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Resource utilization and trophic position of nematodes and harpacticoid copepods in and adjacent to *Zostera noltii* beds

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Abstract

This study examines the resource use and trophic position of nematodes and harpacticoid copepods at the genus/species level in an estuarine food web in *Zostera noltii* beds and in adjacent bare sediments, using the natural abundance of stable carbon and nitrogen isotopes. Microphytobenthos is among the main resources of most taxa, but seagrass-associated resources (i.e. seagrass detritus and epiphytes) also contribute to meiobenthos nutrition, with seagrass detritus being available also in deeper sediments and in unvegetated patches close to seagrass beds. A predominant dependence on chemoautotrophic bacteria was demonstrated for the nematode genus *Terschellingia* and the copepod family Cletodidae. A predatory feeding mode is illustrated for *Paracomesoma* and other Comesomatidae, which were previously considered first-level consumers (deposit feeders) according to their buccal morphology. The considerable variation found in both resource use and trophic level among nematode genera from the same feeding type, and even among congeneric nematode species, shows that interpretation of nematode feeding ecology based purely on mouth morphology should be avoided.

1 Introduction

Seagrass meadows form unique, productive and highly diverse ecosystems throughout the world (Hemminga and Duarte, 2000). They stabilize and enrich sediments, and provide breeding and nursery grounds for various organisms, as well as critical food resources and habitats for many others (Walker et al., 2001). Seagrass beds typically support higher biodiversity and faunal abundance compared to the adjacent unvegetated areas (Edgar et al., 1994) due to both increased food supply and reduced predation risks (Heck Jr. et al., 1989; Ferrell and Bell, 1991). Furthermore, they strongly influence the associated fauna by modifying hydrodynamics (Fonseca and Fisher, 1986) and by altering the energy flux either directly, through release of dissolved organic

carbon into the water column, or indirectly, by contributing to the detritus pool after decomposition (Boström and Bonsdorff, 1997).

Several studies during the last decade have used natural stable isotope ratios to elucidate the principal food sources of macrobenthos in seagrass beds, stressing the importance of seagrass-associated sources and/or microphytobenthos (MPB) (Lepoint et al., 2000; Kharlmamenko et al., 2001; Moncreiff and Sullivan, 2001; Baeta et al., 2009; Carlier et al., 2009; Lebreton et al., 2011; Ouisse et al., 2012; Vafeiadou et al., 2013a). Less information is available for meiobenthos resource utilization in seagrass beds (Vizzini et al., 2000b, 2002a; Baeta et al.,. 2009; Leduc et al., 2009; Lebreton et al., 2011, 2012), with none of the studies including meiofauna at the level of feeding types, families, genera or species. The few studies using natural isotope abundances to unravel food resources of coastal meiofauna at this level (Carman and Fry, 2002; Moens et al., 2002, 2005, 2013; Rzeznik-Orignac et al., 2008) do not pertain to seagrass habitats.

The present study aims to assess the principal carbon sources of the nematode and harpacticoid copepod assemblages, at the species, genus or family level, in *Zostera noltii* Hornem. seagrass beds and in adjacent bare sediments. In light of several stable isotope studies which have stressed the predominant role of MPB as a carbon source to intertidal meiofauna (Moens et al., 2002, 2005; Rzeznik-Orignac et al., 2008; Maria et al., 2012), we hypothesized that MPB would be the principal carbon resource to the majority of taxa in bare sediments. In vegetated sediments, seagrass-associated resources (i.e. seagrass detritus and epiphytes) could also contribute, and higher sedimentation rates would likely raise the contribution of suspended particulate organic matter (SPOM) to meiofauna diets, much like in salt marshes (Moens et al., 2005). We also expected MPB and SPOM to contribute more at the sediment surface than deeper down in the sediment, based on Rudnick's theory (1989) which proposed a different resource utilization by meiofauna in the sediment surface than in deeper layers: fresh phytodetritus would be the principal resource for nematodes living in the upper 2 cm of the sediment, whereas deeper down, nematodes would mainly feed on larger frac-

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tions of buried, more refractory detritus. Thus, we would expect a higher contribution of detrital organic matter than of MPB or SPOM in deeper sediment layers.

So far, nematodes have been classified in feeding guilds based on buccal morphology (Wieser, 1953; Jensen, 1987; Moens and Vincx, 1997). Nevertheless, stable isotope data and in situ observations of living nematodes have shown that such stoma-morphology based guild classifications do not always provide good predictions of nematode resource utilization and even trophic level (Moens et al., 2005). In harpacticoid copepods, there is also no straightforward link between the morphology of the mouth parts and their food resources (Hicks and Coull, 1983; De Troch et al., 2006). Therefore, we also examine the validity of existing mouth-morphology based nematode feeding guilds, based on their trophic position and resource utilization as revealed by the stable isotope data obtained in this study. If current guild classifications represent real functional groupings, then resource utilization and trophic level within feeding guilds should be very similar, while it would differ among guilds.

2 Materials and methods

2.1 Study area and sampling design

Sampling was conducted at the Mira estuary (37°40 N, 8°40 W, SW Portugal), a small mesotidal system with a semidiurnal tidal regime, which together with the Mira River and its surrounding intertidal area is included in the protected Natural Park "Sudoeste Alentejano e Costa Vicentina" (Fig. 1). This estuary is considered relatively undisturbed and free from industrial pollution (Costa et al., 2001). Our study area was located at two sites of the intertidal area at the lower section, ca. 1.5 km from the mouth of the estuary (i.e. sampling site A) and ca. 2 km further upstream (i.e. sampling site B). Due to the low, seasonal and limited freshwater input, the lower section of the estuary has a significant marine signature. In both sites, sediments were sparsely covered with *Zostera noltii*, seagrass vegetation being less dense (ca. 50 % difference) in February 2011

than in June 2010 (Vafeiadou et al., 2013a). These seagrass beds used to be denser in the past, but the vegetation is under recovery after a major collapse in 2008 (Adão et al., 2009; Cunha et al., 2013). Samples were collected on two sampling moments (22 June 2010 and 7 February 2011) to cover two different seasons. We sampled two random stations at each sampling site (i.e. A and B), one located inside the seagrass vegetation (i.e. A1 and B1), the other in adjacent bare sediments (i.e. A2 and B2).

2.2 Sampling of carbon sources and meiobenthos

Fresh seagrass leaves, roots and seagrass detrital material were collected randomly from each vegetated station (i.e. A1 and B1), thoroughly rinsed and carefully scraped off using a cover glass to remove epiphytes, which were collected separately. To obtain bulk sediment organic matter we sampled three replicate cores ($10\,cm^2$) of the upper 6 cm of sediment from all stations. The epipelic fraction of MPB was collected via migration through the lens-tissue method (Eaton and Moss, 1966) one year later than the other samples, but at very similar sampling moments and conditions (February and June 2012), because samples collected during the 2010/2011 campaigns had yielded insufficient MPB biomass for reliable nitrogen isotopic analyses. 1.5 L of seawater was filtered over pre-combusted Whatman GF/F filters to collect SPOM. Seagrass material and bulk sediment samples were oven dried (60 °C) for 48 h before preservation and stored in desiccators; all other samples were stored frozen.

Meiobenthos samples were obtained by forcing hand cores ($10\,cm^2$) to a depth of 6 cm into the sediment at all stations. Each sediment sample was divided in three depth layers: 0–2 cm, 2–4 cm and 4–6 cm. Seven replicate samples were randomly collected from each station within a $100\,m^2$ area and then pooled into one bulk sample considered representative for a particular station. Pooling of replicate samples was done to ensure that enough biomass of several genera/species could be obtained for the stable isotope analyses. Meiobenthos samples were stored frozen prior to elutriation and analysis.

2.3   Preparation of samples for stable isotope analyses

Dried seagrass and bulk sediment samples were homogenised, weighed (0.3–0.7 mg DWT of seagrass, 20–60 mg DWT of sediment), and transferred into silver cups (8 mm × 5 mm, Elemental Microanalysis Ltd.) which had been pre-treated for 4 h at 550 °C to remove organic contamination. Two subsamples were then prepared: the first was acidified with dilute HCl to remove carbonates, the second not, to eliminate any effects of acidification on nitrogen isotopic signatures (Vafeiadou et al., 2013b). A drop of milli-Q water was added to acidified samples which then were oven dried (60 °C) for 48 h. Epiphyte and MPB samples were all acidified since insufficient biomass was available for subsampling. The Whatman GF/F filters were divided in two; only one half was acidified under HCl vapour for 24 h, the other not. All samples were prepared in pre-combusted silver cups.

Meiofauna was elutriated using density centrifugation in Ludox HS40, which does not affect isotope signatures (Moens et al., 2002). No other chemicals were used during processing of the meiofauna samples. The most abundant nematode and copepod taxa were hand-sorted and identified at the genus or family level under a stereomicroscope. Individuals were hand-picked with a fine needle, rinsed several times in milli-Q water to remove adhering particles, and finally transferred into a drop of milli-Q water in pre-combusted aluminium cups (6 mm × 2.5 mm, Elemental Microanalysis Ltd.). The number of specimens transferred into the cups depended on the abundance and individual biomass of the different taxa. We aimed at a sample mass > 5 µg of the element of interest, be it C, N or both. Thus, 10–40 individuals were pooled together for a copepod sample and from 10 to 300 for a nematode sample, depending on their size. In many cases, though, the biomass of the sample was sufficient only for reliable carbon analysis but not for nitrogen analysis. Thus, despite the combined $\delta^{13}C/\delta^{15}N$ analysis per sample, we finally obtained different sample numbers for the $\delta^{13}C$ and $\delta^{15}N$ data, lacking some $\delta^{15}N$ because of the too low N peaks at the analysis. Because of very

low meiofauna abundances below a depth of 2 cm, for most taxa we obtained sufficient biomass for only a single isotope measurement.

2.4 Stable isotope analyses

Isotopic analyses of sources and meiofauna were performed using a ThermoFinnigan Flash 1112 elemental analyser (EA) coupled on-line via a Conflo III interface to a ThermoFinnigan Delta Plus XL isotope ratio mass spectrometer (IRMS), with analytical reproducibility typically $\leq 0.2\,\permil$ for both δ^{13}C and δ^{15}N. All resource samples were measured in He-dilution mode, except for the epiphyte samples. These, as well as all meiofauna samples, were measured without He-dilution. Stable isotope ratios are expressed in units of parts per thousand, according to the formula:

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 10^3,$$

where X is ^{13}C or ^{15}N and R the ratio of ^{13}C/^{12}C or ^{15}N/^{14}N. As external lab standards, we used CH-6 (sucrose) and N1 (ammonium sulphate) from the International Atomic Energy Agency, with δ^{13}C and δ^{15}N values of $-10.4\,\permil$ and $+0.4\,\permil$, respectively.

When measuring samples containing limited biomass, caution is needed when assessing the results of IRMS. Based on prior tests with decreasing mass of standards of known isotopic ratios, we discarded all results of samples yielding amplitudes smaller than 200 mV. We measured external standards for linear corrections of small analytical errors in the obtained delta-values. Further, we routinely corrected the obtained sample delta-values for the contribution of blanks using the formula:

$$\delta_{\text{organic matter}} = (\delta_{\text{sample}} \cdot \text{amplitude}_{\text{sample}}; \delta_{\text{blank}} \cdot \text{amplitude}_{\text{blank}})/\text{amplitude}_{\text{organic matter}},$$

where $\delta_{\text{organic matter}}$ is the real δ-value of the material of interest and amplitude$_{\text{organic matter}}$ = amplitude$_{\text{sample}}$ − amplitude$_{\text{blank}}$. Such "blank correction" is important in samples with low amplitudes, where even small blanks may contribute significantly to the measured δ_{sample} (Moens et al., 2013).

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2.5 Data analysis

For the interpretation of stable isotope data, trophic enrichment factors of $1 \pm 1.2\,‰$ for δ^{13}C and $2.5 \pm 2.5\,‰$ for δ^{15}N were adopted for each level (Vander Zanden and Rasmussen, 2001). Comparisons of stable isotope data of meiobenthos (1) between sampling moments (summer vs. winter) and (2) between vegetated and bare sediments, were performed using paired Student's t tests. For these comparisons, we used only δ^{13}C data of those taxa which occurred in both months or at both types of sediments from the upper 2 cm, due to the limited data obtained for δ^{15}N and from deeper layers. No data transformation was applied since the assumptions of normality and homoscedasticity were met, tested by Cochran's test. The validity of the above comparisons was based on the fact that source isotope signatures did not differ across months or stations (Vafeiadou et al., 2013a). All statistical analyses were performed using Statistica 6 software (StatSoft).

The Bayesian stable isotope mixing model MixSIR (Semmens and Moore, 2008) was applied to the present data, using the application MixSIR Version 1.0.4. for MATLAB (R2013a, The MathWorks), to calculate the relative contributions of potential food sources to the diets of meiofauna. We used δ^{13}C and δ^{15}N of all replicate samples per taxon separately and mean ($\pm$SD) δ^{13}C and δ^{15}N of each resource from both sampling months as input data. Seagrass leaves and roots were excluded from the model because we assumed that no meiofauna studied here are capable of herbivory on living seagrass tissue. Two scenarios were modelled: with and without epiphytes, the latter in order to reduce the number of potential resources and the number of resources with intermediate and overlapping carbon isotopic signatures. Chemoautotrophic bacteria were added as a potential resource for the nematode genera *Terschellingia* and *Sabatieria* and the copepod family Cletodidae, based on their δ^{13}C and literature information (see Sect. 4); we adopted an average δ^{13}C of $-35\pm5\,‰$ for this resource (based on: robinson and Cavanaugh, 1995; Pape et al., 2011; Guilini et al., 2012) and similar δ^{15}N to those of the examined taxa. Mean $\pm$ SD trophic enrichment factors of $1 \pm 1.2\,‰$

and $2.5 \pm 2.5\,‰$ were assumed for δ^{13}C and δ^{15}N, respectively, and adapted accordingly for each trophic level. We ran MixSIR introducing a number of 10 000 iterations, without a priori defined source contribution data. The model was applied separately to each taxon, in seagrass beds and bare sediments, and in the surface and deeper layers.

3 Results

3.1 Stable isotope signatures of carbon resources

Fresh seagrass leaves, roots, and seagrass detritus had comparatively higher δ^{13}C (from $-11.3 \pm 1.7\,‰$ to $-16.0 \pm 1.2\,‰$), while epiphytes, bulk SOM, MPB and SPOM were, to various degrees, more ^{13}C-depleted (δ^{13}C from $-17.8 \pm 0.4\,‰$ to $-24.2 \pm 1.4\,‰$) (Table 1). No significant differences were detected when comparing source δ^{13}C or δ^{15}N data between sampling months ($p > 0.05$ for all), the only exception being MPB, which had more depleted δ^{13}C in February ($-21.0 \pm 1.2\,‰$) than in June ($-19.0 \pm 0.2\,‰$) (for δ^{13}C: $U = 0$; $Z = -2.7$, $N_1 = 4$, $N_2 = 6$, $p = 0.006$ and for δ^{15}N: $U = 0$; $Z = 3$, $N_1 = 4$, $N_2 = 6$, $p = 0.003$; see also Vafeiadou et al., 2013a).

3.2 Stable isotope signatures of meiobenthos

Overall, the present study includes δ^{13}C data of 20 nematode taxa, 16 of which were identified to the genus level (two genera were represented by two species each) and two to the family level (unidentified Comesomatidae and Chromadoridae), as well as four harpacticoid copepod families (Canuellidae, represented here by the genus *Sunaristes*, Cletodidae, Ectinosomatidae and Harpacticidae, this last taxon being present only in deeper sediments) (Tables 2 and 3). δ^{15}N data are available for 8 of the 16 nematode genera and the unidentified Comesomatidae, and for two copepod families (Canuellidae and Cletodidae) (Tables 2 and 3). Although this dataset includes most

of the abundant genera of this nematode assemblage (Table 2), some abundant genera are not represented here because of their low individual biomass, hampering the collection of sufficient biomass for stable isotope analysis.

δ^{13}C of most meiofauna from the upper 2 cm ranged from $-22.7 \pm 1.2\,\permil$ (*Spirinia parasitifera*) to $-11.9\,\permil$ (*Theristus*) (Fig. 2a), and δ^{15}N ranged from $3.9\,\permil$ (*Sunaristes*) to $10.8\,\permil$ (Comesomatidae) (Fig. 2b). The nematode genus *Terschellingia* and the copepod family Cletodidae had much lower δ^{13}C (mean δ^{13}C $\pm$ SD $= -41.7 \pm 2.4\,\permil$ and $-33.2 \pm 5.5\,\permil$, respectively; Fig. 2a) compared to all other meiofauna. *Terschellingia* also had very low δ^{15}N values ($2.8 \pm 1.9\,\permil$; Fig. 2b). Most taxa had δ^{13}C in the range of MPB and epiphytes, whereas *Spirinia parasitifera* and *Sabatieria* sp.2 were more depleted in ^{13}C, with δ^{13}C values close to SPOM ($-24.1 \pm 1.2\,\permil$; Figs. 2a and 3). *Daptonema*, *Metachromadora*, *Spirinia* sp.2, *Ptycholaimellus* and *Theristus* were comparatively enriched in ^{13}C, with values close to those of seagrass detritus ($-16.0 \pm 1.1\,\permil$; Figs. 2a and 3).The comparison of δ^{13}C of meiobenthos from the surface sediment layers between sampling months (i.e. June vs. February) and between stations (i.e. vegetated vs. bare sediments) did not reveal any significant differences ($df = 24$, $t = 0.31$; $p > 0.05$ and $df = 32$, $t = 1.35$; $p > 0.05$, respectively). δ^{15}N data clearly show the presence of more than one trophic level in this nematode assemblage in the upper 2 cm, with *Sphaerolaimus*, *Paracomesoma* and unidentified Comesomatidae belonging to a higher trophic level than all other meiofauna (Figs. 2b and 3).

δ^{13}C and δ^{15}N data from the deeper sediment layers (2–6 cm) are available for a lower number of nematode and copepod taxa due to the overall low meiofauna abundances in these deeper layers (Table 3). Most δ^{13}C ranged from $-29.8\,\permil$ (*Paracanthonchus*) to $-14.4 \pm 0.4\,\permil$ (*Metachromadora*), with the exception of *Terschellingia* and Cletodidae, which had much lower δ^{13}C ($-40.4 \pm 4.5\,\permil$ and $-33.5\,\permil$, respectively; Table 3). The δ^{13}C of most taxa in the deeper sediment layers (i.e. *Anoplostoma*, *Bathylaimus*, *Oncholaimus*, *Paracanthonchus*, *Sphaerolaimus*, *Spirinia parasitifera*) were more ^{13}C-depleted (by $> 4\,\permil$), and closer to those of SPOM than those from the same taxa at the sediment surface, where they had more intermediate values. The δ^{13}C of

Oncholaimus, Paracanthonchus, Sabatieria sp.2, *Spirinia parasitifera* and Harpactici-dae were even more depleted than any measured resource. In contrast, δ^{13}C of the nematodes *Daptonema*, *Metachromadora* and *Spirinia* sp.2 and of the copepod genus *Sunaristes* were in the range of values for epiphytes and seagrass detritus (Table 3).

3.3 Application of the isotope mixing model MixSIR

Applying the isotope mixing model MixSIR to our data we obtained the model esti-mations of proportional contributions of each resource to the diet of each nematode genus/species or copepod family/genus, in seagrass vegetated and bare sediments, and in surface and deeper layers (Table 4). According to the model computations, sea-grass detritus contributed more than other resources to the carbon requirements of *Metachromadora*: for 0.84 and 0.94 in seagrass beds, and for 0.77 and 0.91 in bare sediments (with respect to the 50th and the 95th percentile; see Supplement), when using all four resources. Seagrass detritus was also the predominant carbon source for *Daptonema*, with contributions of 0.72 and 0.89 in seagrass beds and of 0.54 and 0.80 in bare sediments (Table 4). When omitting epiphytes as a candidate resource, the con-tribution of seagrass detritus increased for all taxa. In contrast, SPOM contributed more than other resources to the carbon requirements of *Sphaerolaimus*, for 0.77 and 0.89 in seagrass beds, and for 0.67 and 0.82 in bare sediments, when using all four resources, and of *Paracomesoma,* for 0.80 and 0.92 in seagrass beds, and for 0.72 and 0.86 in bare sediments (Table 4). When omitting epiphytes from the model, the contribution of SPOM increased for all taxa. MPB contributed substantially to the diet of most nema-tode and copepod taxa with intermediate stable carbon signals, together with epiphytes (Table 4), but when omitting the latter, MPB estimated contributions increased. In gen-eral, the fewer the number of resources included in the model, the clearer the estimated contributions of the remaining resources as calculated by MixSIR. As such, excluding epiphytes generally improved the model output. However, one should bear in mind that when MPB would be excluded instead of epiphytes, then the model would often pre-dict a predominant contribution of epiphytes instead of MPB to the diets of a range of

meiofaunal taxa, even in bare sediments. The additional resource, chemoautotrophic bacteria, contributed to the carbon requirements of *Terschellingia* for 0.81 and 0.91, and this to the same extent in seagrass beds and in bare sediments, when using all five resources (Table 4). It also predominantly contributed to the diet of Cletodidae, for 0.46 and 0.61 in seagrass beds. Here, however, SPOM and MPB contributions were also substantial.

4   Discussion

4.1   Resource utilization by meiobenthos inside and adjacent to *Zostera* vegetation

The stable isotope data of resources and consumers obtained in this study suggest that seagrass detritus, epiphytes, MPB and SPOM all contribute to a varying degree to the carbon requirements of meiofauna. In all, the proportional contributions estimated by the isotope mixing model MixSIR agree well with our data interpretation based on the isotope biplots. No significant differences in isotope signatures of nematode and copepod taxa inside seagrass vegetation compared to in adjacent bare sediments were detected, contradicting our hypothesis that MPB would contribute more in bare sediments, whereas seagrass detritus and SPOM would be more important sources inside vegetated sediments. This agrees well with results for macrobenthos from the same ecosystem (Vafeiadou et al., 2013a). Seagrass vegetation has important indirect effects on resource availability, for instance through substrate formation and through the enhancement of SPOM sedimentation (Ouisse et al., 2012). However, seagrass detritus and SPOM are also exported from seagrass beds to adjacent or even more distant locations (Hemminga et al., 1994; Heck et al., 2008). Our results support the idea that carbon inputs associated with seagrass beds extend beyond the vegetation boundaries and contribute to the diet of benthos living adjacent to seagrass vegetation, including representatives of the predominant meiofaunal taxa.

Fresh seagrass leaves and roots, despite their biomass, are generally considered of minor importance as carbon sources for the benthos, mainly as a consequence of their poor nutritional value and high lignocellulose content (Ott and Maurer, 1977; Vizzini et al., 2002a). This is also supported by the results of our study, where the majority of meiofaunal taxa were considerably more depleted in δ^{13}C than seagrass tissue. Nevertheless, the high contribution of seagrass detritus predicted by the mixing model for some nematode genera (i.e. *Daptonema*, *Theristus, Metachromadora, Spirinia* sp.2 and *Ptycholaimellus*), in addition to their relatively enriched δ^{13}C, suggest that they depended to a considerable extent on decomposing seagrass tissue. Based on mouth-morphology derived assumptions on their feeding ecology, these nematode genera have usually been considered as MPB feeders. Our present δ^{13}C data do not point at a major contribution of MPB in the diet of these nematodes. In contrast, they clearly indicate that they feed on *Zostera* detritus, either directly or through grazing on detritivorous (micro)organisms see further under Sect. 4.2.

The predominant associates of seagrass are epiphytic microalgae, which can importantly contribute to the primary productivity in seagrass beds, and have a generally high nutritional value (Kitting et al., 1984; Gambi et al., 1992; Moncreiff and Sullivan, 2001). In our study, they had considerably more depleted carbon isotope signatures than fresh or detrital seagrass material and a variety of meiofauna, in particular several epistratum-feeding nematodes and harpacticoid copepods, had δ^{13}C values closely resembling those of epiphytes. Given the expected importance of microalgae as food to many harpacticoid copepods (De Troch et al., 2005a, b) and epistratum-feeding nematodes (Moens and Vincx, 1997), it is tempting to interpret these results as an important utilization of seagrass epiphytes by meiofauna. However, the carbon isotope signatures of epiphytes in our study overlap with those of MPB, rendering firm conclusions on the relative importance of these resources difficult (see Vafeiadou et al., 2013a).

The few studies which have previously studied resource utilization of intertidal meiofauna at genus or species level have all stressed the importance of MPB as a principal food source for meiofauna (Carman and Fry, 2000; Moens et al., 2002, 2005, 2013;

Rzeznik-Orignac et al., 2008; Maria et al., 2012). Our results revealed a number of epistratum- and deposit-feeding nematodes with intermediate carbon isotope signatures, suggesting they either utilize a mix of more ^{13}C-depleted (e.g. SPOM) and more ^{13}C-enriched (e.g. seagrass detritus) food sources or, more likely, feed predominantly on MPB and/or epiphytes. Since larger seagrass fragments were very scanty on bare sediments, it is unlikely that epiphytes would have substantially contributed to nematode diets in these bare sediments. Given the absence of significant differences in nematode isotope signatures between vegetated and bare sediments, we conclude that MPB is probably the most important carbon source for these nematodes, independent of the habitat where they were collected.

Given the increased sedimentation in seagrass beds, and the high contribution of SPOM in vegetated intertidal areas which are characterised by higher sedimentation (Moens et al., 2005), we expected SPOM to be a comparatively more important carbon source for meiofauna inside *Zostera* patches than in bare sediments in our study area. The carbon isotope signatures of SPOM in our study were clearly more depleted than those of the other potential resources, and in the range of "typical" values for SPOM (comparing with SPOM data from the Mondego Estuary, Portugal; Baeta et al. (2009) and from the Scheldt Estuary, the Netherlands; Moens et al., 2005). This was not, however, reflected in more depleted δ^{13}C signatures of meiofauna inside seagrass vegetation. Isotopic signatures reflecting utilization of SPOM were most prominent in the nematodes *Spirinia parasitifera*, *Sabatieria* sp.2, *Oncholaimus, Sphaerolaimus* and *Paracomesoma*, and in the copepod family Harpacticidae from deeper sediments (2–6 cm). This was the case in both vegetated and bare sediments, except for *Oncholaimus* and Harpacticidae which occurred only in seagrass beds. The increased contributions of SPOM over the other resources resulting from the mixing model for the nematodes *Sphaerolaimus* and*Paracomesoma* also confirm their predominant reliance on this carbon source. However, according to their elevated δ^{15}N see Sect. 4.2 these two genera utilize SPOM indirectly, probably through feeding on prey which rely

on SPOM. Alternatively, it is also possible that the abundant genus *Terschellingia* is among their prey; this nematode has extremely low δ^{13}C values (see below).

Furthermore, our data highlight differential resource utilization between surface (2 cm) and deeper sediment layers (2–6 cm), indicating a shift from MPB to SPOM utilization in deeper sediments for the nematodes *Anoplostoma, Bathylaimus, Oncholaimus, Paracanthonchus, Sphaerolaimus* and *Spirinia parasitifera* and for the copepod family Harpacticidae. Hence, our data partly support Rudnick's (1989) hypothesis of differential resource utilization by surface-inhabiting vs. deeper-dwelling meiofauna. In our study, surface-inhabiting meiofauna primarily utilized MPB and, to a lesser extent, seagrass detritus, epiphytes and SPOM. For meiofauna collected below 2 cm, SPOM was of primary importance. Surface food-addition experiments in subtidal (Ólafsson et al., 1999) and intertidal (Moens et al., 2002) sediments have also demonstrated that nematodes from both surface and deeper sediment layers can consume deposited phytodetritus. However, our results do not support Rudnick's (1989) contention that deeper-dwelling nematodes rely more on refractory organic matter. Among the resources considered in the present study, seagrass detritus is the most refractory, but our data indicate that it was utilized less rather than more by deeper-dwelling nematodes.

The strongly depleted δ^{13}C values of the nematode *Terschellingia* and the copepod family Cletodidae demonstrate different trophic pathways involving utilization of a carbon resource not included in our sampling. Several chemoautotrophic processes yield highly depleted δ^{13}C values. Among them is sulphide oxidation; sulphide-oxidizing bacteria have δ^{13}C values which tend to be (well) below −30 ‰ (Robinson and Cavanaugh, 1995). Hence, our results strongly indicate that *Terschellingia* and Cletodidae rely predominantly or even exclusively on such bacteria, as also supported by the high contributions predicted by the mixing model.

Our data for *Terschellingia* are consistent with previous records (δ^{13}C = −43 ‰) from a mangrove ecosystem (T. Moens, unpublished data; in Bouillon et al., 2008) and from an estuarine intertidal flat in the Oosterschelde, the Netherlands (Moodley et al.,

unpublished data; in Moens et al., 2011). *Terschellingia* is a microvore with a very small buccal cavity, enabling ingestion of only bacteria-sized particles, and tends to be very abundant in hypoxic/anoxic sediments (Steyaert et al., 2007), where chemosynthetic processes can be important. The nematode genera *Terschellingia* and *Sabatieria* have been suggested to feed on sulphide-oxidizing bacteria in deep-sea sediments too (Pape et al., 2011; Guilini et al., 2012). *Sabatieria* sp.2 in our study also had depleted δ^{13}C (-23.4‰ and -28.3‰ in vegetated and bare sediments, respectively). These data together with the mixing model estimations suggest that *Sabatieria* sp.2 partly relied on chemoautotrophic carbon, especially in bare sediments; nevertheless, estimated contributions in vegetated and bare sediments could not be compared as the available data of *Sabatieria* sp.2 in bare sediments do not allow mixing model computations. In contrast, *Sabatieria* sp.1 was more enriched than its congener and probably depended largely on MPB.

Little is known on the autecology and feeding habits of cletodid copepods (Hicks and Coull, 1983), but diatoms, detritus and bacteria have all been listed as their food sources (Ivester and Coull, 1977). However, recent data from a salt marsh gully in the Scheldt Estuary, the Netherlands, confirm our results that sulphide-oxidizing bacteria are the major carbon source for these copepods (Cnudde et al., unpublished data). Further, Grego et al. (2014) found representatives of the family Cletodidae the most resistant copepods to long-term anoxia. Apart from a single mention of equally depleted δ^{13}C of an unidentified harpacticoid copepod from the Oosterscheldt Estuary (Moens et al., 2011), these data provide the first evidence of a trophic association between harpacticoid copepods and chemoautotrophic bacteria. Whether this association involves (selective) grazing on chemoautotrophic bacteria or some form of symbiosis remains unknown, both for the Cletodidae and for *Terschellingia*.

Conceivably, the availability of the different carbon sources may vary seasonally, as seagrass productivity does. Nevertheless, such temporal changes did not qualitatively influence the resource utilization by meiofauna, since the isotope data obtained of consumers and their food sources did not exhibit significant differences between winter

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and summer (see also Vafeiadou et al., 2013a for similar patterns in macrofauna). For carbon sources, this is in agreement with isotope studies in other estuarine seagrass areas and indicates that temporal variability in resource isotopic signatures is limited (Baeta et al., 2009; Lebreton et al., 2012). For the meiofauna, this suggests that most taxa maintain the same resource preferences throughout the year, irrespective of their availability, whereas the resource isotopic signatures do not vary significantly.

4.2 Implications for nematode trophic guild classifications

A clear distinction among trophic levels within the meiofauna analysed is evident from the stable nitrogen isotope data, with *Sphaerolaimus*, *Paracomesoma*, and unidentified Comesomatidae belonging to a higher trophic level than all other nematodes and harpacticoid copepods. Our results on *Sphaerolaimus* are in agreement with trophic guild classifications based on mouth morphology (Moens and Vincx, 1997), and with results from a stable isotope study from the Schelde Estuary, the Netherlands (Moens et al., 2005) and from a mudflat in Marennes-Oléron Bay, French Atlantic coast (Rzeznik-Orignac et al., 2008). Furthermore, predation by *Sphaerolaimus* may have been selective, since its relatively depleted carbon isotope signatures poorly reflect those of the majority of its candidate prey species. On the other hand, the δ^{13}C of *Sphaerolaimus* may also result from predation on *Terschellingia* in addition to feeding on other prey species.

A predatory feeding ecology for *Paracomesoma* and unidentified Comesomatidae is, however, counter to expectations. Comesomatidae are generally considered deposit feeders (Wieser, 1953; Moens and Vincx, 1997), the prime food sources of which in intertidal and shallow subtidal sediments are often microalgae and prokaryotes (Wieser, 1953; Moens and Vincx, 1997; Moens et al., 2005). However, buccal cavities without teeth or tooth-like structures may still serve predatory strategies through ingestion of whole prey (Moens and Vincx, 1997), and a variety of ciliates and flagellates may potentially serve as first-level consumers which could be preyed upon by nematodes such as *Paracomesoma*. Similarly, Moens et al. (2005) found an unexpectedly high

δ^{15}N for *Ascolaimus elongatus*; they also mentioned an unpublished observation of another comesomatid, *Sabatieria*, regurgitating ciliates upon addition of a chemical fixative E. Ólafsson, unpublished observation . Hence, we suggest that *Paracomesoma* and unidentified Comesomatidae obtained most of their carbon through predation on

5 heterotrophic protists or other small prey which in turn depend on various resources.

The nematode genera *Daptonema* and *Theristus* are considered non-selective deposit feeders (Wieser, 1953) or deposit feeders, which ingest suitably sized food particles like microalgae cells (Jensen, 1987; Moens and Vincx, 1997). Diatom grazing has been reported as a main feeding strategy for *Daptonema* from temperate tidal flats,

10 based on observations (Nehring, 1990; Moens and Vincx, 1997) as well as on natural stable carbon isotope signatures (Carman and Fry, 2002; Moens et al., 2002; Rzeznik-Orignac et al., 2008). Nevertheless, the stable isotope signatures of cordgrass and MPB are often in the same range; thus, discrimination between the utilization of these two resources based on stable carbon isotopes can be difficult (see also Couch, 1989).

15 In light of the present results, which show that *Daptonema* can utilize vascular plant detritus, caution is due when discarding vascular-plant derived detrital resources from the diet of this and other nematodes, like *Theristus, Metachromadora, Ptycholaimellus* and *Spirinia*. Documentation of the feeding behaviour of intertidal *Theristus* is scantier than for *Daptonema*, but here too, diatoms have been shown to be a prominent food source

20 based on observations and on stable isotope data (Boucher, 1973; Moens et al., 2013). In general, however, (non-selective) deposit feeders are considered opportunistic feeders capable of ingesting a variety of food particles, including microalgae bacteria, and perhaps also small detrital particles, the latter being strongly supported by the results of this study, with particle size being a major determinant of food selection (Moens and

25 Vincx, 1997).

A strong link between the genera *Metachromadora* and *Ptycholaimellus* and seagrass detritus was unexpected. Both genera were originally considered predators based on their mouth morphology (Wieser, 1953), but observations on feeding behaviour (Moens and Vincx, 1997) and stable isotope data (Moens et al., 2002, 2005)

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have shown that they can predominantly rely on MPB on intertidal flats. As epistrate feeders, they utilize a tooth to pierce food particles before emptying them, or to scrappe off epigrowth from sediment or detrital particles. The present results, however, suggest that they may also utilize microbes associated with vascular plant detritus, a trophic link also suggested for *Ptycholaimellus* from *Spartina* salt marsh sediments (Carman and Fry, 2002). Such differences between studies may point at a considerable flexibility in resource utilization (Moens et al., 2004). Alternatively, different feeding strategies may exist between congeneric species. In any case, these results highlight that the idea that epistratum-feeding nematodes from intertidal and shallow subtidal sediments primarily utilize microalgae cannot be generalized.

Thus, we found unexpected resource utilization patterns for some deposit and epistrate feeders. In addition, we observed considerable variation in both resource use and trophic level among genera from the same feeding type (eg. *Paracomesoma, Sabatieria* sp.2), showing that morphology-based classifications provide very artificial functional groupings. Considering the variation of isotope data among confamiliar and even congeneric species (as observed for Comesomatidae, the two *Sabatieria* species and the two *Spirinia* species in the present study), we strongly recommend avoiding interpretation of resource use and even of trophic level at suprageneric levels. Hence, we clearly demonstrate that the traditional feeding type classifications of nematodes based on buccal morphology can be misleading and should be combined with empirical information for reliable conclusions.

5   Summary

The organic carbon input in the benthic food web in seagrass beds at the Mira estuary derives from various sources, i.e. seagrass detritus, epiphytes, MPB and SPOM, being utilized by nematodes and harpacticoid copepods. Further than that, chemosynthetic carbon is also included in the diet of some taxa in estuarine habitats, most probably via feeding on sulphide-oxidizing bacteria. Seagrass detritus is available also in the

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adjacent to seagrass beds bare sediments, as well as in deeper layers, and one of the main food sources for most taxa, demonstrating the important role of seagrass beds to the estuarine ecosystem. The predatory feeding mode suggested for the expected deposit-feeding Comesomatidae, in addition to the considerable variation in both re-source use and trophic level found for confamiliar or congeneric nematode species, clearly demonstrates that the traditional feeding type classifications based on the morphology of nematodes can be misleading. Therefore, we recommend combining morphology observations with stable isotope analysis at the genus or even species level if possible, in order to clarify the complex feeding ecology of marine nematodes and of meiofauna in general.

Supplementary material related to this article is available online at http://www.biogeosciences-discuss.net/11/1277/2014/bgd-11-1277-2014-supplement.pdf.

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Table 1. Mean (±SD) stable isotope signatures of the potential carbon sources per sampling month (n = number of replicate samples).

Carbon source	n	June		n	February	
		δ^{13}C (‰)	δ^{15}N (‰)		δ^{13}C (‰)	δ^{15}N (‰)
Seagrass fresh leaves	4	−11.26 ± 1.65	4.45 ± 1.08	4	−11.43 ± 0.31	3.55 ± 2.06
Seagrass roots	4	−13.05 ± 2.73	3.5 ± 1.35	4	−12.64 ± 2.26	3.2 ± 1.7
Seagrass detritus	–	–	–	4	−15.97 ± 1.22	3.6 ± 0.61
Epiphytes	2	−17.77 ± 0.4	6 ± 0.28	4	−19.37 ± 2.05	4.75 ± 0.24
MPB	6	−19 ± 0.2	6.4 ± 0.28	4	−21 ± 1.2	9.6 ± 0.15
Bulk sediment organic matter (SOM)						
0–2 cm depth layer	8	−19.53 ± 2.29	4.75 ± 0.31	8	−21.24 ± 0.44	4.63 ± 0.24
2–4 cm depth layer	8	−20.79 ± 0.85	5.41 ± 0.29	8	−20.96 ± 0.73	5.5 ± 0.22
4–6 cm depth layer	8	−20.62 ± 0.91	5.26 ± 0.89	8	−20.92 ± 0.46	5.26 ± 0.7
SPOM	12	−23.61 ± 0.43	7.2 ± 1.47	5	−24.24 ± 1.42	4.23 ± 0.71

Table 2. Relative abundance (%) of nematode genera in *Zostera noltii* beds and stable isotope data of meiofauna from the upper 2 cm in seagrass beds and bare sediments.

Meiofauna	Relative abundance (%)		Mean δ^{13}C ± SD (‰)		Mean δ^{15}N ± SD (‰)	
	Jun	Feb	Seagrass beds	Bare sediments	Seagrass beds	Bare sediments
NEMATODA						
Anoplostoma	0.69	0.74	−19.9		7.1	
Axonolaimus	1.25	5.10		−17.4		
Bathylaimus	0.29	0.35	−16.7 ± 3.7	−16.5		
Chromadoridae			−20.2 ± 2.5			
Comesomatidae			−18.3		10.8	
Daptonema	3.78	7.71	−13.5	−13.7	7	6.6
Metachromadora	2.29	4.37	−13.9 ± 1.6	−13.7 ± 1.5	5.9 ± 0.8	5.8
Odontophora	8.53	6.61		−20.4		
Oncholaimus	1.96	0.59	−17.1			
Paracanthonchus	0.33	0.01	−17.2	−19.2	7.2	
Paracomesoma	8.36	21.87	−21.2	−19.4	10.7	8.9 ± 0.8
Pthycholaimellus	10.97	1.48		−15.0		
Sabatieria sp.1	4.04	3.03	−20.6	−18.0	7.8	
Sabatieria sp.2	4.04	3.03	−23.4	−28.3		
Sphaerolaimus	2.71	4.89	−19.5 ± 1.4	−19.1	10.1 ± 0.1	9.4 ± 0.3
Spirinia parasitifera	10.17	5.15	−18.6 ± 3.4	−22.7	4.6	4.8
Spirinia sp.2	10.17	5.15	−15.9		7.1	7
Terschellingia	18.13	25.33	−40.9 ± 3.39	−41.7	3.5	2.3 ± 2.5
Theristus	0.01	0.01	−12.0			
Viscosia	0.86	0.80	−18.8			
Bulk Nematoda			−20.8		8.9	5.6
COPEPODA						
Cletodidae			−30.9 ± 3.3	−41.2	4.7	
Ectinosomatidae				−18.1		
Sunaristes (Canuellidae)			−19.8	−18.2		3.9
Bulk Copepoda			−21.7 ± 1.7	−18.0	6.3 ± 0.8	4.7

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Table 3. Mean (±SD) stable isotope signatures of meiofauna from the deeper sediment layers (2–6 cm), from all stations (n = number of replicate samples).

Meiofauna	n	$\delta^{13}C \pm SD$ (‰)	n	$\delta^{15}N \pm SD$ (‰)
NEMATODA				
Anoplostoma	2	−21.6 ± 0.1		
Bathylaimus	1	−22.6		
Daptonema	2	−17.5 ± 2.3		
Metachromadora	2	−14.4 ± 0.4		
Oncholaimus	2	−26.1 ± 5.7		
Paracanthonchus	1	−29.8		
Paracomesoma	4	−20.0 ± 1.5	2	7.6 ± 2.1
Sabatieria sp.1	3	−21.1 ± 0.7		
Sabatieria sp.2	1	−28.6		
Sphaerolaimus	1	−23.7	1	7.5
Spirinia parasitifera	3	−27.5 ± 6.2	1	4.1
Spirinia sp.2	3	−15.9 ± 0.6	3	5.9 ± 1.1
Terschellingia	6	−40.4 ± 4.5	1	3.2
Bulk Nematoda	8	−22.3 ± 3.5	2	6.5
COPEPODA				
Cletodidae	1	−33.5		
Harpacticidae	1	−27.0		
Sunaristes (Canuellidae)	1	−15.9		
Bulk Copepoda	7	−22.7 ± 3.9		

Table 4. Proportional contribution of each resource to the carbon requirements of meiofauna taxa in seagrass beds and their adjacent bare sediments, in the surface (2 cm) and deeper sediments (4–6 cm), as computed by the isotope mixing model MixSIR (values given at the median 50th and the 95th percentile, respectively). Abbreviations used: SLD for seagrass detritus, EP for epiphytes, MPB for microphytobenthos, SPOM for suspended particulate organic matter and SBac for sulphur-oxidizing bacteria.

| | Proportional contribution of resources | | | | |
Consumers	SLD	EP	MPB	SPOM	SBac
Seagrass beds (upper 2 cm)					
Anoplostoma	0.12; 0.35	0.15; 0.62	0.10; 0.36	0.54; 0.78	–
Comesomatidae	0.14; 0.40	0.20; 0.62	0.14; 0.49	0.43; 0.69	–
Daptonema	0.72; 0.90	0.13; 0.76	0.06; 0.23	0.04; 0.14	-
Metachromadora	0.84; 0.94	0.07; 0.24	0.04; 0.14	0.03; 0.09	–
Paracanthonchus	0.15; 0.42	0.18; 0.65	0.10; 0.42	0.46; 0.72	–
Paracomesoma	0.04; 0.14	0.06; 0.21	0.06; 0.20	0.80; 0.92	–
Sabatieria sp1	0.23; 0.51	0.19; 0.54	0.14; 0.45	0.17; 0.54	0.15; 0.28
Sphaerolaimus	0.06; 0.18	0.07; 0.24	0.05; 0.18	0.77; 0.89	–
Spirinia parasitifera	0.05; 0.17	0.05; 0.18	0.04; 0.14	0.83; 0.94	–
Spirinia sp2	0.54; 0.79	0.20; 0.69	0.09; 0.34	0.10; 0.30	–
Terschellingia	0.03; 0.10	0.03; 0.12	0.04; 0.14	0.04; 0.15	0.81; 0.91
Cletodidae	0.08; 0.27	0.10; 0.32	0.12; 0.35	0.14; 0.41	0.46; 0.61
Seagrass beds (deeper sediments: 4–6 cm)					
Paracomesoma	0.26; 0.62	0.20; 0.73	0.08; 0.20	0.33; 0.65	–
Sphaerolaimus	0.04; 0.15	0.06; 0.23	0.06; 0.20	0.80; 0.93	–
Spirinia sp2	0.71; 0.87	0.08; 0.43	0.04; 0.16	0.11; 0.27	–
Terschellingia	0.03; 0.13	0.04; 0.14	0.04; 0.16	0.05; 0.17	0.79; 0.90
Bare sediments (upper 2 cm)					
Daptonema	0.55; 0.80	0.21; 0.69	0.11; 0.35	0.07; 0.22	–
Metachromadora	0.78; 0.91	0.09; 0.46	0.05; 0.19	0.03; 0.13	–
Paracomesoma	0.10; 0.25	0.08; 0.29	0.05; 0.18	0.72; 0.86	–
Sphaerolaimus	0.12; 0.29	0.10; 0.37	0.05; 0.19	0.67; 0.83	–
Spirinia parasitifera	0.04; 0.14	0.05; 0.19	0.05; 0.17	0.82; 0.93	–
Spirinia sp2	0.51; 0.77	0.20; 0.70	0.09; 0.35	0.11; 0.33	–
Terschellingia	0.02; 0.09	0.03; 0.11	0.04; 0.13	0.04; 0.15	0.82; 0.91
Sunaristes	0.48; 0.76	0.20; 0.72	0.08; 0.35	0.14; 0.40	–
Bare sediments (deeper sediments: 4–6 cm)					
Paracomesoma	0.14; 0.38	0.20; 0.61	0.17; 0.53	0.41; 0.67	–
Spirinia parasitifera	0.07; 0.22	0.09; 0.37	0.07; 0.25	0.71; 0.88	–

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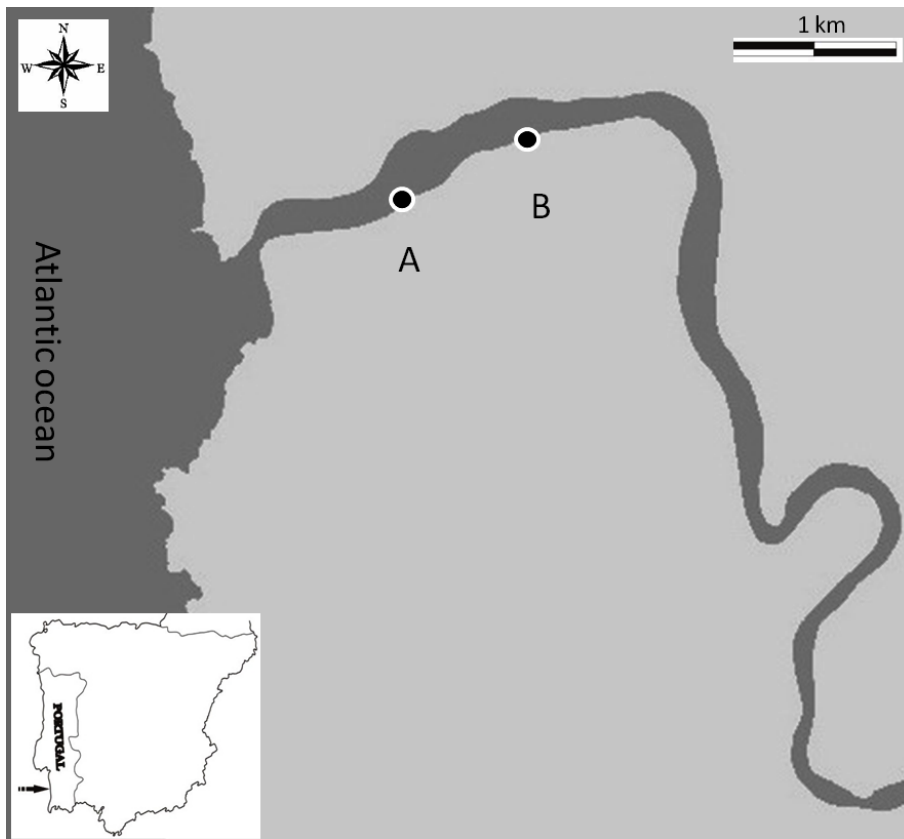
Fig. 1. Map of the study area: Mira Estuary (Portugal) and sampling sites (A and B).
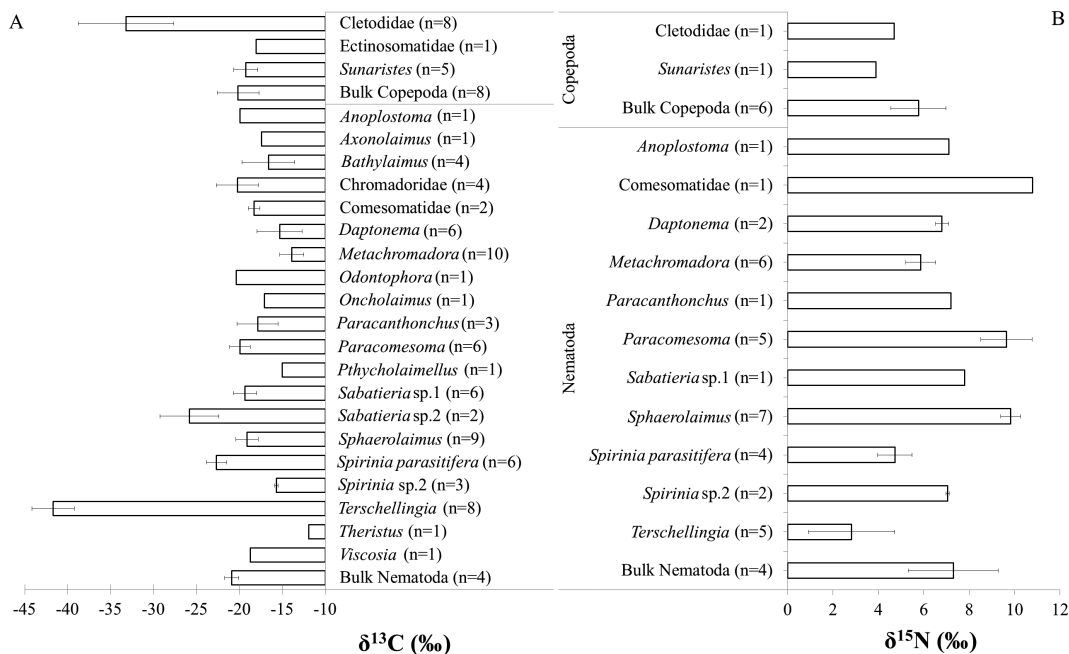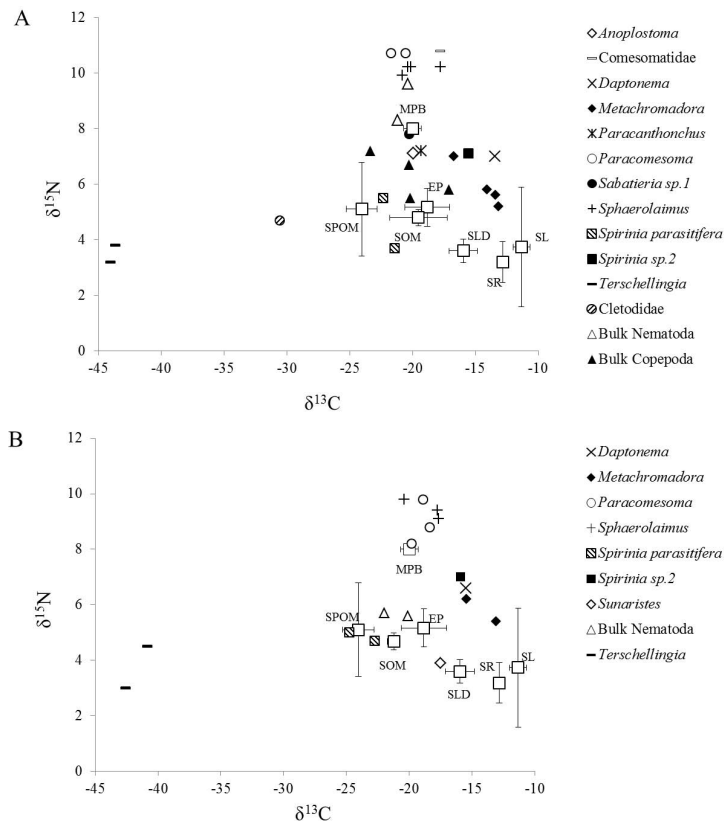
Fig. 2. Stable carbon **(A)** and nitrogen **(B)** isotope signatures of meiobenthos from the upper 2 cm. Data are mean values (±SD) of all replicate samples per taxon, from all months and stations (*n* = number of replicate samples).

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Fig. 3. $\delta^{13}C/\delta^{15}N$ biplots of meiobenthos from the upper 2 cm and their potential resources in seagrass beds **(A)** and bare sediments **(B)**. Resource data are mean values (±SD) of all replicate samples per source material analysed in both months. Abbreviations used: SL, SR and SLD for seagrass leaves, roots and detritus, respectively, EP for epiphytes, MPB for microphytobenthos, SPOM for suspended particulate organic matter and SOM for bulk sediment organic matter.

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