed for macrofauna by Asmus (1987) and were considered to be the most 240 appropriate estimations based on sensitivity analyses from Guesnet et al. (2015).

241

#### 242 2.2.2. Complementary constraints: outputs of isotope mixing models

243 Meiofauna compartments from previous models were partitioned into benthic copepods and trophic groups of nematodes (i.e. selective deposit feeders, non-selective deposit feeders, epigrowth 244 245 feeders and omnivores/predators) and constraints were calculated for these new compartments based 246 on stable isotope data. Stable isotope mixing models MixSIAR (Stock et al., 2018) were applied to isotope data from van der Heijden et al. (2019) to compute the dietary contribution of food sources to 247 benthic copepods and trophic groups of nematodes in all habitats. We used the  $\delta^{13}C$  and  $\delta^{15}N$  values 248 (mean and standard deviation) of the food sources (i.e. suspended particulate organic matter (SPOM), 249 sediment organic matter (SOM) and microphytobenthos from van der Heijden et al. (2019), those of 250 sulfide-oxidizing bacteria from Vafeiadou et al. (2014)) and meiofauna consumers (i.e. benthic 251 252 copepods and trophic groups of nematodes). Complementary information about parametrization of mixing models can be found in van der Heijden et al. (2019). The 90% credibility intervals (CI) provided 253 by the mixing models are reported here and were used as constraints (lower and upper limits) in the 254 255 food web models, following the approach of Pacella et al. (2013).

256

#### 257 2.3. Calculation of LIM solutions

Mass balance of each compartment and constraints were integrated into the LIM-MCMC models. Matrices of the linear equations (A and G) were combined with the vectors of equalities (b) and inequalities (h) to generate the vector of unknown flows (x) (van den Meersche et al., 2009):

261 262

Equality equation:A \* x = bInequality equation: $G * x \ge h$ 

263 264

The vectors x were then estimated by sampling through a solution space using the LIM-MCMC mirror defined by (van den Meersche et al., 2009) and revised by (van Oevelen et al., 2010). A range of possible values for each vector x (flow) was determined based on 500,000 solutions (jump size of 0.5). Model simulations were realized using the *limSolve* package (Soetaert et al., 2017) from van Oevelen et al. (2010). Visual observations of iterated flow values provided information on the stability of the iterations and the completeness of the sampled solution space, and thereby validated the total number of iterations and jumps selected.

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#### 273 2.4. Computation of indices and ratios

Indices and ratios were calculated from the LIM-MCMC estimated solutions and via network analyses in the purpose of (1) determining how flows of organic matter change between food sources and meiofauna trophic groups depending on food source availability and (2) determine how meiofauna mediate the transfer of carbon to higher trophic levels depending on food web characteristics
(e.g. availability of food sources, structures of meiofauna and macrofauna communities). For both
questions, several indices were computed and compared to provide a comprehensive interpretation of
the food web functioning, and to compare roles of meiofauna and macrofauna.

#### 281 2.4.1. Food web indices and ratios

Flows of carbon, omnivory indices and dependency ratios were calculated to determine and 282 analyze trophic relationships between food sources and consumers. Flows of carbon (mg C m<sup>-2</sup> d<sup>-1</sup>) 283 express trophic relationships between food sources and consumers. Omnivory index (formula in 284 285 Appendix B.1) is a ratio expressing the variability of food sources consumed by a consumer (e.g. a trophic group of meiofauna), highlighting its degree of omnivory. Dependency ratio determines 286 287 the dependence of a consumer on a food source through both direct and indirect pathways, providing 288 information about the origin of carbon assimilated by each compartment. Because an atom of carbon 289 can go through several compartments before it is consumed by a particular organism, the sum of 290 dependency ratios can exceed the value of 1.0 (Baird and Ulanowicz, 1989).

291 Production rates, production/biomass ratios and transfer efficiency were computed to determine 292 significance of meiofauna in the carbon transfer through each distinct food web. Production rates were calculated using the export, consumption, egestion and respiration (Production = consumption -293 egestion – respiration – export). Production/biomass ratio, an estimation of the activity per biomass 294 295 unit, was used to determine the activity of a compartment in the habitat. The transfer efficiency was 296 calculated based on inputs, losses due to respiration, exports and outputs as detritus and transfers to 297 higher trophic levels. It highlights the efficiency of the energy transfered from one trophic level to the 298 next (Baird et al., 2004a). Mean transfer efficiency (MTE) was calculated as the geometric mean of 299 transfer efficiencies for trophic level II to IV (Heymans et al., 2014).

Transfer efficiencies originated from Lindeman spines which illustrate food webs as linear food chains with integer trophic levels (Lindeman, 1942; Wulff et al., 1989), for which the inputs, losses due to respiration, exports and output as detritus and transfers to higher trophic levels are detailed. Modified Lindeman spines were used to extract the information for meiofauna. Meiofauna consumers were distributed in their respective trophic levels according to their feeding behavior.

305 2.4.2. Network analysis indices

Four ecosystem network analysis (ENA) indices were computed: Total system throughput (TSTp), Finn cycling index (FCI), internal ascendency (A<sub>i</sub>) and average path length (APL) (formulas in Appendix B.1). These ENA indices provide information about the efficiency of the food webs. TSTp reflects the sum of all network flows within the system (Latham, 2006), and is also considered as the 310 total power generated within the system (Baird et al., 1998). Note the difference between the TSTp and 311 the total system through-flow (TSTf), used by Leguerrier et al. (2003). TSTf, which is the sum of 312 compartmental through-flow (Latham, 2006), is reported here as well to facilitate comparisons. FCI estimates the proportion of organic carbon that flows through loops (i.e. cycles) (Baird et al., 2004b, 313 2004a; Baird and Ulanowicz, 1989; Finn, 1976). Internal ascendency (A<sub>i</sub>) measures the efficiency and 314 definitiveness by which energy is transferred within a food web. Higher Ai highlights increased 315 ecological succession (Baird et al., 2007; Scharler and Baird, 2005). Average path length (APL) defines 316 the average number of compartments through which a unit of energy (i.e. carbon) passes between 317 entering and leaving the food web (Christensen, 1995). This parameter is expected to be higher in food 318 webs with higher flow diversity and cycling (Christensen, 1995; Thomas and Christian, 2001). 319 The indices were calculated from 500,000 estimated flow solutions using the enaR package (Lau et al., 320 321 2017).

322

#### 323 2.5. Statistical methods

324 In order to test the pairwise difference of index values between the habitats, Cliff's delta statistic 325 method (Cliff, 1993; Macbeth et al., 2010) from the effsize package (Torchiano, 2019) was used, following Tecchio et al. (2016). This method uses a non-parametric effect size statistic to estimate the 326 327 probability that a randomly selected value in the first sample is higher than a randomly selected value in the second sample, minus the reverse probability. Whether the difference is due to an effective 328 ecological meaning or sample size alone can be tested by comparing the degree of overlap between the 329 two distributions. Threshold values were used to determine the degree of significance (Romano et al., 330 2006) with low threshold values indicating a similarity between index values (negligible:  $|\delta| < 0.147$ 331 and small  $|\delta| < 0.33$ ) and higher delta values indicating a significant difference between values of both 332 indices (medium  $|\delta| < 0.474$  and large  $|\delta| > 0.474$ ). 333

#### 334 **3.** Results

335

#### 336 *3.1. General characteristics of the food web models*

The food web models of the five habitats from the two ecosystems, the Marennes-Oléron Bay and the Sylt-Rømø Bight, integrated different compartments with varying biomass (Table 1), energy requirements and production estimates which resulted in distinctly different trophic interactions (Fig. 2-4, flow values in Appendix B.2). For meiofauna compartments, constraints that were used to generate flow networks were based on outputs of stable isotope mixing models (Appendix B.3). The carbon flow networks of the five habitats were cast into a simplified construction of each food web (Fig. 2-4) which excludes respiration, import, export and flow to detritus. 344 Higher biomass of microphytobenthos, benthic bacteria, pelagic bacteria, zooplankton and 345 benthic fish were observed in the habitats of the Marennes-Oléron Bay, whereas biomass of seagrass, 346 phytoplankton, benthic deposit feeders, suspension feeders and carnivorous birds were higher in the habitats of the Sylt-Rømø Bight (Table 1). The different habitats in the Sylt-Rømø Bight were generally 347 more similar in terms of compartment biomass compared to the habitats of the Marennes-Oléron Bay. 348 Biomass of meiofauna compartments varied as well between habitats. The dominant trophic groups of 349 meiofauna were non-selective deposit feeders in mudflat SR, epigrowth feeders in seagrass MO and 350 seagrass SR, both non-selective deposit feeders and epigrowth feeders in mudflat MO, and non-351 selective deposit feeders, omnivores/predators and benthic copepods in sandflat SR. Selective deposit 352 feeders had low relative biomass in the mudflats (5%) and seagrass beds (1%) and were nearly absent 353 354 in the sandflat of the Sylt-Rømø Bight.

355 Large proportions of carbon passed through meiofauna in the mudflat of the Marennes-Oléron Bay habitats (60.6%, Fig. 2), due to the higher biomass of meiofauna in the mudflat MO 356 (1352.1 mgC m<sup>-2</sup>). Moderate proportions of carbon flowed through meiofauna in the seagrass MO 357 358 (29.6%, Fig. 2), seagrass SR (32.2%, Fig. 3) and mudflat SR (23.8%, Fig. 3), whereas low proportions of carbon passed through meiofauna in the sandflat SR (9.9%, Fig. 4). Larger proportions of carbon 359 flowed through macrofauna compartments (64.5-69.8%, Fig. 3 and 4) in the Sylt-Rømø Bight habitats, 360 361 where biomass of meiofauna were between 100-fold (seagrass SR) and 200-fold (mudflat SR) lower compared to macrofauna biomass. In the mudflat MO, where meiofauna and macrofauna biomass were 362 similar, the carbon distribution is skewed in favor of meiofauna (Fig. 2). In the seagrass MO moderate 363 proportions of carbon flowed through macrofauna (17.8%, Fig. 2) even though its biomass was 15 times 364 365 higher than meiofauna.



367 Figure 2. Food webs of the mudflat and seagrass bed in the Marennes-Oléron Bay (MO) obtained by linear inverse modeling. The mudflat MO food web model consists of 368 two primary producer compartments (green), two bacteria compartments (blue), two detrital compartments (orange) and 13 consumer compartments (pink). The seagrass MO 369 food web model consists of three primary producer compartments (green), two bacteria compartments (blue), three detrital compartments (orange) and 13 consumer 370 compartments (pink). Arrow thickness indicates the magnitude of the flow between compartments, with exact flow values given in Appendix B.2, and compartment thickness 371 indicates the magnitude of the biomass, with exact biomass given in Table 1. Biomass of SOM and SPOM in mudflat MO are unknown (stippled boxes). Meiofauna 372 compartments are in bold letters. BBA =benthic bacteria, BDF = benthic deposit feeding macrofauna, BFI = benthic fish, BGR = benthic grazing macrofauna, BOM = benthic 373 omnivorous macrofauna, COP = benthic copepods, CBR = carnivorous birds, DOC = dissolved organic carbon, HBR = herbivorous birds, MPB = microphytobenthos, MZO = 374 microzooplankton, NBA = selective deposit feeding nematodes, NDF = non-selective deposit feeding nematodes, NOF = 375 omnivorous/predating nematodes, PBA = pelagic bacteria, PHY = phytoplankton, SPOM = suspended particulate organic matter, SOM = sediment organic matter, SUS =

376 suspension feeding macrofauna, ZOO = mesozooplankton, ZOS = *Zostera noltii* material.



- 378 Figure 3. Food webs of the mudflat and seagrass bed in the Sylt-Rømø Bight (SR) obtained by linear inverse modeling. 379 The mudflat SR food web model consists of two primary producer compartments (green), two bacteria compartments 380 (blue), two detrital compartments (orange) and 11 consumer compartments (pink). The seagrass SR food web model 381 consists of three primary producer compartments (green), two bacteria compartments (blue), two detrital compartments 382 (orange) and 12 consumer compartments (pink). Arrow thickness indicates the magnitude of the flow between 383 compartments, with exact flow values in Appendix B.2, and compartment thickness indicates the magnitude of the 384 biomass, with exact biomass given in Table 1. Meiofauna compartments are in bold. BBA =benthic bacteria, BDF = 385 benthic deposit feeding macrofauna, BFI = benthic fish, BGR = benthic grazing macrofauna, BOM = benthic omnivorous 386 macrofauna, COP = benthic copepods, CBR = carnivorous birds, HBR = herbivorous birds, MPB = microphytobenthos, 387 NBA = selective deposit feeding nematodes, NDF = non-selective deposit feeding nematodes, NEF = epigrowth feeding nematodes, NOM = omnivorous/predating nematodes, PBA = pelagic bacteria, PHY = phytoplankton, SPOM = 388 389 suspended particulate organic matter, SOM = sediment organic matter, SUS = suspension feeding macrofauna, ZOS = 390 Zostera noltii material.
- 391





Figure 4. Food web of the sandflat in the Sylt-Rømø Bight (SR) obtained by linear inverse modeling. This model consists of two primary producer compartments (green), two bacteria compartments (blue), two detrital compartments (orange) and 12 consumer compartments (pink). Arrow thickness indicates the magnitude of the flow between compartments, with exact flow values in Appendix B.2, and compartment thickness indicates the magnitude of the biomass, with exact biomass given in Table 1. Meiofauna compartments are in bold. BBA = benthic bacteria, BDF = benthic deposit feeding macrofauna, BFI = benthic fish, BGR = benthic grazing macrofauna, BOM = benthic omnivorous macrofauna, COP = benthic copepods, CBR = carnivorous birds, MPB = microphytobenthos, MZO = microzooplankton, NBA = selective

- deposit feeding nematodes, NDF = non-selective deposit feeding nematodes, NEF = epigrowth feeding nematodes, NOM
   = omnivorous/predating nematodes, PBA = pelagic bacteria, PHY = phytoplankton, SPOM = suspended particulate
   organic matter, SOM = sediment organic matter, SUS = suspension feeding macrofauna, ZOO = mesozooplankton.
- 403 404

#### 3.2. Flows from food sources to meiofauna and macrofauna

405

#### 406 *3.2.1. Meiofauna and macrofauna feeding behavior*

407 Meiofauna and macrofauna had different feeding behaviors as meiofauna relied merely on a single 408 food source: microphytobenthos (60 to 81% of total consumption); with flows of microphytobenthos to meiofauna ranging from 62.8 (sandflat SR) to 674.9 mgC m<sup>-2</sup> d<sup>-1</sup> (mudflat MO) (Fig. 5). Meiofauna secondary 409 food sources were the SOM (from 17.1 to 102.2 mgC m<sup>-2</sup> d<sup>-1</sup>) and bacteria (from 7.2 to 92.3 mgC m<sup>-2</sup> d<sup>-1</sup>), 410 411 when pelagic food sources (i.e. SPOM and phytoplankton) were poorly used by meiofauna. Macrofauna, on 412 the other hand, relied on a larger diversity of resources but microphytobenthos was their major food source in three of the five habitats (mudflat SR, seagrass MO and seagrass SR), with flows ranging from 91.6 (seagrass 413 MO) to 398.2 mgC m<sup>-2</sup> d<sup>-1</sup> (mudflat SR). Consumption of bacteria, phytoplankton and SOM by macrofauna 414 was much higher in habitats of the Sylt-Rømø Bight (bacteria: from 144.5 to 288.3 mgC m<sup>-2</sup> d<sup>-1</sup>, phytoplankton: 415 from 171.9 to 246.1 mgC m<sup>-2</sup> d<sup>-1</sup>, SOM: from 165.3 to 372.5 mgC m<sup>-2</sup> d<sup>-1</sup>) than in the Marennes-Oléron Bay 416 (bacteria: from 4.5 to 16.8 mgC m<sup>-2</sup> d<sup>-1</sup>, phytoplankton: from < 0.1 to 2.8 mgC m<sup>-2</sup> d<sup>-1</sup>, SOM: from 22.8 to 33.3 417 mgC m<sup>-2</sup> d<sup>-1</sup>). Seagrass material were used very little by meiofauna and macrofauna. 418

419

420 Comparisons of flows between macrofauna and meiofauna highlighted the large differences between 421 habitats. In the Marennes-Oléron Bay habitats, flows from microphytobenthos to benthic primary consumers 422 were higher than the sum of all the other ones. In these habitats, carbon flows of microphytobenthos accounted indeed for about 70% of the total sum of flows, whereas SOM and bacteria only accounted for 11% and 10% 423 424 of the total carbon flows towards benthic consumers, respectively. In the Sylt-Rømø Bight habitats, total 425 carbon flows towards benthic consumers were originating from more diverse sources such as microphytobenthos (21–43%), SOM (20–25%), phytoplankton (13–23%), bacteria (10–21%) and SPOM (3– 426 427 10%). At the scale of consumers, flows towards macrofauna were much higher in the Sylt-Rømø Bight habitats 428 compared to those of the Marennes-Oléron Bay where meiofauna dominated grazing.

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- 430
- 431



432

Figure 5. Flows of carbon from food sources to meiofauna and macrofauna in the mudflats, seagrass beds, and sandflat
in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). SOM = sediment organic matter, SPOM = suspended
particulate organic matter.

436

#### 437 *3.2.2.* Flows from food sources to meiofauna trophic groups

Within the meiofauna, three main feeding strategies were observed among the different trophic groups. 438 First, meiofauna from three trophic groups: non-selective deposit feeding nematodes, epigrowth feeding 439 nematodes and benthic copepods, mostly relying on microphytobenthos with flows from 15.4-303.2 440 mgC m<sup>-2</sup> d<sup>-1</sup>, from 9.9–280.8 mgC m<sup>-2</sup> d<sup>-1</sup> and from 1.8–29.3 mgC m<sup>-2</sup> d<sup>-1</sup>, respectively (Fig. 6, Appendix B.4). 441 442 The high reliance of these consumers on microphytobenthos in all habitats was demonstrated by the 443 dependency ratios, ranging from 0.73 to 0.97 (Fig. 6), and their very low omnivory indices (0.03–0.10; Table 2). Habitat comparisons highlighted that non-selective deposit feeders and epigrowth feeders had much higher 444 445 inputs of microphytobenthos in the mudflats and seagrass beds than in the sandflat SR. Lastly, benthic copepods had a lower relative carbon input from microphytobenthos in seagrass MO than in other habitats. 446

447 Second, selective deposit feeding nematodes relied on more variable food sources (Fig. 6, Appendix 448 B.4). They relied mostly on bacteria in the Marennes-Oléron Bay habitats  $(8.2-35.9 \text{ mgC m}^{-2} \text{ d}^{-1})$ , whereas 449 they mostly used microphytobenthos in the Sylt-Rømø Bight habitats  $(0.5-16.1 \text{ mgC m}^{-2} \text{ d}^{-1})$ . In all habitats 450 except seagrass MO, dependency ratios of selective deposit feeders highlighted that they rely on a large 451 diversity of food sources: microphytobenthos, SOM and bacteria (Fig. 6). In the Marennes-Oléron seagrass 452 bed, the contribution of microphytobenthos and bacteria to the carbon requirements of selective deposit feeders 453 were similar as confirmed by their dependency ratio in this habitat (Fig. 6).

Third, omnivorous/predating nematodes relied on microphytobenthos  $(7.8-61.2 \text{ mgC m}^2 \text{ d}^{-1})$  as well as on other meiofauna  $(10.3-83.6 \text{ mgC m}^2 \text{ d}^{-1})$  (Fig. 6, Appendix B.4), as also demonstrated by their relatively higher omnivory index (0.26 to 0.30, Table 2). Still, dependency ratios demonstrated that omnivores/predators depended mostly on carbon of microphytobenthos origin in all habitats with ratios ranging from 0.75 (seagrass SR) to 0.94 (mudflat MO) (Fig. 6). 459 Table 2. Omnivory indices for trophic groups of nematodes and benthic copepods in the mudflats, seagrass beds, and

Omnivory index									
	Mudflat MO	Mudflat SR	Seagrass MO	Seagrass SR	Sandflat SR				
Nematodes – selective deposit feeders	0.17	0.17	0.25	0.16	0.19				
Nematodes – non-selective deposit feeders	0.05	0.03	0.08	0.07	0.05				
Nematodes – epigrowth feeders	0.07	0.03	0.04	0.08	0.07				
Nematodes – omnivores/predators	0.30	0.26	0.26	0.28	0.28				
Benthic copepods	0.08	0.08	0.05	0.10	0.06				

460 sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR).

461



Figure 6. Flows of carbon (mgC m<sup>-2</sup> d<sup>-1</sup>) from food sources to meiofauna trophic groups (left panel) and dependency ratios of meiofauna trophic groups on food sources (right
panel) in the mudflats, seagrass beds, and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). Trophic groups: selective deposit feeding nematodes,
non-selective deposit feeding nematodes, epigrowth feeding nematodes, omnivorous/predating nematodes and benthic copepods. Primary food sources: microphytobenthos,
sediment organic matter (SOM), bacteria and suspended particulate organic matter (SPOM). Values are displayed in Appendix B.2 (flows of carbon) and Appendix B.5
(dependency ratios).

#### 3.3. Production and transfer efficiency

469

### 470 *3.3.1. Production of food sources*

471 Microphytobenthos was the most important primary producer in all habitats with the largest gross 472 primary production (GPP) ranging from 774.4 (sandflat SR) to 1161.9 mgC m<sup>-2</sup> d<sup>-1</sup> (mudflat MO), and microphytobenthos represented between 47.3% (seagrass SR) to 81.3% (seagrass MO) of the primary 473 474 production (Table 3). The highest GPP of microphytobenthos was measured in the two mudflats, as well as in seagrass MO, while GPP was much lower in seagrass SR and sandflat SR. Other primary producers were also 475 characterized by large difference of GPP between habitats (Table 3). GPP of seagrass was much lower than 476 477 that of microphytobenthos in seagrass MO (45.1 compared to 1043.1 mgC m<sup>-2</sup> d<sup>-1</sup>) and slightly lower than that of microphytobenthos in seagrass SR (685.3 compared to 836.6 mgC m<sup>-2</sup> d<sup>-1</sup>). GPP of phytoplankton varied 478 from 194.2 to 536.0 mgC m<sup>-2</sup> d<sup>-1</sup>, with the highest production occurring in mudflat MO (536.0 mgC m<sup>-2</sup> d<sup>-1</sup>) 479 and sandflat SR (446.5 mgC m<sup>-2</sup> d<sup>-1</sup>). Production of bacteria was more variable than production of 480 481 microphytobenthos, with much higher values in the habitats of the Sylt-Rømø Bight (147.7 to 317.5 mgC m<sup>-2</sup> d<sup>-1</sup>) than in the habitats of the Marennes-Oléron Bay (41.3 to 96.8 mgC m<sup>-2</sup> d<sup>-1</sup>, Table 3). 482

483 Table 3. Primary production of primary producers (with proportion of total primary production in *italic*; %), secondary 484 production of bacteria, meiofauna and macrofauna and production/biomass ratios of meiofauna and macrofauna in the 485 mudflats, seagrass beds, and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). Secondary 486 production of meiofauna and macrofauna are weighted averages of the combined compartments weighted by their 487 biomass.

	Prima	ry production (mg	$C m^{-2} d^{-1}$ )	
Mudflat MO	Mudflat SR	Seagrass MO	Seagrass SR	Sandflat SR
1161.9	1023.1	1043.1	836.6	774.4
68.4%	81.2%	81.3%	47.3%	63.4%
536.0	237.4	194.2	247.5	446.5
31.6%	18.8%	15.1%	13.9%	36.6%
-	-	45.1	685.3	-
		at SR         Seagrass MO         Seagrass SR         Sandflat $023.1$ $1043.1$ $836.6$ $774.4$ $1.2\%$ $81.3\%$ $47.3\%$ $63.4$ $37.4$ $194.2$ $247.5$ $446.6$ $8.8\%$ $15.1\%$ $13.9\%$ $36.6$ - $45.1$ $685.3$ - $3.5\%$ $38.8\%$ $317.5$ $147.5$ Secondary production (mgC m <sup>-2</sup> d <sup>-1</sup> ) $13.2$ $41.3$ $317.5$ $147.5$ $30.6$ $14.5$ $28.4$ $13.0$ $41.3$ $19.8$ $3.3$ $6.8$ Production/biomass ratio (d <sup>-1</sup> ) $0.28$ $0.04$ $0.08$ $0.00$ $.002$ $0.003$ $< 0.001$ $< 0.001$		
	Second	ary production (m	gC m <sup>-2</sup> d <sup>-1</sup> )	
96.8	313.2	41.3	317.5	147.7
34.9	30.6	14.5	28.4	13.6
8.8	41.3	19.8	3.3	6.8
	Pro	duction/biomass ra	tio (d <sup>-1</sup> )	
0.03	0.28	0.04	0.08	0.08
0.007	0.002	0.003	< 0.001	< 0.001
	Mudflat MO 1161.9 68.4% 536.0 31.6% - 96.8 34.9 8.8 0.03 0.03 0.007	Mudflat MO         Mudflat SR           1161.9         1023.1           68.4%         81.2%           536.0         237.4           31.6%         18.8%           -         -           96.8         313.2           34.9         30.6           8.8         41.3           0.03         0.28           0.007         0.002	Primary production (mg           Mudflat MO         Mudflat SR         Seagrass MO           1161.9         1023.1         1043.1           68.4%         81.2%         81.3%           536.0         237.4         194.2           31.6%         18.8%         15.1%           -         -         45.1           3.5%         3.5%           Secondary production (mg           96.8         313.2         41.3           34.9         30.6         14.5           8.8         41.3         19.8           Production/biomass ra           0.03         0.28         0.04           0.007         0.002         0.003	Primary production (mgC m-2 d-1)Mudflat MOMudflat SRSeagrass MOSeagrass SR1161.91023.11043.1836.6 $68.4\%$ $81.2\%$ $81.3\%$ $47.3\%$ $536.0$ $237.4$ 194.2247.5 $31.6\%$ $18.8\%$ $15.1\%$ $13.9\%$ $45.1$ $685.3$ $3.5\%$ $38.8\%$ Secondary production (mgC m-2 d-1)96.8 $313.2$ $41.3$ $317.5$ $34.9$ $30.6$ $14.5$ $28.4$ $8.8$ $41.3$ $19.8$ $3.3$ Production/biomass ratio (d-1) $0.03$ $0.28$ $0.04$ $0.08$ $0.007$ $0.002$ $0.003$ $<0.001$

488

489 3.3.2. Secondary production

Production of macrofauna, ranging 3.3 (seagrass SR) to 41.3 mgC m<sup>-2</sup> d<sup>-1</sup> (mudflat SR), was more 490 variable than that of meiofauna, which ranged from 14.5 (seagrass MO) to 34.9 mgC m<sup>-2</sup> d<sup>-1</sup> (mudflat MO) 491 492 (Table 3). Meiofauna production was higher than those of macrofauna in mudflat MO, seagrass SR and sandflat SR, and relatively similar in mudflat SR and seagrass MO. Meiofauna P/B ratios were much higher than those 493 494 of macrofauna, being from four (mudflat MO) to 800 times higher (seagrass SR). Habitat comparisons 495 highlighted that meiofauna P/B ratios were much higher in the Sylt-Rømø Bight mudflat (0.28  $d^{-1}$ ) than in all 496 other habitats (from 0.03 to 0.09 d<sup>-1</sup>). Macrofauna P/B ratios were higher in the mudflat MO, mudflat SR and 497 seagrass MO than in the other habitats.

498

#### 499 *3.3.3. Transfer efficiency*

In the Marennes-Oléron Bay habitats, the carbon flows from primary food sources 500 501 (i.e. microphytobenthos, seagrass, phytoplankton, SPOM, SOM and bacteria) to meiofauna (269.9-951.7 mgC m<sup>-2</sup> d<sup>-1</sup>) were much higher than the carbon flows to macrofauna (47.0–173.2 mgC m<sup>-2</sup> d<sup>-1</sup>) (Fig. 5). The 502 opposite pattern was observed for the Sylt-Rømø Bight habitats with lower carbon flows to meiofauna (115.6-503 530.5 mgC m<sup>-2</sup> d<sup>-1</sup>) than to macrofauna (884.3–1584.8 mgC m<sup>-2</sup> d<sup>-1</sup>). At the habitat scale, the carbon flow from 504 food sources to meiofauna with the lowest trophic level (level II) was high in the mudflat MO 505  $(804.4 \text{ mgC m}^{-2} \text{ d}^{-1})$ , seagrass SR (443.6 mgCm<sup>-2</sup> d<sup>-1</sup>) and mudflat SR (421.5 mgC m<sup>-2</sup> d<sup>-1</sup>) (Appendix B.6). 506 A moderate carbon flow was observed in seagrass MO (234.1 mgC m<sup>-2</sup> d<sup>-1</sup>) and a particularly low flow was 507 observed in the sandflat SR (97.7 mgC m<sup>-2</sup> d<sup>-1</sup>). The carbon flow from food sources to macrofauna with the 508 lowest trophic level (level II) was high in the Sylt-Rømø Bight habitats (501.3–1033.5 mgC m<sup>-2</sup> d<sup>-1</sup>) compared 509 510 to the moderate flow in the seagrass MO (150.3 mgCm<sup>-2</sup> d<sup>-1</sup>) and the particular low flow in mudflat MO (42.2 mgC m<sup>-2</sup> d<sup>-1</sup>) (Appendix B.7). 511

512

The carbon flows from meiofauna to higher trophic levels  $(12.6-39.2 \text{ mgC m}^{-2} \text{ d}^{-1})$  were relatively similar to or slightly higher than those from macrofauna  $(18.3-30.1 \text{ mgC m}^{-2} \text{ d}^{-1}; \text{ Table 4})$  in all habitats, except for mudflat SR. In these habitats, meiofauna represented between 40% and 66% of the carbon requirements of higher trophic levels. On the contrary, in the mudflat SR the carbon flows to higher trophic levels were mainly originating from macrofauna (137.1 mgC m<sup>-2</sup> d<sup>-1</sup>; 74%) with much lower contributions for meiofauna (49.1 mgC m<sup>-2</sup> d<sup>-1</sup>; 26%).

519

Large differences were also observed between habitats when comparing the diversity of organisms relying on meiofauna (Table 4). In the mudflat MO flows from meiofauna were equally divided over benthic omnivorous macrofauna (59%) and benthic fish (41%), whereas flows from meiofauna to higher trophic levels mostly ended up in one single consumer group in other habitats, benthic omnivorous macrofauna (99%) in seagrass MO and benthic fishes (> 95%) in Sylt-Rømø Bight habitats. Macrofauna of the seagrass SR and sandflat SR were also mostly assimilated by one group of consumers (> 95%; carnivorous birds), whereas

- 526 macrofauna had multiple consumers in other habitats (i.e. benthic omnivorous macrofauna, benthic fish and
- 527 carnivorous birds).
- 528
- 529 Table 4. Flows from meiofauna (Meio) and macrofauna (Macro) to higher trophic levels (mgC m<sup>-2</sup> d<sup>-1</sup>) in the mudflats,
- 530 seagrass beds, and sandflat of the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). Higher trophic levels are:
- benthic omnivorous macrofauna (BOM), benthic fish (BFI) and carnivorous birds (CBR).

	Mudflat MO		dflat MO Mudflat SR		Seagra	iss MO	Seagr	ass SR	Sandf	Sandflat SR		
	Meio	Macro	Meio	Macro	Meio	Macro	Meio	Macro	Meio	Macro		
BOM	7.4	4.8	49.1	1.3	0.2	0.1	19.6	8.1	39.2	0.5		
BFI	5.2	2.1	< 0.1	0.2	19.5	11.4	1.1	1.4	< 0.1	0.4		
CBR	-	11.4	-	135.6	-	18.6	-	9.4	-	18.9		

Losses by respiration and egestion were also very different between meiofauna-all integer trophic 533 534 levels—and macrofauna (Table 5). Meiofauna represented lower respiration (1.7 to 22.3%) compared to macrofauna (27.0 and 60.3%). For egestion, the opposite pattern was observed, as it was slightly higher for 535 meiofauna (40.9-90.7%) compared to that of macrofauna (38.9-68.2%). Comparisons between habitats 536 highlighted that losses due to respiration of meiofauna were higher in mudflat MO (15.4–19.3%) and sandflat 537 SR (12.4-22.3%) than in other habitats (< 6.5%). For macrofauna, the loss by respiration was the highest in 538 seagrass MO (60.2–60.3%) compared to m other habitats (27.0–48.0%). Moreover, loss by meiofauna due to 539 egestion was lower in sandflat SR (40.9–73.0%) than in other habitats (70.0–90.7%). No clear pattern was 540 observed for relative losses by macrofauna due to egestion. 541

542

Table 5. Relative contributions of respiration and egestion to the total meiofauna and macrofauna outflows (%) in the
 mudflats, seagrass beds, and sandflat of the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). Roman

545 numbers represent the different integer trophic levels that originated from the Lindeman spines (Appendix B.6 and B.7).

	Meiofauna									
Outflow		Re	spirati	on			F	Egestior	1	
Trophic level	II	III	IV	V	VI	Π	III	IV	V	VI
Mudflat MO	19.3	17.7	15.4	-	-	70.0	76.1	82.9	-	-
Mudflat SR	1.9	1.7	1.7	-	-	75.7	79.6	82.3	-	-
Sandflat SR	12.4	17.7	22.3	-	-	40.9	59.7	73.0	-	-
Seagrass MO	5.3	5.0	6.4	-	-	78.4	79.5	74.2	-	-
Seagrass SR	4.8	4.3	4.2	-	-	76.2	84.8	90.7	-	-

	Macrofauna										
Outflow		Re	espirati	on			ŀ	gestio	n		
Trophic level	II	III	IV	V	VI	II	III	IV	V	VI	
Mudflat MO	27.0	29.3	29.6	29.6	29.6	48.3	50.1	50.4	50.4	50.4	
Mudflat SR	39.7	37.4	42.6	45.0	-	56.5	58.2	51.9	54.8	-	
Sandflat SR	48.0	41.6	29.1	29.4	-	45.1	56.0	67.5	68.2	-	

Seagrass MO	60.3	60.2	-	-	-	39.4	38.9	-	-	-
Seagrass SR	43.0	41.6	27.6	29.2	-	53.8	53.8	53.4	56.3	-

547 As a result, the differences between meiofauna and macrofauna in carbon inflows and outflows 548 (i.e. consumption by higher trophic levels, losses due to respiration and returns due to egestion) led to much higher transfer efficiencies (TEs) of meiofauna (16.2–31.3%) than of macrofauna (2.5–15.9%) in all habitats 549 except in mudflat MO (Fig. 7). TE of meiofauna ( $11.5 \pm 2.1 \%$ ) in mudflat MO was much lower than TE of 550 macrofauna (23.1  $\pm$  2.1 %). Different patterns were observed for the mean transfer efficiencies (MTEs) of 551 integer trophic levels II to IV (Fig. 7), with higher MTEs in mudflat MO ( $12.7 \pm 1.2\%$ ), mudflat SR 552  $(11.9 \pm 2.2\%)$  and seagrass SR  $(10.2 \pm 2.2\%)$  compared to sandflat SR  $(8.0 \pm 2.0\%)$  and seagrass MO 553 554  $(6.8 \pm 3.6\%).$ 

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556

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Figure 7. Transfer efficiency (TE) of the whole food web, meiofauna and macrofauna for the mudflats, seagrass beds,
and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). Mean TE for the food web is the geometric
mean from integer trophic level II-IV (± standard deviation; see Appendix B.8). For meiofauna and macrofauna a
weighted average is used (± weighted standard deviation).

562 3.4. Network analysis

The food webs of the five studied habitats presented a distinct structure, with an obvious discrimination 563 of the seagrass MO. Seagrass MO had among the lowest values for the average path length (APL), internal 564 ascendency (A<sub>i</sub>) and Finn cycling index (FCI), whereas the total system throughput (TSTp) was among the 565 highest compared to all other habitats (Fig. 8). Mudflat MO and mudflat SR were characterized by the longest 566 567 food chain (i.e. high APL), highest internal organization (i.e. high A<sub>i</sub>), and the highest recycling (i.e. high FCI) 568 whereas seagrass SR and sandflat SR had intermediate values. As demonstrated by their higher values of TSTp, 569 a higher quantity of carbon flows through the food webs of the Marennes-Oléron Bay habitats compared to 570 those of the Sylt-Rømø Bight habitats.



Figure 8. Ecological network analysis indices for the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay
(MO) and the Sylt-Rømø Bight (SR): total system throughput (TSTp; top left), average path length (top right), internal
ascendency (A<sub>i</sub>; bottom left) and Finn cycling index (bottom right). Letters displayed above boxes indicate groups of
samples with similar indices using the Cliff's delta statistics (Appendix B.9).

- 576 4. Discussion
- 577

#### 578 4.1. Importance of microphytobenthos as a food source for meiofauna

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### 580 *4.1.1. Reliance on microphytobenthos*

As evidenced by the five different models, meiofauna mostly relied on microphytobenthos in all 581 habitats, whereas macrofauna relied on a wider variety of food sources. Carbon flows from microphytobenthos 582 indeed represented between 60 (i.e. 62.8 mgC m<sup>-2</sup> d<sup>-1</sup>) and 81% (i.e. 674.9 mgC m<sup>-2</sup> d<sup>-1</sup>) of the total flows 583 584 between food sources and meiofauna in the different studied habitats. The high reliance of meiofauna on microphytobenthos confirmed the outcomes of the combined trophic marker approach carried out on the same 585 586 habitats by van der Heijden et al. (2019). This major role of microphytobenthos in both ecosystems and all habitats highlights the importance of this food source compared to other primary producers, even when the 587 588 latter have much higher biomass (e.g. seagrass material). Microphytobenthos therefore has a pivotal role as a 589 food source in soft-bottom coastal habitats.

590

591 Importance of microphytobenthos as a food source likely stems from its short turnover times (0.1-7.9)days) and high production (774–1162 mgC m<sup>-2</sup> d<sup>-1</sup>). More importantly so, these rates (Degré et al., 2006) and 592 593 microphytobenthos biomass (Lebreton et al., 2009; van der Heijden et al., 2018) are generally much more constant all year round than those of other potential sources, resulting in a reliable food source constantly 594 595 available. Phytoplankton and seagrass follow strong seasonal fluctuations in biomass and production over a 596 year, mostly blooming during spring and summer seasons, while inputs of detrital material mostly occur in fall 597 and winter (Asmus and Asmus, 1985; Lebreton et al., 2009; Struski and Bacher, 2006; van der Heijden et al., 598 2018). Moreover, microphytobenthos has a high nutritional quality (Cebrián, 1999), opposed to seagrass 599 material and a fortiori detrital material. Indeed, these latter have a low nutritional value (Vizzini et al., 2002) 600 and are generally characterized by more refractory compounds (i.e. resistant to biological degradation; Klump 601 et al., 1989) and are therefore poorly consumed by both meiofauna and macrofauna (Lebreton et al., 2011a). Meiofauna are known to actively migrate towards (Moens et al., 1999a) or selectively feed on high quality 602 603 food sources (Azovsky et al., 2005; Estifanos et al., 2013).

604

#### 605 *4.1.2.* Differences of food source reliance between meiofauna feeding types

606 The degree of which meiofauna relied on microphytobenthos in each habitat differed depending on meiofauna feeding types, as demonstrated by the flows and network properties derived from the five habitats 607 608 models. The various meiofauna feeding types could be gathered in three main groups according to their reliance 609 on microphytobenthos. First group: non-selective deposit feeding nematodes, epigrowth feeding nematodes 610 and benthic copepods, which had a high reliance on microphytobenthos as indicated by their dependency ratios 611 to microphytobenthos (0.73–0.97) and very low omnivory indices (0.03-0.10). For these groups, most of the 612 carbon was originating from microphytobenthos (56 to 91%) in all habitats (carbon flows from 2 to 303 mgC m<sup>-2</sup> d<sup>-1</sup>). A slightly lower reliance on microphytobenthos as observed on the seagrass bed and sandflat of 613 the Sylt-Rømø Bight (56-70%) may be related to differences in terms of availability, e.g. no biofilm in the 614 615 sandflat, as productions are in the same order of magnitude in all habitats. The importance of 616 microphytobenthos as a food source for epigrowth feeders and benthic copepods has been demonstrated 617 through grazing experiments before (Rzeznik-Orignac and Fichet, 2012), and is in agreement with the morphology of the buccal cavity of epigrowth feeders, optimized for the consumption of diatoms (Moens and 618 Vincx, 1997a; Wieser, 1953). Epigrowth feeder buccal cavities are fitted with a tooth used to pierce diatoms, 619 620 making it easier to assimilate them.

621

Second group: omnivorous/predating nematodes largely relied on carbon of microphytobenthos origin as indicated by their dependency ratios (0.77–0.94). This associated to their relatively higher omnivory index (0.26–0.30) compared to other groups of meiofauna highlighted that these consumers relied both directly and indirectly on microphytobenthos. This indirect reliance on microphytobenthos was linked to the predation on meiofauna from lower trophic groups (i.e., non-selective deposit feeders and epigrowth feeders), themselves feeding on microphytobenthos (Rzeznik-Orignac et al., 2008; Vafeiadou et al., 2014; van Oevelen et al., 2006).

629 Third group: selective deposit feeding nematodes, which relied on a larger variety of food sources, as 630 reflected by their relatively higher omnivory indices and the similar values of dependency to benthic bacteria, SOM, as well as microphytobenthos. The buccal cavity morphology of selective deposit feeders is adapted to 631 632 efficiently feed on bacteria (Wieser, 1953), and this high reliance on bacteria was confirmed by carbon flows. 633 Interestingly, bacteria mainly used microphytobenthos and SOM as substrates (Boschker et al., 2000; van der 634 Heijden et al., 2019). As a result, selective deposit feeders rely as well on organic matter primarily produced 635 by microphytobenthos, but in an indirect way, as this organic matter is mostly routed through bacteria before 636 being assimilated by these nematodes. Consequently, although the direct consumption was low, the 637 dependency on microphytobenthos was high, when considering direct and indirect interactions.

638

639 The fact that the meiofauna from these different feeding types mostly relied on microphytobenthos 640 while they could access to other food sources clearly highlights that other features of food sources (i.e. quality, productivity) must be considered in addition to biomass when carrying out food web studies. These results 641 also highlight the importance of considering the different feeding types of meiofauna when determining trophic 642 643 relationships. Indeed, even if we highlighted that meiofauna rely mostly on one single food source (i.e. 644 microphytobenthos), the trophic pathways from this food source when fresh and its ultimate assimilation by 645 meiofauna may vary depending on feeding types (i.e. direct consumption, indirect consumption via grazing on 646 bacteria or predation on other nematodes). This diversity of pathways involved in transfers of organic matter 647 may have implications for the general properties of the food webs (e.g. higher diversity of flows) and changes 648 of meiofauna community structure may affect the functioning of the food webs as well. In addition, even if 649 meiofauna mostly rely on carbon primarily originating from microphytobenthos, some other food sources may 650 also be of high importance to meiofauna given that limited knowledge is available on carbon processing within 651 the meiofauna compartment. Information on direct predator-prey interactions between meiofauna organisms 652 is scarce and meiofaunal feeding modes are known to be flexible (e.g. facultative feeding behavior; (Moens et 653 al., 1999b). As a result, this compartment should be treated in a similar way as macrofauna and aggregating 654 meiofauna trophic groups into a single compartment should be avoided whenever possible.

655

#### 656 4.2. Important role of meiofauna in soft-bottom coastal food webs

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#### 658 *4.2.1.* Evidences about important role of meiofauna

A large proportion of the energy passed through meiofauna in the different soft-bottom habitats (i.e. 31.2% on average), besides some important differences: minimum of 10% in sandflat SR and maximum of 61% in mudflat MO. The important role of meiofauna as a trophic mediator between primary producers and higher consumers was highlighted by the flows to (116–952 mgC m<sup>-2</sup> d<sup>-1</sup>) and from meiofauna (13–49 mgC m<sup>-2</sup> d<sup>-1</sup>). These flows are in the range of flows to (47–1290 mgC m<sup>-2</sup> d<sup>-1</sup>) and from macrofauna (18–137 mgC m<sup>-2</sup> d<sup>-1</sup>). Focusing merely on the contribution of meiofauna and macrofauna to the diet of higher trophic

665 level consumers (i.e. benthic omnivorous macrofauna, benthic fish and carnivorous birds) the relative 666 contribution of meiofauna as a food source to higher trophic levels ranges from 26 to 66%. However, distinct 667 patterns were observed between habitats about the proportion of energy passing through meiofauna and macrofauna. At the ecosystem scale, more energy passed through macrofauna (65–70%) when compared to 668 669 the meiofauna (10-32%) in the Sylt-Rømø Bight, while the opposite pattern was observed in the Marennes-670 Oléron Bay (i.e. macrofauna: 5–18%, meiofauna: 30–61%). This is very likely related to the much larger 671 biomass of macrofauna (100 to 200 times more) in the Sylt-Rømø Bight than in the Marennes-Oléron Bay. 672 Despite the smaller amount of energy that passed through meiofauna in seagrass SR and sandflat SR, a larger 673 proportion of the energy for higher trophic levels originated from meiofauna (meiofauna: 52-66%; 674 macrofauna: 34-48%). At the habitat scale, a larger proportion of energy passed through meiofauna in the mudflat of the Marennes-Oléron Bay (61%) compared to all other habitats (10–32%). Consequently, a much 675 676 lower amount of energy passed through macrofauna in mudflat MO (5%), while biomass of meiofauna and 677 macrofauna were similar. This much higher amount of energy transiting through meiofauna is very likely related to the close connection between meiofauna and microphytobenthos, which is very productive and 678 679 highly available in this habitat as it forms a biofilm at the sediment surface. In addition, more diverse consumer 680 groups relied on meiofauna in the mudflat of the Marennes-Oléron Bay, whereas meiofauna was consumed by 681 one dominant higher trophic level consumer in all other habitats, i.e. benthic fish (seagrass MO) or benthic 682 omnivorous macrofauna (Sylt-Rømø Bight habitats).

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#### 4.2.2. How can meiofauna play this important role?

686 The important role of meiofauna in the functioning of the five habitats is very likely related to their high production (14–35 mgC m<sup>-2</sup> d<sup>-1</sup>) and P/B ratios (0.03–0.28 d<sup>-1</sup>). Indeed, meiofauna production was either 687 similar (in the seagrass MO and in the mudflat SR), or even higher (2 to 9 times, in all other habitats), than 688 689 macrofauna production. These productions were generally in agreement with previous estimations (10 to 80 mgC m<sup>-2</sup> d<sup>-1</sup>) (Chardy and Dauvin, 1992; Danovaro et al., 2002; Escaravage et al., 1989). The high 690 production of meiofauna combined with similar and/or lower biomass compared to macrofauna resulted in 691 692 much higher P/B ratios than for the macrofauna, i.e. from 4 to 1000 times. Higher production and P/B ratios of meiofauna compared to macrofauna is known to be related to their higher turn-over rates (at least five times 693 694 higher than that of macrofauna: Gerlach, 1971; Moens and Vincx, 1997b) and higher weight-specific metabolic 695 rates (up to 21 times higher than for macrofauna: Kuipers et al., 1981).

Meiofauna also play a major role in the different studied food webs as trophic mediator, as confirmed by the transfer efficiency of meiofauna (i.e. 20% on average) which was higher than the transfer efficiency of macrofauna (i.e. 12% on average) and much higher than the mean transfer efficiency of the whole food webs (i.e. 10% on average). Meiofauna also have a high nutritional value (Coull, 1999) and their concentration in the surface sediment layer make them a very available and valuable food source to consumers (Castel et al., 1989; Leduc and Probert, 2011; van der Heijden et al., 2018). The important role of meiofauna 702 as a food source for juvenile benthic feeding fish (e.g. mullets, gobies, flatfish, grunts and croakers) was 703 demonstrated in mudflats (Carpentier et al., 2014; Gordon and Duncan, 1979; Lassere et al., 1975; Smith and 704 Coull, 1987; Smith et al., 1984), sandflats (Castel and Lasserre, 1982; Gee, 1987; Hicks, 1984; Pihl, 1985) and salt marshes (Lebreton et al., 2013, 2011b). As a result, meiofauna can help fulfil the nutritional needs of 705 706 higher trophic level organisms, that are eventually harvestable by humans. However, the exact fate of 707 meiofauna remains unclear (Giere, 2009) and further research should focus on the flows from meiofauna to 708 higher trophic levels in food webs. Meiofauna should at least not be neglected in coastal ecosystem assessments 709 and should be treated similarly to macrofauna.

710 711

#### 4.3. Close relationship between food web efficiency and assimilation of high-quality food sources

712 Mudflat MO, mudflat SR and seagrass SR were the most efficient food webs with a high mean transfer efficiency (MTE: 10.2-12.7%; Heymans et al., 2014), associated with the highest internal ascendency 713 (A<sub>i</sub>: 6946–9339 mgC m<sup>-2</sup> d<sup>-1</sup>; Baird et al., 2007) and the highest average path length (APL: 3.1-4.1; 714 715 Hutchinson, 1959; Slobodkin, 1960). These high MTEs are explained by the structure of the studied food webs, 716 in which the carbon is constrained to flow through specific trophic pathways, resulting in the high A<sub>i</sub>. Thus, 717 the link between a predator and its main prey items is based on preferences whereas indirect consumption on the same prey is limited. In this way the losses of carbon by respiration, egestion and export are limited, as 718 719 suggested by the APL, and the carbon flows through longer and more efficient trophic chains. The highest 720 efficiencies of these three habitats are very likely related to the large flows from high quality food sources (836–996 mgC m<sup>-2</sup> d<sup>-1</sup>), that fulfill the energy requirements of organisms, prevent them from diversifying their 721 722 diet and favor higher assimilation. In the core of this efficient trophic chain is the meiofauna that have 723 consumed up to 40% of the GPP and that are among the main prey for higher trophic levels. The lower 724 efficiency in the sandflat SR was related to lower microphytobenthos production and a resulting lower input from this high-quality food source to primary consumers (607 mgC m<sup>-2</sup> d<sup>-1</sup>). However, the energy was very 725 726 efficiently transferred from primary consuming meiofauna to higher trophic levels partially related to the high 727 relative biomass of omnivores/predating nematodes. As reported by Campanyà-Llovet et al. (2017), the lowest 728 trophic levels have the strongest response to changes in food quality. Thus, caution should be taken when 729 aggregating smaller organisms in the lower trophic levels of food webs, e.g. meiofauna, since these organisms generally assimilate large proportions of the flows coming from high-quality food sources. 730

731 The link between food web efficiency and assimilation of high-quality primary food sources is less clear in seagrass MO. Low MTE (6.8%), A<sub>i</sub> (4974 mgC m<sup>-2</sup> d<sup>-1</sup>) and APL (1.8) clearly demonstrate a low 732 733 efficiency, however, the flows from primary producers to primary consumers were dominated by high-quality 734 food sources (70.5%), despite the low input when compared to other habitats (391 mgC m<sup>-2</sup> d<sup>-1</sup>). This could be 735 related to the lower proportion of available carbon that is transferred to higher trophic levels, as indicated by 736 the low APL. Further investigations are needed to clarify this point, to determine if this is for ecological 737 (e.g. low recycling or high export) or mathematical reasons (i.e. the topology of the model). The recycling was 738 very low in seagrass MO, as highlighted by the very low FCI (2.4%) when compared to other habitats (7.3–

13.1%). This low recycling may be related to the poorly used detrital pool in seagrass MO (26%) when compared to other habitats (62–80%). The food web efficiency might have been affected by this low recycling, since food web efficiency includes both the efficiency of energy transfers from primary producers to herbivores and then carnivores as well as from detrital material to detritivores and then carnivores. Therefore, the low consumption of detritus by detritivores might have an indirect effect on the lower transfer efficiency of trophic level II and III in seagrass MO.

#### 745 5. Conclusion

The analysis of five coastal food web models highlighted the importance of the trophic pathway 746 between microphytobenthos and meiofauna in soft-bottom intertidal habitats. Microphytobenthos was indeed 747 the most important primary producer and the most important food resource for meiofauna in these habitats 748 (63-675 mgC m<sup>-2</sup> d<sup>-1</sup>), even when high loads of seagrass material were present. The important role of 749 meiofauna was highlighted by their high throughput (average: 31.2%), high production (14–35 mgC m<sup>-2</sup> d<sup>-1</sup>) 750 751 and transfer efficiency (11-28%). As a result, meiofauna are responsible for a large part of the production as 752 well as for the carbon flows from microphytobenthos towards higher trophic levels, and thus are very important in the functioning of intertidal soft-bottom habibats. On the contrary, the slower-growing macrofauna are more 753 754 accountable for energy storage and rely on a larger diversity of food sources. Therefore, these two 755 compartments appear to provide complementary ecosystem functions. They should thus be considered with 756 the same level of precision when building food web models, especially since a close positive relationship was 757 highlighted between the assimilation of high-quality food sources by primary consumers, e.g. meiofauna and 758 macrofauna, and the overall food web efficiency.

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760 The close link between microbiota and meiofauna and the use of available primary sources 761 (i.e. microphytobenthos) by meiofauna make these consumers a key compartment in the functioning of food 762 webs in soft-bottom habitats (Schratzberger and Ingels, 2017). Although most trophic groups of meiofauna revealed a high reliance on microphytobenthos in all habitats, through direct (herbivory) or indirect (carnivory) 763 764 flows, some meiofauna trophic groups relied on bacteria and SOM, with direct consequences on the carbon 765 use and its distribution within the food web. The diversity in feeding behavior and their significance in the carbon flow justify the partitioning of meiofauna into different compartments, as traditionally done for 766 macrofauna in most food web studies. We therefore argue that feeding types of meiofauna should be considered 767 768 as separate compartments in future studies. Coupling state-of-the-art methods (i.e. molecular techniques, 769 trophic markers and stomach content) should be commonly used to quantify carbon flows from/to meiofauna 770 with higher precision and thus refine the role of this key compartment in the functioning of coastal habitats.

771

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