

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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ABSTRACT

Meiofauna are known to have an important role on many ecological processes, although, their role in food web dynamics is often poorly understood, partially as they have been an overlooked and under sampled organism group. Here, we used quantitative food web modeling to evaluate the trophic relationship between meiofauna and their food sources and how meiofauna can mediate the carbon flow to higher trophic levels in five contrasting soft-bottom intertidal habitats (including seagrass beds, 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 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 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 represented the largest flow in all habitats and resulted in high production of meiofauna independent of 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 sources, with varying contributions of bacteria, microphytobenthos and sediment organic matter. Ecological network analyses (e.g. cycling, throughput and ascendancy) of the modeled systems highlighted the close positive relationship between the food web efficiency and the assimilation of high-quality food sources by primary consumers, e.g. meiofauna and macrofauna. Large proportions of these flows can be attributed to trophic groups of meiofauna. The sensitivity of the network properties to the representation of meiofauna in the models leads to recommending a greater attention in ecological data monitoring and integrating meiofauna into food web models.

Keywords: food web model; linear inverse model; meiofauna; microphytobenthos; stable isotope mixing models; intertidal habitats

1. Introduction

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 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 Murison, 1973), and to the methodological issues when studying them, due to their small size (Carman and Fry, 2002; Moens et al., 2005). Methodological improvements (Leduc et al., 2009; Vafeiadou et 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 deep-sea ecosystems, the metabolic importance of meiofauna can sometimes overtake that of macrofauna—a compartment which has been highly studied unlike meiofauna—(Giere, 2009; Schwinghamer et al., 1986) with meiofauna’s metabolic rate being reported 21 times higher than that of macrofauna in a tidal flat (Kuipers et al., 1981). Nowadays meiofauna are known to take part in many ecological functions, e.g., sediment stabilization, biochemical cycling and food web dynamics (Schratzberger and Ingels, 2018). A better comprehension of ecological functions of meiofauna in coastal food webs requires considering meiofauna at the ecosystem scale, following a holistic approach. Indeed, because meiofauna mediates flows of organic matter between primary producers and higher trophic level consumers (Leguerrier et al., 2003; Pascal et al., 2019), assessments about the role of meiofauna should consider two aspects: (1) the interaction between meiofauna and their food sources and (2) the fate of meiofauna.

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., 2005; Vafeiadou et al., 2014) and quantifications of carbon fluxes from lower trophic levels to meiofauna are scarce (Danovaro et al., 2002; van Oevelen et al., 2006). In bare sediment systems, meiofauna have been reported to feed mainly on microphytobenthos (Moens et al., 2014; Rzeznik-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 abundant taxon of meiofauna, have a very diverse feeding behavior, i.e., herbivory, bacterivory, or omnivory/carnivory (Wieser, 1953), and can be classified into various trophic groups. Feeding behavior and abundances of nematodes from these trophic groups might change depending on availability, quantity and quality of food sources (Giere, 2009; Moens et al., 2013). Non-selective deposit feeders for example feed on various food sources such as microphytobenthos, bacteria and detritus, and their diet changes depending on the availability of these food sources (Moens and Vincx, 1997a; Rzeznik-Orignac et al., 2008). It has also been demonstrated that meiofauna, especially benthic copepods, may control microphytobenthos biomass (Blanchard, 1991; Montagna et al., 1995) as well

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

Many unknowns remain about the fate of meiofauna in benthic food webs. For a long time there 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 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⁻² year⁻¹; Chardy and Dauvin, 1992; Danovaro et al., 2002) due to their elevated turnover rate (Kuipers et al., 1981), despite their general 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 fatty acids (Watanabe et al., 1983), are sufficient to fulfill a predator's needs (Coull, 1999), explaining their preference as prey for higher trophic levels (Danovaro et al., 2007). However, knowledge about carbon fluxes from meiofauna to higher trophic levels and determination of their transfer efficiency remain scarce (Danovaro et al., 2002; Schratzberger and Ingels, 2018). Danovaro et al. (2007) estimated that more than 75% of the total meiofauna production is channeled to higher trophic levels in soft-bottom habitats. However, meiofauna consists of a diversity of organisms which have different feeding strategies (i.e. trophic groups; Wieser, 1953). The fate of these trophic groups in food webs most likely varies due to their relative biomasses among meiofauna, which can differ a lot between 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 a need to consider meiofauna trophic groups in food web assessments, and inter-habitat comparison can help at understanding how changes in trophic groups' biomass affect the role of meiofauna in coastal food webs.

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, temporally integrated snapshot of the complete food web and its flows using a combination of field and relevant literature data (Niquil et al., 2011; Vézina and Platt, 1988) and it is a powerful method in estimating unmeasured flows within an ecosystem (Degré et al., 2006; Leguerrier et al., 2003; Pacella et al., 2013). Combined with the Markov chain Monte Carlo method, it provides the probability 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 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 making (de la Vega et al., 2018; Schückel et al., 2018). One of these food web characteristics, the efficiency with which carbon energy is transferred and assimilated, can be linked to the quality and

quantity of primary food sources (Marcarelli et al., 2011). The lower trophic levels of food webs (e.g. meiofauna and macrofauna) have the strongest response to changes in food quality whereas the 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, 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 typically been the case for meiofauna as they are described as a single compartment in most recent steady-state mass-balanced food web models, or at best are split into nematodes and benthic copepods (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 studies on single specimens (Herman and Vranken, 1988; Vranken and Heip, 1986). Therefore, separating meiofauna into major trophic groups is necessary if a better understanding of their 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 consumption flows of meiofauna trophic groups in food web models (Pacella et al., 2013; van Oevelen et al., 2010).

Using food web models, the general aim of this study was to determine how the roles of meiofauna and the food web efficiency can differ in coastal ecosystems depending on the composition 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 relate to those of macrofauna, and (3) the relationship between the food web efficiency and the composition of food sources. Finally, we provide recommendations on including meiofauna in future food web modeling studies. In this aim, five contrasting different intertidal habitats in terms of food sources and meiofauna group composition—providing several food web scenarios—were compared: habitats influenced by inputs of continental organic matter vs. habitats mostly influenced by marine inputs, habitats characterized by high loads of detrital matter vs. habitats with low loads of detrital matter, habitats with different communities of benthic microalgae. The food web models of these intertidal habitats of the Marennes-Oléron Bay and of the Sylt-Rømø Bight were compared using quantitative flow values and food web properties.

2. Material and methods

2.1. Study sites and carbon flow networks

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

were compared to determine how the role of meiofauna differs depending on the composition of food 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 detrital matter (i.e. seagrass bed), one characterized by a lower load of detrital matter and by a community of microphytobenthos dominated by epipellic diatoms (i.e. mudflat), and one characterized 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 of these habitats in two different ecosystems: one influenced by continental inputs of organic matter, 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 Bight in Germany (Asmus and Asmus, 2005, 1985). As sandflats are not a typical habitat in the Marennes-Oléron Bay, this habitat could not be considered in this ecosystem. As a result, seagrass beds and mudflats were studied in both the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR), while 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 SR) (Fig. 1). These different habitats are characterized by different plant and animal communities that were previously described: seagrass MO (Lebreton, 2009; Lebreton et al., 2009), mudflat MO (Haubois et al., 2005; Rzeznik-Orignac et al., 2003), Sylt-Rømø Bight habitats (Asmus and Asmus, 2000, 2005, 1998, 1993; Asmus and Bauerfeind, 1994; Gätje and Reise, 1998), and additional information can be found in van der Heijden et al. (2018).

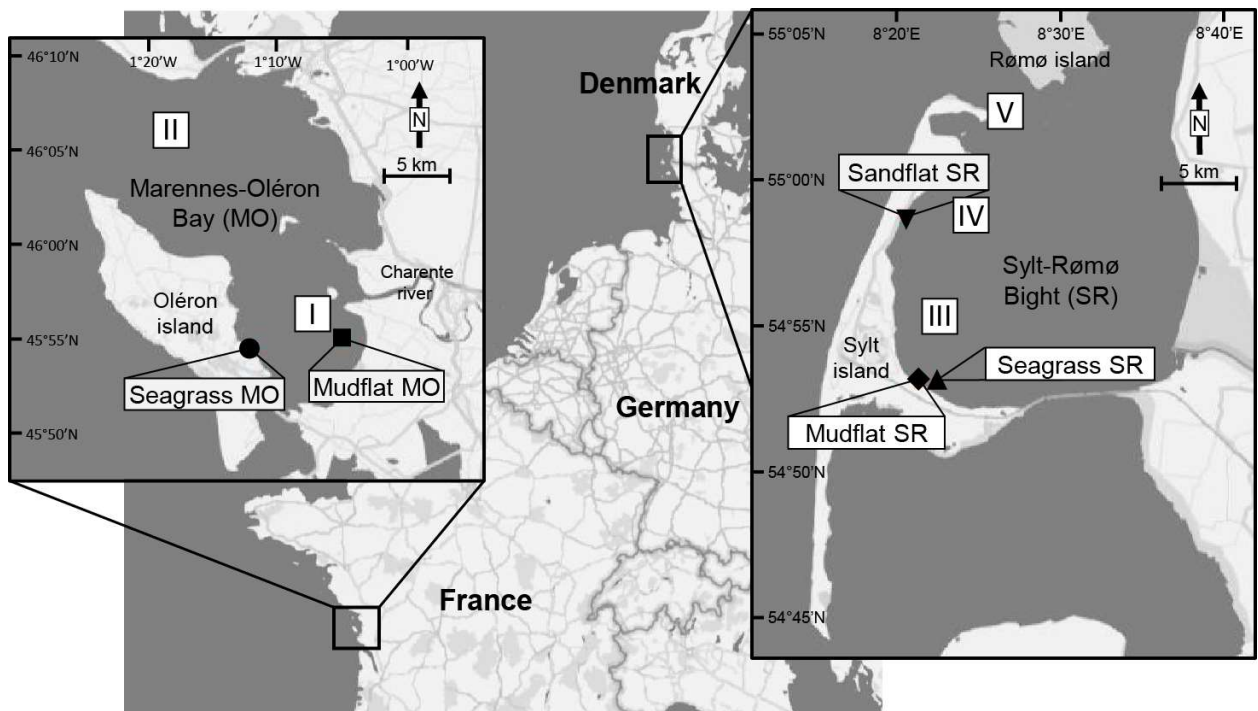


Figure 1. Study sites in the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) along the European Atlantic coast. Pelagic sampling stations, where samples for suspended

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

2.2. Linear inverse model construction

Linear inverse ecosystem models with Markov chain Monte Carlo (LIM-MCMC) were built to determine carbon flows in the five habitats on a daily basis ($\text{mgC m}^{-2} \text{d}^{-1}$) using the R software (R Core Team, 2019). The flow estimations originated from annual averages but are expressed as daily averages here. Annual averages were chosen in order to smoothen the daily and seasonal fluctuations that occur 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 to construct the flow networks of these habitats originated from established models (Baird et al., 2007; Leguerrier et al., 2003; Pacella et al., 2013; Saint-Béat et al., 2014, 2013). New models focused on meiofauna and thus represented the diversity of this group at a higher resolution. Consequently, meiofauna was partitioned into five compartments according to their trophic group: selective deposit feeding nematodes, non-selective deposit feeding nematodes, epigrowth feeding nematodes, omnivorous/predating nematodes and benthic copepods. Recent *in situ* data on biomass (Table 1; van der Heijden et al., 2018) and on diets (used in stable isotope mixing models; van der Heijden et al., 2019) were used to constrain food web models. The prior established models aggregated meiofauna into two compartments, allowing us to compare the effects of this two-compartment partitioning versus 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 order to have a homogeneous topology of food web models (i.e. number of compartments), required when comparing different systems (Table 1; Baird and Ulanowicz, 1993).

Table 1. Abbreviations (Abbr.) and biomass of compartments used in the food web models of the mudflats, seagrass beds and sandflat in the Marennnes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). NA = no data 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

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.

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

The models of habitats from the Sylt-Rømø Bight (i.e. mudflat SR, seagrass SR and sandflat 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 (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 inequalities by increasing or reducing the equality value with 30%. These ranges correspond with seasonal fluctuations observed for macrofauna by Asmus (1987) and were considered to be the most appropriate estimations based on sensitivity analyses from Guesnet et al. (2015).

2.2.2. *Complementary constraints: outputs of isotope mixing models*

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 feeders and omnivores/predators) and constraints were calculated for these new compartments based 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 benthic copepods and trophic groups of nematodes in all habitats. We used the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean and standard deviation) of the food sources (i.e. suspended particulate organic matter (SPOM), sediment organic matter (SOM) and microphytobenthos from van der Heijden et al. (2019), those of sulfide-oxidizing bacteria from Vafeiadou et al. (2014)) and meiofauna consumers (i.e. benthic 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 by the mixing models are reported here and were used as constraints (lower and upper limits) in the food web models, following the approach of Pacella et al. (2013).

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):

$$\text{Equality equation: } A * x = b$$

$$\text{Inequality equation: } G * x \geq h$$

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.

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.

2.4.1. Food web indices and ratios

Flows of carbon, omnivory indices and dependency ratios were calculated to determine and analyze trophic relationships between food sources and consumers. Flows of carbon ($\text{mg C m}^{-2} \text{ d}^{-1}$) express trophic relationships between food sources and consumers. Omnivory index (formula in 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 the dependence of a consumer on a food source through both direct and indirect pathways, providing information about the origin of carbon assimilated by each compartment. Because an atom of carbon can go through several compartments before it is consumed by a particular organism, the sum of dependency ratios can exceed the value of 1.0 (Baird and Ulanowicz, 1989).

Production rates, production/biomass ratios and transfer efficiency were computed to determine significance of meiofauna in the carbon transfer through each distinct food web. Production rates were calculated using the export, consumption, egestion and respiration ($\text{Production} = \text{consumption} - \text{egestion} - \text{respiration} - \text{export}$). Production/biomass ratio, an estimation of the activity per biomass unit, was used to determine the activity of a compartment in the habitat. The transfer efficiency was calculated based on inputs, losses due to respiration, exports and outputs as detritus and transfers to higher trophic levels. It highlights the efficiency of the energy transferred from one trophic level to the next (Baird et al., 2004a). Mean transfer efficiency (MTE) was calculated as the geometric mean of 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.

2.4.2. Network analysis indices

Four ecosystem network analysis (ENA) indices were computed: Total system throughput (TSTp), Finn cycling index (FCI), internal ascendancy (A_i) 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

total power generated within the system (Baird et al., 1998). Note the difference between the TSTp and the total system through-flow (TSTf), used by Leguerrier et al. (2003). TSTf, which is the sum of 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, 2004a; Baird and Ulanowicz, 1989; Finn, 1976). Internal ascendancy (A_i) measures the efficiency and definitiveness by which energy is transferred within a food web. Higher A_i highlights increased ecological succession (Baird et al., 2007; Scharler and Baird, 2005). Average path length (APL) defines the average number of compartments through which a unit of energy (i.e. carbon) passes between entering and leaving the food web (Christensen, 1995). This parameter is expected to be higher in food webs with higher flow diversity and cycling (Christensen, 1995; Thomas and Christian, 2001). The indices were calculated from 500,000 estimated flow solutions using the *enaR* package (Lau et al., 2017).

2.5. Statistical methods

In order to test the pairwise difference of index values between the habitats, Cliff's delta statistic 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 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 ecological meaning or sample size alone can be tested by comparing the degree of overlap between the two distributions. Threshold values were used to determine the degree of significance (Romano et al., 2006) with low threshold values indicating a similarity between index values (negligible: $|\delta| < 0.147$ and small $|\delta| < 0.33$) and higher delta values indicating a significant difference between values of both indices (medium $|\delta| < 0.474$ and large $|\delta| > 0.474$).

3. Results

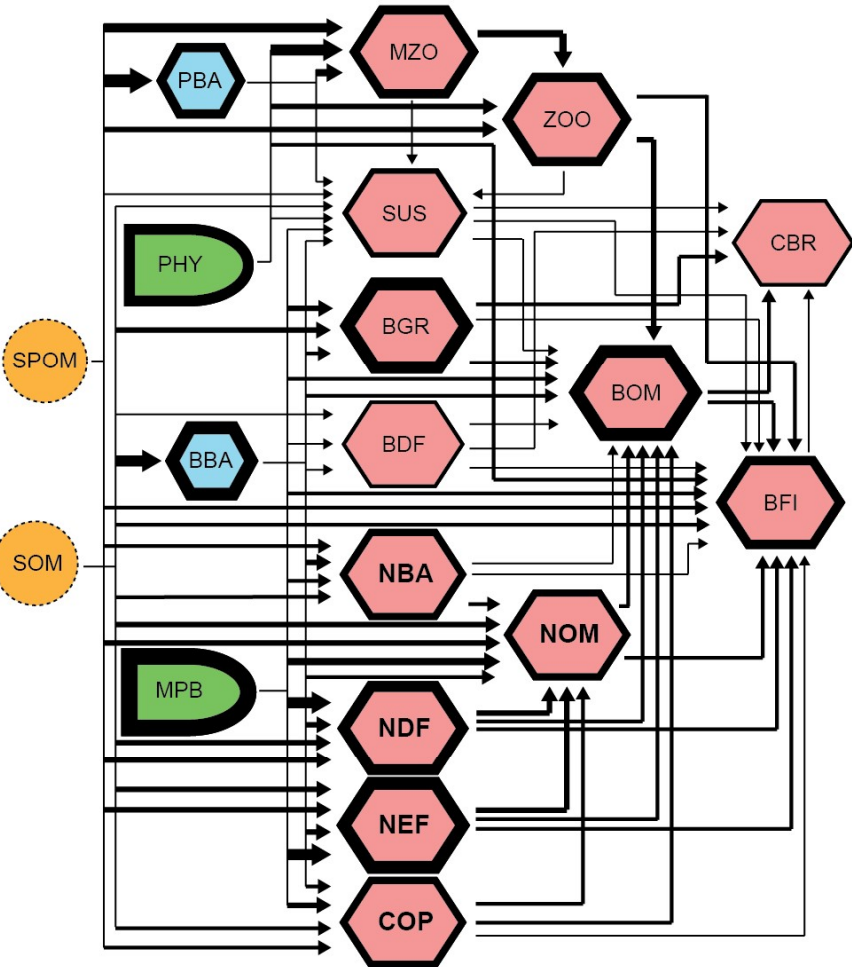
3.1. General characteristics of the food web models

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.

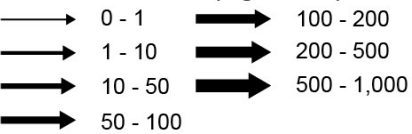
Higher biomass of microphytobenthos, benthic bacteria, pelagic bacteria, zooplankton and benthic fish were observed in the habitats of the Marennes-Oléron Bay, whereas biomass of seagrass, phytoplankton, benthic deposit feeders, suspension feeders and carnivorous birds were higher in the habitats of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

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 (1352.1 mgC m⁻²). Moderate proportions of carbon flowed through meiofauna in the seagrass MO (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 flowed through macrofauna compartments (64.5–69.8%, Fig. 3 and 4) in the Sylt-Rømø Bight habitats, 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 similar, the carbon distribution is skewed in favor of meiofauna (Fig. 2). In the seagrass MO moderate proportions of carbon flowed through macrofauna (17.8%, Fig. 2) even though its biomass was 15 times higher than meiofauna.

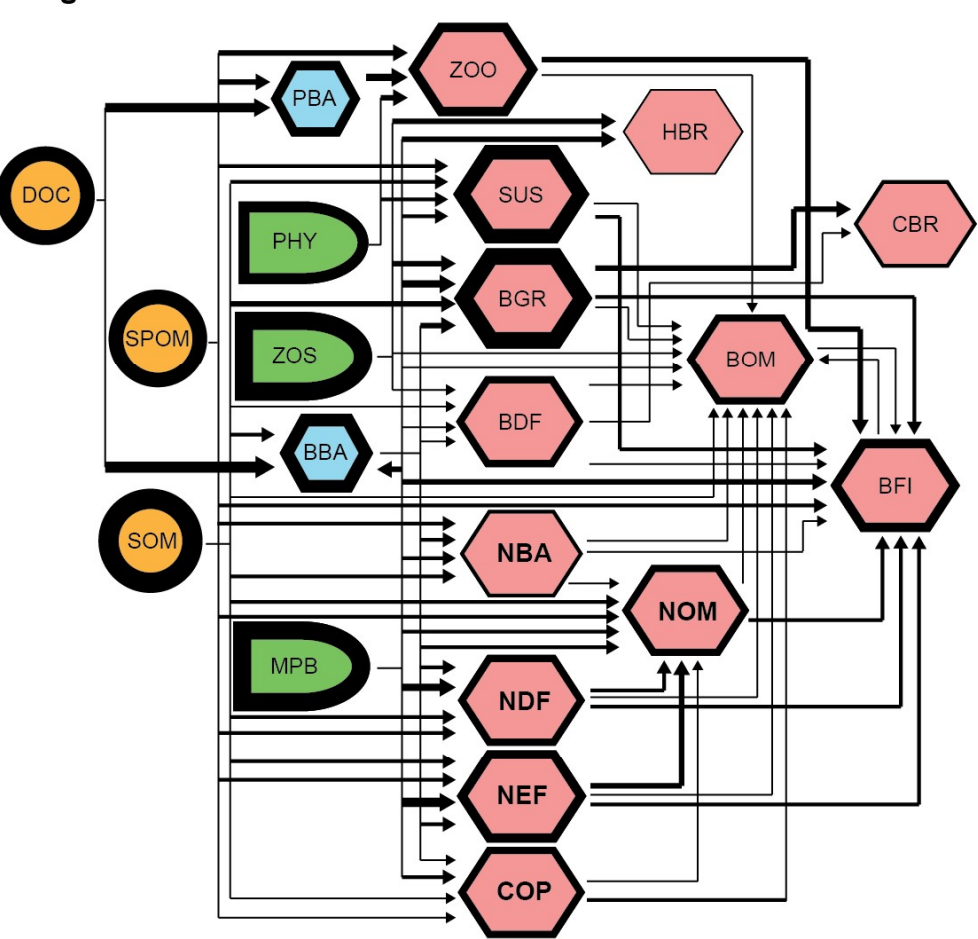
Mudflat MO



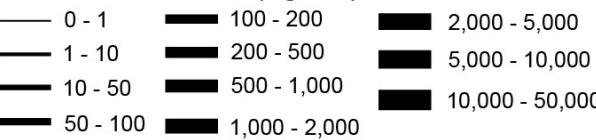
Flows of carbon ($\text{mgC m}^{-2} \text{d}^{-1}$)



Seagrass MO

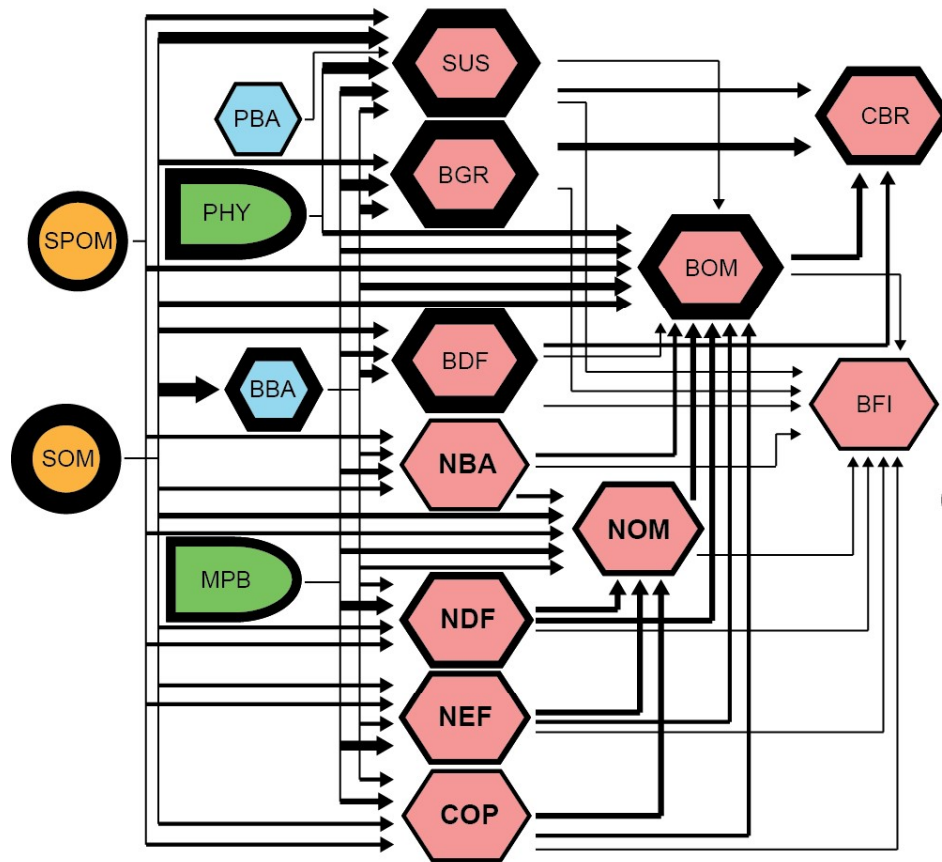


Biomass (mgC m^{-2})

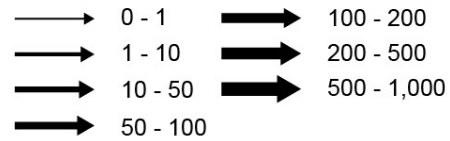


367 **Figure 2.** Food webs of the mudflat and seagrass bed in the Marennes-Oléron Bay (MO) obtained by linear inverse modeling. The mudflat MO food web model consists of
368 two primary producer compartments (green), two bacteria compartments (blue), two detrital compartments (orange) and 13 consumer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

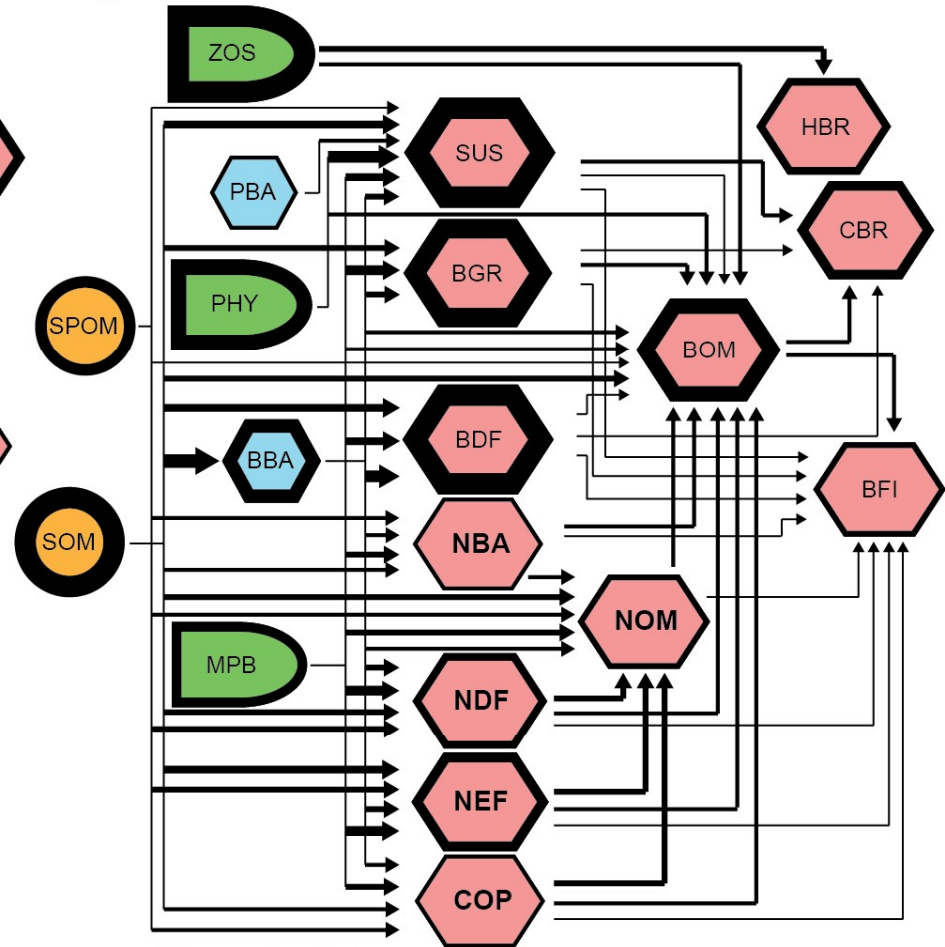
Mudflat SR



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



Seagrass SR



Biomass (mgC m^{-2})

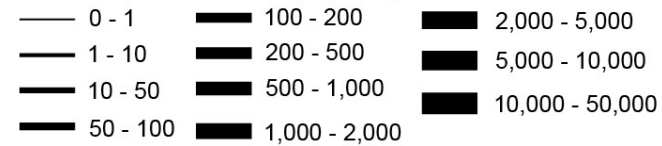


Figure 3. Food webs of the mudflat and seagrass bed in the Sylt-Rømø Bight (SR) obtained by linear inverse modeling. The mudflat SR food web model consists of two primary producer compartments (green), two bacteria compartments (blue), two detrital compartments (orange) and 11 consumer compartments (pink). The seagrass SR food web model consists of three 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, HBR = herbivorous birds, MPB = microphytobenthos, 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, ZOS = *Zostera noltii* material.

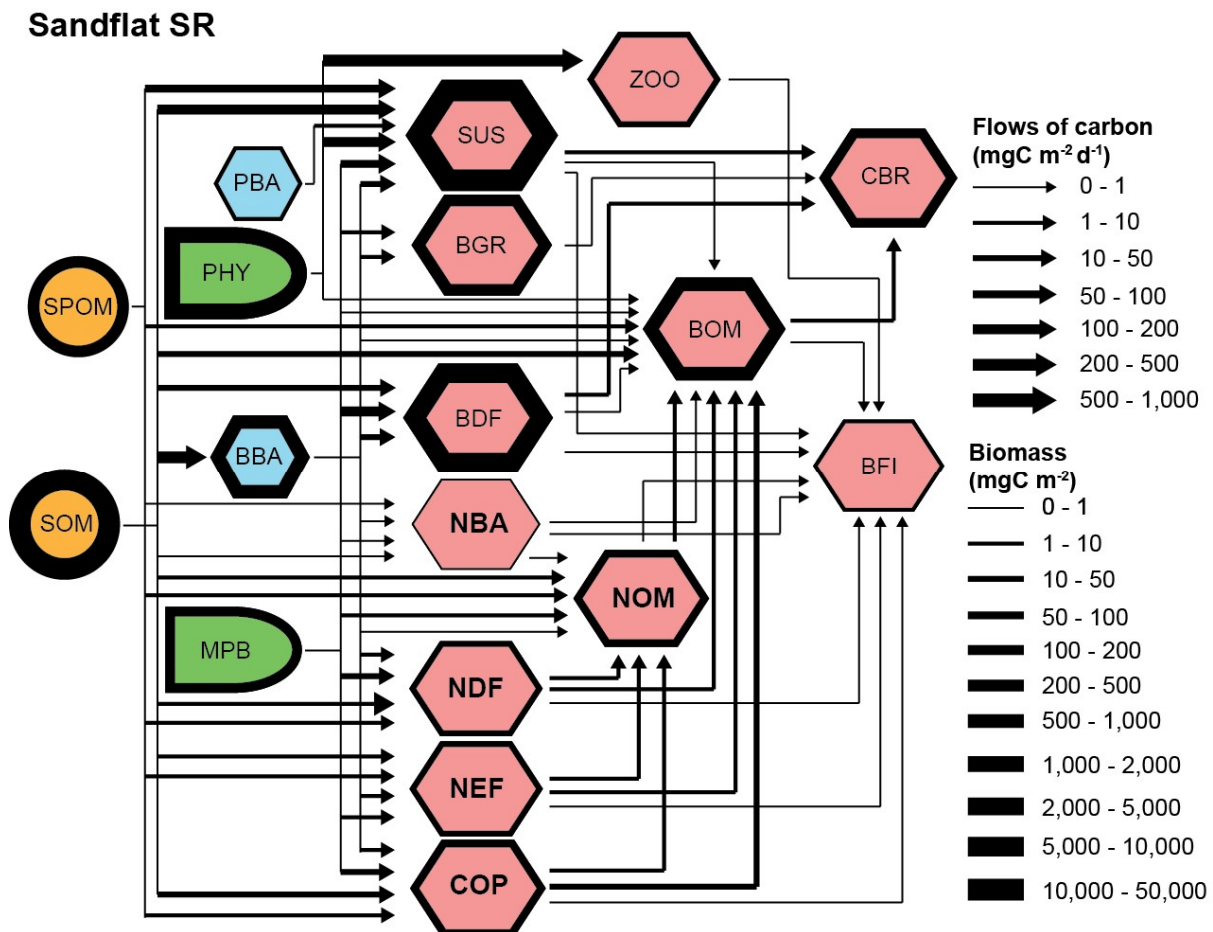


Figure 4. Food web of the sandflat in the Sylt-Rømø Bight (SR) obtained by linear inverse modeling. This model consists of two primary producer compartments (green), two bacteria compartments (blue), two detrital compartments (orange) and 12 consumer compartments (pink). Arrow thickness indicates the 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.

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

3.2.1. *Meiofauna and macrofauna feeding behavior*

Meiofauna and macrofauna had different feeding behaviors as meiofauna relied merely on a single 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⁻² d⁻¹ (mudflat MO) (Fig. 5). Meiofauna secondary 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), when pelagic food sources (i.e. SPOM and phytoplankton) were poorly used by meiofauna. Macrofauna, on 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 MO) to 398.2 mgC m⁻² d⁻¹ (mudflat SR). Consumption of bacteria, phytoplankton and SOM by macrofauna was much higher in habitats of the Sylt-Rømø Bight (bacteria: from 144.5 to 288.3 mgC m⁻² d⁻¹, phytoplankton: 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 (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 mgC m⁻² d⁻¹). Seagrass material were used very little by meiofauna and macrofauna.

Comparisons of flows between macrofauna and meiofauna highlighted the large differences between habitats. In the Marennes-Oléron Bay habitats, flows from microphytobenthos to benthic primary consumers 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% of the total carbon flows towards benthic consumers, respectively. In the Sylt-Rømø Bight habitats, total 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 (3–10%). At the scale of consumers, flows towards macrofauna were much higher in the Sylt-Rømø Bight habitats compared to those of the Marennes-Oléron Bay where meiofauna dominated grazing.

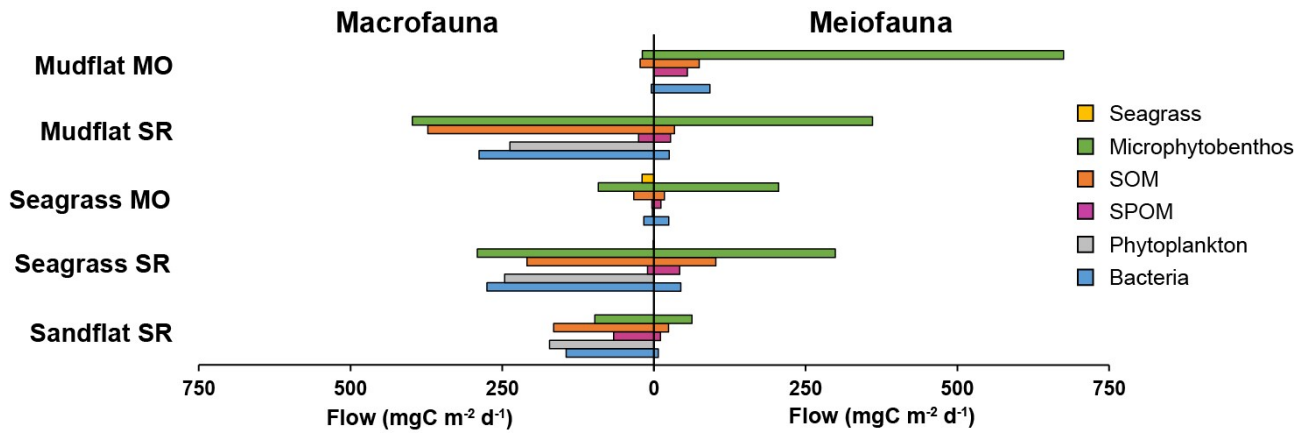


Figure 5. Flows of carbon from food sources to meiofauna and macrofauna in the mudflats, seagrass beds, and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). SOM = sediment organic matter, SPOM = suspended particulate organic matter.

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. First, meiofauna from three trophic groups: non-selective deposit feeding nematodes, epigrowth feeding nematodes and benthic copepods, mostly relying on microphytobenthos with flows from 15.4–303.2 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). The high reliance of these consumers on microphytobenthos in all habitats was demonstrated by the 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 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.

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

Third, omnivorous/predating nematodes relied on microphytobenthos (7.8–61.2 mgC m⁻² d⁻¹) as well as on other meiofauna (10.3–83.6 mgC m⁻² 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
 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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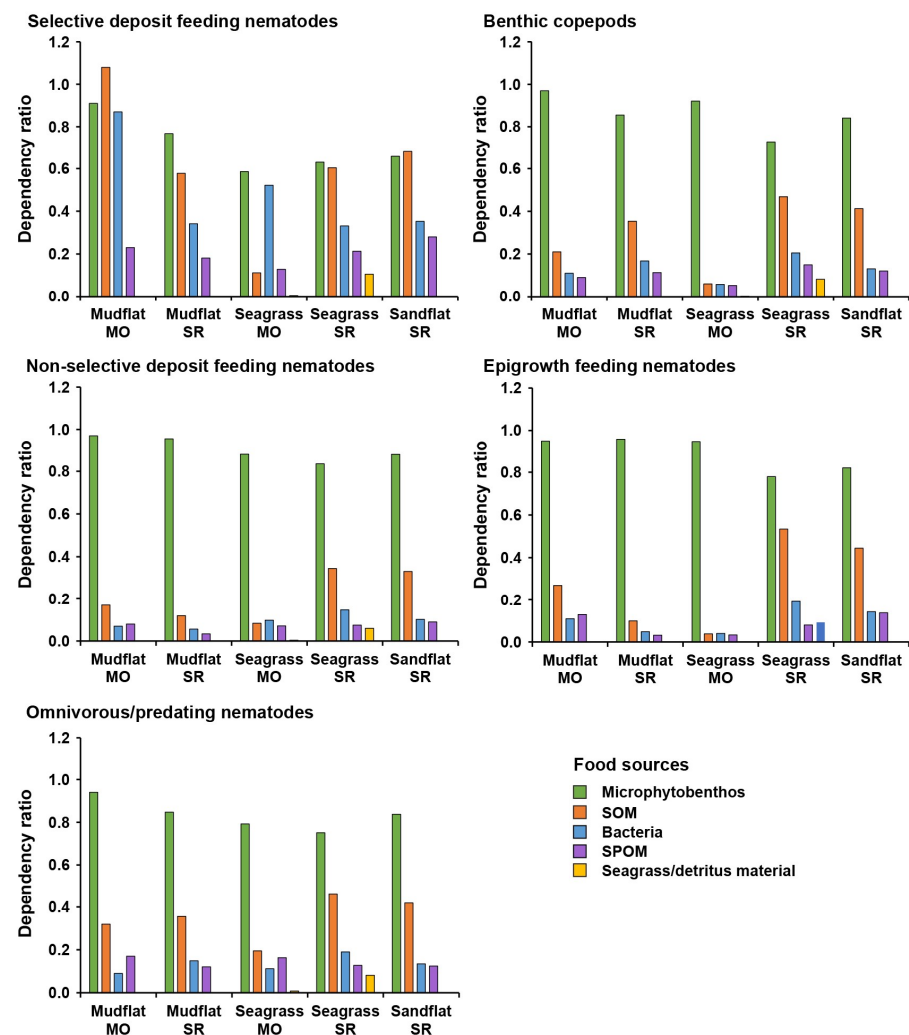
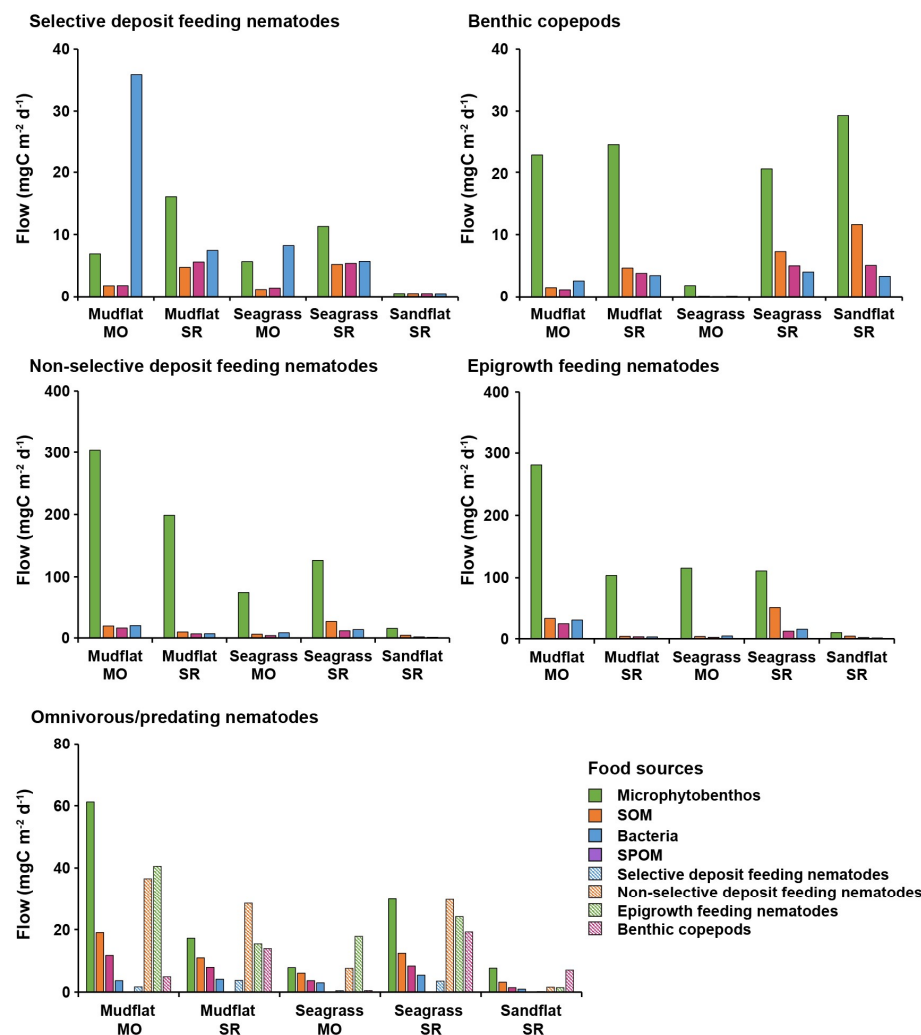


Figure 6. Flows of carbon ($\text{mgC m}^{-2} \text{d}^{-1}$) from food sources to meiofauna trophic groups (left panel) and dependency ratios of meiofauna trophic groups on food sources (right panel) in the mudflats, seagrass beds, and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (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).

3.3. Production and transfer efficiency

3.3.1. Production of food sources

Microphytobenthos was the most important primary producer in all habitats with the largest gross primary production (GPP) ranging from 774.4 (sandflat SR) to 1161.9 mgC m⁻² d⁻¹ (mudflat MO), and microphytobenthos represented between 47.3% (seagrass SR) to 81.3% (seagrass MO) of the primary 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 characterized by large difference of GPP between habitats (Table 3). GPP of seagrass was much lower than that of microphytobenthos in seagrass MO (45.1 compared to 1043.1 mgC m⁻² d⁻¹) and slightly lower than that of microphytobenthos in seagrass SR (685.3 compared to 836.6 mgC m⁻² d⁻¹). GPP of phytoplankton varied 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) and sandflat SR (446.5 mgC m⁻² d⁻¹). Production of bacteria was more variable than production of microphytobenthos, with much higher values in the habitats of the Sylt-Rømø Bight (147.7 to 317.5 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).

Table 3. Primary production of primary producers (with proportion of total primary production in *italic*; %), secondary production of bacteria, meiofauna and macrofauna and production/biomass ratios of meiofauna and macrofauna in the mudflats, seagrass beds, and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). Secondary production of meiofauna and macrofauna are weighted averages of the combined compartments weighted by their 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)				
	Mudflat MO	Mudflat SR	Seagrass MO	Seagrass SR	Sandflat SR
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)				
	Mudflat MO	Mudflat SR	Seagrass MO	Seagrass SR	Sandflat SR
Meiofauna	0.03	0.28	0.04	0.08	0.08
Macrofauna	0.007	0.002	0.003	< 0.001	< 0.001

3.3.2. Secondary production

Production of macrofauna, ranging 3.3 (seagrass SR) to 41.3 mgC m⁻² d⁻¹ (mudflat SR), was more variable than that of meiofauna, which ranged from 14.5 (seagrass MO) to 34.9 mgC m⁻² d⁻¹ (mudflat MO) (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 of macrofauna, being from four (mudflat MO) to 800 times higher (seagrass SR). Habitat comparisons highlighted that meiofauna P/B ratios were much higher in the Sylt-Rømø Bight mudflat (0.28 d⁻¹) than in all other habitats (from 0.03 to 0.09 d⁻¹). Macrofauna P/B ratios were higher in the mudflat MO, mudflat SR and seagrass MO than in the other habitats.

3.3.3. *Transfer efficiency*

In the Marennes-Oléron Bay habitats, the carbon flows from primary food sources (i.e. microphytobenthos, seagrass, phytoplankton, SPOM, SOM and bacteria) to meiofauna (269.9–951.7 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 opposite pattern was observed for the Sylt-Rømø Bight habitats with lower carbon flows to meiofauna (115.6–530.5 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 food sources to meiofauna with the lowest trophic level (level II) was high in the mudflat MO (804.4 mgC m⁻² d⁻¹), seagrass SR (443.6 mgC m⁻² d⁻¹) and mudflat SR (421.5 mgC m⁻² d⁻¹) (Appendix B.6). A moderate carbon flow was observed in seagrass MO (234.1 mgC m⁻² d⁻¹) and a particularly low flow was observed in the sandflat SR (97.7 mgC m⁻² d⁻¹). The carbon flow from food sources to macrofauna with the lowest trophic level (level II) was high in the Sylt-Rømø Bight habitats (501.3–1033.5 mgC m⁻² d⁻¹) compared to the moderate flow in the seagrass MO (150.3 mgC m⁻² d⁻¹) and the particular low flow in mudflat MO (42.2 mgC m⁻² d⁻¹) (Appendix B.7).

The carbon flows from meiofauna to higher trophic levels (12.6–39.2 mgC m⁻² d⁻¹) were relatively similar to or slightly higher than those from macrofauna (18.3–30.1 mgC m⁻² d⁻¹; 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⁻² d⁻¹; 74%) with much lower contributions for meiofauna (49.1 mgC m⁻² d⁻¹; 26%).

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

macrofauna had multiple consumers in other habitats (i.e. benthic omnivorous macrofauna, benthic fish and carnivorous birds).

Table 4. Flows from meiofauna (Meio) and macrofauna (Macro) to higher trophic levels (mgC m⁻² d⁻¹) in the mudflats, 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		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

Losses by respiration and egestion were also very different between meiofauna—all integer trophic 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 meiofauna (40.9–90.7%) compared to that of macrofauna (38.9–68.2%). Comparisons between habitats highlighted that losses due to respiration of meiofauna were higher in mudflat MO (15.4–19.3%) and sandflat SR (12.4–22.3%) than in other habitats (< 6.5%). For macrofauna, the loss by respiration was the highest in seagrass MO (60.2–60.3%) compared to m other habitats (27.0–48.0%). Moreover, loss by meiofauna due to egestion was lower in sandflat SR (40.9–73.0%) than in other habitats (70.0–90.7%). No clear pattern was observed for relative losses by macrofauna due to egestion.

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

Meiofauna										
Outflow Trophic level	Respiration					Egestion				
	II	III	IV	V	VI	II	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 Trophic level	Respiration					Egestion				
	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	-

As a result, the differences between meiofauna and macrofauna in carbon inflows and outflows (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 except in mudflat MO (Fig. 7). TE of meiofauna (11.5 ± 2.1 %) in mudflat MO was much lower than TE of macrofauna (23.1 ± 2.1 %). Different patterns were observed for the mean transfer efficiencies (MTEs) of integer trophic levels II to IV (Fig. 7), with higher MTEs in mudflat MO ($12.7 \pm 1.2\%$), mudflat SR ($11.9 \pm 2.2\%$) and seagrass SR ($10.2 \pm 2.2\%$) compared to sandflat SR ($8.0 \pm 2.0\%$) and seagrass MO ($6.8 \pm 3.6\%$).

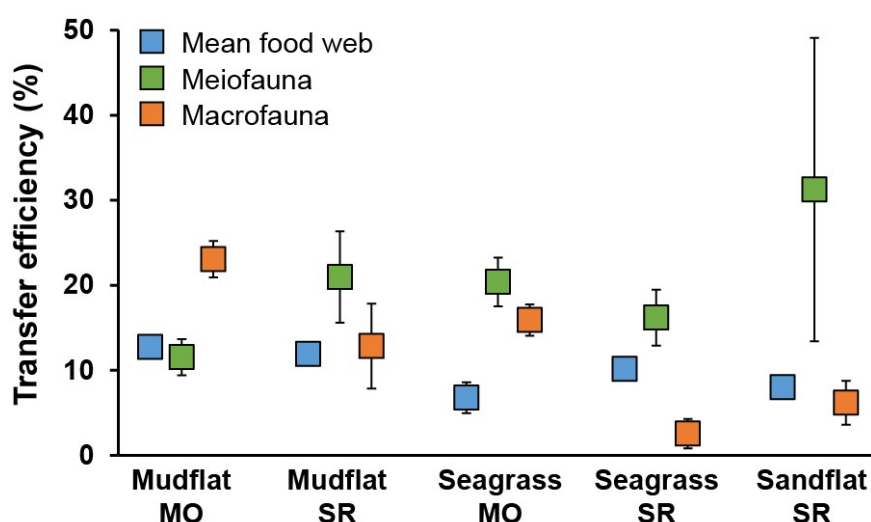


Figure 7. Transfer efficiency (TE) of the whole food web, meiofauna and macrofauna for the mudflats, seagrass beds, and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR). Mean TE for the food web is the geometric mean from integer trophic level II-IV (\pm standard deviation; see Appendix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

3.4. Network analysis

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

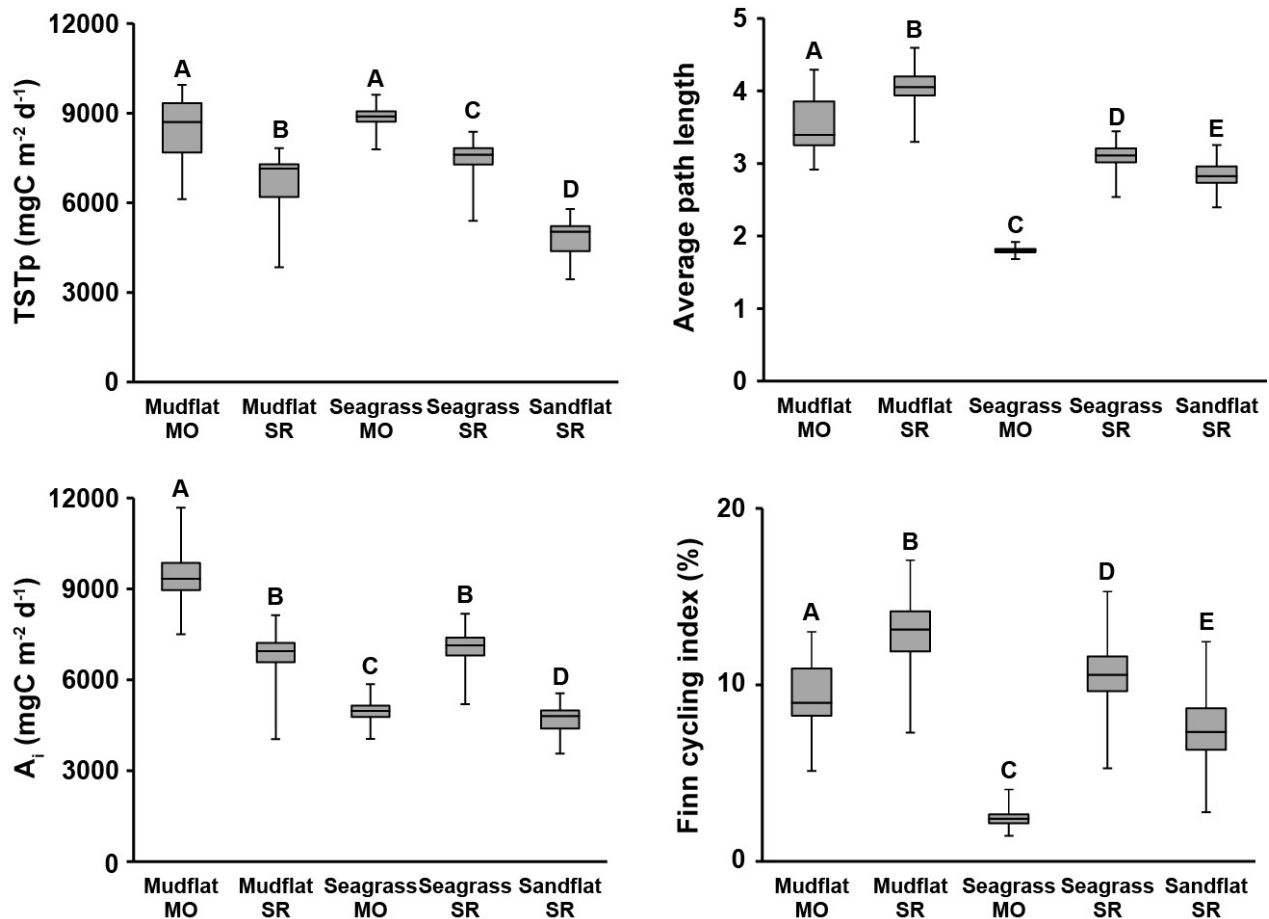


Figure 8. Ecological network analysis indices for the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR): total system throughput (TSTp; top left), average path length (top right), internal ascendency (A_i; bottom left) and Finn cycling index (bottom right).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

4. Discussion

4.1. Importance of microphytobenthos as a food source for meiofauna

4.1.1. Reliance on microphytobenthos

As evidenced by the five different models, meiofauna mostly relied on microphytobenthos in all habitats, whereas macrofauna relied on a wider variety of food sources. Carbon flows from microphytobenthos 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 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 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 latter have much higher biomass (e.g. seagrass material). Microphytobenthos therefore has a pivotal role as a food source in soft-bottom coastal habitats.

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⁻² d⁻¹). More importantly so, these rates (Degré et al., 2006) and 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 available. Phytoplankton and seagrass follow strong seasonal fluctuations in biomass and production over a year, mostly blooming during spring and summer seasons, while inputs of detrital material mostly occur in fall and winter (Asmus and Asmus, 1985; Lebreton et al., 2009; Struski and Bacher, 2006; van der Heijden et al., 2018). Moreover, microphytobenthos has a high nutritional quality (Cebrián, 1999), opposed to seagrass material and *a fortiori* detrital material. Indeed, these latter have a low nutritional value (Vizzini et al., 2002) and are generally characterized by more refractory compounds (i.e. resistant to biological degradation; Klump 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 food sources (Azovsky et al., 2005; Estifanos et al., 2013).

4.1.2. Differences of food source reliance between meiofauna feeding types

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 models. The various meiofauna feeding types could be gathered in three main groups according to their reliance on microphytobenthos. First group: non-selective deposit feeding nematodes, epigrowth feeding nematodes and benthic copepods, which had a high reliance on microphytobenthos as indicated by their dependency ratios to microphytobenthos (0.73–0.97) and very low omnivory indices (0.03–0.10). For these groups, most of the carbon was originating from microphytobenthos (56 to 91%) in all habitats (carbon flows from 2 to 303 mgC m⁻² d⁻¹). A slightly lower reliance on microphytobenthos as observed on the seagrass bed and sandflat of the Sylt-Rømø Bight (56–70%) may be related to differences in terms of availability, e.g. no biofilm in the sandflat, as productions are in the same order of magnitude in all habitats. The importance of microphytobenthos as a food source for epigrowth feeders and benthic copepods has been demonstrated 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 Vincx, 1997a; Wieser, 1953). Epigrowth feeder buccal cavities are fitted with a tooth used to pierce diatoms, making it easier to assimilate them.

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).

Third group: selective deposit feeding nematodes, which relied on a larger variety of food sources, as 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 efficiently feed on bacteria (Wieser, 1953), and this high reliance on bacteria was confirmed by carbon flows. Interestingly, bacteria mainly used microphytobenthos and SOM as substrates (Boschker et al., 2000; van der Heijden et al., 2019). As a result, selective deposit feeders rely as well on organic matter primarily produced by microphytobenthos, but in an indirect way, as this organic matter is mostly routed through bacteria before being assimilated by these nematodes. Consequently, although the direct consumption was low, the dependency on microphytobenthos was high, when considering direct and indirect interactions.

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

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

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⁻² d⁻¹) and from meiofauna (13–49 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 mgC m⁻² d⁻¹). Focusing merely on the contribution of meiofauna and macrofauna to the diet of higher trophic

level consumers (i.e. benthic omnivorous macrofauna, benthic fish and carnivorous birds) the relative contribution of meiofauna as a food source to higher trophic levels ranges from 26 to 66%. However, distinct 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 the meiofauna (10–32%) in the Sylt-Rømø Bight, while the opposite pattern was observed in the Marennes-Oléron Bay (i.e. macrofauna: 5–18%, meiofauna: 30–61%). This is very likely related to the much larger biomass of macrofauna (100 to 200 times more) in the Sylt-Rømø Bight than in the Marennes-Oléron Bay. Despite the smaller amount of energy that passed through meiofauna in seagrass SR and sandflat SR, a larger proportion of the energy for higher trophic levels originated from meiofauna (meiofauna: 52–66%; 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 lower amount of energy passed through macrofauna in mudflat MO (5%), while biomass of meiofauna and 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 highly available in this habitat as it forms a biofilm at the sediment surface. In addition, more diverse consumer groups relied on meiofauna in the mudflat of the Marennes-Oléron Bay, whereas meiofauna was consumed by one dominant higher trophic level consumer in all other habitats, i.e. benthic fish (seagrass MO) or benthic omnivorous macrofauna (Sylt-Rømø Bight habitats).

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

The important role of meiofauna in the functioning of the five habitats is very likely related to their 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 similar (in the seagrass MO and in the mudflat SR), or even higher (2 to 9 times, in all other habitats), than macrofauna production. These productions were generally in agreement with previous estimations ($10\text{ to }80\text{ mgC m}^{-2}\text{ d}^{-1}$) (Chardy and Dauvin, 1992; Danovaro et al., 2002; Escaravage et al., 1989). The high production of meiofauna combined with similar and/or lower biomass compared to macrofauna resulted in 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 higher than that of macrofauna: Gerlach, 1971; Moens and Vincx, 1997b) and higher weight-specific metabolic 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

as a food source for juvenile benthic feeding fish (e.g. mullets, gobies, flatfish, grunts and croakers) was demonstrated in mudflats (Carpentier et al., 2014; Gordon and Duncan, 1979; Lassere et al., 1975; Smith and 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 higher trophic level organisms, that are eventually harvestable by humans. However, the exact fate of meiofauna remains unclear (Giere, 2009) and further research should focus on the flows from meiofauna to higher trophic levels in food webs. Meiofauna should at least not be neglected in coastal ecosystem assessments and should be treated similarly to macrofauna.

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

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 ascendancy (A_i : 6946–9339 $\text{mgC m}^{-2} \text{d}^{-1}$; Baird et al., 2007) and the highest average path length (APL: 3.1–4.1; Hutchinson, 1959; Slobodkin, 1960). These high MTEs are explained by the structure of the studied food webs, in which the carbon is constrained to flow through specific trophic pathways, resulting in the high A_i . Thus, 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 suggested by the APL, and the carbon flows through longer and more efficient trophic chains. The highest efficiencies of these three habitats are very likely related to the large flows from high quality food sources (836–996 $\text{mgC m}^{-2} \text{d}^{-1}$), that fulfill the energy requirements of organisms, prevent them from diversifying their diet and favor higher assimilation. In the core of this efficient trophic chain is the meiofauna that have consumed up to 40% of the GPP and that are among the main prey for higher trophic levels. The lower 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 $\text{mgC m}^{-2} \text{d}^{-1}$). However, the energy was very efficiently transferred from primary consuming meiofauna to higher trophic levels partially related to the high relative biomass of omnivores/predating nematodes. As reported by Campanyà-Llovet et al. (2017), the lowest trophic levels have the strongest response to changes in food quality. Thus, caution should be taken when 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.

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_i (4974 $\text{mgC m}^{-2} \text{d}^{-1}$) and APL (1.8) clearly demonstrate a low efficiency, however, the flows from primary producers to primary consumers were dominated by high-quality food sources (70.5%), despite the low input when compared to other habitats (391 $\text{mgC m}^{-2} \text{d}^{-1}$). This could be related to the lower proportion of available carbon that is transferred to higher trophic levels, as indicated by the low APL. Further investigations are needed to clarify this point, to determine if this is for ecological (e.g. low recycling or high export) or mathematical reasons (i.e. the topology of the model). The recycling was 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.

5. Conclusion

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

The close link between microbiota and meiofauna and the use of available primary sources (i.e. microphytobenthos) by meiofauna make these consumers a key compartment in the functioning of food 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) flows, some meiofauna trophic groups relied on bacteria and SOM, with direct consequences on the carbon 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 macrofauna in most food web studies. We therefore argue that feeding types of meiofauna should be considered as separate compartments in future studies. Coupling state-of-the-art methods (i.e. molecular techniques, trophic markers and stomach content) should be commonly used to quantify carbon flows from/to meiofauna with higher precision and thus refine the role of this key compartment in the functioning of coastal habitats.

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