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Seasonal dependence on seagrass detritus and trophic niche partitioning in four copepod eco-morphotypes

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ABSTRACT

Benthic copepods dominate meiofaunal communities from marine phytodetritus, both in terms of numerical abundance and species diversity. Nevertheless, ecological factors driving copepod co-existence and population dynamics are still largely unknown. Here, we aimed to explore feeding habits of four copepod species commonly found in Mediterranean seagrass detritus accumulations, representing distinct eco-morphotypes (planktonic, phytal, epibenthic and mesopsammic). Joint use of fatty acid and stable isotope trophic markers showed that co-occurring harpacticoid copepods have diversified diets. Contrary to what was expected, microphytobenthos does not serve as their main food source. Instead, we found evidence from both techniques that major food items include heterotrophic biomass, macro-epiphytes and, depending on eco-morphology and season, of seagrass detritus-derived organic matter. Isotopic niches suggested that eco-morphotypes showed resource segregation. This segregation varies temporally, and partial overlap occurs between niches of phytal and epibenthic eco-morphotypes in some seasons. Our results highlight that, contrary to what is often assumed for meiofaunal consumers, considerable trophic diversity exists among copepod assemblages. They also indicate that, through multiple non-exclusive possible mechanisms, copepods could constitute a major link between seagrass detritus and associated biomass and higher trophic levels (namely macroinvertebrates and juvenile fish).

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1. Introduction

Seagrass meadows are net autotrophic ecosystems and key components of carbon cycle in marine coastal areas (Champenois and Borges, 2012). An important proportion of seagrass and macroalgae productivity is exported as shed biomass, accumulating on the sea bottom to form habitats called 'exported macrophytodebris accumulations' (hereafter EMAs) (e.g. Vetter, 1995; Hyndes and Lavery, 2005; Lepoint et al., 2006; Boudouresque et al., 2016) and fuelling the detrital pool (Cebrian, 2002). The endemic and highly productive Neptune grass, *Posidonia oceanica* (L.) Delile, covers from 25 to 45.10³ km² and the meadows it forms represent one of the dominant ecosystems found in the coastal Mediterranean (Pasqualini et al., 1998). EMAs formed by *P. oceanica* dead leaves are ubiquitous features of shallow areas of the Mediterranean Sea (Boudouresque et al., 2016). These patches of necromass accumulation are heterogeneous in their composition, being variable in thickness, size, and persistence in the environment (i.e. from very ephemeral to year-along presence) (Boudouresque et al., 2016). Their

occurrence and persistence in the environment are determined by the local *P. oceanica* biomass cycle, by the local hydrodynamics and by the sea bottom morphology (Ricart et al., 2015).

Marine macrophytodebris is considered an important trophic subsidies for food webs in many marine, estuarine, salt marsh, or terrestrial systems, both in temperate and tropical areas (Bouillon and Connolly, 2009; Heck Jr et al., 2008), providing habitats for many organisms (Como et al., 2008; Duggins et al., 2016; Mancinelli and Rossi, 2002; Vetter, 1995). Nevertheless, most literature focuses on macro- and megafauna, and smaller animals (i.e. meiofauna, animals with a body size between 38 µm and 1 mm) have received comparatively little attention. Small crustaceans (i.e. harpacticoid copepods) are the dominant taxa of meiofauna colonizing EMAs and represent up to 10⁵ individuals per square meter (Mascart et al., 2015b). The copepod assemblages found in *P. oceanica* EMAs are diverse, and different morphotypes (sensu Noodt (1969)) can be found among the necromass. These morphotypes have different biological traits, behavioural patterns, and occupy different micro-habitats. Phytal (i.e. often flattened copepods, mobile but strongly associated to macrophyte substrate, often grasping dead or living plant) and epibenthic eco-morphotypes (i.e. free-living benthic copepods, less associated to a substrate, able to live on and often in sediment) are dominant, but truly planktonic (i.e. copepods living in the water column) and

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mesopsammic (i.e. copepods living inside sediment but sometimes able to live as epibenthic copepods) species are also encountered (Mascart et al., 2015b). Given those differences, it is likely that feeding habits, and therefore the role of these copepods in EMAs' food web functioning differs. In other environments, trophic niches of copepod species belonging to the same eco-morphotype can be different (Arroyo et al., 2006; Azovsky et al., 2005; Carman and Fry, 2002; Carman and Thistle, 1985; De Troch et al., 2006b; Pace and Carman, 1996; Steinarsdóttir et al., 2010). How resource partitioning determines co-existence of dominant eco-morphotypes in EMAs remains unknown.

Because of their short life cycle and high turnover rates, harpacticoid copepod communities respond rapidly to organic matter inputs, and their life cycles are closely coupled to these inputs (Danovaro et al., 2002). In addition, EMAs are seasonally pulse-sourced by dead seagrass leaves and the epiphytic community covering them (Mascart et al., 2015b; Remy et al., 2017). Therefore, food item availability fluctuates over time, and this could have consequences for copepod trophic ecology and food partitioning between the different copepod eco-morphotypes (Mascart et al., 2015b).

Stable isotope (SI) analyses of carbon and nitrogen allow identification and quantification of food sources that are assimilated into the tissues of consumers over time. Fatty acid (FA) profiling complements stable isotope analysis as a second biomarker, providing additional information on the feeding ecology of meiofauna (Cnudde et al., 2015; De Troch et al., 2012; Leduc et al., 2009), as several FAs can be used as markers for specific food sources (Dalsgaard et al., 2003; El-Sabaawi et al., 2009).

By combining stable isotope ratios and fatty acid profiles, we aimed to study the trophic ecology of four co-occurring species of copepods, representing four dominant eco-morphotypes of *Posidonia* litter meiofauna (Noodt, 1969): *Diosaccus tenuicornis* (phytal type, harpacticoid), *Tisbe furcata* (epibenthic type, harpacticoid), *Ectinosoma dentatum* (mesopsammic type, harpacticoid) and *Calanus arcuicornis* (water column type, calanoid) (Fig. 1). Specifically, we addressed 4 questions and put forward the following hypotheses.

1) What are the food sources sustaining copepod consumers in seagrass detritus accumulations? While copepods are typically regarding as depending mostly on microphytobenthos, we

hypothesized that their food items in EMAs are diverse because available food sources are diverse.

- 2) Do different copepod eco-morphotypes exhibit resource segregation? Despite the “black box” approach generally applied to meiofaunal consumers in ecological literature (i.e. meiofaunal consumers are considered ecologically redundant and feeding on the same items regardless of consumer species) (Danovaro et al., 2002), we hypothesized that the 4 species studied here can have different diets and occupy different niches, and that this could facilitate co-existence of these abundant consumers.
- 3) Does copepod trophic ecology vary seasonally? Given the high turnover of copepod populations, we expect their feeding habits in EMAs to change temporally as food availability and composition varies seasonally.
- 4) Do copepods feed on dead seagrass tissue? In saltmarsh ecosystems, copepods assimilate detritus-derived organic matter and, like macrofauna, depend on dead plant material not only as a shelter but also as a food source (Couch, 1989). Therefore, we expect that it is also the case in seagrass detritus accumulation. Using trophic markers, we aim to explicitly test that, and to propose mechanisms through which copepods could feed on and assimilate seagrass detritus.

2. Materials and methods

2.1. Study site and field sampling

A sandy patch close to a continuous *P. oceanica* seagrass meadow was located near the STARESO marine research station (University of Liège) in the Revellata Bay (Calvi Bay, Corsica, France, NW Mediterranean; 42°35'N, 8°43'E). Sampling of consumers and their potential food sources (macrophytodebris, epiphytes, drifted macroalgae and particulate organic matter) was carried out at a depth of 10 m on a seasonal basis. Four sampling events were conducted, each representing a season, namely winter (February 2012), spring (May 2012), summer (August 2011) and autumn (October 2011). 30 L plastic bags were used to hand-collect copepod consumers and food sources, as well as the seagrass detritus, with which they are associated. Subsequently, the collected material was kept alive in a 0.75 m³ aquarium with 38

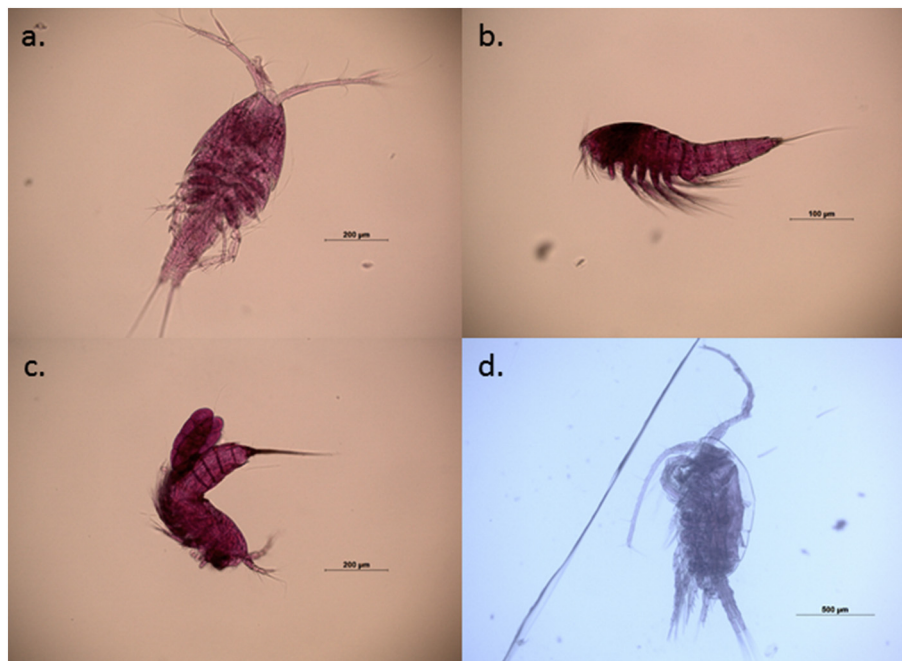


Fig. 1. Pictures of focal copepods: a. *Tisbe furcata*; b. *Ectinosoma dentatum*; c. *Diosaccus tenuicornis*; d. *Clausocalanus arcuicornis*.

μm filtered seawater. The content of the aquarium was sequentially rinsed over three mesh size sieves: a 10 mm mesh size to collect vegetal fraction (i.e. potential food sources), a 1 mm mesh size to exclude macrofauna, and finally a 38 μm mesh size to retain copepods. The sampled EMA food sources consisted of a heterogeneous mixture of (Abdulkadir and Tsuchiya, 2008) dead *P. oceanica* leaf litter fragments (leaves with attached epiphytes), (Anderson et al., 2008) drift (epilithic) macroalgae, and (Arroyo et al., 2006) living shoots of *P. oceanica* comprising rhizomes and living leaves. Epiphytes present on *P. oceanica* leaves were scraped off using razor blades. The fourth food source, the suspended particulate organic matter (SPOM), was collected about 1 m above the seafloor with Niskin bottles (2.5 L) handled by SCUBA divers. The content was afterwards vacuum-filtered onto pre-combusted glass fibre filters (Whatman GF/F, diameter 47 mm). In Revellata Bay, SPOM composition is seasonally variable, but generally dominated by phytoplankton biomass, except during and after storm when re-suspended detritic material may represent a large proportion of its composition (Dauby et al., 1995).

In a second stage, the 38 μm fraction holding the copepods was kept in a 20 L aquarium with an air stone to collect living copepods using positive phototactic attraction, in a setup similar to that used by Svensson et al. (2010). By means of a stereomicroscope, individuals were subsequently determined using the identification keys and reference books by Boxshall and Hasley (2004) and Lang (1948, 1965), and separated by species. The copepods were placed in filtered seawater overnight to empty their gut contents. The four most abundant copepod species (Mascart et al., 2015b) (Fig. 1), each belonging to a different ecomorphological type (Mascart et al., 2015a) were selected: *Diosaccus tenuicornis* (phytal type harpacticoid), *Tisbe furcata* (epibenthic type harpacticoid), *Ectinosoma dentatum* (mesopsammic type harpacticoid) and *Calanus arcuicornis* (water column type calanoid). Replicates were realised by pooling individuals, to have enough biomass for reliable measurements (i.e. for stable isotopes: 60–100 individuals per replicate, fatty acids: 120–200 individuals). We have excluded gravid female as eggs may affect the FA content of the copepods. All consumer and food source samples were stored at $-80\text{ }^{\circ}\text{C}$ for FA profiling and $-20\text{ }^{\circ}\text{C}$ for SI analyses.

2.2. Lipid extraction and fatty acid analysis

Prior to the lipid extraction, food sources and copepod samples were freeze-dried and transferred to glass vials. Lipid extraction, fatty acid methylation, and analysis of fatty acid methyl esters (FAMES) were executed according to the methods used in De Troch et al. (2012), including a lipid hydrolysis and fatty acid methylation achieved by a one-step derivatization method modified after Abdulkadir and Tsuchiya (2008). FAMES were injected at a temperature of $250\text{ }^{\circ}\text{C}$ in splitless mode (1 μL for food sources and 5 μL for copepods) into a gas chromatograph (HP 6890 N, Agilent, USA) with a capillary column (J&W HP88, Agilent, USA), coupled to a mass spectrometer (HP 5973, Agilent, USA). Quantification of individual FAMES was accomplished with internal standard C19:0 (Fluka 74208, Sigma-Aldrich, USA). Concerns about analytical error were raised in the profiles yielded for the *Ectinosoma dentatum* copepod, and the latter were thus not taken into account. Therefore, the FA profiles of only 3 copepod species are shown in this study: *Calanus arcuicornis*, *Tisbe furcata* and *Diosaccus tenuiremis*. The FA shorthand notation A:BwX was used, where A represents the number of carbon atoms, B gives the number of double bounds, and X gives the position of the double bound closest to the terminal methyl group (Guckert et al., 1985). FAs were reported as percentage of the total fatty acids (% TFA \pm SD) and grouped as saturated (SAFA), monounsaturated (MUFA), and polyunsaturated (PUFA) FAs.

2.3. Stable isotope ratio analysis

Food sources were dried at $60\text{ }^{\circ}\text{C}$ for 96 h, and, with the exception of SPOM filters, ground to a homogenous powder using a ball-mill (Retsch

Mixer Mill MM301). The attached epiphytes and drift macroalgae material were subdivided into two parts for acidification, to remove inorganic carbonates prior to carbon measurements. Acidification was done by fumigation of HCl vapours (fuming HCl, 37%, overnight). Stable isotope ratios of carbon (hereafter, $\delta^{13}\text{C}$) were measured on acidified material, and stable isotope carbon ratios of nitrogen (hereafter, $\delta^{15}\text{N}$) on non-acidified material. Ground food source samples (2–3 mg) were subsequently loaded into tin capsules for isotopic measurements. Regarding the consumers, pooled copepod individuals were transferred into a droplet of MilliQ water in a tin capsule ($8 \times 5\text{ mm}$, Elemental Microanalysis), and subsequently dried at $60\text{ }^{\circ}\text{C}$ for 24 h. They were then precisely weighed ($\pm 0.001\text{ mg}$) (Metler Toledo, XS3DU). Copepods were not acidified, considering the very low carbonate content of their exoskeletons.

Isotopic ratios and elemental content measurements were performed using an isotopic ratio mass spectrometer (IsoPrime100, Isoprime, UK) interfaced in continuous flow with an elemental analyser (vario MICRO cube, Elementar, Germany). Isotope ratios of C and N were reported conventionally (Coplen, 2011), using standard delta (δ) notation relative to their respective international standards, Vienna-Pee Dee Belemnite (V-PDB) and atmospheric N_2 .

Reference gases CO_2 and N_2 , as well as certified reference materials (i.e. sucrose (IAEA-C6; $\delta^{13}\text{C} = -10.8 \pm 0.3\text{‰}$) and ammonium sulfate (IAEA-N2; $\delta^{15}\text{N} = 20.3 \pm 0.3\text{‰}$) obtained from the International Atomic Energy Agency (IAEA, Vienna, Austria)), were used for calibration. The analytical precision was assessed by procedural blanks, internal replicates (i.e. glycine and in-house crustacean and seagrass reference materials) and isotopic certified materials (i.e. IAEA-C6 and IAEA-N2). Standard deviations on replicate measurements presented hereafter were 0.1‰ for $\delta^{13}\text{C}$ and 0.2‰ for $\delta^{15}\text{N}$. Neither chemical lipid extractions nor a posteriori lipid corrections were performed; this is due to the often limited relevance of a posteriori corrections for aquatic invertebrates containing high proportions of chitin in addition to lipids and proteins (Logan et al., 2008).

2.4. Data analyses

Stable isotope data were normalised by subtracting means and dividing by SD, in order to place them on comparable measurement scales and to homogenize variances between groups. The variance of sources and consumers was then compared using a two-way multivariate PERMANOVA with fixed factors (Month-Source or Month-Species, respectively) to determine whether the food sources or consumer species differed significantly through time. A PERMANOVA model generated pseudo F-statistics and P-values based on 999 permutations of the data, computed from a Euclidean distances resemblance matrix (Anderson et al., 2008). Prior to making the decision to use this analysis, normality and homoscedasticity assumptions were tested (P-values of the Hawkins test < 0.05). The disadvantage of this analysis of variance is the difficulty in distinguishing the source of the variation (due to location or dispersion). Therefore, homogeneity of dispersion was tested with a PERMDISP procedure, using distances among centroids calculated at the lowest level (Quinn and Keough, 2002).

All data analyses for FAs were performed on relative (%) FA concentrations. Therefore, a similarity percentages (SIMPER) analysis was preferred to identify the main harpacticoid copepod species, primarily providing differentiation between the seasons. An analysis of similarity (ANOSIM) was carried out to test whether the defined communities were significantly different. All the above-mentioned analyses were performed with the Primer 6.1.11 software (Clarke and Gorley, 2006) with the PERMANOVA add-on (Anderson et al., 2008). A significance level of $P < 0.05$ was used in all tests.

To estimate the consumer's assimilated diet, several Bayesian mixing models have been developed (reviewed by Phillips et al. (2014)). The stable isotope mixing model, SIAR (Stable Isotope Analysis in R) (Parnell et al., 2010), was used to estimate the relative

contribution of different food sources to the diet of the four copepod species. SIAR 4.2 was fitted in R 3.2.2 (R Core Team, 2014), including isotopic compositions of each individual, isotopic compositions of food sources (mean \pm SD), and trophic enrichment factors (TEFs; expressed as mean \pm SD) that correspond to the net isotopic composition change between a consumer and its ingested food source(s). Some sources were combined, as isotopic composition of autotrophs can overlap (Phillips et al., 2005). Accordingly, some food items did not display significant differences in their isotopic composition. Therefore, the following potential sources were combined: dead leaf litter and living *P. oceanica* shoots (PERMANOVA for every month: for $\delta^{13}\text{C}$, all $P > 0.061$ and for $\delta^{15}\text{N}$, all $P > 0.196$); and the drift macroalgae and scraped epiphytes from the *P. oceanica* leaves (PERMANOVA for every month: for $\delta^{13}\text{C}$, all $P > 0.097$ and for $\delta^{15}\text{N}$, all $P > 0.348$). After combination, three significantly different potential food sources (PERMANOVA per month for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ $P = 0.001$) were used in the mixing models: (Abdulkadir and Tsuchiya, 2008) macrophytodebris, i.e. primarily dead and living *P. oceanica* seagrass leaves without epiphytes; (Anderson et al., 2008) epiphytes, i.e. the scraped leaf epiphytes and drift (epilithic) macroalgae; and (Arroyo et al., 2006) suspended particulate organic matter.

Since there are no specific TEFs for the taxa studied here, we used widely applicable values from (McCutchan et al., 2003), i.e. $0.40 \pm 1.20\%$ for C and $2.30 \pm 1.61\%$ for N (mean \pm SD, in each case).

In addition, it has been proposed that the variability of isotopic composition of a population or a species (i.e. its isotopic niche) can be used as a proxy to assess the trophic niche of this population or species, and/or the degree of individual specialisation in the population (Bearhop et al., 2004; Jackson et al., 2011). This concept of isotopic niche has also been developed through numerical methods (Jackson et al., 2011). The Stable Isotope Bayesian Ellipses in R (SIBER) set of functions from the aforementioned SIAR 4.2 R package was used to describe isotopic niches and quantify their essential parameters. The yielded standard ellipses, containing ~40% of the data (centred on the mean and SDs of the bivariate data as semi-axes), and standard ellipse area (SEA), were used to delineate an isotopic niche space for each species. The areas of ellipses were estimated using the SEA_c correction for small sample size, as outlined in Jackson et al. (2011). The areas of these ellipses were also estimated using Bayesian modelling (SEA_B , 106 iterations), and direct inter-group pairwise comparisons of SEA_B were performed. Model solutions were presented using credibility intervals of probability density

function distributions. Pairwise comparisons were considered meaningful when the probability of occurrence exceeded 95%.

3. Results

3.1. Fatty acid profiling

A total of 17 FAs were identified in the potential food sources, i.e., those yielding a fatty acid percentage above 0.5% in at least one of the samples (Table 1). The relative FA contribution of sources showed a similar composition, with relatively high amounts of SAFAs, especially in the macrophytodebris, compared to the epiphyte samples (mean of $72.4 \pm 9.3\%$ and $55.4 \pm 5.1\%$, respectively). The most abundant SAFA was 16:0 (palmitic acid) with mean contributions of $30.8 \pm 2.0\%$ for macrophytodebris and $36.0 \pm 3.7\%$ for epiphytes. Other abundant SAFAs were 26:0 (cerotic acid) and 28:0 (montanic acid), especially in macrophytodebris, with a respective contribution of $11.3 \pm 5.2\%$ and $13.6 \pm 4.5\%$. The MUFAs and PUFAs of the macrophytodebris represented a similar share ($12.1 \pm 4.0\%$ and $14.0 \pm 5.0\%$, respectively). Conversely, in the epiphytes, PUFAs were more abundant than MUFAs ($27.5 \pm 7.5\%$ and $19.7 \pm 3.4\%$, respectively). The three most abundant MUFAs were 16:1 ω 7 (palmitoleic acid), 18:1 ω 7 (*cis*-vaccenic acid), and 18:1 ω 9 (oleic acid) (Table 1). The most frequently-encountered PUFAs in the epiphyte source were 20:4 ω 6 (arachidonic acid or ARA) and 20:5 ω 3 (eicosapentaenoic acid or EPA) ($9.4 \pm 3.2\%$ and $8.5 \pm 4.2\%$, respectively). The most abundant PUFAs in the macrophytodebris were 18:2 ω 6 (linoleic acid; $5.0 \pm 2.9\%$) and 18:3 ω 3 (α -linolenic acid; $3.7 \pm 1.5\%$). Both sources were clearly separated according to their PUFA profile (ANOSIM, $R = 1$, $P < 0.001$). A less pronounced distinction between months was visible (ANOSIM, $R = 0.667$, $P < 0.001$). SIMPER analysis showed a dissimilarity of 26.6% between these sources. The main FAs responsible (48.6 cumulated %) for the dissimilarity were long-chained: 26:0 (14.2%), 28:0 (13.1%), 20:4 ω 6 (10.9%) and 20:5 ω 3 (10.5%). Regarding the different months, the macrophytodebris collected in October differed most from the other months, with the largest dissimilarity between October and August (21.8%). For the epiphytes, May was separated most clearly from the other months, with the largest dissimilarity between May and August (15.9%).

In the four consumer copepod species, a total of 19 FAs were identified (Table 2). Compared to the food sources, three FAs were not present

Table 1
Relative FA composition (%) of food sources. All values are mean \pm standard deviation. Only FAs contributing for $>0.5\%$ are listed. MPD = macrophytodebris and EPI = epiphytes. n.d. = not detected. SPOM FA data comes from Michel et al., 2015.

	February		May		August		October		SPOM
	MPD	EPI	MPD	EPI	MPD	EPI	MPD	EPI	
14:0	4.3 \pm 0.63	4.21 \pm 0.74	3.58 \pm 0.02	5.24 \pm 2.05	2.48 \pm 1.02	4.91 \pm 0.63	5.48 \pm 0.55	4.29 \pm 0.55	7.58 \pm 0.60
15:0	0.41 \pm 0.07	2 \pm 0.2	0.12 \pm 0.03	1.07 \pm 0.17	0.32 \pm 0.1	1.4 \pm 0.17	0.37 \pm 0.07	1.26 \pm 0.47	1.05 \pm 0.05
16:0	31.2 \pm 3.35	37.83 \pm 2.54	32.8 \pm 5.29	33.8 \pm 2.9	31.44 \pm 2.62	32.21 \pm 2.06	28.02 \pm 2.17	40.22 \pm 5.15	28.1 \pm 0.27
16:1 ω 7	4.23 \pm 0.97	6.7 \pm 1.64	6.03 \pm 2.83	4.3 \pm 3.42	7.18 \pm 0.57	9.62 \pm 0.97	1.4 \pm 0.16	3.99 \pm 0.48	9.41 \pm 0.81
16:1 ω 5	n.d.	1.23 \pm 0.26	n.d.	2.54 \pm 0.88	n.d.	0.52 \pm 0.29	n.d.	1.12 \pm 0.41	0.50 \pm 0.03
17:0	0.29 \pm 0.2	1.23 \pm 0.14	0.57 \pm 0.21	0.94 \pm 0.21	0.43 \pm 0.06	0.95 \pm 0.14	0.4 \pm 0.08	1.31 \pm 0.1	0.45 \pm 0.10
18:0	6.87 \pm 1.55	6.06 \pm 0.16	6.98 \pm 3.39	3.75 \pm 0.22	8.49 \pm 0.8	4.85 \pm 0.92	3.22 \pm 2.39	5.45 \pm 0.45	10.4 \pm 0.13
18:1 ω 9	2.36 \pm 0.54	6.45 \pm 0.65	3.5 \pm 1.19	7.64 \pm 5.26	3.57 \pm 1.03	4.74 \pm 1.22	1.9 \pm 1.01	6.97 \pm 2.38	7.59 \pm 0.03
18:1 ω 7	4.63 \pm 1.65	8.74 \pm 3.09	5.65 \pm 2.28	7.41 \pm 4.16	4.64 \pm 0.11	2.82 \pm 1.17	3.51 \pm 0.86	3.97 \pm 0.67	1.77 \pm 0.26
18:2 ω 6	9.05 \pm 1.9	3.54 \pm 0.99	5.28 \pm 1	3.39 \pm 0.53	2.22 \pm 0.58	6.78 \pm 0.72	3.42 \pm 0.79	5.49 \pm 3.1	5.07 \pm 0.12
18:3 ω 3	2.25 \pm 0.38	3.41 \pm 1.89	2.6 \pm 1.09	3.96 \pm 1.26	4.49 \pm 0.81	6.51 \pm 0.9	5.33 \pm 1.03	5.02 \pm 2.29	1.23 \pm 0.04
20:4 ω 6	0.87 \pm 1.41	7.6 \pm 1.32	2.36 \pm 2.56	5.89 \pm 2.64	6.07 \pm 1.33	12.44 \pm 1.08	0.65 \pm 0.57	11.64 \pm 0.93	2.72 \pm 0.31
20:5 ω 3	0.15 \pm 0.13	13.79 \pm 2.86	2.37 \pm 2.91	3.58 \pm 0.98	8.43 \pm 2.69	9.02 \pm 1.43	0.32 \pm 0.45	7.75 \pm 7.01	5.61 \pm 0.17
22:0	0.3 \pm 0.26	n.d.	n.d.	0.11 \pm 0.33	0.34 \pm 0.3	0.28 \pm 0.08	1.83 \pm 0.34	1.31 \pm 2.06	0.50 \pm 0.12
24:0	3.75 \pm 1.12	0.58 \pm 0.62	3.25 \pm 1.38	1.84 \pm 0.14	2.32 \pm 0.47	1.23 \pm 0.42	7.93 \pm 0.45	0.61 \pm 0.37	n.a.
26:0	10.47 \pm 3.16	0.63 \pm 0.57	9.72 \pm 2.24	4.67 \pm 0.42	7.88 \pm 0.79	1.09 \pm 0.13	19.6 \pm 3.1	1.23 \pm 0.34	n.a.
28:0	10.54 \pm 2.09	2.14 \pm 0.56	17.31 \pm 7.83	9.51 \pm 1.4	8.83 \pm 0.55	1.8 \pm 0.91	17.62 \pm 1.78	1.65 \pm 0.63	n.a.
Σ SAFA	68.13 \pm 3.89	54.67 \pm 3.53	74.32 \pm 11.54	60.94 \pm 1.13	62.55 \pm 3.25	48.72 \pm 2	84.47 \pm 1.47	57.33 \pm 3.66	50.22 \pm 0.10
Σ MUFA	11.22 \pm 0.3	23.11 \pm 5.15	15.18 \pm 6.28	21.88 \pm 4.53	15.39 \pm 0.68	17.71 \pm 3.64	6.82 \pm 0.97	16.04 \pm 2.59	22.31 \pm 1.01
Σ PUFA	12.33 \pm 3.53	28.34 \pm 2.99	12.61 \pm 5.13	16.82 \pm 1.14	21.21 \pm 4.06	34.76 \pm 1.17	9.71 \pm 1.11	29.9 \pm 12.79	27.47 \pm 0.91

Table 2

Relative FA composition (%) of copepods. All values are mean \pm standard deviation. Only FAs contributing for >0.5% are listed. CA = *Clausocalanus arcuicornis*, TF = *Tisbe furcata* and DT = *Diosaccus tenuicornis*. n.d. = not detected.

	February			May			August			October		
	CA	TF	DT	CA	TF	DT	CA	TF	DT	CA	TF	DT
14:0	5.35 \pm 0.58	2.67 \pm 0.55	4.12 \pm 0.16	7.54 \pm 0.87	3.5 \pm 0.79	4.55 \pm 0.47	4.69 \pm 0.67	4.53 \pm 0.17	3.56 \pm 0.28	5.28 \pm 1.05	2.26 \pm 0.69	3.64 \pm 1.1
α 15:0	3.31 \pm 0.97	5.74 \pm 1.32	1.64 \pm 0.09	2.68 \pm 0.13	2.98 \pm 1.84	2.22 \pm 0.07	3.32 \pm 0.62	2.83 \pm 0.42	2.48 \pm 1.02	3.2 \pm 0.18	1.1 \pm 0.07	0.82 \pm 0.18
15:0	3.2 \pm 0.12	1.55 \pm 0.36	1.41 \pm 0.1	2.74 \pm 0.16	3.93 \pm 1.95	3.28 \pm 1.72	3.36 \pm 0.59	3.39 \pm 0.68	2.94 \pm 0.56	3.13 \pm 0.3	1.08 \pm 0.38	0.94 \pm 0.28
16:0	54.11 \pm 9.84	21.06 \pm 3.93	35.02 \pm 0.94	36.99 \pm 5.75	23.66 \pm 3.75	47.25 \pm 2.94	59.46 \pm 3.98	41.21 \pm 1.24	41.33 \pm 6	52.2 \pm 3.79	22.79 \pm 1.52	40.92 \pm 5.52
16:1 ω 7	3.47 \pm 0.69	11.83 \pm 0.08	7.93 \pm 0.41	3.47 \pm 1.34	12.87 \pm 3.07	5.84 \pm 1.04	3.64 \pm 0.05	7.43 \pm 1.33	6.13 \pm 1.58	3.47 \pm 0.22	7.94 \pm 3.54	8.55 \pm 3.34
17:0	2.56 \pm 0.67	4.47 \pm 0.74	4.18 \pm 0.35	9.35 \pm 0.28	4.35 \pm 0.7	3.97 \pm 0.7	2.57 \pm 0.05	4.42 \pm 1.66	3.92 \pm 0.58	5.15 \pm 0.96	2.7 \pm 0.46	1.84 \pm 0.27
18:0	27.38 \pm 5.2	13.33 \pm 2.67	18.8 \pm 0.8	24.59 \pm 2.31	24.31 \pm 5.88	21.58 \pm 2.64	21.38 \pm 3.58	22.99 \pm 2.94	25.75 \pm 3.64	22.28 \pm 1.73	14.28 \pm 3.19	17.06 \pm 2.6
18:1 ω 9	n.d.	4.52 \pm 0.45	2.28 \pm 0.23	10.01 \pm 2.79	2.34 \pm 0.47	2.61 \pm 1.85	0.29 \pm 0.2	2.56 \pm 2.22	1.72 \pm 0.59	3.6 \pm 1.27	3.88 \pm 2.01	2.45 \pm 0.67
18:1 ω 7	0.64 \pm 0.32	7.36 \pm 0.75	2.55 \pm 0.17	6.23 \pm 1.53	3.01 \pm 3.19	2.93 \pm 1.63	2 \pm 1.35	3.16 \pm 1.88	3.47 \pm 2.05	2.82 \pm 0.49	3.75 \pm 1.48	2.2 \pm 0.6
18:2 ω 6	n.d.	1.88 \pm 0.38	3.62 \pm 1.08	1.34 \pm 0.45	n.d.	1.57 \pm 1.09	0.35 \pm 0.35	0.74 \pm 0.45	0.32 \pm 0.56	0.67 \pm 0.14	2.33 \pm 0.49	1.7 \pm 0.95
18:3 ω 3	n.d.	0.5 \pm 0.86	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	0.19 \pm 0.32	n.d.
18:4 ω 3	n.d.	1.33 \pm 0.34	n.d.	n.d.	2.34 \pm 3.61	0.26 \pm 0.45	n.d.	0.87 \pm 1.13	1.3 \pm 1.69	n.d.	0.97 \pm 0.4	0.75 \pm 0.12
20:0	n.d.	0.29 \pm 0.51	0.56 \pm 0.49	0.57 \pm 0.58	n.d.	n.d.	0.14 \pm 0.14	0.09 \pm 0.09	0.18 \pm 0.2	1.18 \pm 1.61	0.26 \pm 0.1	0.57 \pm 0.14
20:4 ω 6	n.d.	2.09 \pm 0.59	3.07 \pm 0.44	2.09 \pm 3.06	1.01 \pm 0.08	2 \pm 0.38	n.d.	1.63 \pm 1.14	0.73 \pm 0.37	0.12 \pm 0.05	1.89 \pm 0.51	1.44 \pm 1.26
20:5 ω 3	n.d.	1.22 \pm 0.37	0.39 \pm 0.03	0.07 \pm 0.05	0.92 \pm 0.18	0.19 \pm 0.19	n.d.	0.38 \pm 0.05	0.32 \pm 0.2	n.d.	1.47 \pm 0.23	0.56 \pm 0.17
22:0	n.d.	0.65 \pm 0.58	1.31 \pm 0.35	0.26 \pm 0.23	1.16 \pm 0.03	1.51 \pm 0.63	0.06 \pm 0.06	0.94 \pm 0.19	1.06 \pm 0.43	0.09 \pm 0.02	1.65 \pm 0.43	3.48 \pm 1.6
22:6 ω 3	n.d.	18.41 \pm 7.38	8.39 \pm 0.99	0 \pm 0	14.99 \pm 1.78	n.d.	n.d.	5 \pm 0.59	5.07 \pm 4.48	n.d.	28.77 \pm 3	9.41 \pm 8.17
23:0	n.d.	0.47 \pm 0.41	0.81 \pm 0.7	0 \pm 0	1.84 \pm 2.05	1.9 \pm 2.87	n.d.	1.24 \pm 0.81	0.22 \pm 0.19	n.d.	0.76 \pm 0.16	0.78 \pm 0.38
24:0	n.d.	0.66 \pm 0.57	3.92 \pm 0.54	0 \pm 0	1.65 \pm 0.82	1.01 \pm 0.8	n.d.	0.88 \pm 0.29	1.3 \pm 0.15	n.d.	1.95 \pm 0.55	2.89 \pm 2.08
Σ SAFA	95.91 \pm 4.16	50.87 \pm 10.2	71.76 \pm 2.89	84.73 \pm 3.56	67.36 \pm 4.67	87.26 \pm 7.43	94.99 \pm 0.58	82.53 \pm 2.26	82.73 \pm 3.73	92.5 \pm 0.74	48.82 \pm 5	72.95 \pm 5.94
Σ MUFA	4.11 \pm 1	23.7 \pm 1.13	12.76 \pm 0.73	19.71 \pm 5.63	17.52 \pm 2.05	11.39 \pm 4.51	5.9 \pm 1.55	13.15 \pm 3.51	11.32 \pm 1.01	9.89 \pm 1.82	15.56 \pm 6.98	13.2 \pm 4.54
Σ PUFA	n.d.	25.43 \pm 9.1	15.48 \pm 2.23	3.5 \pm 3.01	19.27 \pm 5.34	4.03 \pm 1.83	0.35 \pm 0.35	8.62 \pm 1.17	7.75 \pm 5.05	0.79 \pm 0.16	35.62 \pm 2.24	13.85 \pm 10.08

Table 3

Annual mean of stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of food sources and consumers (%o, mean \pm SD). Summary of pair-wise comparisons of means between seasons and associated *P*-values. MPD = Macrophytodebris; EPI = Epiphytes; SPOM = Suspended particulate organic matter. PORT: STARESO harbour site; OSCE: Oscelluccia site.

	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
	Annual mean (%o)		Pair-Wise tests		Annual mean (%o)		Pair-Wise tests	
	PORT	OSCE	Comparisons	<i>P</i> -value(s)	PORT	OSCE	Comparisons	<i>P</i> -value(s)
Sources								
MPD	-12.7 \pm 0.3	-12.8 \pm 0.1	Feb \neq May; May \neq Aug; May \neq Oct	0.001; 0.001; 0.001	1.8 \pm 0.1	1.2 \pm 0.2	\neq	<0.05
EPI	-14.5 \pm 1.3	-15.9 \pm 1.3	Feb \neq Oct; May \neq Oct; Aug \neq Oct	0.001; 0.007; 0.001	1.2 \pm 0.4	1.0 \pm 0.0	Aug = Oct	0.341
SPOM	-23.3 \pm 0.9	-24.8 \pm 1.1	May = Aug	0.823	1.7 \pm 0.6	1.7 \pm 0.7	=	>0.05
Consumers								
<i>Clausocalanus arcuicornis</i>	-21.9 \pm 1.2	-20.9 \pm 1.4	Aug \neq Oct	0.043	3.1 \pm 0.6	2.9 \pm 0.6	Feb = May; Aug = Oct	0.786; 0.141
<i>Tisbe furcata</i>	-18.9 \pm 0.9	-19.1 \pm 0.9	Feb \neq Oct; Oct \neq May	0.003; 0.007	2.8 \pm 0.4	2.8 \pm 0.3	=	>0.05
<i>Diosaccus tenuicornis</i>	-18.2 \pm 1.3	-17.9 \pm 1.2	Aug = Oct	0.189	3.0 \pm 0.4	3.0 \pm 0.5	Feb \neq Aug; May \neq Aug; Aug \neq Oct	0.001; 0.012; 0.013
<i>Ectinosoma dentatum</i>	-18.0 \pm 2.5	-18.1 \pm 2.0	Aug = Oct	0.439	1.5 \pm 0.5	1.6 \pm 0.4	Feb = May; Aug = Oct	0.168; 0.168

in the consumers: 26:0, 28:0, and 16:1 ω 6. Four FAs were restricted to the copepods' profiles: 18:4 ω 3 (stearidonic acid), 20:0 (eicosanoic acid), 22:6 ω 3 (docosahexaenoic acid or DHA), and 23:0 (tricosylic acid). The SAFAs were the most important class, accounting on average for $92.0 \pm 5.1\%$ in *C. arcuicornis*, $78.7 \pm 7.5\%$ in *D. tenuiremis*, and $62.0 \pm 15.8\%$ in *T. furcata*. The predominant SAFAs were 16:0 and 18:0, representing on average $39.7 \pm 12.8\%$ and $21.1 \pm 5.1\%$, respectively, across all species. The MUFAs were more abundant in *T. furcata*, where they accounted for $17.5 \pm 4.5\%$ of the total FA composition. Palmitoleic acid (16:1 ω 7) was the most abundant MUFA in this species, with $10.0 \pm 2.7\%$. It also dominated the MUFA composition of *D. tenuiremis* ($7.1 \pm 1.33\%$). A very low and variable amount of MUFAs was found in *C. arcuicornis* ($9.9 \pm 7.0\%$). *C. arcuicornis* presented an even lower and more variable amount of PUFAs ($1.2 \pm 1.6\%$). Strangely, no DHA (22:6 ω 3) was found in *C. arcuicornis*, contrasting with *T. furcata* and *D. tenuiremis*, where it was the most important PUFA, with $16.8 \pm 9.8\%$ and $5.7 \pm 4.2\%$, respectively. ANOSIM revealed a subtle difference among months for all species (ANOSIM, $R = 0.691$, $P < 0.001$). In addition, a stronger difference among species was visible (ANOSIM, $R = 0.893$, $P < 0.001$), separating *C. arcuicornis* from the other two species, mainly based on the DHA levels, which contributed most to the dissimilarities with *T. furcata* and *D. tenuiremis* (20.3% and 13.3%, respectively). Conversely, differences in the FA of *T. furcata* and *D. tenuiremis* were less clear, with dissimilarity between the two species being only 17.39%. Moreover, these two species FA compositions only differed between May and February (PERMANOVA, pair-wise, $P(\text{MC}) = 0.018$ and 0.016 , respectively). Those relatively weak differences were mostly driven by the lower MUFA and PUFA content of *T. furcata* during those months (Table 2).

3.2. Stable isotope compositions

$\delta^{13}\text{C}$ values of food sources ranged from -28.1% (SPOM February) to -11.3% (macrophytodebris August). On an annual basis, epiphytes ($\delta^{13}\text{C} = -17.2 \pm 1.9\%$) exhibited the largest temporal difference in their $\delta^{13}\text{C}$ values. The highest values were found in October (-13.2%) and the lowest values were noted in August (-20.4%). Macrophytodebris showed the highest $\delta^{13}\text{C}$ values, with a mean isotopic composition of $-13.1 \pm 0.8\%$. SPOM was always the most ^{13}C -depleted food source (average $-25.4 \pm 1.4\%$), with significant differences among months, except between May and August. The two-way PERMANOVA showed significant effects of both month and source factors for carbon composition (Table 3).

$\delta^{15}\text{N}$ values of food sources ranged from 0.2% (epiphytes, August) to 4.6% (Epiphytes, May). Food sources displayed significantly different isotopic composition across months, except for SPOM, where no difference occurred (annual mean: $1.7 \pm 0.2\%$). The epiphyte and macrophytodebris sources showed a similar annual mean $\delta^{15}\text{N}$ with values of $2.0 \pm 1.1\%$ and $2.1 \pm 0.9\%$, respectively. However, epiphytes showed a large fluctuation among months (Pair-wise, $P = 0.467$).

$\delta^{13}\text{C}$ values of consumers ranged from -24.9% (*Clausocalanus arcuicornis*, February) to -15.3% (*Diosaccus tenuiremis*, February) (Fig. 2). On an annual basis, *C. arcuicornis* displayed the lowest $\delta^{13}\text{C}$ values, and showed no significant difference in $\delta^{13}\text{C}$ values among months (annual mean of $-21.4 \pm 1.4\%$) except between August and October (Table 3). The other three species did not show any significant difference in their annual mean $\delta^{13}\text{C}$. However, temporal $\delta^{13}\text{C}$ fluctuations, especially for *D. tenuiremis* and *Ectinosoma dentatum* (Table 3). These species had similar $\delta^{13}\text{C}$ in August and October. *D. tenuiremis* reached its lowest $\delta^{13}\text{C}$ values in February and its highest in May. On the contrary, *E. dentatum* showed its lowest $\delta^{13}\text{C}$ values in February.

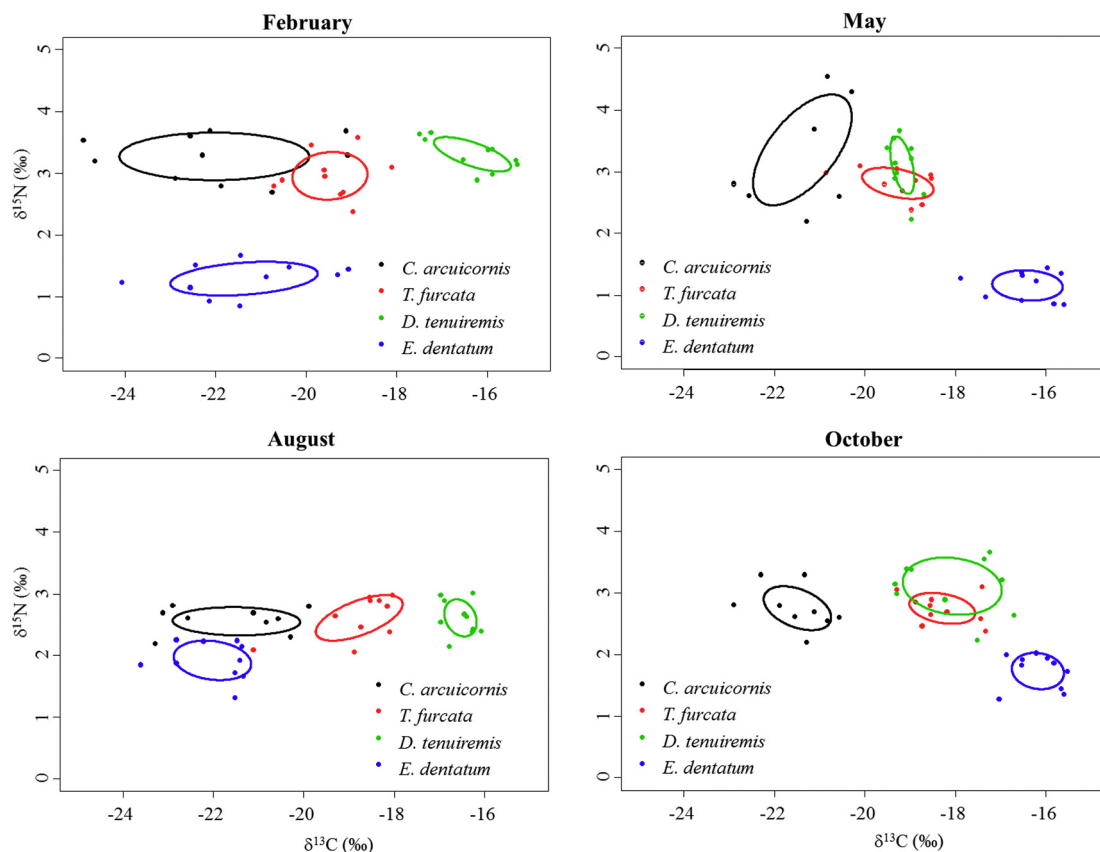


Fig. 2. Stable isotope compositions of the four copepod species sampled in macrophytodebris accumulations. Points are measurements on copepods pools ($n = 30$ – 100 depending upon copepod size), and solid lines are bivariate standard ellipses that represent core isotopic niches of consumers. a. February; b. May; c. August; d. October.

$\delta^{15}\text{N}$ values of consumers ranged from 0.9‰ (*C. arcuicornis*, May) to 4.5‰ (*E. dentatum*, May) (Fig. 2). *Tisbe furcata* showed the most constant $\delta^{15}\text{N}$ value over the year, in contrast to *C. arcuicornis* and *E. dentatum* (Table 3). Both these species showed their lowest $\delta^{15}\text{N}$ values in May and their highest $\delta^{15}\text{N}$ values in August.

3.3. Isotopic niches

Bivariate standard ellipses (Fig. 2), representing core isotopic niches of consumers, indicated that, except for *D. tenuiremis* and *T. furcata* in May and October, ellipses occupied different parts of the isotopic space, without overlapping. Along the carbon axis, ellipse position in the isotopic space of *D. tenuiremis* and *E. dentatum* changed drastically according to sampling dates. In May and February, SEA_B calculations suggested that, in over 99.90% of model runs, ellipse area (Fig. 3) of *C. arcuicornis* was greater than those of the other three species. However, in August, *D. tenuiremis* showed the smallest ellipse areas in over 99.95% of model runs, when all other ellipses showed similar areas.

The ellipse area of *C. arcuicornis* decreased from February to August in over 99.98% of model runs. They were more constant for the other three species (except *E. dentatum* in February and *D. tenuiremis* in October, when they were larger).

3.4. Stable isotopic mixing model

SIAR modelling results showed that *C. arcuicornis* mainly assimilated food sources coming from a planktonic environment (Fig. 4) (upper and lower limit of a 95% credibility interval – hereafter C.I. 95% – for all seasons: 35–82%). This contribution was the lowest in August (C.I. 95%: 35–63%; mode = 46%) and the highest in October (C.I. 95%: 66–82%; mode = 75%). Although sometimes contributing to the diet of *C. arcuicornis*, the other two food sources showed a wide range of possible

contribution (i.e. very wide 95% C.I.). Nevertheless, contributions by macrophytodebris were generally low (upper and lower limit of C.I. 95%: 0–30%). They were the lowest in October (0–19%; mode = 4%) and the highest in August (C.I. 95%: 0–30%; mode = 13%). All three food sources seemed to contribute significantly to the diet of *T. furcata*, *D. tenuiremis* and *E. dentatum*, except in May, when epiphytes seemed to contribute only a little. However, the credibility intervals of model solutions were often very wide. Macrophytodebris seemed to contribute significantly to the diet of these three species, as the model never gave contributions equal to zero. Strong seasonal variability seemed to be present for *D. tenuiremis* and *E. dentatum* (Fig. 4).

4. Discussion

4.1. What are the food sources sustaining copepod consumers in seagrass detritus accumulations?

Stable isotope and fatty acid profiling indicated that the food sources of this copepod assemblage are relatively diverse and not dominated by microphytobenthos. Isotopic modelling showed that the diet of the four eco-morphotypes analysed was unlikely dominated by only one food source, and was clearly different between benthic (i.e. the 3 harpacticoid) and planktonic species.

The planktonic species (calanoid) found in the EMA clearly showed isotopic compositions and fatty acid profiles which reflect feeding on phytoplankton in the water column. Indeed, in the Calvi Bay, $\delta^{13}\text{C}$ of SPOM always show more negative values than benthic primary producers found in the bay, excepted for sciaphilous algae (Lepoint et al., 2000). Nevertheless, even for this species, our results showed potential contribution of benthic food sources to their diet.

According to literature, harpacticoid copepods can consume a large spectrum of food sources, depending on food availability in a particular

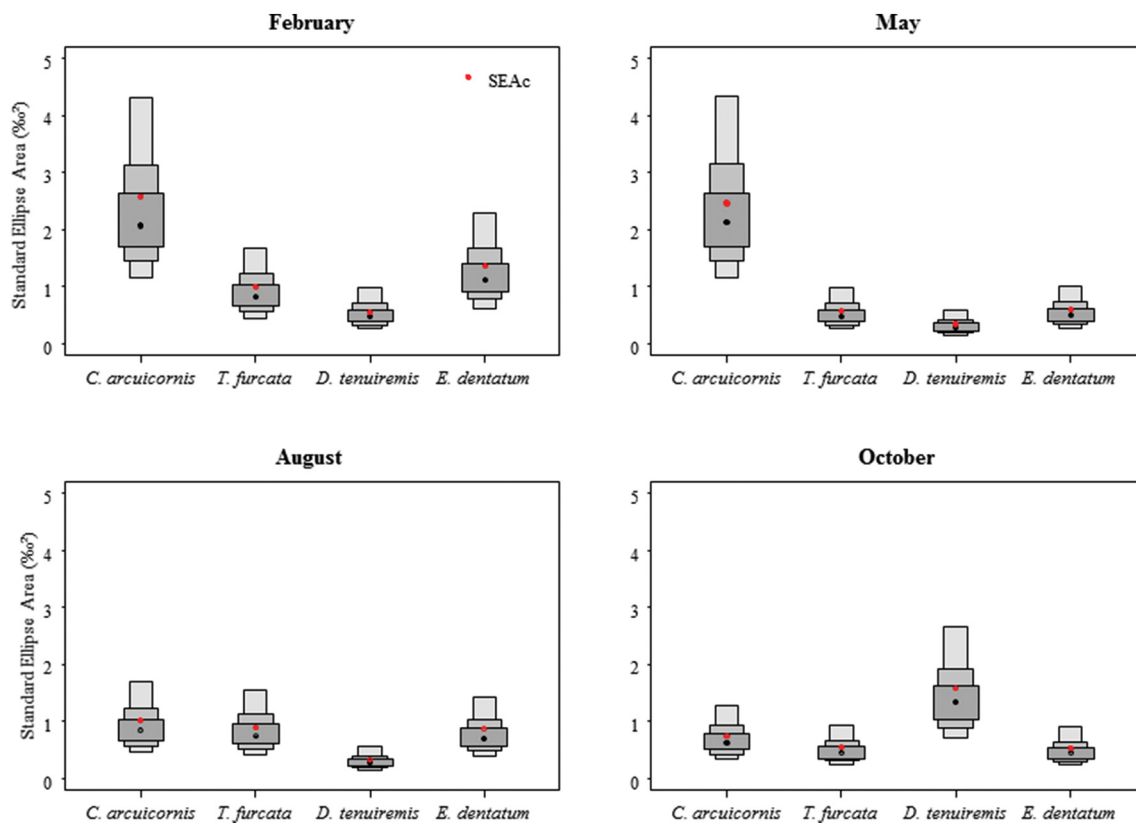


Fig. 3. Boxplots of model-estimated bivariate standard ellipse area (SEA_B) for each copepod species in each season. Dark, median and light grey boxes are respectively the 50%, 75% and 95% credibility intervals of the probability density function distributions of the model's solutions, and black dots are the modes of these distributions. Red dots are the SEA_C values associated with each group. a. February; b. May; c. August; d. October. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

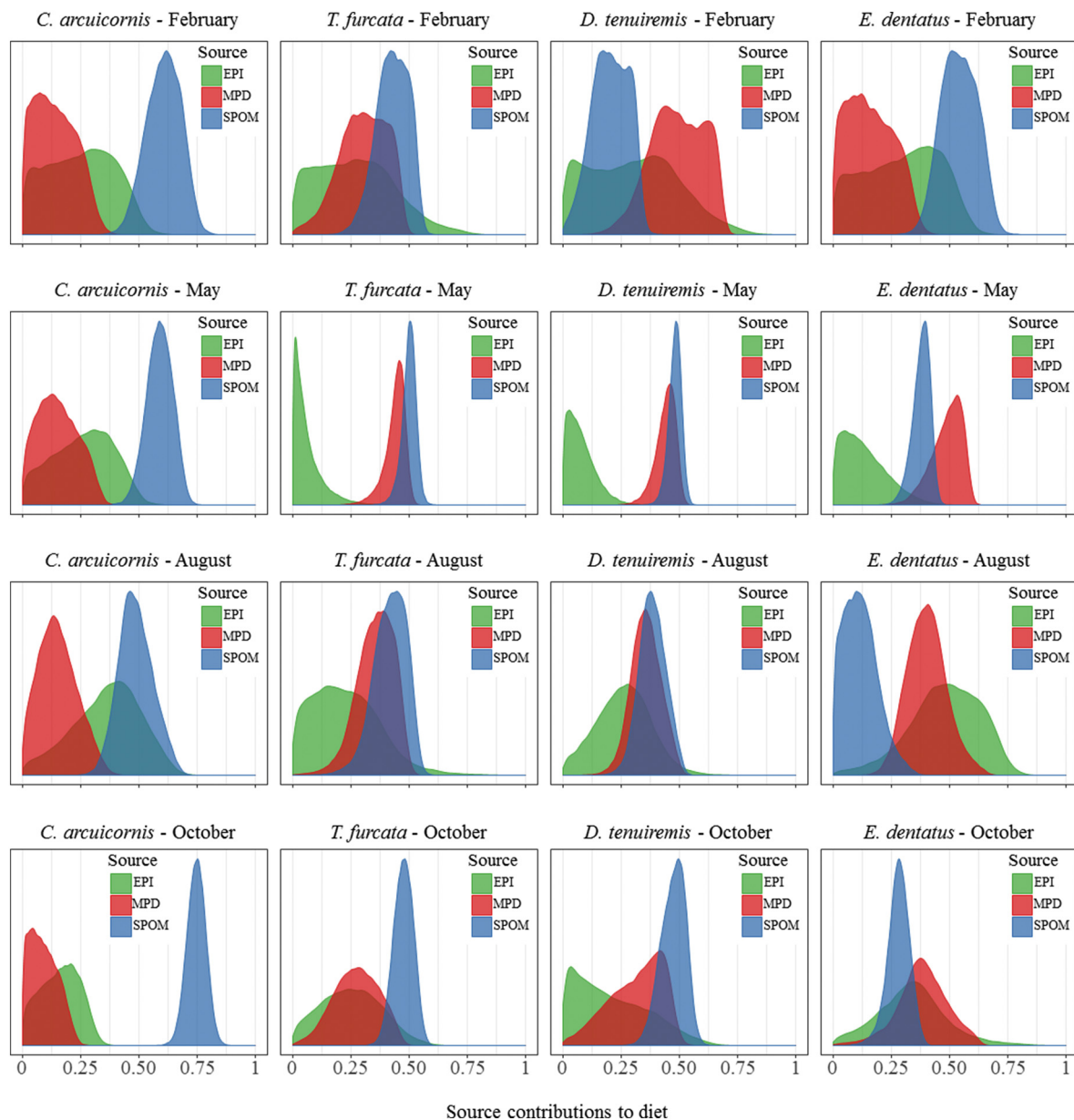


Fig. 4. Distribution of posterior probability density function of the relative contribution of macrophytodebris (MPD), epiphytic and drift macroalgae (EPI), and suspended particulate organic matter (SPOM) for each copepod (line) at each sampling date (column), computed using the SIAR model.

habitat. In intertidal and subtidal habitats, copepod diet mostly consists of microscopic algae assemblages, i.e. microphytobenthos (De Troch et al., 2005; Evrard et al., 2010; Rzeznik-Orignac et al., 2008). Here, FA profiles of copepods indicate that feeding on diatoms – which are part of the sessile epiphytes – could occur, as 16:1 ω 7 and 20:5 ω 3 marker compounds (Dalsgaard et al., 2003) were present. However, the ratio between 16:1 ω 7 and 16:0, often used as an indicator of high diatom contribution to diet, was rather low compared to intertidal copepods, who mainly feed on microphytobenthos (Kharlamenko et al., 2001). Contrary to the suggestion by Couch (1989), this indicates that, in EMAs, diatoms are not dominant in the diet of copepods.

In our study, macroepiphytes (both sessile fauna and flora) and drift epilithic macroalgae (i.e. macroalgae ripped from surrounding rocks) seemed to be part of the copepods' diet. In the study site, epiphytes and drift algae represented around 10% of EMA biomass each (Mascart et al., 2015b). Both food sources could be valuable for copepods in terms of nutrient and fatty acid content, as they are not necromass in the litter. Epiphytes were already previously found as food source for

copepods living in *P. oceanica* canopy (Mascart et al., 2013) and for many other crustaceans, such as amphipods (Michel et al., 2015). In Australian coastal waters, macroalgae consumption in seagrass-dominated litter has also been documented (Hyndes and Lavery, 2005).

Uprooted living seagrass, often found in high abundance in EMA, were not consumed by copepods, as no typical FAs from living seagrass were found in copepods' tissues (Kharlamenko et al., 2001). FA profiles of live seagrass blades differ significantly from seagrass detritus, due to the loss of some FAs during decay and the presence of bacterial FAs in detritus (Kharlamenko et al., 2001; Leduc et al., 2009; Michel et al., 2015).

Our isotopic modelling indicated that carbon coming from seagrass detritus often constituted a non-negligible part of the copepods' diets (particularly in the case of harpacticoids). This is in accordance with the diet of copepods in *P. oceanica* meadow sediments (Danovaro et al., 2002), *Zostera noltii* meadow sediments (Lebreton et al., 2012; Vafeiadou et al., 2014), and in salt marshes (Couch, 1989), or in *Amphibolis* sp. and *Posidonia* spp. detritus accumulations (Hyndes and Lavery, 2005).

Seagrass leaf detritus itself is mostly constituted of carbon and refractory nitrogen associated with structural carbohydrates. In this refractory material, microbial biomass can constitute the majority of the nitrogen and fatty acids available for consumers (Newell et al., 1989). Even if photo-autotrophic organisms are present, heterotrophic biomasses (eukaryotic and bacterial) are also very abundant on and inside degrading leaves (see scanning electron microscope images in (Lepoint et al., 2006)). Bacteria are a possible food source for harpacticoid copepods (Rieper, 1978). In our study, the presence of 14:0, 15:0 and 17:0, and 18:1ω7 could indicate a contribution of bacterial biomass to copepod diet (Cnudde et al., 2015; Jaschinski et al., 2008). Other heterotrophs (fungi, protists) are also potentially ingested by copepods, but our approach cannot determinate this potential contribution to the copepod diet.

The overall picture painted by our data is that harpacticoid copepods inhabiting detritus accumulations display a relatively diverse diet, dominated by heterotrophic, epiphytic/algae, and seagrass detritus food items. On the contrary, the planktonic eco-morphotype found in the litter appears to mostly rely on the water column for its nutrition.

4.2. Do different copepod eco-morphotypes exhibit resource segregation?

Our data indicated that different eco-morphotypes can exhibit different isotopic niches and different diets, meaning that there is in partitioning of resources offered by EMAs among the four investigated species. Food partitioning and dietary specialisation is often observed in meiofauna inhabiting coastal sediments (Rzeznik-Orignac et al., 2008) or macrophyte habitats (Steinarsdóttir et al., 2010). High feeding selectivity has been documented for nematodes grazing on bacteria and microphytobenthos (Moens et al., 2006), relating to a specific diversity of prey and consumers (De Meester et al., 2016). Specific feeding preferences have also been demonstrated for copepods (e.g. Carman and Thistle, 1985), sometimes with a selectivity at species level (i.e. diatom species) or related to particle characteristics (i.e. diatom sizes) (De Troch et al., 2006a). This resource partitioning is one of the mechanisms sustaining high biodiversity and high consumer biomass at a local scale.

The planktonic copepods analysed here had markedly separated isotopic niches as a consequence of both distinct diets and/or habitats (Fig. 2). Indeed, isotopic niches are related both to trophic niche (i.e. when different diets at population or species level reflect different isotopic niches) and to the habitats in which animals feed (i.e. when different habitats have different isotopic baselines, and animals shifting between habitats may integrate these different isotopic baselines) (Flaherty and Ben-David, 2010 and Phillips et al., 2014). *C. arcuicornis* individuals regularly found in the litter would probably shift between water column and litter (e.g. diel migration, or refuge during windy events). Nevertheless, isotopic data evidenced significant contributions of benthic food sources in the diet of *C. arcuicornis* too. This means that, in shallow coastal areas, EMAs support coupling between planktonic and benthic food webs. This coupling does not necessarily imply an important transfer of seagrass detritus carbon to the pelagic ecosystem as SIAR modelling showed a very low contribution of seagrass material to the diet of *C. arcuicornis*. More likely, epiphytic and microphytobenthic biomass appear as the preferential benthic food sources used by *C. arcuicornis*. Nevertheless, considering its abundance in litter accumulations (10^3 ind·m⁻² during zooplankton bloom) (Mascart et al., 2015b), this species could channel significant matter fluxes between benthic and pelagic compartments.

The mesopsammic species *E. dentatum* also had a distinct isotopic niche compared to other harpacticoid eco-morphotypes. As with *C. arcuicornis*, this species may be found in two habitats, namely EMA and sediment under the EMAs. This may explain the particular $\delta^{15}\text{N}$ value observed for this species, which is representative of sediment organic matter in the study area (Michel et al., 2015).

Isotopic niches of the other two eco-morphotypes, which are more associated with substrate surface (sediment or phytal), were partly

overlapping or were completely separated, depending on the season. These may be related to the relative abundance of the food sources they exploited (i.e. epiphytes, seagrass detritus) and the relative level of competition between these two species (i.e. their relative abundance, which was not assessed here).

Generally speaking, the fact that isotopic niches differed between copepods showing different body morphologies indicated segregation of resources in this particular environment.

4.3. Do copepod trophic ecology vary seasonally?

The four eco-morphotypes investigated displayed a certain level of variability in their respective isotopic composition according to sampling period. A part of this variability is linked to baseline shifts (i.e. temporal variability of isotopic composition of food sources, cf. Tables 3), independent of actual trophic shifts. This confirms the importance to sample food sources in a period compatible with consumer assimilation to assess this baseline shift and properly parameterize the mixing model, as we have done here.

Application of a mixing model using season-specific data for food sources also showed that contributions of food sources to diet varied seasonally. Seasonal diet shifts in benthic copepods are probably related to food availability (i.e. microbial or epiphytic biomass vs. detritus biomass) or nutritive quality. The strongest seasonal shift in isotopic composition was observed for the mesopsammic *E. dentatum*, and this could be explained by a seasonal shift in both trophic resources and habitat (sediment vs. EMA). Indeed, Mascart et al. (2015a) have shown an active and rapid colonization of EMA from sediment by this species.

Phytal and epibenthic eco-morphotypes shared part of their isotopic niches in May and October but not in February and August. In terms of diet, our data indicated species-specific changes between the relative importance of epiphytic resources *sensu lato* (i.e. epiphytic macroalgae, microbial biomass, etc.), and seagrass. Such segregation/overlap between trophic niches has already been documented in phytal habitats (e.g. Arroyo et al., 2006; Steinarsdóttir et al., 2010), suggesting that harpacticoid copepods colonizing phytal environments interact and, potentially, compete for food sources (Arroyo et al., 2006). Temporal changes in food availability (i.e. epiphytic and microbial biomass) (Mascart et al., 2015b), but also quality (detritus ageing, enrichment by microbial biomass, fatty acid composition), are probably the main drivers of trophic competition and trophic niche partitioning between these two eco-morphotypes, tightly associated to phytal habitats. These resource pulses have been demonstrated to have an important effect on macrofauna biodiversity in studied EMAs (Remy et al., 2017).

In addition, our data indicate that species found in litter showed high trophic plasticity, regardless of their eco-morphotype. Indeed, all species observed in the litter were also found on living *P. oceanica* leaves in the seagrass bed, where food source composition, availability, and quality are different, compared to seagrass litter accumulations (Mascart et al., 2013). In the canopy of *P. oceanica*, diatoms colonizing leaves as microepiphytes are likely a major food source for phytal and epibenthic eco-morphotypes, and the contribution from seagrass organic matter is probably reduced.

4.4. Do copepod feed on dead seagrass material?

All 3 harpacticoid copepods analysed here seemed to rely, to some extent, on organic matter originating from seagrass detritus. This conclusion arises from our isotopic data, as $\delta^{13}\text{C}$ allowed us to distinguish seagrass carbon from other sources. Harpacticoid copepods are known to bioconvert short-chain FA into long-chain FA (De Troch et al., 2012). This mechanism of bioconversion is an essential tool in case of low food quality as it allows them to make their own PUFA or increase their PUFA level. This may represent a possible explanation why some copepod species can deal better with detritus as possible food than other species. Three mechanisms could explain this important

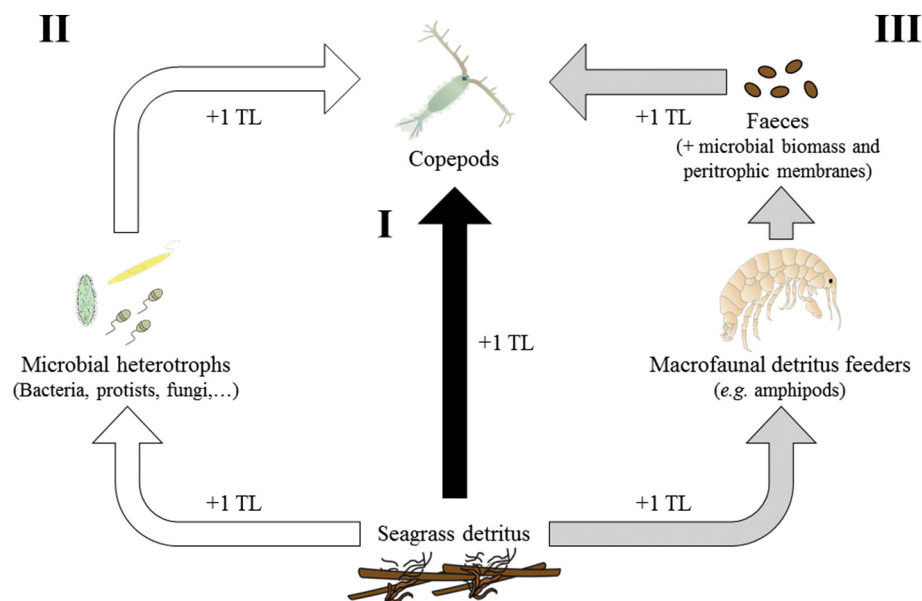


Fig. 5. Possible mechanisms explaining the assimilation of seagrass detritus organic matter by benthic copepods. 1. Direct ingestion of fine detritus particles; 2. Indirect assimilation of processed material via microbial biomass; 3. Indirect assimilation of processed material via faeces of detritus-feeding macrofauna. TL: Trophic level.

observation in terms of energy flow (Fig. 5). The first hypothesis would be that direct copepod grazing on macrophytodebris could occur. However, copepods are considered to feed selectively on individual particles (e.g. plankton, microphytobenthos) or to browse on the substrate surface, as the morphology of their mouth are not adapted to cutting large pieces of material. Detritus material nevertheless fragments rapidly due to physical effect of water motion and consumption by detritivores; therefore, fine material is often the majority of the *Posidonia* detritus pool (Mateo and Romero, 1997). This size is potentially compatible with direct ingestion by copepods; particularly epibenthic and mesopsammic ecomorphotypes, or planktonic ones when particles are resuspended in the water column (following a storm for example).

Second, seagrass carbon could be assimilated indirectly by copepods via microbial intermediates. Seagrass detritus are colonized by various microorganisms (bacteria, fungi, protists) that degrade detritus biomass. The isotopic composition of carbon assimilated by microbial biomass is only slightly affected by isotopic fractionation, meaning that the isotopic composition of heterotrophic microbial biomass could be very close to that of detritus biomass (seagrass detritus, in this case) (Bouillon and Boschker, 2006). Such indirect transfer is often considered to be dominant in seagrass meadow sediments, for example, because of the refractory character of detritus itself (Danovaro, 1996). This has also been hypothesized for salt marshes (Couch, 1989). Indirect transfer of seagrass carbon would add a trophic step between detritus biomass and copepods, but this trophic step between microbial biomass and copepods would not necessarily result in an increase of $\delta^{15}\text{N}$ as demonstrated for planktonic copepods (Gutiérrez-Rodríguez et al., 2014).

The third hypothesis is that a second indirect routing could happen via the consumption of faeces produced by detritus-feeding macrofauna. Indeed, this compartment is dominated by detritus-feeding amphipods (i.e. *Gammarella fucicola* and *Gammarus aequicauda*) that ingest large quantity of seagrass detritus (Lepoint et al., 2006; Remy, 2016). Their faeces, partly digested and enriched by microbes and peritrophic membranes, could be a valuable food source for copepods. Coprophagy is documented in harpacticoid copepods, particularly ones with small mandibular processes (De Troch et al., 2005). Arroyo et al. (2006) observed phytal harpacticoid copepods swimming around their own faecal mounds, and carrying considerable amount of faecal material within their furca. This is also a feeding mechanism found in planktonic copepods, particularly in the oligotrophic area where this study was done (Frangoulis et al., 2011).

This third hypothesis would also introduce (at least) one trophic step between seagrass detritus and copepods (Fig. 5). Therefore, these three mechanistic hypotheses do not have the same efficiencies in terms of energetic transfer of seagrass material to upper trophic levels (such as macrofauna and fish juveniles). Nevertheless, considering the abundance of copepods in the litter (10^4 – 10^5 individuals \cdot m^{-2} or 10–100 individuals \cdot g^{-1} DM) (Mascart et al., 2015b), and the fact they are an important prey for many fish juveniles, this could constitute an important transfer of seagrass C to higher trophic levels. In *Amphibolis* sp. and *Posidonia* spp. detritus accumulations, detrital seagrass material may be specifically fuelled into the food web by harpacticoid copepods, rather than by all detritivores (Hyndes and Lavery, 2005). This highlights the fact that meiofaunal populations are often key players in seagrass organic matter transfer to higher trophic levels, both in seagrass meadow sediments and in detritus accumulations (Danovaro et al., 2002).

To conclude, our data demonstrated that, in this detritus environment, different copepod species and eco-morphotypes feed on various sources and adopt different trophic strategies. The relatively diverse diet was dominated by heterotrophic food items, epiphytes and/or algae, and seagrass detritus. Copepod feeding strategies change over time. This means that the food web associated with litter accumulations is more complex than previously thought, and can change according to seagrass litter composition and availability. Copepods could contribute importantly to the transfer of seagrass organic matter to higher trophic levels, and, as in pelagic ecosystems, constitute a key link between microbial biomass and bigger animals (such as macrofauna and fish larvae or juveniles).

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References

- Abdulkadir, S., Tsuchiya, M., 2008. One-step method for quantitative and qualitative analysis of fatty acids in marine animal samples. *J. Exp. Mar. Biol. Ecol.* 354, 1–8.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for Primer: Guide to Software and Statistical Methods. PRIMER-E, Plymouth.
- Arroyo, N.L., Aarnio, K., Bonsdorff, E., 2006. Drifting algae as a means of re-colonizing defaunated sediments in the Baltic Sea. A short-term microcosm study. *Hydrobiologia* 554, 83–95.
- Azovsky, A.I., Saburova, M.A., Chertoprood, E.S., Polikarpov, I.G., 2005. Selective feeding of littoral harpacticoids on diatom algae: hungry gourmands? *Mar. Biol.* 148, 327–337.
- Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., Macleod, H., 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *J. Anim. Ecol.* 73, 1007–1012.
- Boudouresque, C.F., Pergent, G., Pergent-Martini, C., Ruitton, S., Thibaut, T., Verlaque, M., 2016. The necromass of the *Posidonia oceanica* seagrass meadow: fate, role, ecosystem services and vulnerability. *Hydrobiologia* 781, 25–42.
- Bouillon, S., Boschker, H.T.S., 2006. Bacterial carbon sources in coastal sediments: a cross-system analysis based on stable isotope data of biomarkers. *Biogeosciences* 3, 175–185.
- Bouillon, S., Connolly, R.M., 2009. Carbon exchange among tropical coastal ecosystems. *Ecological Connectivity among Tropical Coastal Ecosystems*. Springer Netherlands, pp. 45–70.
- Boxshall, G.A., Hasley, S.H., 2004. *An Introduction to Copepods Diversity*. The Ray Society, London.
- Carman, K.R., Fry, B., 2002. Small-sample methods for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of the diets of marsh meiofaunal species using natural-abundance and tracer-addition isotope techniques. *Mar. Ecol. Progr. Ser.* 240, 85–92.
- Carman, K.R., Thistle, D., 1985. Microbial food partitioning by three species of benthic copepods. *Mar. Biol.* 88, 143–148.
- Cebrian, J., 2002. Variability and control of carbon consumption, export, and accumulation in marine communities. *Limnol. Oceanogr.* 47, 11–22.
- Champerois, W., Borges, A.V., 2012. Seasonal and interannual variations of community metabolism rates of a *Posidonia oceanica* seagrass meadow. *Limnol. Oceanogr.* 57, 347–361.
- Clarke, K.R., Gorley, R.N., 2006. PRIMER v6. In: PRIMER-E (Ed.), *User Manual/Tutorial*, Plymouth.
- Cnudde, C., Moens, T., Werbrouck, E., Lepoint, G., Van Gansbeke, D., De Troch, M., 2015. Trophodynamics of estuarine intertidal harpacticoid copepods based on stable isotope composition and fatty acid profiles. *Mar. Ecol. Progr. Ser.* 524, 225–239.
- Como, S., Magni, P., Baroli, M., Casu, D., De Falco, G., Floris, A., 2008. Comparative analysis of macrofaunal species richness and composition in *Posidonia oceanica*, *Cymodocea nodosa* and leaf litter beds. *Mar. Biol.* 153, 1087–1101.
- Coplen, T.B., 2011. Guidelines and recommended terms for expression of stable-isotope ratio and gas-ratio measurements results. *Rapid Commun. Mass Spectrom.* 25, 2538–2560.
- Couch, C.A., 1989. Carbon and nitrogen stable isotopes of meiobenthos and their food resources. *Estuar. Coast. Shelf Sci.* 28, 433–441.
- Dalsgaard, J., St. John, M., Kattner, G., Müller-Navarra, D., Hagen, W., 2003. Fatty acid trophic markers in the pelagic marine environment. *Adv. Mar. Biol.* 46, 225–340.
- Danovaro, R., 1996. Detritus-bacteria-meiofauna interactions in a seagrass bed (*Posidonia oceanica*) of the NW Mediterranean. *Mar. Biol.* 127, 1–13.
- Danovaro, R., Gambi, C., Mirto, S., 2002. Meiofaunal production and energy transfer efficiency in a seagrass *Posidonia oceanica* bed in the western Mediterranean. *Mar. Ecol. Progr. Ser.* 234, 95–104.
- Dauby, P., Bale, A.J., Bloomer, N., Canon, C., Ling, R.D., Norro, A., Robertson, J.E., Simon, A., Théate, J.-M., Watson, A.J., Frankignoulle, M., 1995. Particle fluxes over a Mediterranean seagrass bed: a one year case study. *Mar. Ecol. Progr. Ser.* 126, 233–246.
- De Meester, N., Gingold, R., Rigaux, A., Derycke, S., Moens, T., 2016. Cryptic diversity and ecosystem functioning: a complex tale of differential effects on decomposition. *Oecologia* 182, 559–571.
- De Troch, M., Steinarsdóttir, M.B., Chepurnov, V., Ólafsson, E., 2005. Grazing on diatoms by harpacticoid copepods: species-specific density-dependent uptake and microbial gardening. *Aquat. Microb. Ecol.* 39, 135–144.
- De Troch, M., Chepurnov, V., Gheerardyn, H., Vanreusel, A., Ólafsson, E., 2006a. Is diatom size selection by harpacticoid copepods related to grazer body size? *J. Exp. Mar. Biol. Ecol.* 332, 1–11.
- De Troch, M., Van Gansbeke, D., Vincx, M., 2006b. Resource availability and meiofauna in sediment of tropical seagrass beds: local versus global trends. *Mar. Env. Res.* 61, 59–73.
- De Troch, M., Boeckx, P., Cnudde, C., Van Gansbeke, D., Vanreusel, A., Vincx, M., Caramujo, M.J., 2012. Bioconversion of fatty acids at the basis of marine food webs: insights from a compound-specific stable isotope analysis. *Mar. Ecol. Progr. Ser.* 465, 53–67.
- Duggins, D.O., Gómez-Buckley, M.C., Buckley, R.M., Lowe, A.T., Galloway, A.W.E., Dethier, M.N., 2016. Islands in the stream: kelp detritus as faunal magnets. *Mar. Biol.* 163, 1–10.
- El-Sabaawi, R., Dower, J.F., Kainz, M., Mazumder, A., 2009. Characterizing dietary variability and trophic positions of coastal calanoid copepods: insight from stable isotopes and fatty acids. *Mar. Biol.* 156, 225–237.
- Evrard, V., Soetaert, K., Heip, C.H.R., Huettel, M., Xenopoulos, M.A., Middelburg, J.J., 2010. Carbon and nitrogen flows through the benthic food web of a photic subtidal sandy sediment. *Mar. Ecol. Progr. Ser.* 416, 1–16.
- Flaherty, E.A., Ben-David, M., 2010. Overlap and partitioning of the ecological and isotopic niches. *Oikos* 119, 1409–1416.
- Frangoulis, C., Skliris, N., Lepoint, G., Elkalay, K., Goffart, A., Pinnegar, J.K., Hecq, J.-H., 2011. Importance of copepod carcasses versus faecal pellets in the upper water column of an oligotrophic area. *Estuar. Coast. Shelf Sci.* 92, 456–463.
- Guckert, J.B., Antworth, C.P., Nichols, P.D., White, D.C., 1985. Phospholipid, ester-linked fatty acid profiles as reproducible assays for changes in prokaryotic community structure of estuarine sediments. *FEMS Microbiol. Ecol.* 31, 147–158.
- Gutiérrez-Rodríguez, A., Décima, M., Popp, B.N., Landry, M.R., 2014. Isotopic invisibility of protozoan trophic steps in marine food webs. *Limnol. Oceanogr.* 59, 1590–1598.
- Heck Jr, K.L., Carruthers, T.J.B., Duarte, C.M., Randall Hughes, A., Kendrick, G., Orth, R.J., Williams, S.W., 2008. Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. *Ecosystems* 11, 1198–1210.
- Hyndes, G.A., Lavery, P.S., 2005. Does transported seagrass provide an important trophic link in unvegetated, nearshore areas? *Estuar. Coast. Shelf Sci.* 63, 633–643.
- Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER - stable isotope Bayesian ellipses in R. *J. Anim. Ecol.* 80, 595–602.
- Jaschinski, S., Brepohl, D.C., Sommer, U., 2008. Carbon sources and trophic structure in an eelgrass *Zostera marina* bed, based on stable isotope and fatty acid analyses. *Mar. Ecol. Progr. Ser.* 358, 103–114.
- Kharlamenko, V.I., Kiyashko, S.I., Imbs, A.B., Vyshkvartzev, D.I., 2001. Identification of food sources of invertebrates from the seagrass *Zostera marina* community using carbon and sulfur stable isotope ratio and fatty acid analyses. *Mar. Ecol. Progr. Ser.* 220, 103–117.
- Lang, K., 1948. *Monographie der Harpacticiden*. Håkan Ohlssons boktryckeri, Lund.
- Lang, K., 1965. *Copepoda Harpacticoida From the Californian Pacific Coast*. Almqvist & Wiksell, Stockholm.
- Lebreton, B., Richard, P., Galois, R., Radenac, G., Brahmia, A., Colli, G., Grouazel, M., André, C., Guillou, G., Blanchard, G.F., 2012. Food sources used by sediment meiofauna in an intertidal *Zostera noltii* seagrass bed: a seasonal stable isotope study. *Mar. Biol.* 159, 1537–1550.
- Leduc, D., Probert, P.K., Duncan, A., 2009. A multi-method approach for identifying meiofaunal trophic connections. *Mar. Ecol. Progr. Ser.* 383, 95–111.
- Lepoint, G., Nyssen, F., Gobert, S., Dauby, P., Bouquegneau, J.M., 2000. Relative impact of a seagrass bed and its adjacent epilithic algal community in consumer diets. *Mar. Biol.* 136, 513–518.
- Lepoint, G., Cox, A.S., Dauby, P., Poulicek, M., Gobert, S., 2006. Food sources of two detritivore amphipods associated with the seagrass *Posidonia oceanica* leaf litter. *Mar. Biol. Res.* 2, 355–365.
- Logan, J.M., Jardine, T.D., Miller, T.J., Bunn, S.E., Cunjak, R.A., Lutcavage, M.E., 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *J. Anim. Ecol.* 77, 838–846.
- Mancinelli, G., Rossi, L., 2002. The influence of allochthonous leaf detritus on the occurrence of crustacean detritivores in the soft-bottom macrobenthos of the Po River Delta Area (northwestern Adriatic Sea). *Estuar. Coast. Shelf Sci.* 54, 849–861.
- Mascart, T., Lepoint, G., De Troch, M., 2013. Meiofauna and harpacticoid copepods in different habitats of a Mediterranean seagrass meadow. *J. Mar. Biol. Assoc. U. K.* 93, 1557–1566.
- Mascart, T., Augusto, L., Lepoint, G., Remy, F., de Troch, M., 2015a. How do harpacticoid copepods colonize detrital seagrass leaves? *Mar. Biol.* 162, 929–943.
- Mascart, T., Lepoint, G., Deschoemaeker, S., Binard, M., Remy, F., De Troch, M., 2015b. Seasonal variability of meiofauna, especially harpacticoid copepods, in *Posidonia oceanica* macrophytodebris accumulations. *J. Sea Res.* 95, 149–160.
- Mateo, M.A., Romero, J., 1997. Detritus dynamics in the seagrass *Posidonia oceanica*: elements for an ecosystem carbon and nutrient budget. *Mar. Ecol. Progr. Ser.* 151, 43–53.
- McCutchan, J.H.J., Lewis, W.M.J., Kendall, C., McGrath, C.C., 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102, 378–390.
- Michel, L.N., Dauby, P., Gobert, S., Graeve, M., Nyssen, F., Thelen, N., Lepoint, G., 2015. Dominant amphipods of *Posidonia oceanica* seagrass meadows display considerable trophic diversity. *Mar. Ecol. Progr. Ser.* 36, 969–981.
- Moens, T., Traunspurger, W., Bergtold, M., 2006. *Feeding ecology of free-living benthic nematodes*. *Freshwater Nematodes: Ecology and Taxonomy*. CABI Publishing, pp. 105–131.
- Newell, S.Y., Fallon, R.D., M. J.D., 1989. Decomposition and microbial dynamics for standing, naturally positioned leaves of salt-marsh grass *Spartina alterniflora*. *Mar. Biol.* 101, 471–481.
- Noodt, W., 1969. In: H., N.C. (Ed.), *Ecology of the copepoda*. First International Conference on Meiofauna. Smithsonian Institution Press, Tunis, pp. 97–102.
- Pace, M.C., Carman, K.R., 1996. Interspecific differences among meiobenthic copepods in the use of microalgal food resources. *Mar. Ecol. Progr. Ser.* 143, 77–86.
- Parnell, A.C., Inger, R., Bearhop, S., Jackson, A.L., 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS One* 5.
- Pasqualini, V., Pergent-Martini, C., Clabaut, P., Pergent, G., 1998. Mapping of *Posidonia oceanica* using aerial photographs and side scan sonar: application off the island of Corsica (France). *Estuar. Coast. Shelf Sci.* 47, 359–367.
- Phillips, D.L., Newsome, S.D., Gregg, J.W., 2005. Combining sources in stable isotope mixing models: alternative methods. *Oecologia* 144, 520–527.
- Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X., Ward, E.J., 2014. Best practices for use of stable isotope mixing models in food-web studies. *Can. J. Zool.* 92, 823–835.
- Quinn, G.G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- R Core Team, 2014. *R: A Language and Environment for Statistical Computing*. (R Foundation for Statistical Computing, <http://www.R-project.org/>, Vienna, Austria).

- Remy, F., 2016. Characterization, Dynamics and Trophic Ecology of Macrofauna Associated to Seagrass Macrophytodetritus Accumulations (Calvi Bay, Mediterranean Sea). PhD Thesis University of Liège, Liège, p. 324.
- Remy, F., Gobert, S., Lepoint, G., 2017. Effects of an experimental resource pulse on the macrofaunal assemblage inhabiting seagrass macrophytodetritus. *Belg. J. Zool.* 147, 1–15.
- Ricart, A.M., Dalmau, A., Pérez, M., Romero, J., 2015. Effects of landscape configuration on the exchange of materials in seagrass ecosystems. *Mar. Ecol. Prog. Ser.* 532, 89–100.
- Rieper, M., 1978. Bacteria as food for marine harpacticoid copepods. *Mar. Biol.* 45, 337–345.
- Rzeznik-Orignac, J., Boucher, G., Fichet, D., Richard, P., 2008. Stable isotope analysis of food source and trophic position of intertidal nematodes and copepods. *Mar. Ecol. Prog. Ser.* 359, 145–150.
- Steinarsdóttir, M.B., Ingólfsson, A., Ólafsson, E., 2010. Field evidence of differential food utilization of phytal harpacticoids collected from *Fucus serratus* indicated by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes. *Estuar. Coast. Shelf Sci.* 88, 160–164.
- Svensson, C.J., Hyndes, G.A., Lavery, P.S., 2010. An efficient method for collecting large samples of live copepods free from detritus. *Mar. Fresh. Res.* 61, 621–624.
- Vafeiadou, A.M., Materatski, P., Adão, H., De Troch, M., Moens, T., 2014. Resource utilization and trophic position of nematodes and harpacticoid copepods in and adjacent to *Zostera noltii* beds. *Biogeosciences* 11, 4001–4014.
- Vetter, E.W., 1995. Detritus-based patches of high secondary production in the nearshore benthos. *Mar. Ecol. Prog. Ser.* 120, 251–262.