



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

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Received: 25 January 2018 / Accepted: 25 September 2018 / Published online: 9 October 2018
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Abstract

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

Responsible Editor: M. Huettel.

Reviewed by undisclosed experts.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00227-018-3419-7>) contains supplementary material, which is available to authorized users.

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Introduction

Soft-bottom intertidal habitats are highly productive (Underwood and Kromkamp 1999; Hemminga and Duarte 2000), fueling complex food webs and providing food resources for a large diversity of top consumers like fish and birds (Day et al. 1989; Duarte and Cebrián 1996) via trophic pathways going through meiofauna (Chardy and Dauvin 1992) and macrofauna (Haubois et al. 2005). Meiofauna, here defined as metazoans associated with sediments with a size range from 40 to 500 μm , are considered as an important trophic component in the functioning of coastal ecosystems. They have an intermediate trophic position (Leguerrier et al. 2003; Giere 2009) and high secondary production (from 4 to 29 gC m^{-2} year⁻¹) (Escaravage et al. 1989; Chardy and Dauvin 1992; Danovaro et al. 2002) that often exceeds that of the macrofauna (Giere 2009). Meiofauna are connected to the microorganisms in the food web via the consumption of microalgae and bacteria (Rzeznik-Orignac et al. 2003; Vafeiadou et al. 2014) and to the food webs of macroconsumers, especially via their consumption by small benthic fish and

predatory invertebrates (Coull 1999). Nematodes are the most dominant group in meiofauna; their food resources can be very specific, or in the contrary, relatively diverse, and their buccal cavity is very distinct based on these feeding types. This morphological trait has been used for decades to define feeding types (Wieser 1953; Warwick 1971; Heip et al. 1985) and some more recent methods [i.e., feeding behavior experiments; (Moens and Vincx 1997), trophic markers (Moens et al. 2005)] permitted to revise or precise the feeding types of some genera (e.g., assort of *Metachromadora* from omnivores/predators to epigrowth feeders).

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

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

temporal and spatial variations of the food sources and those of meiofauna community structure.

Materials and methods

Study sites

Marennes-Oléron Bay

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

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

Sylt-Rømø Bight

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

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

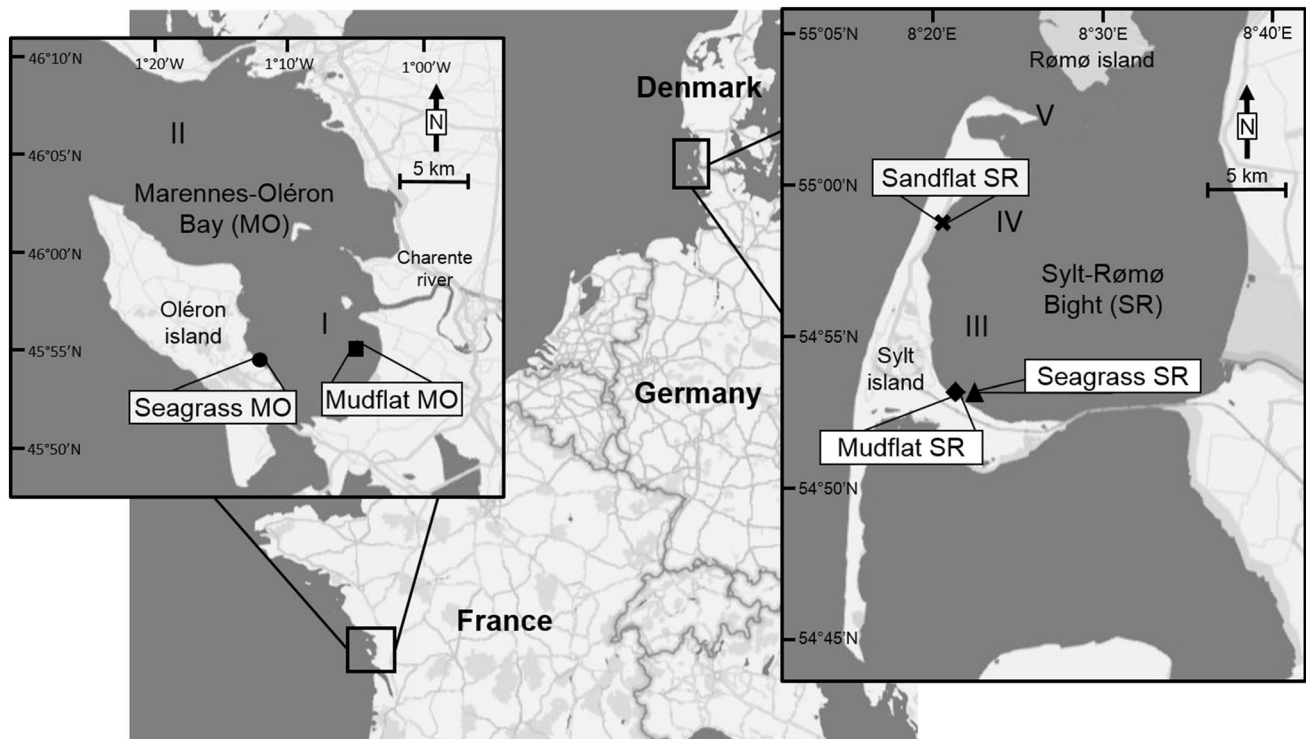


Fig. 1 Sampling stations of the mudflats, seagrass beds and sandflat in the Marennnes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) along the European coast. Pelagic sampling stations, where samples

for suspended particulate organic matter were taken, are indicated by roman numbers in both Marennnes-Oléron Bay (I–II) and Sylt-Rømø Bight (III–V)

Field sampling and laboratory processes

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

Sediment grain size

Sediment samples ($n = 3$) were collected randomly with cores ($\phi = 4$ cm) and were split into 0–1 cm and 1–5 cm depth fractions. Sediment grain size was determined by laser granulometry analyses for the sediment from the seagrass bed and mudflats (Mastersize 2000, Malvern Instruments Limited, United Kingdom). The freeze-dried sediment of these habitats was rehydrated before analyses in order to avoid the use of ultrasound to disaggregate the sediment. Sediment grain size of freeze-dried samples from the sandflat of the Sylt-Rømø Bight was determined by dry sieving.

Samples were classified based on their median sediment grain size after Wentworth (1922).

Benthic primary producers, composite sources and bacteria

For all stations, sampling was carried out in two seasons, in spring (from May 17 to June 17, 2016) and in autumn (from November 14 to December 15, 2016), to compare a season with a high primary production with a season with a high load of detrital matter. Sampling was carried out during low tide, starting about 1 h before lowest water level.

Samples for sediment organic matter (SOM), detritus, and seagrass leaves and roots (3 replicates) were taken using cores ($\phi = 19$ cm) which were separated into two layers (a surface layer from 0 to 1 cm, a sub-surface layer from 1 to 5 cm). The collected material was gently sieved on a 500 μ m mesh screen (1 mm for sandflat SR samples) after which the upper fraction was sorted in seagrass leaves, roots and detritus (brown to black colored leaves and roots). All samples were freeze dried and then weighed (± 0.001 g). Carbon to dry weight ratios were determined on each sample: a small amount was ground to a fine and homogeneous powder using a ball mill (MM 400, Retsch, Germany) and carbon content was determined using an elemental analyzer (Flash EA 1112, Thermo Scientific, Italy). Sub-samples were collected

in the lower fraction (SOM), freeze dried, and ground using a mortar and pestle. Chlorophyll *a* and organic carbon concentrations were determined in sub-samples by fluorimetry (TD-700, Turner Designs, USA) using the method of Lorenzen (1966) and elemental analyses (Flash EA 1112, Thermo Scientific, Italy), respectively. Chlorophyll *a* values were converted into carbon biomass using the conversion ratio (47.63) provided by de Jonge (1980) and used as a proxy of fresh material of microalgae origin (i.e., microphytobenthos and trapped phytoplankton) in sediment, thereafter called “benthic microalgae”. Carbonates were removed prior to elemental analyses by adding HCl at 2 mol L⁻¹ drop-by-drop on SOM samples until cessation of bubbling. Subsequently, samples were dried at 60 °C to constant weight, freeze dried and ground again.

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

Suspended particulate organic matter

Sampling of the suspended particulate organic matter (SPOM) was conducted by collecting samples of surface water during high tide, in the same timeframe as the benthic samples. Water was sampled at two stations (I and II) in the Marennes-Oléron Bay and three stations (III, IV and V) in the Sylt-Rømø Bight (Fig. 1). Station I, in the north of the Brouage mudflat, represented the water mass covering the mudflat MO station. Station II, near the inlet of the Marennes-Oléron bay, represented the water mass influencing the seagrass MO station. Station II is regularly sampled in the framework of the SOMLIT surveys (data provided by “Service d’Observation en Milieu Littoral, INSU-CNRS, La Rochelle station”). Water samples collected at stations III and IV represented water masses covering the sandflat SR (III), and the mudflat SR and seagrass SR stations (IV),

respectively. Station V, near the entrance of the Sylt-Rømø Bight, represented the SPOM originating from the North Sea.

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

Meiofauna

Meiofauna were sampled for taxonomic composition, density (ind. m⁻²) and biomass (gC m⁻²) estimations at the same time as benthic primary producers and composite sources. Three replicates were collected randomly in a ten square meters area using cores ($\phi = 4$ cm). Cores were separated into two layers (0–1 cm and 1–5 cm) to study the changes of meiofauna communities related to sediment depth. Samples were sieved with a 500- μ m mesh to eliminate macrofauna and large detritus. Meiofauna were extracted from the sediment using Ludox HS-40 (Sigma Aldrich, France) (de Jonge and Bouwman 1977) and retrieved with a 40- μ m mesh sieve (Higgins and Thiel 1988). From each replicate, 100 nematodes were haphazardly taken with fine tweezers (#55, Dumont, Switzerland), mounted on slides in anhydrous glycerol to prevent dehydration (Seinhorst 1959) and examined microscopically. The taxonomic composition of the nematode community was determined at least to the genera level based on these 100 individuals according to the identification keys of Platt and Warwick (1983, 1988), and Warwick et al. (1998). Density was calculated for each genera as number of individuals per m² (ind. m⁻²) and relative abundance as the percent composition of each genera relative to the total number of organisms. Species diversity indices were calculated on 100 individuals for each replicate at the five habitats for the two seasons. Community structure of the other meiofauna groups was not determined due to low densities. Nematodes were allocated into four trophic groups according to Wieser (1953) as follows: selective deposit feeders (1A), non-selective deposit feeders (1B), epigrowth feeders (2A), and omnivores/predators (2B). Various nematode genera, including at least one of each from the 4 different feeding groups, were selected for determination of individual dry weight and carbon content. Between 10 and 200 nematodes from the same genera were picked for dry weight determination, freeze dried and weighed (± 1 μ g) using a microbalance (ME 5, Sartorius, Germany). Organic

carbon composition was determined using an elemental analyzer (Flash EA 1112, Thermo Scientific, Italy). Mean biomass of species-specific nematodes and benthic copepods was used to convert the density of nematodes into grams of carbon per m² and dry weight per m² (Supplementary material, Appendix 1).

Data treatment and statistical methods

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

Results

Sediment grain size

Sediment of the mudflats and seagrass beds consisted of a mixture of sand (29–64%), silt (29–58%) and clay (7–15%), while the sandflat consisted mainly of sand (98%) (Fig. 2).

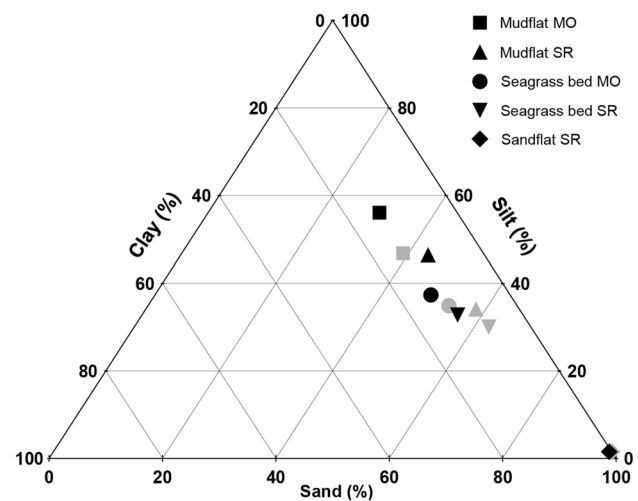


Fig. 2 Ternary diagram presenting the sediment composition of the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in spring (gray symbols) and autumn (black symbols). Separation by size for clay ($< 3.9 \mu\text{M}$), silty ($3.9\text{--}63 \mu\text{M}$),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

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

Potential food sources

The total biomass of benthic food sources ranged from 67.4 (sandflat SR, autumn) to 447.4 gC m^{-2} (mudflat SR, spring) (Fig. 3c, e). SOM was dominant in all habitats sources with proportions ranging from 29.3 to 94.5%, representing 19.8 (sandflat SR, autumn) to 290.3 gC m^{-2} (mudflat MO, autumn). Benthic microalgae were the second most dominant food source, with biomass ranging from 7.1 gC m^{-2} (3.7%, mudflat MO, spring) to 70.3 gC m^{-2} (22.6%, seagrass SR, spring). Detrital matter was found mainly in the two seagrass beds and mudflat SR with 4.3 (1.0%, mudflat SR, spring) to 45.5 gC m^{-2} (16.7%, seagrass bed MO, autumn). In the seagrass beds, leaves and roots were occurring with biomass ranging from 1.6 (0.5%, seagrass SR, autumn) to 15.0 gC m^{-2} (5.1%, seagrass MO, spring) and 0.3 (0.1%, seagrass SR, autumn) to 24.4 gC m^{-2} (8.2%, seagrass MO, autumn). Bacteria represented the lowest biomass in all habitats with 0.6 (0.9%, sandflat SR, autumn) to 20.1 gC

m^{-2} (4.5%, mudflat SR, spring). Some differences of food source biomass could be observed between the surface and the sub-surface layers, always with higher biomass in the surface layer when they occurred: detrital matter in mudflat SR in spring and in seagrass MO in autumn, bacteria in mudflat SR in spring, and benthic microalgae in all habitats in all seasons except for mudflat SR and sandflat SR in autumn (two-way ANOVA with Tukey post hoc test, highest p value 0.032).

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

Some differences occurred at the seasonal scale as well, with higher biomass of primary producers in spring when a difference occurred. Such a pattern was observed for benthic microalgae in sandflat SR, seagrass SR and seagrass MO, and for seagrass leaves in seagrass bed MO (two-way ANOVA with Tukey post hoc test, $p < 0.001$). Bacteria

biomass of mudflat SR and seagrass SR was also higher in spring compared to autumn (two-way ANOVA followed by Tukey post hoc test, $p < 0.001$). About detrital matter, seasonal changes followed an opposite pattern when they occurred, with an increase in biomass of detritus from spring to autumn in mudflat SR and seagrass MO (two-way ANOVA with Tukey post hoc test, $p < 0.001$). SOM biomass was stable between spring and autumn (two-way ANOVA with Tukey post hoc test, lowest p value 0.44).

Regarding quality of potential food sources in the different habitats, they varied from being partly detrital in sandflat SR (57–63%) to being almost completely made out of detrital matter in mudflat MO (from 93 to 99%). Carbon: chlorophyll *a* (C:chl *a*) ratios of SOM were higher in mudflat MO (1201.4), mudflat SR (681.8) and seagrass MO (504.6) compared to seagrass SR (221.4) and sandflat SR (72.3; two-way ANOVA with Tukey post hoc test, $p < 0.001$, Table 1). SOM had much higher C:chl *a* ratios in the sub-surface layer than in the surface layer (two-way ANOVA with Tukey post hoc test, $p < 0.001$). Variation in C:chl *a* ratios between spring and autumn was not observed (two-way ANOVA, lowest p value 0.33, Table 1). Proportions of SOM that were originating from fresh microalgae (i.e., microphytobenthos and trapped phytoplankton) ranged from 3.6 (mudflat MO, spring) to 71.1% (sandflat SR, autumn, Table 1). These proportions were much higher in sandflat SR (66.6%) and seagrass SR (22.0%) than in mudflat SR (7.0%) and mudflat MO (4.0%, two-way ANOVA with Tukey post hoc test, Table 1). Quantities of SPOM ranged between 0.32 and 0.54 gC L^{-1} . Minor variations between habitats observed within SPOM are reported in the supplementary material (Appendix 4).

Meiofauna community structure

The meiofauna community was dominated by nematodes with relative abundance ranging from 41.7% (sandflat SR, surface layer, spring) to 100% (mudflat MO, sub-surface layer, spring), except for the surface layer of sandflat SR

Table 1 Carbon: chlorophyll *a* ratios (mean \pm standard deviation, $n=3$) and percentage of carbon originating from fresh microalgae (mean \pm standard deviation, %, $n=3$) in sediment organic matter

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

Letters displayed after mean values indicate grouping of similar samples (two-way ANOVA with Tukey post hoc tests, $p < 0.05$)

(SOM) in the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in spring and autumn

where benthic copepods dominated (55.5%, Fig. 4). Three other meiofauna taxa occurred in the different habitats: foraminifera (0–7.4%), polychaetes (0–5.3%), and ostracods (0–0.4%). Total meiofauna density was higher in the surface layer than in the sub-surface layer in all habitats (two-way ANOVA with Tukey post hoc test, highest *p* value 0.033). Mean meiofaunal density of both layers combined ranged from 1.7×10^5 ind. m^{-2} (mudflat SR, autumn) to 3.4×10^6 ind. m^{-2} (mudflat MO, autumn, Appendix 5). Meiofauna densities (both layers combined) were similar between spring and autumn, except in seagrass SR where densities were higher in spring (two-way ANOVA with Tukey post hoc test, highest *p* value 0.020, Table 2).

The total biomass of nematodes (both layers combined) ranged from 0.053 $gC\ m^{-2}$ (1.6×10^5 ind. m^{-2} , mudflat SR, autumn) to 1.541 $gC\ m^{-2}$ (2.9×10^6 ind. m^{-2} , mudflat MO, spring, Fig. 3f). Nematode density and biomass were higher in the surface layers than in the sub-surface layers (two-way ANOVA with Tukey post hoc test, highest *p* value

0.042). Nematodes from the surface layers dominated the contribution to the total biomass in all habitats, with lowest proportions in seagrass SR (54.0%) and mudflat SR (55.4%) and higher proportions in sandflat SR (82.3%), mudflat MO (83.3%) and seagrass SR (95.7%). At the habitat scale, nematode density and biomass were much higher in mudflat MO (density: 3.0×10^6 ind. m^{-2} ; biomass: 1.257 $gC\ m^{-2}$) than in all other habitats (two-way ANOVA with Tukey post hoc test, *p* < 0.001, Table 2, Appendix 5). Nematode biomass in the seagrass beds ranged from 0.146 (seagrass MO, autumn) to 0.459 $gC\ m^{-2}$ (seagrass SR, spring). Nematode biomass of the mudflat SR and sandflat SR ranged from 0.054 (mudflat SR, autumn) to 0.150 $gC\ m^{-2}$ (mudflat SR, spring). Some temporal variations occurred as well, with higher nematode densities in spring in seagrass SR and higher nematode biomass in spring in mudflat MO (two-way ANOVA with Tukey post hoc test, highest *p* value 0.005, Table 2).

Total biomass of benthic copepods, which were merely present in the surface layers, ranged from 0.003 $gC\ m^{-2}$

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

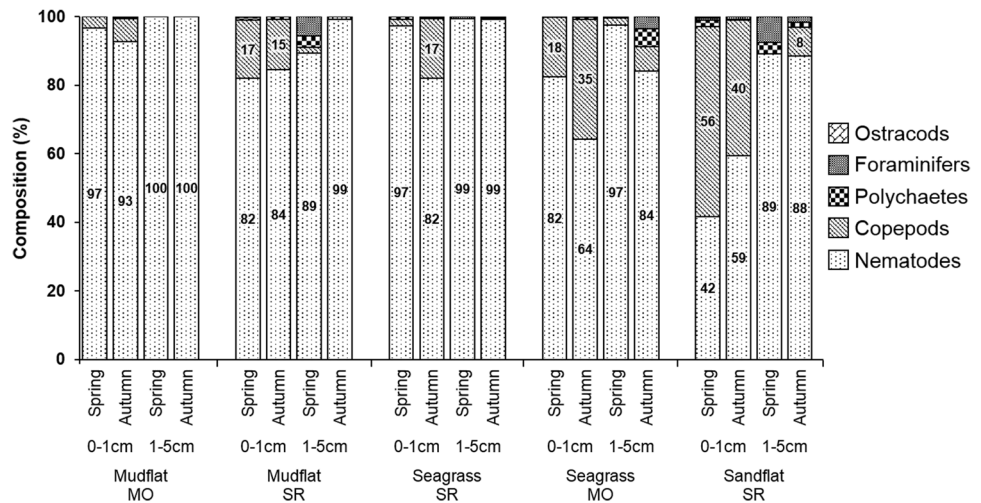


Table 2 Results of the two-way ANOVA for differences in total meiofauna, nematode, and benthic copepod density and nematode and benthic copepod biomass across habitats and seasons

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

Values in bold indicate a significant difference ($\alpha \leq 0.05$)

Df degree of freedom, F F statistic, P probability

(1.0×10^4 ind. m^{-2} , mudflat SR, autumn) to $0.110 \text{ gC } m^{-2}$ (1.7×10^5 ind. m^{-2} , mudflat MO, spring, Fig. 3f). Copepod biomass of the mudflat MO ($0.095 \text{ gC } m^{-2}$) was much higher than in the mudflat SR ($0.006 \text{ gC } m^{-2}$), while copepod density was higher in the seagrass MO than in the seagrass SR and mudflat SR (two-way ANOVA with Tukey post hoc test, $p < 0.001$). Densities and biomass of benthic copepods were similar in spring and autumn (two-way ANOVA with Tukey post hoc test, lowest p value 0.178, Table 2).

Nematode community structure

Five-thousand and four-hundred nematodes were determined at genus and/or species level. A total of 139 species, belonging to 65 genera and 20 families, were found at the five habitats in both the Marennes-Oléron Bay and the Sylt-Rømø Bight. Eight genera represented 70% of the community in the surface layer of all habitats combined: *Daptonema* (1B, 18%), *Chromadorita* (2A, 10%), *Metachromadora* (2A, 10%), *Sabatieria* (1B, 10%), *Ptycholaimellus* (2A, 7%), *Spirinia* (2A, 6%), *Terschellingia* (1A, 5%), and *Praeacanthonchus* (2A, 4%). Four genera represented 70% of the community in the sub-surface layer of all habitats combined: *Terschellingia* (1A, 28%), *Sabatieria* (1B, 25%), *Spirinia* (2A, 13%), and *Metachromadora* (2A, 6%). The surface layer had a higher number of genera (from 3 to 9 genera, mean: 5.8) that represented 75% of the community

compared to the sub-surface layer (from 2 to 9 genera, mean: 3.4) for all habitats. The ten most dominant genera per habitat, season and sediment layer are presented in the supplementary material (Appendix 6). Species richness varied from 8 to 28, Hill's diversity from 2.3 to 19.1, and species evenness from 0.41 to 0.88 (Table 3). Species richness, diversity and evenness decreased with depth at all habitats (two-way ANOVA, $p < 0.001$, Table 4). Species richness and evenness were higher at the seagrass MO than at the mudflat SR and the seagrass SR (two-way ANOVA with Tukey post hoc test, $p < 0.001$). Hills diversity was higher at the seagrass MO than at all other habitats (two-way ANOVA with Tukey post hoc test, $p < 0.001$). There was no difference in diversity and evenness between seasons (two-way ANOVA, lowest p value 0.126, Table 4).

Community compositions, based on proportions of benthic copepods and of trophic groups of nematodes, were similar between the two mudflats (besides the very large difference of biomass), as highlighted by the average hierarchical cluster analysis ($p < 0.05$, Fig. 3b). The sandflat SR and the two seagrass beds had similar communities as well. The difference of trophic structures between the mudflats and the other habitats was related to the higher proportions of selective deposit feeders (1A) and of non-selective deposit feeders (1B) in the mudflats. The mudflat MO was dominated by genera belonging to non-selective deposit feeders (36%, $0.579 \text{ gC } m^{-2}$), epigrowth feeders (34%, 0.525 gC

Table 3 Number of nematode genera, Hill's diversity (N_1), and species evenness (J') in the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in spring and autumn ($n = 3$)

Layer (in cm)	Mudflat MO		Mudflat SR		Seagrass SR		Seagrass MO		Sandflat SR											
	Spring		Autumn		Spring		Autumn		Spring		Autumn									
	0-1	1-5	0-1	1-5	0-1	1-5	0-1	1-5	0-1	1-5	0-1	1-5								
Species richness	22	11	21	13	23	12	15	13	16	11	16	12	24	19	23	14	20	12	21	18
Hill's diversity (N_1)	14	5	12	6	13	4	9	5	7	3	6	4	15	12	14	8	11	6	12	7
Species evenness (J')	0.9	0.6	0.8	0.7	0.8	0.6	0.8	0.6	0.7	0.5	0.6	0.6	0.8	0.9	0.8	0.8	0.8	0.7	0.8	0.7

Table 4 Results of the two-way ANOVA for differences in species richness, Hill's diversity (N_1), and species evenness (J') between habitats, sediment layers and season in the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay and the Sylt-Rømø Bight

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

Values in bold indicate a significant difference ($\alpha \leq 0.05$)

Df degree of freedom, F F statistic, P probability

m^{-2}), and selective deposit feeders (25%, 0.071 gC m^{-2}) with *Terschellingia* (1A, 22%, 0.055 gC m^{-2}), *Comesa* (1B, 14%, 0.082 gC m^{-2}) and *Ptycholaimellus* (2A, 13%, 0.048 gC m^{-2}) being the most common genera (Fig. 3d). At the mudflat SR, the non-selective deposit feeders dominated (55%), and the most abundant genera were *Sabatieria* (1B, 43%, 0.042 gC m^{-2}) and *Terschellingia* (1A, 13%, 0.004 gC m^{-2}). The seagrass bed SR was dominated by epigrowth feeders with the genera *Spirinia* (2A, 46%, 0.225 gC m^{-2}) and *Chromadorita* (2A, 16%, 0.026 gC m^{-2}). The seagrass bed MO was dominated by various genera belonging to epigrowth feeders (31%, 0.165 gC m^{-2}) and non-selective deposit feeders (29%, 0.061 gC m^{-2}). There, the biomass of nematodes was dominated by the epigrowth feeder genera *Metachromadora* (7%, 0.035 gC m^{-2}). The sandflat SR was dominated by genera belonging to epigrowth feeders (35%, 0.023 gC m^{-2}) and non-selective deposit feeders (19%, 0.040 gC m^{-2}), with the genera *Microlaimus* (2A, 15%, 0.006 gC m^{-2}) and *Daptonema* (1B, 13%, 0.028 gC m^{-2}) being the most common.

Relationships between environmental parameters and meiofauna trophic structure

The PCA on the environmental variables explained 63.2% of the total variation (Axis 1: 39.9%, Axis 2: 23.3%, Fig. 5a). Axis 1 highlights a positive relationship between SPOM, benthic microalgae and sediment grain size. At

the opposite, when biomass of benthic microalgae, SPOM and sediment grain size was low, quantities of SOM were higher, as well as bacteria and detritus biomass, and carbon:chlorophyll *a* ratios of SOM. Axis 2 demonstrates that biomass of bacteria increased with biomass of SOM, SPOM, and benthic microalgae. Sandflat SR is defined by larger sediment grain size, higher biomass of benthic microalgae and of SPOM, as highlighted on Axis 1. Axis 1 also discriminates seagrass SR from mudflat SR, mudflat MO and seagrass MO (autumn), the later ones being characterized with lower biomass of benthic microalgae and SPOM and/or higher carbon:chlorophyll *a* ratios of SOM, and higher biomass of SOM and detritus. In spring Axis 2 discriminates well the mudflat and seagrass bed in the Marennes-Oléron Bay compared to the Sylt-Rømø Bight, which could be due to higher biomass of bacteria (mudflat SR) and/or benthic microalgae (seagrass SR). In terms of temporal variations, Axis 1 highlights low variation in environmental variables between spring and autumn except for seagrass MO, which could be due to a significant increase in biomass of detritus from spring to autumn in this habitat. Axis 2 highlights a stronger temporal variation (Fig. 5a), especially in seagrass SR, seagrass MO and mudflat SR. For seagrass SR, this could be due to a decrease in bacteria, benthic microalgae, SPOM and SOM biomass from spring to autumn, as well as an increase in detrital matter, while changes in seagrass MO may be related to opposite patterns. For mudflat SR, variations

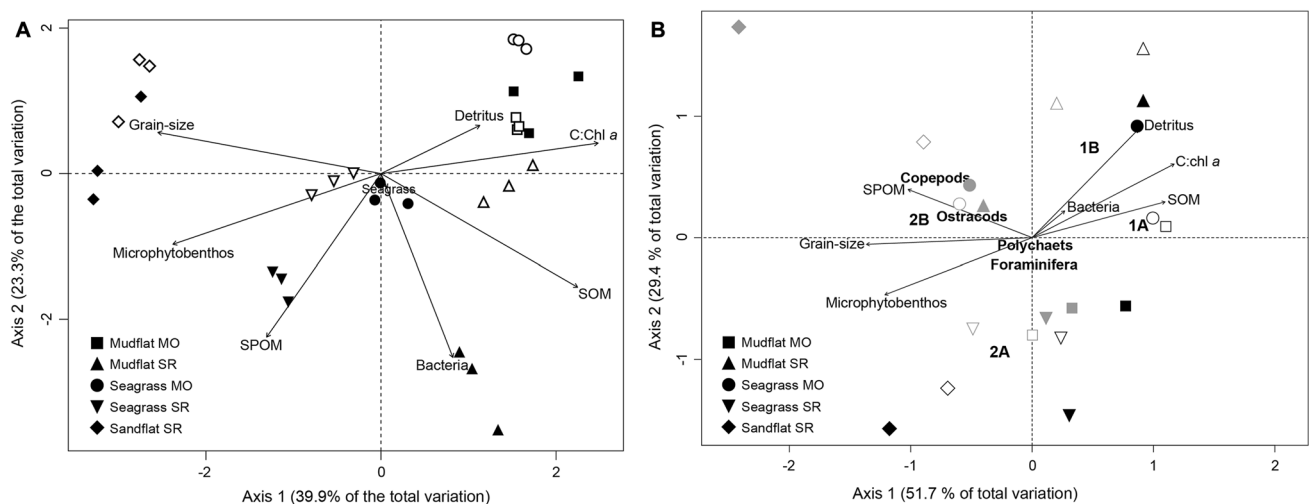


Fig. 5 **a** Principal component analyses for the environmental factors (arrows) plotted for the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in spring (closed symbols) and autumn (open symbols). **b** Redundancy relationship analyses of environmental factors (arrows) selected with stepwise forward procedure plotted against the different groups of meiofauna (benthic copepods, polychaetes, foraminifers, ostracods and trophic groups of nematodes) and the surface (gray symbols) and

sub-surface layers (black symbols) of the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in spring (closed symbols) and autumn (open symbols). *SPOM* suspended particulate organic matter, *SOM* sediment organic matter, *1A* nematodes, selective deposit feeders, *1B* nematodes, non-selective deposit feeders, *2A* nematodes, epigrowth feeders, *2B* nematodes, omnivores/predators

could be explained by the decrease in biomass of benthic microalgae and bacteria and/or the increase in detritus biomass from spring to autumn.

The redundancy analyses (RDA) represented 51.8% of the total variation and 81.1% of the constrained variation (Fig. 5b). Fresh seagrass material was excluded from the RDA after stepwise forward selection of constraints due to collinearity ($vif.cca > 10$). Axis 1 explains 33.0% of the total variation and 51.8% of the constrained variation. Axis 2 explains 18.8% of the total variation and 29.4% of the constrained variation. Both axes significantly explain the model, which highlights relationships between differences of communities and environmental parameters, particularly biomass of benthic microalgae, SPOM, detritus, SOM, carbon:chlorophyll *a* ratios and sediment grain size. Patterns highlighted by Axis 1 about environmental parameters were similar as those highlighted in the PCA: there was a positive relationship between benthic microalgae and SPOM biomasses, and sediment grain size. At the opposite, when benthic microalgae, SPOM and detritus biomasses were low, the carbon:chlorophyll *a* ratio was higher, as well as biomasses of SOM, bacteria and detritus. Differences of meiofauna trophic structure within habitats are mainly explained by sediment grain size, carbon:chlorophyll *a* ratio of SOM, and biomasses of SOM, SPOM, detritus, benthic microalgae, and bacteria (Fig. 5). The two major groups affected by changes in abiotic and biotic parameters were nematodes and benthic copepods. Selective deposit feeders and non-selective deposit feeders occurred mainly within habitats where biomasses of SOM, detritus and bacteria were high (i.e., surface layers of mudflat SR in autumn sub-surface layers of mudflat SR in both seasons, sub-surface layers of seagrass MO in both seasons, and sub-surface layers of mudflat MO in autumn). Epigrowth feeders dominated in habitats where benthic microalgae were an important driving factor (i.e., surface layers of mudflat MO in both seasons, sub-surface layers of mudflat MO in spring, surface and sub-surface layers of seagrass SR in both seasons, and sub-surface layers of sandflat SR in both seasons). Omnivore/predatory nematodes, benthic copepods and other meiofauna taxa occurred in habitats with high biomass of benthic microalgae and SPOM, as well as large sediment grain size (i.e., surface and sub-surface layers of sandflat SR in both seasons and surface layers of seagrass MO in both seasons, and surface layers of mudflat SR in spring).

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

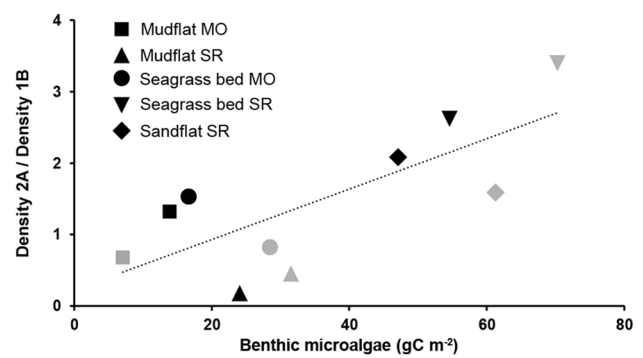


Fig. 6 Relationship between the biomass of benthic microalgae and the ratio between densities of epigrowth feeders (2A) and densities of non-selective deposit feeders (1B) in the mudflats, seagrass beds and sandflat in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in spring (gray symbols)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

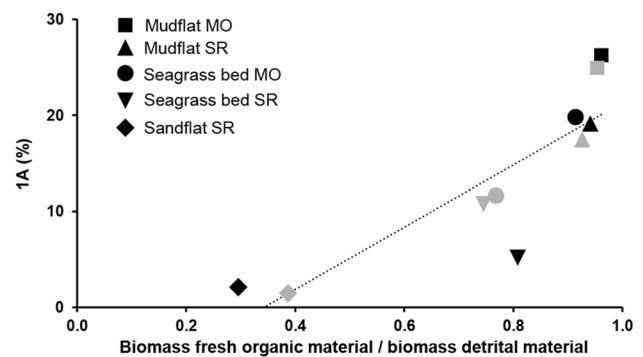


Fig. 7 Relationship between the ratio of fresh organic material to detrital material and the relative abundance of selective deposit feeders (1A) in the mudflats, seagrass beds and sandflats in the Marennes-Oléron Bay (MO) and the Sylt-Rømø Bight (SR) in spring (gray symbols) and autumn (black symbols).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

of detrital material (i.e., SOM and detritus) ($F[1, 8] = 23.1, p < 0.01, r^2 = 0.74$, Fig. 7).

Discussion

Habitat description

The different habitats compared in this study are characterized by a broad range of abiotic and biotic factors. This provides a good framework to determine how changes in these parameters, particularly potential food resources, may influence meiofauna community structure. Biomass of benthic microalgae was much higher in habitats with a larger sediment grain size (sandflat SR and seagrass SR) as already observed in the Marennes-Oléron Bay (Guarini et al. 1998), and benthic microalgae, therefore, represented a much higher proportion of the SOM in these habitats. This pattern is quite

unusual, as habitats with large sediment grain size generally support less microphytobenthos biomass than habitats with small sediment grain size (Cammen 1991; de Jong and de Jonge 1995). Estimations of benthic microalgae biomass were based on chlorophyll *a* measurements and therefore included trapped fresh phytoplankton. Trapped phytoplankton represents a lower proportion of fresh microalgae material than benthic microphytobenthos, although some variations can occur depending on seasons and locations (Asmus 1983; Lebreton et al. 2012). Microphytobenthos community structure and its production may change as well depending on habitats: muddy sediments are usually dominated by large epipelagic diatoms (Thornton et al. 2002; Azovsky et al. 2004) whereas small epipsammic diatoms are the main taxa in sandy habitats (Asmus and Bauerfeind 1994; Azovsky et al. 2004). Benthic microalgae production can be very high in muddy sediments (i.e., $372 \text{ gC m}^{-2} \text{ year}^{-1}$ in mudflat MO) (Pinckney and Zingmark 1993; Leguerrier et al. 2003) and, under favorable conditions, epipelagic diatoms can double their standing stock on a daily basis (Underwood and Paterson 1993). All these changes of biomass, community structure and production rates likely affect the use of this food resource by meiofauna.

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

Loads of detritus were high in seagrass beds, the largest ones being measured in seagrass MO, probably due to the much higher biomass of seagrass roots in this habitat compared to seagrass SR. The higher load of detrital matter in mudflat SR compared to mudflat MO is much likely related to the proximity between the mudflat and the seagrass bed in the Sylt-Rømø Bight, highlighting that seagrass material

can be exported to bare systems. The presence of seagrass in intertidal systems may also indirectly affect the composition of the detrital organic matter available to meiofauna and meiofauna distribution in the sediment (Marbà et al. 2006). The complex root structure of seagrass beds indeed plays a role for the amount of fine particles and detritus associated with the shallow oxic zone in vegetated sediments (Wetzel et al. 2001), as well as in the release of oxygen and dissolved organic matter by the roots (Pedersen et al. 1998). Nevertheless, seagrass material is generally poorly used by most of the consumers as fresh or as detrital material (Danovaro 1996; Vizzini et al. 2002). The presence of seagrass and detritus as well as smaller sediment grain size also affected the abundance of bacteria within the studied habitats. Much lower biomass of bacteria was observed in habitats with lower quantities of detrital matter and SOM and in habitats with coarser sediment (i.e., sandflat), likely due to the reduced surface for bacteria colonization (Dale 1974; Mayer 1994).

Meiofauna community structure: spatial and temporal variations

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

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

Table 5 Density (ind. $m^{-2} \times 10^6$) and biomass (in $gC\ m^{-2}$ and/or $g\ dry\ weight\ m^{-2}$) of nematodes and benthic copepods in mudflats, seagrass beds (*Zostera* spp.) and sandflats from this study and from the available literature about marine soft-bottom intertidal systems

Habitat type	Location	Density		Biomass (g dry weight m^{-2})		Biomass ($gC\ m^{-2}$)		References
		Nematodes	Copepods	Nematodes	Copepods	Nematodes	Copepods	
Mudflat	Papanui Inlet, New Zealand	2.1–3.2	0.5–1.1	0.163	0.125	<i>0.05</i>	<i>0.04</i>	Leduc and Probert (2011)
	Danish Wadden Sea, Denmark	0.22		0.03–0.4		<i>0.01–0.12</i>		Smidt (1951)
	Sylt-Rømø Bight, Germany	0.28	0.03	0.233	0.015	0.102	0.006	This study
	Cornwall, U.K.	1.1				<i>0.48</i>		Ellison (1984)
	Marennes-Oléron Bay, France	2.1				<i>0.92</i>		Rzeznik-Orignac et al. (2003)
	Sylt-Rømø Bight, Germany	2.4	0.07			<i>1.05</i>	<i>0.02</i>	Armonies and Hellwig-Armonies (1987)
	Lynher estuary, U.K.	0.8–22.9		1.4–3.4		<i>0.43–1.49</i>		Warwick and Price (1979)
	Marennes-Oléron Bay, France					0.2–1.5	< 0.09	Pascal (2008)
	Marennes-Oléron Bay, France	3.03	0.13	6.070	0.346	1.257	0.095	This study
	South Carolina, U.S.A.	2.3–4.4				<i>1.01–1.93</i>		Sikora and Sikora (1982)
European estuaries	0.13–14.5				<i>0.06–6.35</i>		Soetaert et al. (1995)	
Seagrass bed	Papanui Inlet, New Zealand	4.9–5.2	< 0.04	0.480	< 0.009	<i>0.15</i>	<i>< 0.003</i>	Leduc and Probert (2011)
	Marennes-Oléron Bay, France	0.65	0.21	1.303	0.459	0.294	0.078	This study
	Sylt-Rømø Bight, Germany	0.81	0.04	0.819	0.015	0.351	0.006	This study
	Sylt-Rømø Bight, Germany	2.0				<i>0.88</i>		Armonies and Hellwig-Armonies (1987)
	Arcachon Bay, France	5.5–8.0		2.4–5.3		<i>0.74–2.32</i>		Castel et al. (1989) and Escaravage et al. (1989)
	Mira estuary, Portugal	1.8–3.3				<i>0.79–1.46</i>		Materatski et al. (2018)
	Marennes-Oléron Bay, France					2.75	0.36	Lebreton (2009)
Sandflat	North Sea intertidal sandflats	0.15	0.11			<i>0.07</i>	<i>0.03</i>	Kotwicki et al. (2005a)
	Sylt-Rømø Bight, Germany	0.22	0.14	0.303	0.130	0.124	0.050	This study
	Arcachon Bay, France	0.7–1.2		0.8–1.3		<i>0.25–0.57</i>		Castel et al. (1989) and Escaravage et al. (1989)
	Oosterschelde, Netherlands	5.0	0.13	2.0	0.2	<i>0.61</i>	<i>0.06</i>	Smol et al. (1994)
	Sylt-Rømø Bight, Germany	2.3	3.5			<i>1.01</i>	<i>1.00</i>	Armonies and Hellwig-Armonies (1987)
	European intertidal flats	0.24–4.1	< 0.35			<i>0.11–1.80</i>	<i>< 0.10</i>	Hicks and Coull (1983) and Kotwicki et al. (2005b)

Average conversion factors used to estimate biomass in $gC\ m^{-2}$ from densities are: nematodes: 2.28×10^6 , benthic copepods: 3.49×10^6 , and from biomass (in $g\ dry\ weight\ m^{-2}$) are: nematodes: 3.26, benthic copepods: 3.40. Converted values are in italic

diversity as species richness was higher in the most dense seagrass bed (Marennes-Oléron) between the two studied ones. Hill's diversity was also higher in seagrass MO than in

all other habitats, which could be partially linked to habitat complexity as well (Austen et al. 1998; Steyaert et al. 2003; Giere 2009). Proportions of omnivore/predatory nematodes

increased as well when complexity increased due to larger sediment grain size as previously observed in sandflats of several other coastal ecosystems (Warwick 1971; Steyaert et al. 2003). This could be explained by the increase of foraging efficiency of predators with an increase in sediment grain size (Gallucci et al. 2005).

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

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

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

Changes in benthic microalgae biomass influenced the community structure of nematodes: relative abundance of epigrowth feeders, relying on benthic microalgae, were reduced when biomass of this food source decreased. Such a relationship between biomass of benthic microalgae and density of epigrowth feeders had already been observed in a subtidal seagrass meadow (Danovaro and Gambi 2002) and during grazing experiments (Rzeznik-Orignac and Fichet 2012). Buccal cavities of epigrowth feeders are appropriate for consumption of benthic microalgae, due to the presence of a dorsal tooth which is used to pierce diatoms (Wieser 1953; Moens and Vincx 1997). A relationship was also observed between biomass of benthic microalgae and relative abundances of benthic copepods and omnivores/predators. However, this relationship may be partly mediated by sediment grain size as benthic microalgae biomass (this study) and relative abundance of benthic copepods increase when sediment get coarser (Hicks and Coull 1983). Nevertheless, the much higher biomass of benthic microalgae in the sandflat compared to SOM suggests that consumers rely—at least partly—directly (i.e., copepods) or indirectly

(i.e., omnivores/predators) on benthic microalgae in this habitat. Such a dependence to benthic microalgae as a food source has been demonstrated for benthic copepods (Leduc et al. 2009).

At a more global scale (i.e., whole meiofauna, all habitats combined), no general pattern could be observed between benthic microalgae biomass and those of nematodes and benthic copepods. Some other parameters should probably be taken into account to better consider relationships between this food resource and consumers. Benthic microalgae can indeed reach very high production rates and are a food source of high quality (Cebrián 1999). The high primary production of benthic microalgae in mudflat MO ($372 \text{ gC m}^{-2} \text{ year}^{-1}$; Leguerrier et al. 2003) and high grazing pressure on this food source by the large biomass of nematodes (Blanchard 1991) could explain the lack of relationship between benthic microalgae and meiofauna biomass within these habitats. Quality is of high importance as well: Moens et al. (1999b) suggested that meiofauna migrate actively towards food sources. In addition to epigrowth feeders, several studies demonstrated that deposit feeders rely on microalgae (Moens and Vincx 1997; Rzeznik-Orignac et al. 2003; Vafeiadou et al. 2014) likely due to the better quality of microalgae. A relationship between density of nematodes belonging to these feeding groups and microalgae has been observed (Moens et al. 1999a). In particular, grazing experiments using ^{14}C labeled diatoms indicated the dependence of a non-selective deposit feeding nematode (*Daptonema*), an epigrowth feeding nematode (*Metachromadora*) and benthic copepods on microalgae (Rzeznik-Orignac and Fichet 2012). Vafeiadou et al. (2014), using stable isotopes, confirmed that non-selective deposit feeding nematodes, epigrowth feeding nematodes and benthic copepods can largely rely on benthic microalgae in sparsely covered seagrass beds. Besides their very specific buccal cavity, it is also worth noting that epigrowth feeders can be opportunistic as well, and rely on other food resources (e.g., bacteria and/or fungi; Iken et al. 2001). As a result, benthic microalgae are often considered as the principal food source for nematodes and benthic copepods (Moens et al. 2005; Rzeznik-Orignac et al. 2008; Maria et al. 2012).

Benthic microalgae followed an opposite pattern than detrital material (SOM and detritus), with decreasing biomass of benthic microalgae when detrital material increased. SOM biomass was stable between spring and autumn, as well as between surface and sub-surface layers, but large variations were observed between the different habitats (i.e., much lower biomass in sandflat SR). The relative abundance of non-selective deposit feeders, closely related to detrital matter based on the RDA, decreased when biomass of SOM was lowered. Higher SOM quality in the surface sediment layers could lead to higher biomass, density and diversity of nematodes in the surface layer compared to the

sub-surface layer. As a result, the important role of SOM is very likely related to its very high amount, as well as variations in quality between the studied systems. A relationship between SOM and density of non-selective deposit feeders was also recognized in a subtidal seagrass meadow (Danovaro and Gambi 2002), while a grazing experiment indicated that the non-selective and selective deposit feeding nematode species assimilated predominantly SOM and bacteria (Tietjen and Lee 1977). The non-selective deposit feeders can, therefore, be considered as opportunistic feeders, which may change feeding strategies depending on the availability of food sources (Moens and Vincx 1997; Rzeznik-Orignac et al. 2008).

As a result, SOM and benthic microalgae appear to be important biotic factors driving the nematode community structure and, *a fortiori*, the composition of meiofauna assemblages as nematodes represent a large proportion of the meiofauna in coastal ecosystems (Armonies and Hellwig-Armonies 1987; Rzeznik-Orignac et al. 2003; Leduc and Probert 2011).

Role of bacteria as a food source?

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

Multivariate analyses demonstrated as well a relationship between relative abundances of non-selective deposit

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

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

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

Conclusion

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

Acknowledgements This study forms part of the Ph.D. thesis of L. van der Heijden. This work was financially supported by the University of La Rochelle through a grant provided by the 'Ministère de l'Enseignement Supérieur et de la Recherche'. This work was supported by the CNRS through the CNRS research chair provided to B. Lebreton. Financial support was provided by the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, as well as the University of La Rochelle (Mobility for doctoral students) and the German Academic Exchange Service (DAAD: short-term research grant, 2017, no. 57314023). We acknowledge P. Pineau, B. Hüssel, S. Horn, M. Burgdorf, M. Paar and N. Lachaussée for their support during fieldwork, and G. Guillou and C. Labruno for their support in the analyses. We thank Q. Bernier for his help in sample processing and analysis. Finally, L. van der Heijden thanks the members of his Ph.D. committee, M. Graeve, N. Niquil and G. Blanchard, for their guidance, as well as two anonymous reviewers whose comments greatly improved the manuscript.

Compliance with ethical standards

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

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

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