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1 **Quantitative food web modeling unravels the importance of the**
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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
41 chain Monte Carlo technique, with increased resolution of the meiofauna compartments (i.e. biomass
42 and feeding ecology of the different trophic groups of meiofauna) compared to most previous modeling
43 studies. These models highlighted that the flows between the highly productive microphytobenthos and
44 the meiofauna compartments play an important role in transferring carbon to the higher trophic levels,
45 typically more efficiently so than macrofauna. The pathway from microphytobenthos to meiofauna
46 represented the largest flow in all habitats and resulted in high production of meiofauna independent of
47 habitat. All trophic groups of meiofauna, except for selective deposit feeders, had a very high
48 dependency on microphytobenthos. Selective deposit feeders relied instead on a wider range of food
49 sources, with varying contributions of bacteria, microphytobenthos and sediment organic matter.
50 Ecological network analyses (e.g. cycling, throughput and ascendancy) 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
61 coastal and marine ecosystems (Moens et al., 2011; Schratzberger and Ingels, 2018), e.g. roles in trophic
62 processes, energy flows (Leguerrier et al., 2003; Moens et al., 2013). This lack of interest is likely
63 related to the belief that meiofauna were a “trophic dead end” (Heip and Smol, 1975; McIntyre and
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;
67 Leguerrier et al., 2003), weakening the “trophic dead end” hypothesis. For example, in intertidal and
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.

79
80 Interactions between meiofauna and their resources are complex due to the large variety of
81 potential food sources (e.g. microalgae, detrital matter, bacteria; Lebreton et al., 2012; Moens et al.,
82 2005; Vafeiadou et al., 2014) and quantifications of carbon fluxes from lower trophic levels to
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
86 (Lebreton et al., 2012; Leduc et al., 2009; Vafeiadou et al., 2014). Nematodes, generally the most
87 abundant taxon of meiofauna, have a very diverse feeding behavior, i.e., herbivory, bacterivory, or
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

98 Many unknowns remain about the fate of meiofauna in benthic food webs. For a long time there
99 was a controversy about the fate of meiofauna in benthic food webs (Heip et al., 1992), whether
100 meiofauna was a dead end in the food web (Heip and Smol, 1975; McIntyre and Murison, 1973), or an
101 important link between primary producers and higher trophic levels (Coull, 1990; Schückel and
102 Kröncke, 2013). Meiofauna production is high (from 4 to 29 gC m⁻² year⁻¹; Chardy and Dauvin, 1992;
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
105 ratios (Couch, 1989), high levels of amino acids (Vilela, 1992; Watanabe et al., 1978) and essential
106 fatty acids (Watanabe et al., 1983), are sufficient to fulfill a predator's needs (Coull, 1999), explaining
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
115 meiofauna by higher trophic levels (Magnhagen et al., 2007; Schückel et al., 2013). Therefore, there is
116 a need to consider meiofauna trophic groups in food web assessments, and inter-habitat comparison can
117 help at understanding how changes in trophic groups' biomass affect the role of meiofauna in coastal
118 food webs.

119

120 Linear inverse modeling is a useful tool to describe the functioning of a food web at the habitat
121 or the ecosystem scale (Baird et al., 2007; Leguerrier et al., 2007). It generates a static, mass-balanced,
122 temporally integrated snapshot of the complete food web and its flows using a combination of field and
123 relevant literature data (Niquil et al., 2011; Vézina and Platt, 1988) and it is a powerful method in
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
127 complexity of the modeled food web (Johnson et al., 2009; Kones et al., 2006). Based on the estimated
128 flow-networks, several food web characteristics can be defined, such as efficiencies, recycling and
129 dependencies (Niquil et al., 2011), which can in turn be useful in ecosystem management and policy
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
135 (Campanyà-Llovet et al., 2017), highlighting different responses for various trophic groups. However,
136 species are often aggregated in lower trophic levels of the food web due to difficulties in taxonomic
137 identification and in segregating the energetics of smaller individuals (Baird et al., 2009). This has
138 typically been the case for meiofauna as they are described as a single compartment in most recent
139 steady-state mass-balanced food web models, or at best are split into nematodes and benthic copepods
140 (Baird et al., 2007; Leguerrier et al., 2007, 2003; Pacella et al., 2013). Model input data (i.e. constraints)
141 for meiofauna trophic groups are indeed scarce (Baird et al., 2009) and often derived from experimental
142 studies on single specimens (Herman and Vranken, 1988; Vranken and Heip, 1986). Therefore,
143 separating meiofauna into major trophic groups is necessary if a better understanding of their
144 relationships with specific food sources and the role of these organisms in food webs is wanted. Trophic
145 marker based approaches (e.g. stable isotopes), however, has shown successful to better constrain
146 consumption flows of meiofauna trophic groups in food web models (Pacella et al., 2013; van Oevelen
147 et al., 2010).

148

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

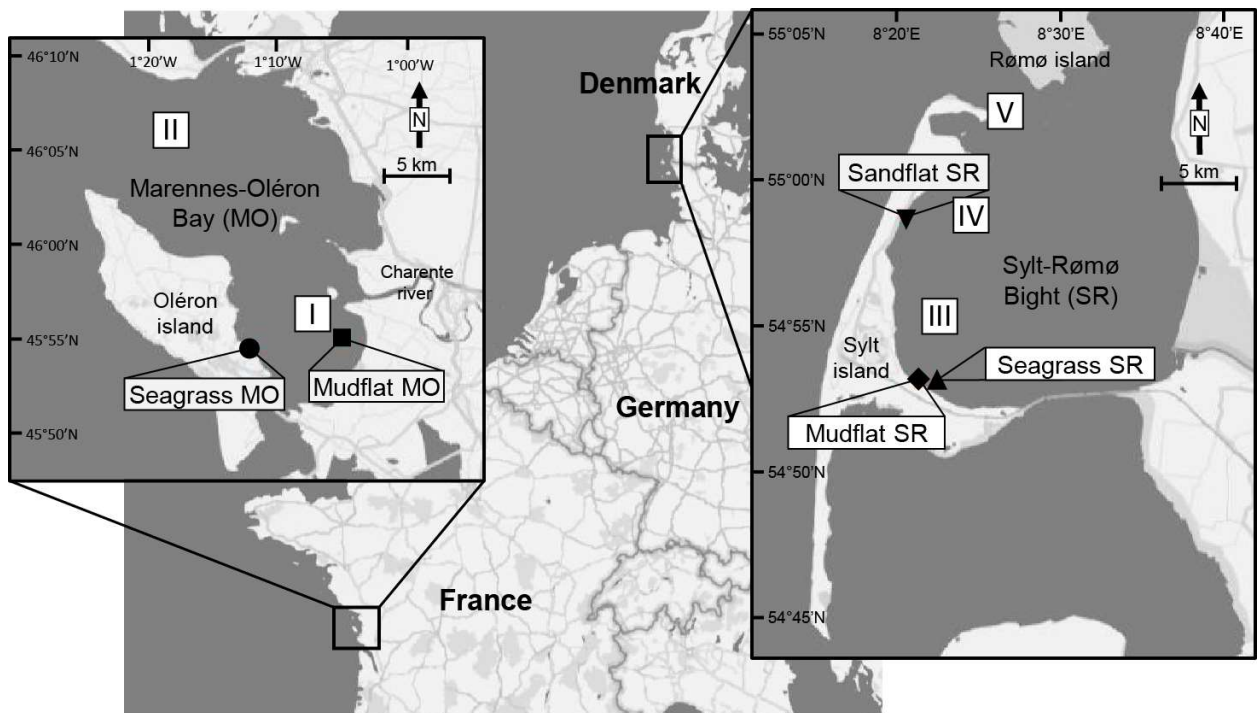
162

163 **2. Material and methods**

164 **2.1. Study sites and carbon flow networks**

165 Five benthic-pelagic coupled carbon flow networks were built, characterized by different food
166 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
 169 autochthonous food sources, three types of habitats were studied: one characterized by high loads of
 170 detrital matter (i.e. seagrass bed), one characterized by a lower load of detrital matter and by a
 171 community of microphytobenthos dominated by epipellic diatoms (i.e. mudflat), and one characterized
 172 by a low load of detrital matter and by a community of microphytobenthos dominated by epipsammic
 173 diatoms (i.e. sandflat). To consider the role of allochthonous food sources, we studied the functioning
 174 of these habitats in two different ecosystems: one influenced by continental inputs of organic matter,
 175 i.e. the Marennes-Oléron Bay in France, into which the Charente river flows (Gouleau et al., 2000), and
 176 one with little direct continental inputs, hence influenced mainly by marine inputs, i.e. the Sylt-Rømø
 177 Bight in Germany (Asmus and Asmus, 2005, 1985). As sandflats are not a typical habitat in the
 178 Marennes-Oléron Bay, this habitat could not be considered in this ecosystem. As a result, seagrass beds
 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
 181 flow networks (i.e. one per habitat: mudflat MO, mudflat SR, seagrass MO, seagrass SR, and sandflat
 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 Marennnes-Oléron Bay (I-II) and
 191 Sylt-Rømø Bight (III-V).

192

193 **2.2. Linear inverse model construction**

194 Linear inverse ecosystem models with Markov chain Monte Carlo (LIM-MCMC) were built to
 195 determine carbon flows in the five habitats on a daily basis ($\text{mgC m}^{-2} \text{d}^{-1}$) using the R software (R Core
 196 Team, 2019). The flow estimations originated from annual averages but are expressed as daily averages
 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.,
 199 2004b; Baird and Ulanowicz, 1989). Most constraints, except for meiofauna constraints, that were used
 200 to construct the flow networks of these habitats originated from established models (Baird et al., 2007;
 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
 210 (i.e. benthic deposit feeders, benthic grazers, suspension feeders and benthic omnivores/predators) in
 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 Marennnes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). NA = no data
 216 available; - = compartment absent.

		Mudflat	Seagrass	Sandflat	Mudflat	Seagrass
		MO	MO	SR	SR	SR
Number of compartments		19	21	17	17	20
Number of flows		123	138	100	96	108
Compartment	Abbr.	Biomass (mg C m^{-2})				
Terrestrial						
Carnivorous birds	CBR	7.0	6.0	121.3	174.7	417.3
Herbivorous birds	HBR	-	1.0	-	-	71.7
Benthic						
Microphytobenthos	MPB	3125.0	9250.0	130.0	120.0	120.0
<i>Zostera noltii</i> (seagrass tissues)	ZOS	-	6133.3	-	-	30890.0
Benthic bacteria	BBA	947.0	947.0	625.0	625.0	625.0
Nematodes – selective deposit feeders	NBA	70.5	4.6	0.3	5.5	2.0
Nematodes – non-selective deposit feeders	NDF	496.9	60.8	40.3	58.2	58.2

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

217

218 2.2.1. Established model constraints

219 The model of mudflat MO was based on data provided by Leguerrier et al. (2003),
 220 Degré et al. (2006), Saint-Béat et al. (2014) (Appendices A.1 and A.2). Original compartments of this
 221 previous model were used as a basis for the other food web models and therefore no aggregations were
 222 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*,
 228 *Crangon crangon*, and *Cerebratulus marginatus*), and suspension feeders (*Cerastoderma edule*,
 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

233 The models of habitats from the Sylt-Rømø Bight (i.e. mudflat SR, seagrass SR and sandflat
 234 SR) were based on data provided by Baird et al. (2007) and modified by Saint-Béat et al. (2013)
 235 (Appendices A.4 to A.6). For these models fewer minimum and maximum values of flow constraints
 236 (mainly production and consumption constraints) were known compared to models of the
 237 Marennes-Oléron Bay. Equalities, provided by Saint-Béat et al. (2013), were therefore converted to
 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
244 trophic groups of nematodes (i.e. selective deposit feeders, non-selective deposit feeders, epigrowth
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
247 isotope data from van der Heijden et al. (2019) to compute the dietary contribution of food sources to
248 benthic copepods and trophic groups of nematodes in all habitats. We used the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values
249 (mean and standard deviation) of the food sources (i.e. suspended particulate organic matter (SPOM),
250 sediment organic matter (SOM) and microphytobenthos from van der Heijden et al. (2019), those of
251 sulfide-oxidizing bacteria from Vafeiadou et al. (2014)) and meiofauna consumers (i.e. benthic
252 copepods and trophic groups of nematodes). Complementary information about parametrization of
253 mixing models can be found in van der Heijden et al. (2019). The 90% credibility intervals (CI) provided
254 by the mixing models are reported here and were used as constraints (lower and upper limits) in the
255 food web models, following the approach of Pacella et al. (2013).

256

257 2.3. *Calculation of LIM solutions*

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

261

262 Equality equation: $A * x = b$

263 Inequality equation: $G * x \geq h$

264

265 The vectors x were then estimated by sampling through a solution space using the LIM-MCMC
266 mirror defined by (van den Meersche et al., 2009) and revised by (van Oevelen et al., 2010). A range
267 of possible values for each vector x (flow) was determined based on 500,000 solutions (jump size of
268 0.5). Model simulations were realized using the *limSolve* package (Soetaert et al., 2017) from van
269 Oevelen et al. (2010). Visual observations of iterated flow values provided information on the stability
270 of the iterations and the completeness of the sampled solution space, and thereby validated the total
271 number of iterations and jumps selected.

272

273 2.4. *Computation of indices and ratios*

274 Indices and ratios were calculated from the LIM-MCMC estimated solutions and via network
275 analyses in the purpose of (1) determining how flows of organic matter change between food sources
276 and meiofauna trophic groups depending on food source availability and (2) determine how meiofauna

277 mediate the transfer of carbon to higher trophic levels depending on food web characteristics
278 (e.g. availability of food sources, structures of meiofauna and macrofauna communities). For both
279 questions, several indices were computed and compared to provide a comprehensive interpretation of
280 the food web functioning, and to compare roles of meiofauna and macrofauna.

281 2.4.1. *Food web indices and ratios*

282 Flows of carbon, omnivory indices and dependency ratios were calculated to determine and
283 analyze trophic relationships between food sources and consumers. Flows of carbon ($\text{mg C m}^{-2} \text{ d}^{-1}$)
284 express trophic relationships between food sources and consumers. Omnivory index (formula in
285 Appendix B.1) is a ratio expressing the variability of food sources consumed by a consumer
286 (e.g. a trophic group of meiofauna), highlighting its degree of omnivory. Dependency ratio determines
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
293 calculated using the export, consumption, egestion and respiration (Production = consumption –
294 egestion – respiration – export). Production/biomass ratio, an estimation of the activity per biomass
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 transferred 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).

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

305 2.4.2. *Network analysis indices*

306 Four ecosystem network analysis (ENA) indices were computed: Total system throughput
307 (TSTp), Finn cycling index (FCI), internal ascendancy (A_i) and average path length (APL) (formulas in
308 Appendix B.1). These ENA indices provide information about the efficiency of the food webs. TSTp
309 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
313 estimates the proportion of organic carbon that flows through loops (i.e. cycles) (Baird et al., 2004b,
314 2004a; Baird and Ulanowicz, 1989; Finn, 1976). Internal ascendancy (A_i) measures the efficiency and
315 definitiveness by which energy is transferred within a food web. Higher A_i highlights increased
316 ecological succession (Baird et al., 2007; Scharler and Baird, 2005). Average path length (APL) defines
317 the average number of compartments through which a unit of energy (i.e. carbon) passes between
318 entering and leaving the food web (Christensen, 1995). This parameter is expected to be higher in food
319 webs with higher flow diversity and cycling (Christensen, 1995; Thomas and Christian, 2001).
320 The indices were calculated from 500,000 estimated flow solutions using the *enaR* package (Lau et al.,
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,
326 following Tecchio et al. (2016). This method uses a non-parametric effect size statistic to estimate the
327 probability that a randomly selected value in the first sample is higher than a randomly selected value
328 in the second sample, minus the reverse probability. Whether the difference is due to an effective
329 ecological meaning or sample size alone can be tested by comparing the degree of overlap between the
330 two distributions. Threshold values were used to determine the degree of significance (Romano et al.,
331 2006) with low threshold values indicating a similarity between index values (negligible: $|\delta| < 0.147$
332 and small $|\delta| < 0.33$) and higher delta values indicating a significant difference between values of both
333 indices (medium $|\delta| < 0.474$ and large $|\delta| > 0.474$).

334 3. **Results**

335

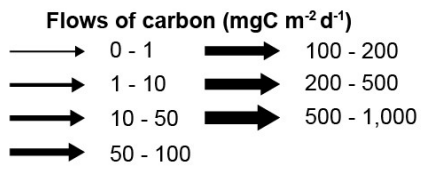
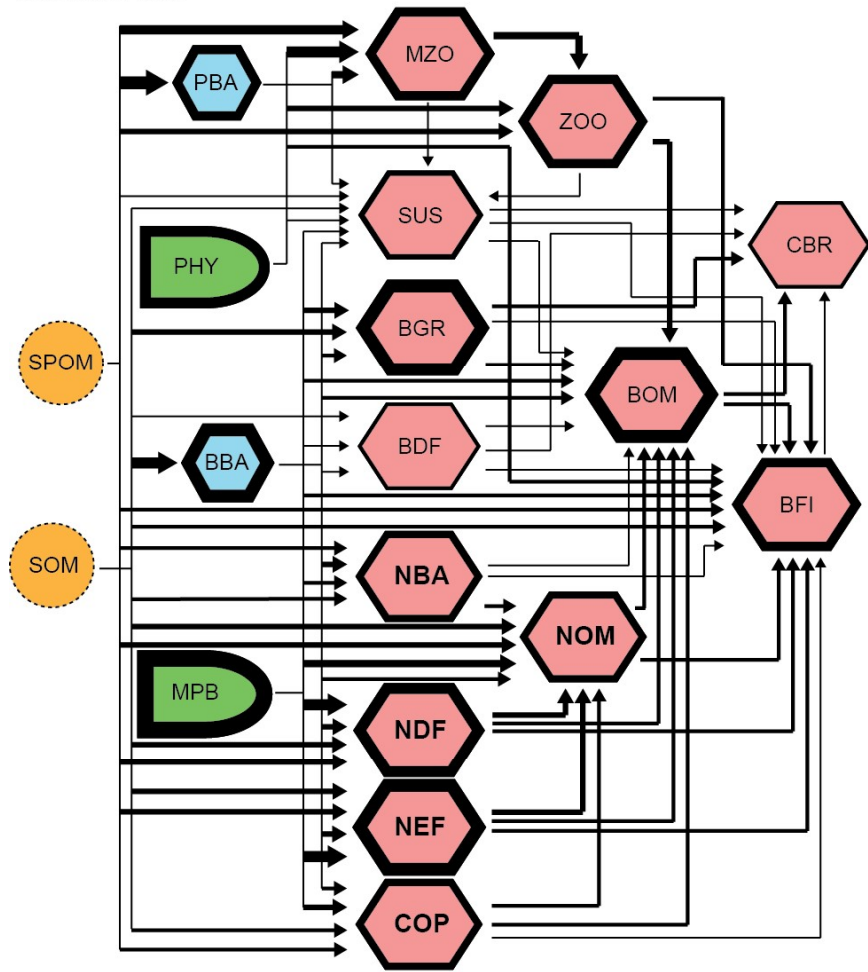
336 3.1. *General characteristics of the food web models*

337 The food web models of the five habitats from the two ecosystems, the Marennes-Oléron Bay
338 and the Sylt-Rømø Bight, integrated different compartments with varying biomass (Table 1), energy
339 requirements and production estimates which resulted in distinctly different trophic interactions (Fig.
340 2-4, flow values in Appendix B.2). For meiofauna compartments, constraints that were used to generate
341 flow networks were based on outputs of stable isotope mixing models (Appendix B.3). The carbon flow
342 networks of the five habitats were cast into a simplified construction of each food web (Fig. 2-4) which
343 excludes respiration, import, export and flow to detritus.

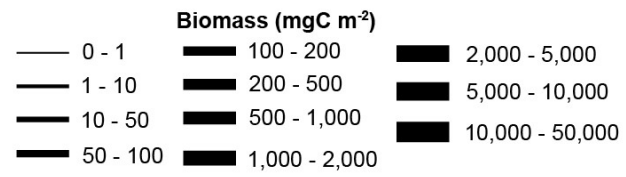
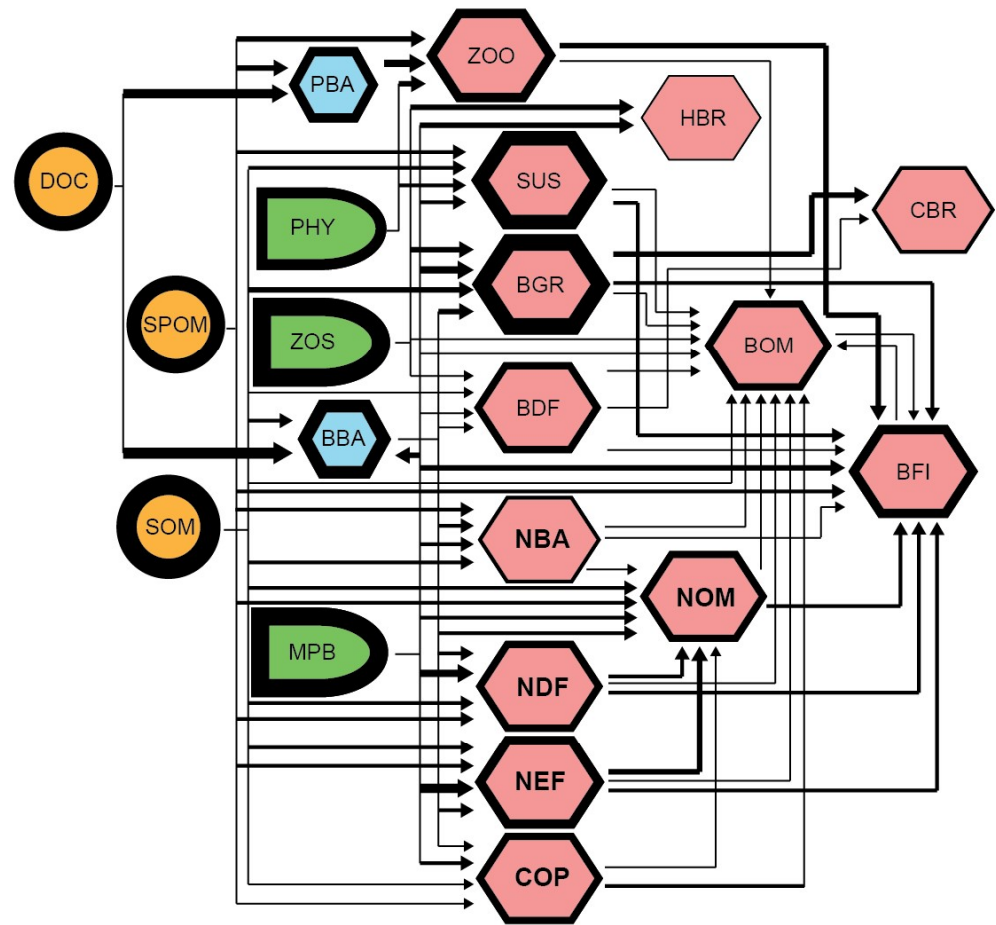
344 Higher biomass of microphytobenthos, benthic bacteria, pelagic bacteria, zooplankton and
345 benthic fish were observed in the habitats of the Marennes-Oléron Bay, whereas biomass of seagrass,
346 phytoplankton, benthic deposit feeders, suspension feeders and carnivorous birds were higher in the
347 habitats of the Sylt-Rømø Bight (Table 1). The different habitats in the Sylt-Rømø Bight were generally
348 more similar in terms of compartment biomass compared to the habitats of the Marennes-Oléron Bay.
349 Biomass of meiofauna compartments varied as well between habitats. The dominant trophic groups of
350 meiofauna were non-selective deposit feeders in mudflat SR, epigrowth feeders in seagrass MO and
351 seagrass SR, both non-selective deposit feeders and epigrowth feeders in mudflat MO, and non-
352 selective deposit feeders, omnivores/predators and benthic copepods in sandflat SR. Selective deposit
353 feeders had low relative biomass in the mudflats (5%) and seagrass beds (1%) and were nearly absent
354 in the sandflat of the Sylt-Rømø Bight.

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

Mudflat MO

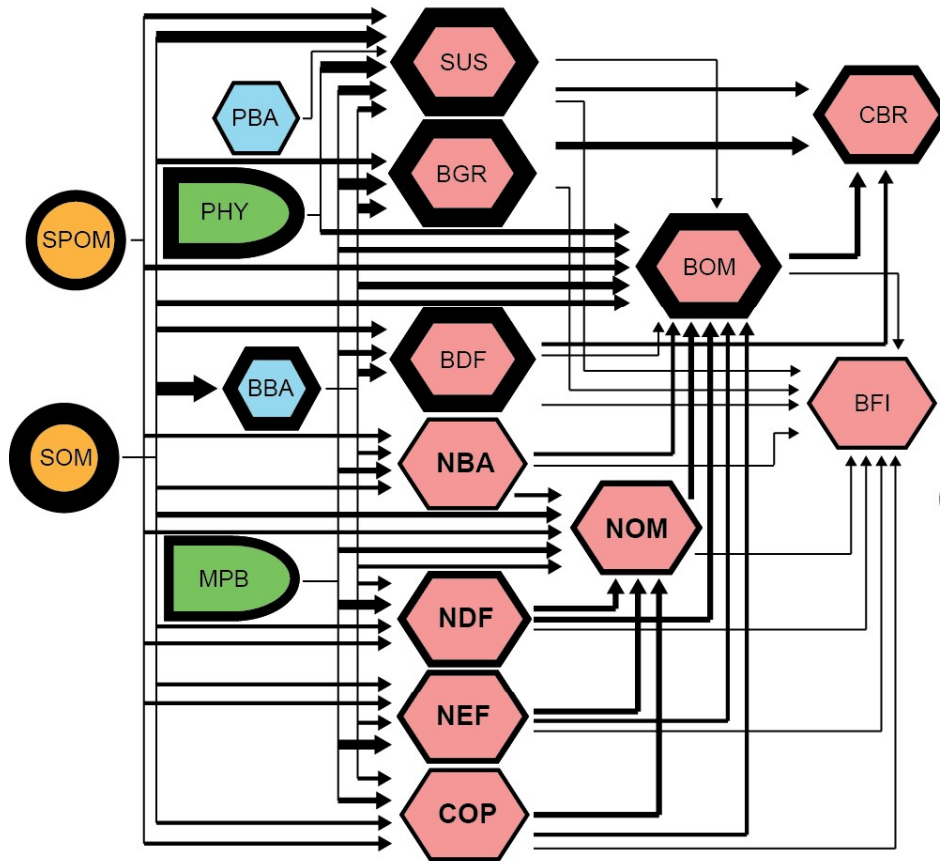


Seagrass MO

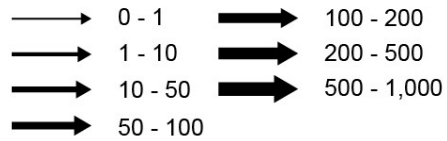


367 **Figure 2.** Food webs of the mudflat and seagrass bed in the Marennes-Oléron Bay (MO) obtained by linear inverse modeling. The mudflat MO food web model consists of
368 two primary producer compartments (green), two bacteria compartments (blue), two detrital compartments (orange) and 13 consumer 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, NEF = epigrowth feeding nematodes, NOM =
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.

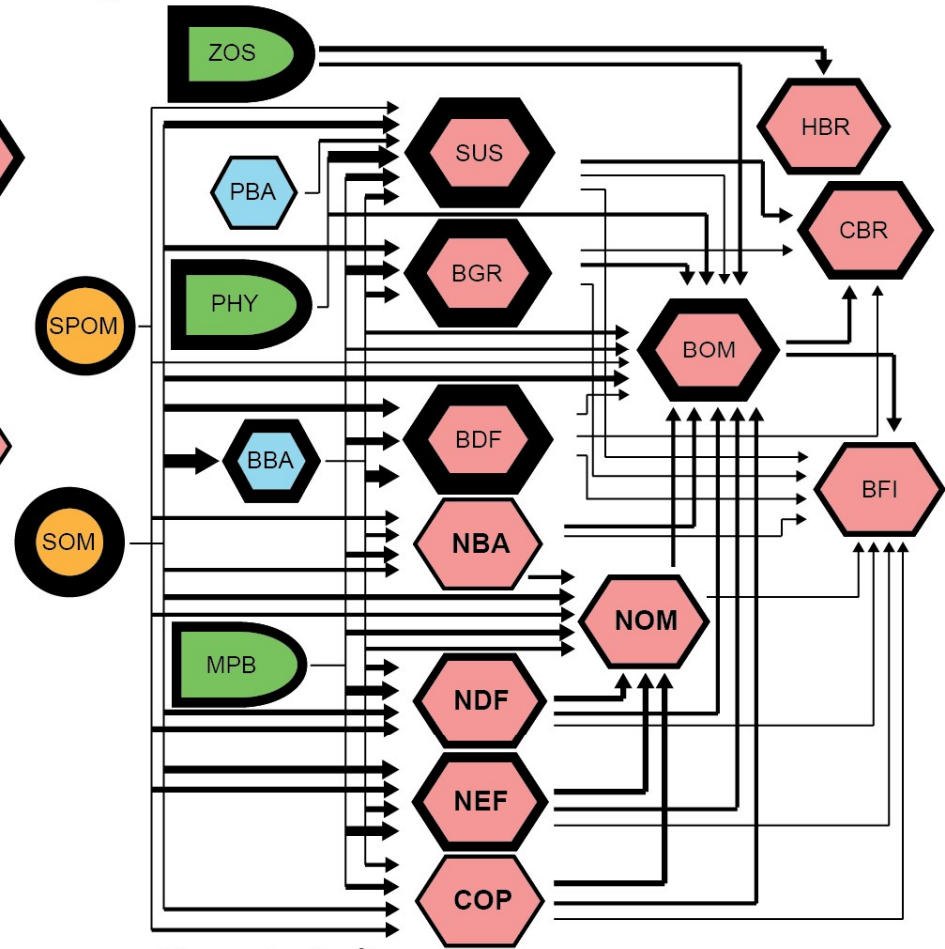
Mudflat SR



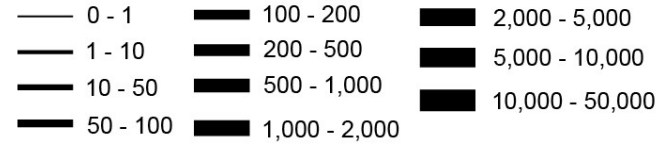
Flows of carbon ($\text{mgC m}^{-2} \text{d}^{-1}$)



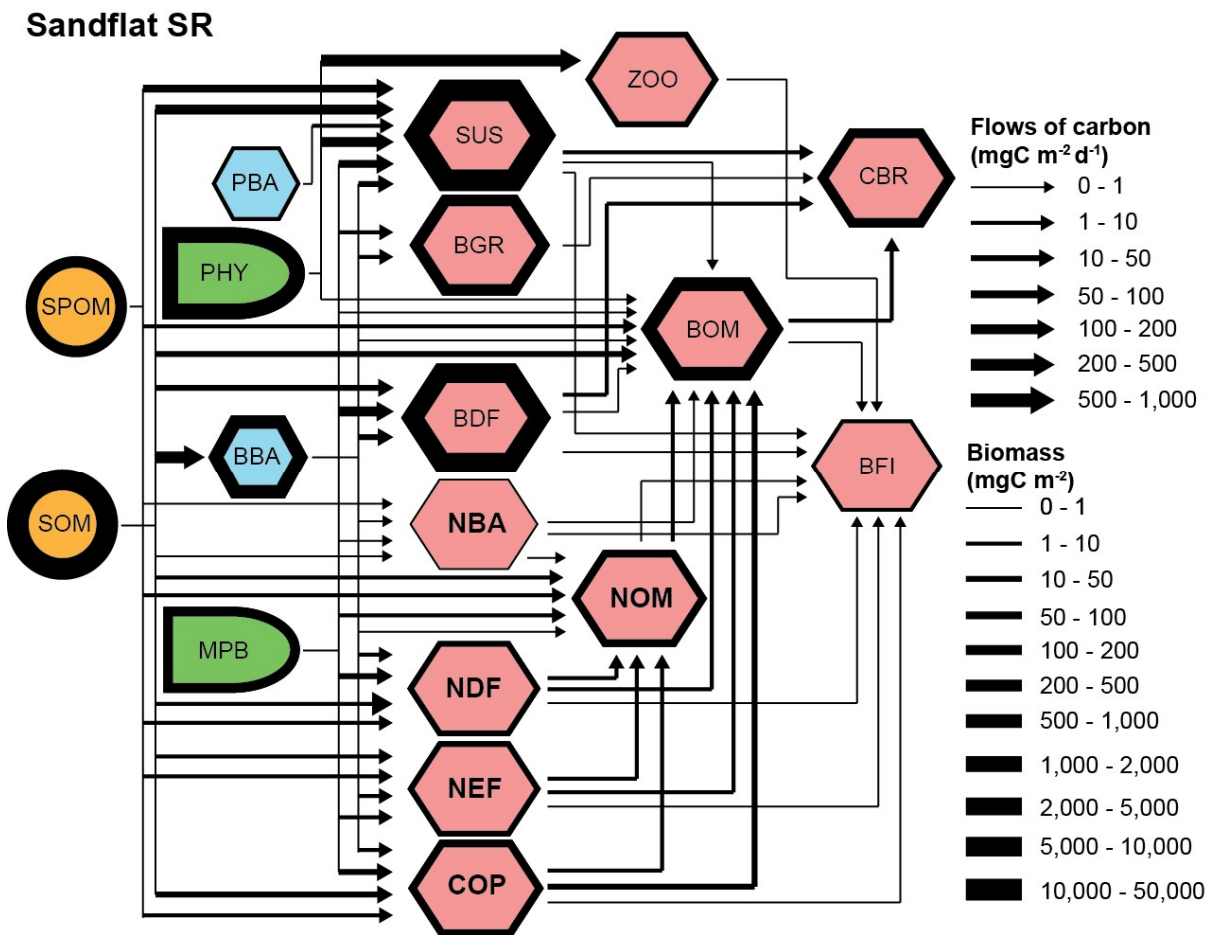
Seagrass SR



Biomass (mgC m^{-2})



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



392
 393 **Figure 4.** Food web of the sandflat in the Sylt-Rømø Bight (SR) obtained by linear inverse modeling. This model consists
 394 of two primary producer compartments (green), two bacteria compartments (blue), two detrital compartments (orange)
 395 and 12 consumer compartments (pink). Arrow thickness indicates the magnitude of the flow between compartments, with
 396 exact flow values in Appendix B.2, and compartment thickness indicates the magnitude of the biomass, with exact
 397 biomass given in Table 1. Meiofauna compartments are in bold. BBA = benthic bacteria, BDF = benthic deposit feeding
 398 macrofauna, BFI = benthic fish, BGR = benthic grazing macrofauna, BOM = benthic omnivorous macrofauna, COP =
 399 benthic copepods, CBR = carnivorous birds, MPB = microphytobenthos, MZO = microzooplankton, NBA = selective

400 deposit feeding nematodes, NDF = non-selective deposit feeding nematodes, NEF = epigrowth feeding nematodes, NOM
401 = omnivorous/predating nematodes, PBA = pelagic bacteria, PHY = phytoplankton, SPOM = suspended particulate
402 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
409 meiofauna ranging from 62.8 (sandflat SR) to 674.9 mgC m⁻² d⁻¹ (mudflat MO) (Fig. 5). Meiofauna secondary
410 food sources were the SOM (from 17.1 to 102.2 mgC m⁻² d⁻¹) and bacteria (from 7.2 to 92.3 mgC m⁻² d⁻¹),
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
413 three of the five habitats (mudflat SR, seagrass MO and seagrass SR), with flows ranging from 91.6 (seagrass
414 MO) to 398.2 mgC m⁻² d⁻¹ (mudflat SR). Consumption of bacteria, phytoplankton and SOM by macrofauna
415 was much higher in habitats of the Sylt-Rømø Bight (bacteria: from 144.5 to 288.3 mgC m⁻² d⁻¹, phytoplankton:
416 from 171.9 to 246.1 mgC m⁻² d⁻¹, SOM: from 165.3 to 372.5 mgC m⁻² d⁻¹) than in the Marennes-Oléron Bay
417 (bacteria: from 4.5 to 16.8 mgC m⁻² d⁻¹, phytoplankton: from < 0.1 to 2.8 mgC m⁻² d⁻¹, SOM: from 22.8 to 33.3
418 mgC m⁻² d⁻¹). Seagrass material were used very little by meiofauna and macrofauna.

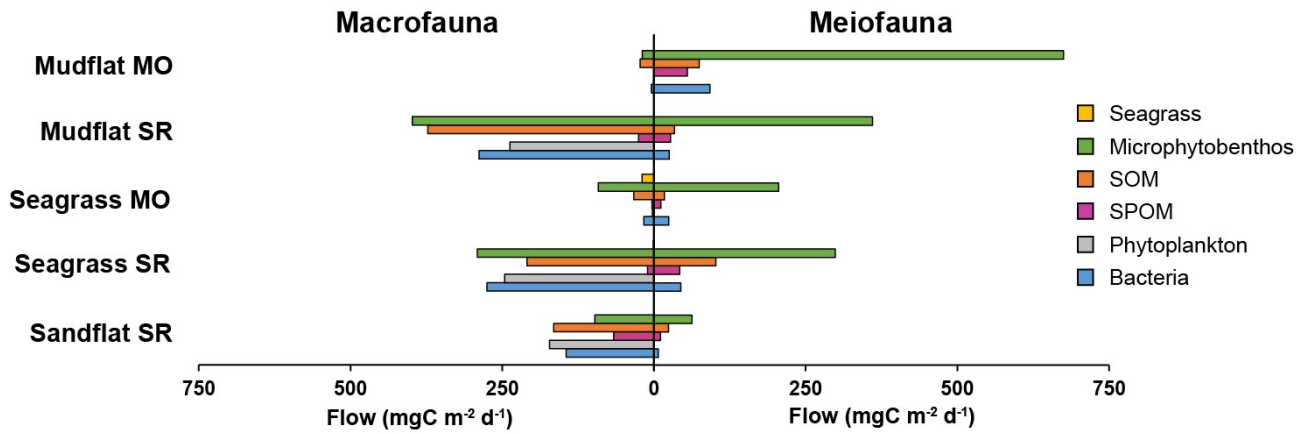
419

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
423 indeed for about 70% of the total sum of flows, whereas SOM and bacteria only accounted for 11% and 10%
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
426 microphytobenthos (21–43%), SOM (20–25%), phytoplankton (13–23%), bacteria (10–21%) and SPOM (3–
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.

429

430

431



432
 433 **Figure 5.** Flows of carbon from food sources to meiofauna and macrofauna in the mudflats, seagrass beds, and sandflat
 434 in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). SOM = sediment organic matter, SPOM = suspended
 435 particulate organic matter.

436
 437 *3.2.2. Flows from food sources to meiofauna trophic groups*

438 Within the meiofauna, three main feeding strategies were observed among the different trophic groups.
 439 First, meiofauna from three trophic groups: non-selective deposit feeding nematodes, epigrowth feeding
 440 nematodes and benthic copepods, mostly relying on microphytobenthos with flows from 15.4–303.2
 441 mgC m⁻² d⁻¹, from 9.9–280.8 mgC m⁻² d⁻¹ and from 1.8–29.3 mgC m⁻² d⁻¹, respectively (Fig. 6, Appendix B.4).
 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
 444 2). Habitat comparisons highlighted that non-selective deposit feeders and epigrowth feeders had much higher
 445 inputs of microphytobenthos in the mudflats and seagrass beds than in the sandflat SR. Lastly, benthic
 446 copepods had a lower relative carbon input from microphytobenthos in seagrass MO than in other habitats.

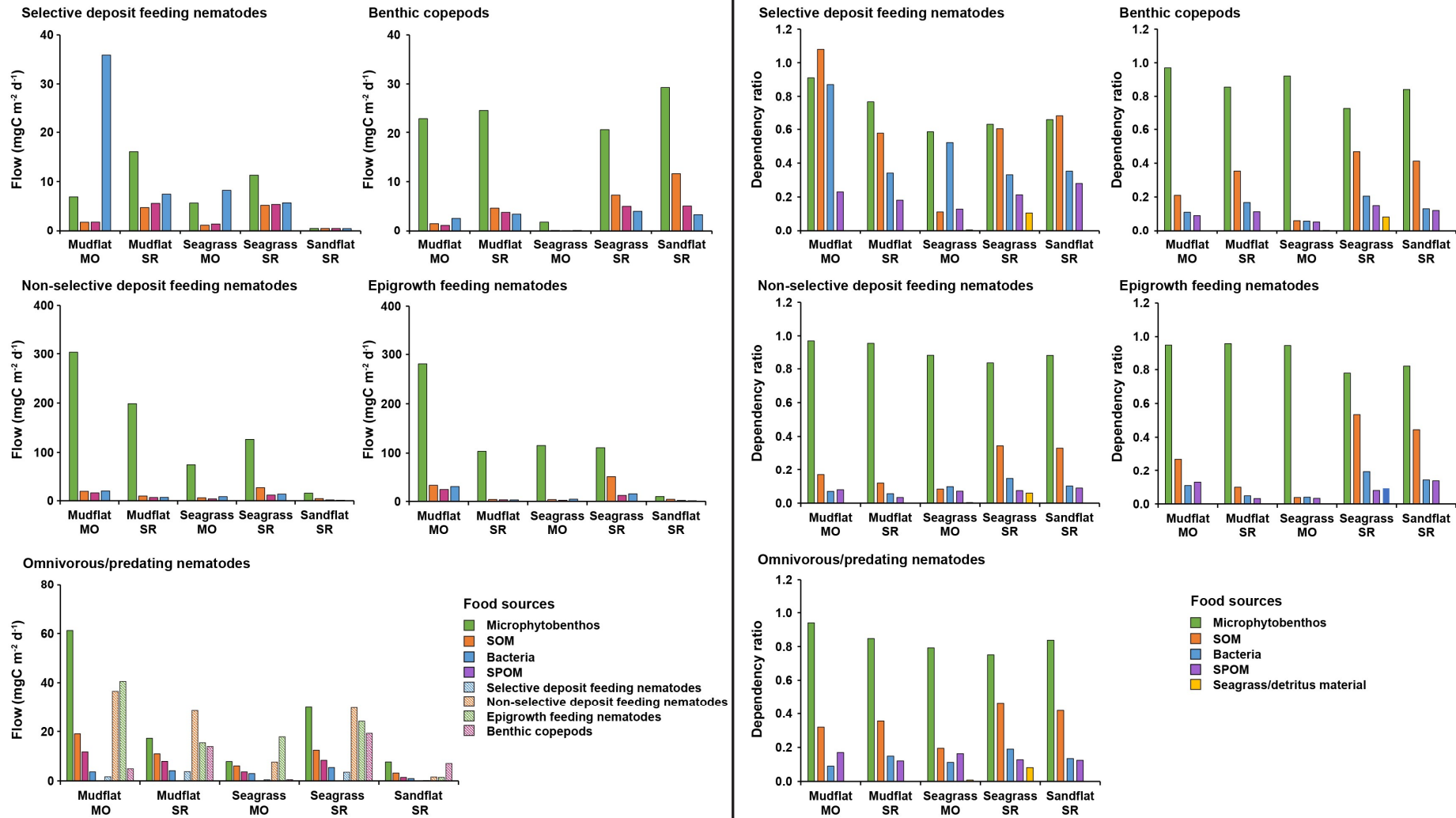
447 Second, selective deposit feeding nematodes relied on more variable food sources (Fig. 6, Appendix
 448 B.4). They relied mostly on bacteria in the Marennes-Oléron Bay habitats (8.2–35.9 mgC m⁻² d⁻¹), whereas
 449 they mostly used microphytobenthos in the Sylt-Rømø Bight habitats (0.5–16.1 mgC m⁻² 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).

454 Third, omnivorous/predating nematodes relied on microphytobenthos (7.8–61.2 mgC m⁻² d⁻¹) as well
 455 as on other meiofauna (10.3–83.6 mgC m⁻² d⁻¹) (Fig. 6, Appendix B.4), as also demonstrated by their relatively
 456 higher omnivory index (0.26 to 0.30, Table 2). Still, dependency ratios demonstrated that omnivores/predators
 457 depended mostly on carbon of microphytobenthos origin in all habitats with ratios ranging from 0.75 (seagrass
 458 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
 460 sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR).

	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

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Figure 6. Flows of carbon (mgC m⁻² d⁻¹) 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).

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

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.

	Primary production (mgC m ⁻² d ⁻¹)				
	Mudflat MO	Mudflat SR	Seagrass MO	Seagrass SR	Sandflat SR
Microphytobenthos	1161.9	1023.1	1043.1	836.6	774.4
	<i>68.4%</i>	<i>81.2%</i>	<i>81.3%</i>	<i>47.3%</i>	<i>63.4%</i>
Phytoplankton	536.0	237.4	194.2	247.5	446.5
	<i>31.6%</i>	<i>18.8%</i>	<i>15.1%</i>	<i>13.9%</i>	<i>36.6%</i>
Seagrass	-	-	45.1	685.3	-
			<i>3.5%</i>	<i>38.8%</i>	
Secondary production (mgC m ⁻² d ⁻¹)					
Bacteria	96.8	313.2	41.3	317.5	147.7
Meiofauna	34.9	30.6	14.5	28.4	13.6
Macrofauna	8.8	41.3	19.8	3.3	6.8
Production/biomass ratio (d ⁻¹)					
Meiofauna	0.03	0.28	0.04	0.08	0.08
Macrofauna	0.007	0.002	0.003	< 0.001	< 0.001

488

489 **3.3.2. Secondary production**

490 Production of macrofauna, ranging 3.3 (seagrass SR) to 41.3 mgC m⁻² d⁻¹ (mudflat SR), was more
491 variable than that of meiofauna, which ranged from 14.5 (seagrass MO) to 34.9 mgC m⁻² d⁻¹ (mudflat MO)
492 (Table 3). Meiofauna production was higher than those of macrofauna in mudflat MO, seagrass SR and sandflat
493 SR, and relatively similar in mudflat SR and seagrass MO. Meiofauna P/B ratios were much higher than those
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⁻¹). 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*

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

512

513 The carbon flows from meiofauna to higher trophic levels (12.6–39.2 mgC m⁻² d⁻¹) were relatively
514 similar to or slightly higher than those from macrofauna (18.3–30.1 mgC m⁻² d⁻¹; Table 4) in all habitats, except
515 for mudflat SR. In these habitats, meiofauna represented between 40% and 66% of the carbon requirements of
516 higher trophic levels. On the contrary, in the mudflat SR the carbon flows to higher trophic levels were mainly
517 originating from macrofauna (137.1 mgC m⁻² d⁻¹; 74%) with much lower contributions for meiofauna
518 (49.1 mgC m⁻² d⁻¹; 26%).

519

520 Large differences were also observed between habitats when comparing the diversity of organisms
521 relying on meiofauna (Table 4). In the mudflat MO flows from meiofauna were equally divided over benthic
522 omnivorous macrofauna (59%) and benthic fish (41%), whereas flows from meiofauna to higher trophic levels
523 mostly ended up in one single consumer group in other habitats, benthic omnivorous macrofauna (99%) in
524 seagrass MO and benthic fishes (> 95%) in Sylt-Rømø Bight habitats. Macrofauna of the seagrass SR and
525 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⁻² d⁻¹) in the mudflats,
 530 seagrass beds, and sandflat of the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). Higher trophic levels are:
 531 benthic omnivorous macrofauna (BOM), benthic fish (BFI) and carnivorous birds (CBR).

	Mudflat MO		Mudflat SR		Seagrass MO		Seagrass SR		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

532

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

542

543 **Table 5.** Relative contributions of respiration and egestion to the total meiofauna and macrofauna outflows (%) in the
 544 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										
<i>Outflow</i>	Respiration					Egestion				
	<i>Trophic level</i>	II	III	IV	V	VI	II	III	IV	V
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	-	-

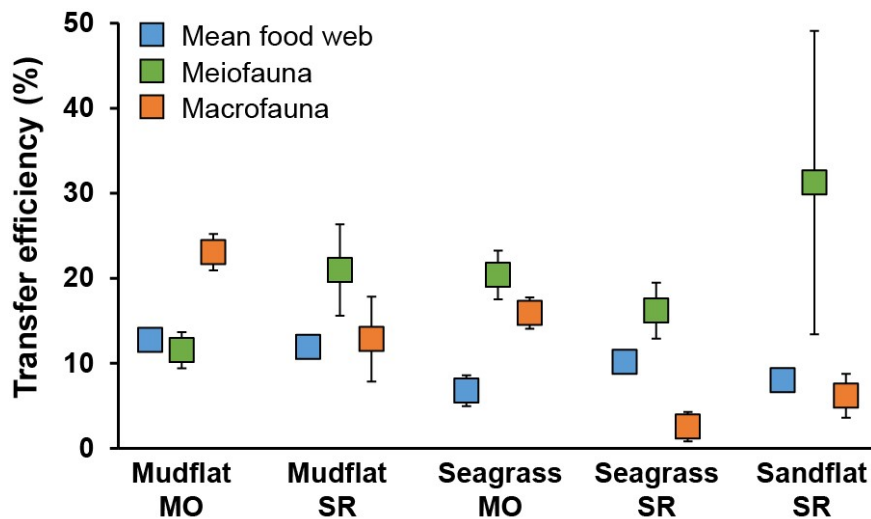
Macrofauna										
<i>Outflow</i>	Respiration					Egestion				
	<i>Trophic level</i>	II	III	IV	V	VI	II	III	IV	V
Mudflat MO	27.0	29.3	29.6	29.6	29.6	48.3	50.1	50.4	50.4	50.4
Mudflat SR	39.7	37.4	42.6	45.0	-	56.5	58.2	51.9	54.8	-
Sandflat SR	48.0	41.6	29.1	29.4	-	45.1	56.0	67.5	68.2	-

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	-

546

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
549 higher transfer efficiencies (TEs) of meiofauna (16.2–31.3%) than of macrofauna (2.5–15.9%) in all habitats
550 except in mudflat MO (Fig. 7). TE of meiofauna (11.5 ± 2.1 %) in mudflat MO was much lower than TE of
551 macrofauna (23.1 ± 2.1 %). Different patterns were observed for the mean transfer efficiencies (MTEs) of
552 integer trophic levels II to IV (Fig. 7), with higher MTEs in mudflat MO (12.7 ± 1.2 %), mudflat SR
553 (11.9 ± 2.2 %) and seagrass SR (10.2 ± 2.2 %) compared to sandflat SR (8.0 ± 2.0 %) and seagrass MO
554 (6.8 ± 3.6 %).

555



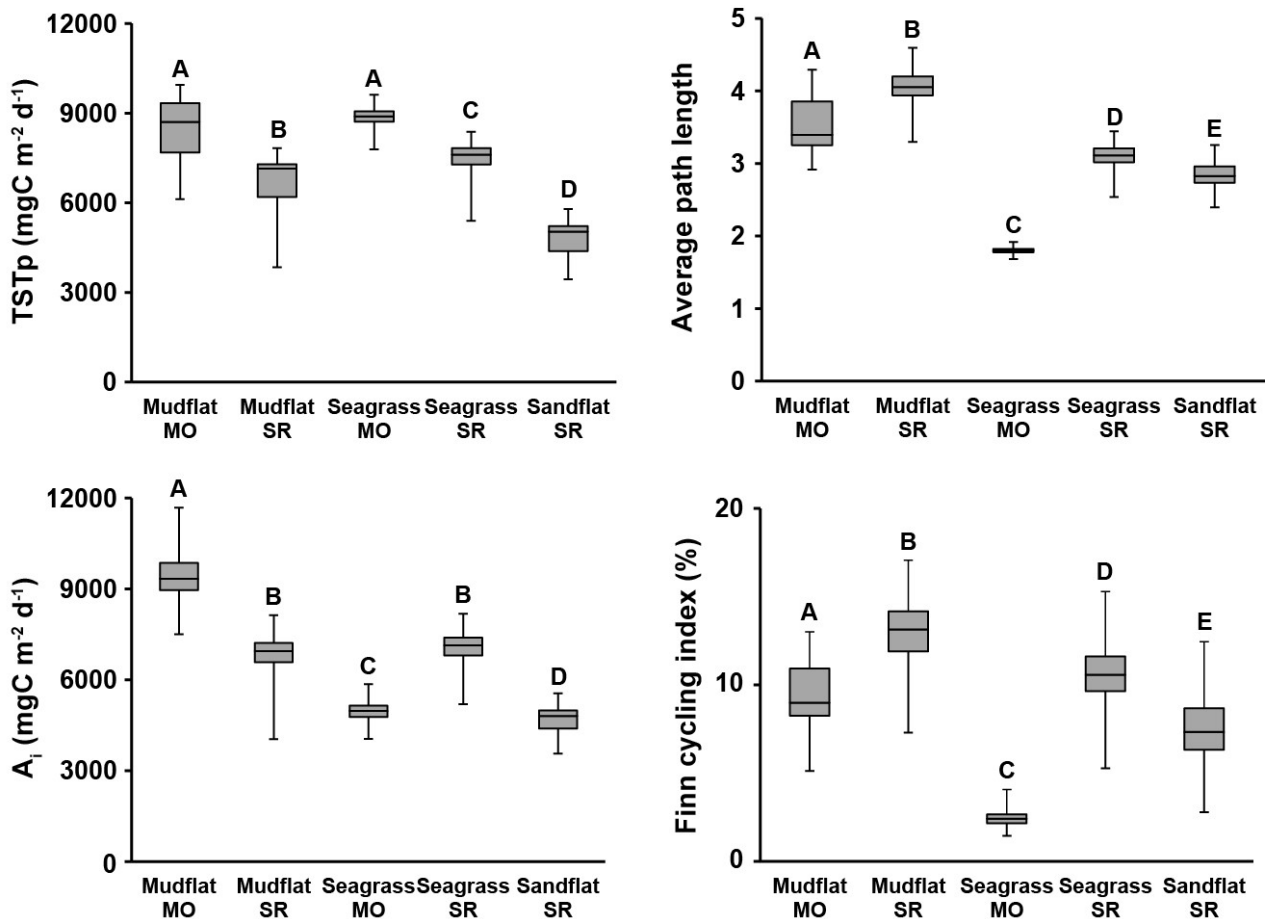
556

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

561

562 3.4. Network analysis

563 The food webs of the five studied habitats presented a distinct structure, with an obvious discrimination
564 of the seagrass MO. Seagrass MO had among the lowest values for the average path length (APL), internal
565 ascendancy (A_i) and Finn cycling index (FCI), whereas the total system throughput (TSTp) was among the
566 highest compared to all other habitats (Fig. 8). Mudflat MO and mudflat SR were characterized by the longest
567 food chain (i.e. high APL), highest internal organization (i.e. high A_i), 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.



571
 572 **Figure 8.** Ecological network analysis indices for the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay
 573 (MO) and the Sylt-Rømø Bight (SR): total system throughput (TSTp; top left), average path length (top right), internal
 574 ascendency (A_i; bottom left) and Finn cycling index (bottom right). Letters displayed above boxes indicate groups of
 575 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**

579

580 **4.1.1. Reliance on microphytobenthos**

581 As evidenced by the five different models, meiofauna mostly relied on microphytobenthos in all
 582 habitats, whereas macrofauna relied on a wider variety of food sources. Carbon flows from microphytobenthos
 583 indeed represented between 60 (i.e. 62.8 mgC m⁻² d⁻¹) and 81% (i.e. 674.9 mgC m⁻² d⁻¹) of the total flows
 584 between food sources and meiofauna in the different studied habitats. The high reliance of meiofauna on
 585 microphytobenthos confirmed the outcomes of the combined trophic marker approach carried out on the same
 586 habitats by van der Heijden et al. (2019). This major role of microphytobenthos in both ecosystems and all
 587 habitats highlights the importance of this food source compared to other primary producers, even when the
 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
592 days) and high production (774–1162 mgC m⁻² d⁻¹). More importantly so, these rates (Degré et al., 2006) and
593 microphytobenthos biomass (Lebreton et al., 2009; van der Heijden et al., 2018) are generally much more
594 constant all year round than those of other potential sources, resulting in a reliable food source constantly
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).
602 Meiofauna are known to actively migrate towards (Moens et al., 1999a) or selectively feed on high quality
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
607 meiofauna feeding types, as demonstrated by the flows and network properties derived from the five habitats
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
613 mgC m⁻² d⁻¹). A slightly lower reliance on microphytobenthos as observed on the seagrass bed and sandflat of
614 the Sylt-Rømø Bight (56–70%) may be related to differences in terms of availability, e.g. no biofilm in the
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
618 morphology of the buccal cavity of epigrowth feeders, optimized for the consumption of diatoms (Moens and
619 Vincx, 1997a; Wieser, 1953). Epigrowth feeder buccal cavities are fitted with a tooth used to pierce diatoms,
620 making it easier to assimilate them.

621

622 Second group: omnivorous/predating nematodes largely relied on carbon of microphytobenthos origin
623 as indicated by their dependency ratios (0.77–0.94). This associated to their relatively higher omnivory index
624 (0.26–0.30) compared to other groups of meiofauna highlighted that these consumers relied both directly and
625 indirectly on microphytobenthos. This indirect reliance on microphytobenthos was linked to the predation on
626 meiofauna from lower trophic groups (i.e., non-selective deposit feeders and epigrowth feeders), themselves
627 feeding on microphytobenthos (Rzeznik-Orignac et al., 2008; Vafeiadou et al., 2014; van Oevelen et al., 2006).

628

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,
631 SOM, as well as microphytobenthos. The buccal cavity morphology of selective deposit feeders is adapted to
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,
641 productivity) must be considered in addition to biomass when carrying out food web studies. These results
642 also highlight the importance of considering the different feeding types of meiofauna when determining trophic
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**

657

658 *4.2.1. Evidences about important role of meiofauna*

659 A large proportion of the energy passed through meiofauna in the different soft-bottom habitats
660 (i.e. 31.2% on average), besides some important differences: minimum of 10% in sandflat SR and maximum
661 of 61% in mudflat MO. The important role of meiofauna as a trophic mediator between primary producers and
662 higher consumers was highlighted by the flows to (116–952 mgC m⁻² d⁻¹) and from meiofauna (13–49
663 mgC m⁻² d⁻¹). These flows are in the range of flows to (47–1290 mgC m⁻² d⁻¹) and from macrofauna (18–137
664 mgC m⁻² d⁻¹). 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
668 macrofauna. At the ecosystem scale, more energy passed through macrofauna (65–70%) when compared to
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
675 mudflat of the Marennes-Oléron Bay (61%) compared to all other habitats (10–32%). Consequently, a much
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
678 related to the close connection between meiofauna and microphytobenthos, which is very productive and
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).

683

684 4.2.2. *How can meiofauna play this important role?*

685

686 The important role of meiofauna in the functioning of the five habitats is very likely related to their
687 high production ($14\text{--}35\text{ mgC m}^{-2}\text{ d}^{-1}$) and P/B ratios ($0.03\text{--}0.28\text{ d}^{-1}$). Indeed, meiofauna production was either
688 similar (in the seagrass MO and in the mudflat SR), or even higher (2 to 9 times, in all other habitats), than
689 macrofauna production. These productions were generally in agreement with previous estimations (10 to
690 $80\text{ mgC m}^{-2}\text{ d}^{-1}$) (Chardy and Dauvin, 1992; Danovaro et al., 2002; Escaravage et al., 1989). The high
691 production of meiofauna combined with similar and/or lower biomass compared to macrofauna resulted in
692 much higher P/B ratios than for the macrofauna, i.e. from 4 to 1000 times. Higher production and P/B ratios
693 of meiofauna compared to macrofauna is known to be related to their higher turn-over rates (at least five times
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).

696 Meiofauna also play a major role in the different studied food webs as trophic mediator, as confirmed
697 by the transfer efficiency of meiofauna (i.e. 20% on average) which was higher than the transfer efficiency of
698 macrofauna (i.e. 12% on average) and much higher than the mean transfer efficiency of the whole food webs
699 (i.e. 10% on average). Meiofauna also have a high nutritional value (Coull, 1999) and their concentration in
700 the surface sediment layer make them a very available and valuable food source to consumers
701 (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
705 salt marshes (Lebreton et al., 2013, 2011b). As a result, meiofauna can help fulfil the nutritional needs of
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
713 efficiency (MTE: 10.2–12.7%; Heymans et al., 2014), associated with the highest internal ascendancy
714 (A_i : 6946–9339 mgC m⁻² d⁻¹; Baird et al., 2007) and the highest average path length (APL: 3.1–4.1;
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_i . Thus,
717 the link between a predator and its main prey items is based on preferences whereas indirect consumption on
718 the same prey is limited. In this way the losses of carbon by respiration, egestion and export are limited, as
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
721 (836–996 mgC m⁻² d⁻¹), that fulfill the energy requirements of organisms, prevent them from diversifying their
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
725 from this high-quality food source to primary consumers (607 mgC m⁻² d⁻¹). However, the energy was very
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
730 generally assimilate large proportions of the flows coming from high-quality food sources.

731 The link between food web efficiency and assimilation of high-quality primary food sources is less
732 clear in seagrass MO. Low MTE (6.8%), A_i (4974 mgC m⁻² d⁻¹) and APL (1.8) clearly demonstrate a low
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⁻² d⁻¹). 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–

739 13.1%). This low recycling may be related to the poorly used detrital pool in seagrass MO (26%) when
740 compared to other habitats (62–80%). The food web efficiency might have been affected by this low recycling,
741 since food web efficiency includes both the efficiency of energy transfers from primary producers to herbivores
742 and then carnivores as well as from detrital material to detritivores and then carnivores. Therefore, the low
743 consumption of detritus by detritivores might have an indirect effect on the lower transfer efficiency of trophic
744 level II and III in seagrass MO.

745 **5. Conclusion**

746 The analysis of five coastal food web models highlighted the importance of the trophic pathway
747 between microphytobenthos and meiofauna in soft-bottom intertidal habitats. Microphytobenthos was indeed
748 the most important primary producer and the most important food resource for meiofauna in these habitats
749 (63–675 mgC m⁻² d⁻¹), even when high loads of seagrass material were present. The important role of
750 meiofauna was highlighted by their high throughput (average: 31.2%), high production (14–35 mgC m⁻² d⁻¹)
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
753 in the functioning of intertidal soft-bottom habitats. On the contrary, the slower-growing macrofauna are more
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.

759
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
763 revealed a high reliance on microphytobenthos in all habitats, through direct (herbivory) or indirect (carnivory)
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
766 carbon flow justify the partitioning of meiofauna into different compartments, as traditionally done for
767 macrofauna in most food web studies. We therefore argue that feeding types of meiofauna should be considered
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.

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787

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