

# Meiofauna and harpacticoid copepods in different habitats of a Mediterranean seagrass meadow

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*This study investigated whether associated meiobenthic communities, especially harpacticoid copepods, differed amongst habitats. Five pre-defined habitats within and next to the Posidonia oceanica seagrass meadow were sampled: living seagrass canopy leaves (LL), small (SMF) and large (LMF) macrophytodebris fragment accumulations and sand, bare (BS) and covered (CS). The highest meiofauna abundances were recorded in the BS for the core sampled habitats (BS, CS, SMF and LMF) and in the LMF for seagrass material habitats (SMF, LMF and LL). Harpacticoid copepods were the most abundant taxon in all habitats. The assemblage composition at copepod family level showed two distinct habitats clusters: a leaf (LMF and LL) and a sediment cluster (BS, CS and SMF). Subsequently, stable isotope analyses were conducted to analyse the relationship between copepods and their potential food sources in seagrass material habitats. Based on  $\delta^{13}\text{C}$  isotopic analyses and SIAR mixing model, harpacticoid copepods relied for 70% on epiphytes and for 30% on P. oceanica leaf material in the LMF and LL habitats.*

**Keywords:** meiofauna, harpacticoid copepods, seagrass, detritus, *Posidonia oceanica*, stable isotopes

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## INTRODUCTION

The endemic *Posidonia oceanica* (L.) Delile, the dominant seagrass in the Mediterranean Sea, is a long-living organism displaying considerable autumnal leaf fall (Pergent *et al.*, 1997). The macrophytodebris is scattered by currents and waves, and accumulates *in situ* or is exported to adjacent habitats where it degrades and often becomes predominant (Mateo *et al.*, 2003; Cardona *et al.*, 2007). Accumulation of macrophytodebris on sand patches adjacent to the seagrass meadow can be substantial, i.e. several hundred cubic metres, especially in relative enclosed systems (Cebrian & Duarte, 2001). These patches are ephemeral environments which remain for a few days to several months depending on the degradation rate and hydrodynamics of the area (Mateo & Romero, 1997). The accumulated materials are heterogeneous, mainly composed of phytodebris (variable in size and degradation status), but also of living seagrass shoots and macroalgae. Macrophytodebris nutritional quality is low due to its high lignocellulose content and its nutritional depletion by N-resorption and recycling before abscission (Lepoint *et al.*, 2002). Nevertheless, macrophytodebris is typically colonized by epiphytic organisms, i.e. all organisms associated with phytal habitats (leaves) such as e.g. heterotrophic microbial communities (bacteria and fungi), autotrophes (e.g. epiphytic diatoms), protists,

meiofauna and macrofauna (Danovaro, 1996; Gallmetzer *et al.*, 2005). The latter two refer to metazoans passing through a 1 mm sieve retained on a 38  $\mu\text{m}$  screen and retained on a 1 mm sieve, respectively. A possible reason for the high colonization is that macrophytodebris create the conditions for the development of a high structural diversity of associated communities. This condition is generated on one hand by physical fragmentation, due to hydrodynamism or biological fragmentation through foraging behaviour. On the other hand by the higher nutritional quality of the epiphytic organisms compared to macrophytodebris and also the accessibility of those epiphytic organisms that serve as food sources (hereafter referred to as epiphytes) for associated consumers. These consumers are likely to be crucial for the degradation and transport of organic matter to higher trophic levels. For example, macrofauna (juvenile fish prey) is known to ingest detritus with their associated epiphytes and microbial communities (Romero *et al.*, 1992; Vizzini *et al.*, 2002; Mateo *et al.*, 2003; Lepoint *et al.*, 2006; Sturaro *et al.*, 2010). As such, seagrass ecosystems hold a significant fraction of autotrophic biomass (Duarte *et al.*, 2005) that is passed indirectly to higher trophic levels. It can thus be assumed that these ecosystems are macrophytodebris based (Romero *et al.*, 1992; Mateo & Romero, 1997; Pergent *et al.*, 1997).

Little is known on the exact role of meiofauna in the macrophytodebris accumulations. *Posidonia oceanica* beds are hotspots for meiofaunal production ranging between 7.5 and 13.2  $\text{g C m}^{-2}\text{yr}^{-1}$  (Danovaro *et al.*, 2002). These values are comparable to the ones reported for seagrass systems in general, but are higher than the meiofaunal production in the Atlantic, the North Sea or the Baltic Sea. Meiofauna

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organisms occur in high densities, have a high turnover rate and most probably spend their entire lifecycle on or around the same substrate (Giere, 2009). They are known to feed on a wide variety of food sources, including epiphytic biofilm (Hicks & Coull, 1983; Caramujo *et al.*, 2008; De Troch *et al.*, 2008, 2009). Meiofaunal studies mainly focus on patterns of occurrence in sediment habitats (Danovaro *et al.*, 2000; Mirto *et al.*, 2010) or in the epiphytal canopy environment (Hall & Bell, 1993). Studies combining both habitats are very limited (Bell *et al.*, 1984; De Troch *et al.*, 2001) and hardly focus on the third non-negligible habitat in this system, namely the macrophytodebris accumulation on sand patches (Dimech *et al.*, 2006). The present study aimed to characterize the meiofaunal community and diversity in different habitat types, namely seagrass canopy, adjacent sand and macrophytodebris accumulations. In addition to the structural diversity of meiofauna, a more functional approach concentrating on harpacticoid copepods is included. Hence, natural stable isotope signatures ( $\delta^{13}\text{C}$ ) are used to trace food sources in consumers (Fry *et al.*, 1987; Lepoint *et al.*, 2000; Vizzini *et al.*, 2002). Potential food sources and harpacticoid copepods from the different habitats were analysed to infer their diet and to study what are the main food sources for harpacticoid copepods at the basis of the food web in the seagrass ecosystem. As the trophic position of copepods in the sediments has been already documented (Carrier *et al.*, 2007; Wyckmans *et al.*, 2007), the present research will clarify which part of the seagrass ecosystem is consumed by harpacticoid copepods, i.e. the macrophytodebris matter, the epiphytic biofilm or the living leaves.

## MATERIALS AND METHODS

### Sampling site and strategy

Samples were collected in the Revellata Bay (Gulf of Calvi, Corsica, north-west Mediterranean) at the Punta Oscelluccia site ( $42^{\circ}35'\text{N}$   $8^{\circ}43'\text{E}$ ) (Figure 1). The sampling site was located close to a sandy patch and in a *Posidonia oceanica* meadow facing the Oscelluccia peninsula (Punta Oscelluccia).

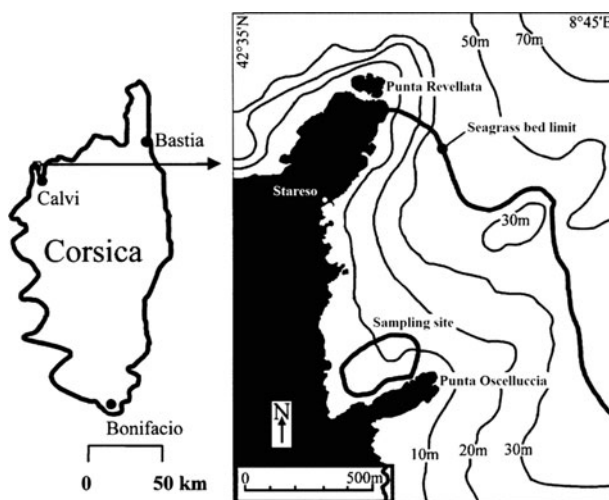


Fig. 1. Location of the Revellata Bay within the sampling site and the *Posidonia oceanica* meadow isobaths with lower depth distribution limit. Adapted from Gobert *et al.* (2003)

At the study site, *P. oceanica* seagrass meadows cover about 50% of the total bay surface down to a depth of 38 m (Bay, 1984) and are ranked among the most productive *P. oceanica* beds in the north-west Mediterranean (Pergent-Martini *et al.*, 1994). Samples were taken in August 2009, which correlates with the start of the autumnal leaf fall cycle. Sampling was carried out at a depth of 10 m by SCUBA divers during day time. The salinity, around 38, and the water temperature, around  $26^{\circ}\text{C}$ , remained stable during the entire sampling campaign.

Five potential habitats for meiofauna were collected in triplicate. The meadow leaves stratum, living leaves of the *P. oceanica* canopy (abbreviation: LL) represented a first potential habitat. Two different types of *P. oceanica* macrophytodebris accumulated on adjacent sand patches were included as other habitat options: large macrophytodebris fragments (abbreviation: LMF) comprising leaf lengths from 0 to 30 cm of *P. oceanica* and small macrophytodebris fragments (abbreviation: SMF) comprising leaf length restricted from 0 to 3 cm of *P. oceanica*. Finally, two sand habitats of adjacent sand patches were sampled: bare sand (abbreviation: BS) and sand covered by macrophytodebris material of *P. oceanica* (abbreviation: CS).

Living *P. oceanica* shoots representing the living leaves stratum (LL) were cut off at the sediment–water interface and put in 2 l plastic jars. The large macrophytodebris fragments (LMF) and small macrophytodebris fragments (SMF) were sampled using a 25 cm diameter tube randomly placed on the macrophytodebris patch. All macrophytodebris present inside the tube were scooped off from the seafloor by hand and collected in 2 l plastic jars. For the sand samples (BS and CS), 20 cm<sup>2</sup> surface area and 5 cm deep cores of bare sand were collected. In order to clear the covered sand sample present underneath the macrophytodebris material, the latter was very carefully moved aside to avoid fine sediment being brought in suspension and to get access to the bare sand. All jars were closed under water to ensure no loss of material or contamination of the samples. Standardization over all samples was not possible due to the different sampling techniques. Therefore two standardizations were made: one to compare all cored samples (BS, CS, SMF and LMF) per unit of surface (10 cm<sup>-2</sup>) and one to compare all seagrass material (SMF, LMF, LL) per unit of dry weight (g<sup>-1</sup>DW).

### Community characterization

In order to extract the attached meiofauna, a 8% MgCl<sub>2</sub>-solution was added to stun the organisms (Hulings & Gray, 1971). Samples were afterwards rinsed twice over a 1 mm mesh sieve to exclude macrofauna and on a 38 μm mesh sieve to retain the meiofauna, prior to preservation with a 4% formaldehyde seawater solution. In the laboratory, the 38 μm–1 mm fraction of each replicate was centrifuged three times with Ludox HS40 (specific density of 1.18 g/dm<sup>3</sup>). Meiofauna was stained with rose Bengal before being sorted and enumerated at a higher taxon level based on Higgins & Thiel (1988) using a Wild M5 binocular. One hundred harpacticoid copepods were randomly picked and stored in 75% ethanol. Copepods were mounted on glycerine slides for further identification to copepod family level using the identification keys and reference books by Boxshall & Hasley (2004) and Lang (1948, 1965).

## Environmental data

The samples for the community characterization were also used to assess the total organic carbon content (TOC). Subsamples were weighed after being dried at 60°C for 72 h. TOC was measured after acidification with HCl and pulverization for 30 minutes of the dried material. TOC analyses were carried out with a ThermoFinnigan Flash1112 elemental analyser using the method of Niewenhuize *et al.* (1994).

## Trophic biomarkers

For stable isotope analysis separate qualitative samples were taken from the seagrass material habitats. The two macrophytodetritus habitats (SMF and LMF) were sampled using 30 l bags where the material was scooped in by hand. The living leaves habitat was sampled by cutting five shoots at the sediment interface. All samples were afterwards kept in aquaria in order to collect harpacticoid copepods using positive phototaxis attraction and a pipette. The extracted copepods were rinsed and placed overnight in filtered seawater to empty their gut content. Two potential food sources including leaves (living or as macrophytodetritus) without and with associated epiphytes were collected according to the technique used by Dauby & Poulicek (1995). The leaves without epiphytes, the epiphytes and the copepod samples (60 ind. sample<sup>-1</sup> in order to have a sufficient amount of carbon for reliable measurements) were stored directly after collection in liquid nitrogen at -80°C. All the samples were dried afterwards for 24 h at 60°C and loaded into tin capsules for isotopic measurements with a C-N-S elemental analyser (Carlo Erba, Italy) coupled to a mass spectrometer (VG Optima, Micromass, UK). Prior to the encapsulation all seagrass material potential food sources were ground, except for harpacticoid copepods. The isotopic data were expressed as  $\delta$  value (‰) relative to the VPDB (Vienna Pee Dee Belemnite) carbon standard. Reference material used to calibrate was IAEA (International Atomic Energy Agency) CH-6 ( $\delta^{13}\text{C} = -10.4 \pm 0.2\text{‰}$ ). The standard deviation of repeated  $\delta^{13}\text{C}$  measurements of the internal standard was  $\pm 0.2\text{‰}$ .

Contribution of potential food sources to the carbon pool of harpacticoid copepods was estimated by a SIAR mixing model developed in R (Parnell *et al.*, 2010). The model was run for 500,000 iterations and the first 50,000 iterations were discarded. Isotopic ratios of copepods and food sources were compared considering a trophic enrichment of  $0.2 \pm 0.6\text{‰}$  for  $\delta^{13}\text{C}$  (adapted from Vander Zanden (2001)). In this study only the mode and lowest and highest 0.95% confidence interval (CI) were detailed. The value used in the model was the overall mean of epiphytes from the two other habitats ( $-20.0 \pm 1.0\text{‰}$ ), due to the lack of data on epiphytes from small macrophytodetritus fragments. To reduce the number of food sources and to avoid bias, the model was run with two sources (epiphytes and leaves without attached epiphytes), except for the small macrophytodetritus fragments where no separation of epiphytes was possible, leaves with epiphytes were used. The living leaves and macrophytodetritus with associated epiphytes were not considered in the mixing models since this source was a combination of two other potential food sources and therefore biasing the mixing model outcome.

## Data analysis

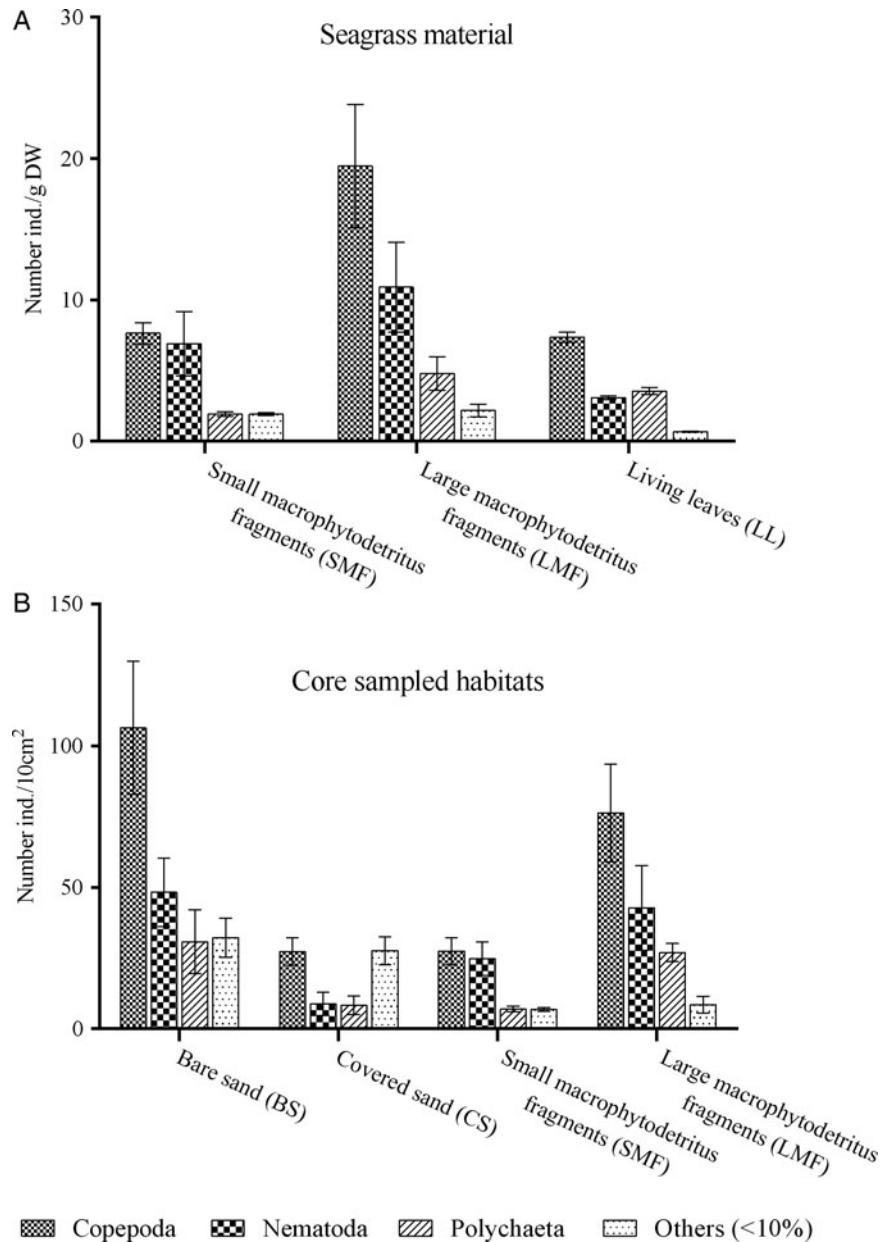
Diversity indices were calculated using  $S$ , the number of meiofauna taxa or copepod families,  $N_{\text{inf}}$ , the dominance index, the reciprocal of the proportional abundance of the most common taxon or family (reciprocal of the Berger–Parker index),  $J'$ , the Pielou evenness index and  $H'$ , the Shannon–Wiener diversity index based on the natural logarithm (ln). A resemblance matrix based on Bray–Curtis similarities was constructed from the log transformed abundances for meiofaunal taxa and harpacticoid copepod families. A cluster analysis based on the Bray–Curtis similarity matrix was performed to explore community structure similarities among the different habitats using the group average linkage method. Prior to the cluster analysis an analysis of similarity (ANOSIM) was carried out to test whether the defined communities (based on habitats) were significantly different. A similarity percentages (SIMPER) analysis based on a Bray–Curtis similarity matrix of the harpacticoid copepod composition was done to reveal which families characterize and discriminate each habitat. All the above mentioned analyses were performed with the Primer 6.0 software (Clarke & Gorley, 2006). Differences in composition among all habitats were tested by means of a one-way analysis of variance (ANOVA) done on relative data. *A posteriori* comparisons were carried out with the Tukey test using 95% confidence limits. Significant differences among two habitats were tested by means of a *t*-test. The ANOVAs, Tukey tests, *t*-tests and graphs were made using GraphPad 5.04 for Windows (GraphPad Software, La Jolla, California BSA).

## RESULTS

### Meiofauna communities

For meiofauna abundances the standardization against surface area yielded a decreasing trend:  $217.5 \pm 92.8$  ind.10 cm<sup>-2</sup> (BS),  $146.2 \pm 63.6$  ind.10 cm<sup>-2</sup> (LMF),  $72.1 \pm 26.7$  ind.10 cm<sup>-2</sup> (CS) and  $57.8 \pm 20.2$  ind.10 cm<sup>-2</sup> (SMF) (Figure 2A). In terms of meiofaunal densities, all four cored habitats were significantly different (one-way ANOVA,  $F(3,8) = 4.75$ ,  $P = 0.0035$ ). The Tukey test comparison revealed that only BS and SMF were significantly different from each other (Tukey,  $P < 0.05$ ). Standardization against dry weight generated the following decreasing trend:  $39.4 \pm 4.1$  ind.g<sup>-1</sup>DW (LMF),  $14.9 \pm 3.0$  ind.g<sup>-1</sup> DW (SMF) and  $13.9 \pm 2.0$  ind.g<sup>-1</sup> DW (LL) (Figure 2B). Regarding meiofaunal densities, all three seagrass material habitats were significantly different (one-way ANOVA,  $F(2,6) = 54.42$ ,  $P < 0.0001$ ). The Tukey test comparison revealed that only SMF and LL were not significantly different from each other (Tukey,  $P > 0.05$ ).

In relation to relative composition, 88% of all organisms belonged to three taxa: copepods, nematodes and polychaetes. Copepods represented the highest average relative abundance of  $49.4 \pm 3.4\%$  with a maximum of  $54.1 \pm 4.8\%$  in LFM. Nematodes accounted on average for  $23.3 \pm 6.8\%$  with a maximal density of  $32.3 \pm 6.4\%$  in SFM. Polychaetes accounted on average for  $15.0 \pm 5.1\%$  with a maximum of  $24.1 \pm 2.2\%$  in the LL. The remaining 12% consisted of, in order of decreasing abundance: juvenile Amphipoda, nauplii, Ostracoda, Tanaidacea, Isopoda, Halacarida, Turbellaria,



**Fig. 2.** Mean meiofauna densities per habitat type. (A) Mean densities in  $\text{gDW}^{-1}$ ; (B) mean densities in  $10 \text{ cm}^{-2}$  surface area. Error bars represent the standard deviation ( $N = 3$ ).

Leptostraca, Oligochaeta, Tardigrada, Decapoda, Chaetognatha, Cnidaria, Pycnogonida, Cumacea and Paguroidea.

The meiofaunal community did not show any significant difference among the habitats in terms of assemblage structure (ANOSIM,  $R = 0.37$ ,  $P = 0.001$ ), with an overall similarity of 84% (SIMPER). The diversity indices showed no significant differences among all five habitats ( $t$ -test,  $p$ -values  $> 0.05$ ) (Table 1).

### Copepoda family composition

For harpacticoid copepod abundances, standardization against surface area yielded the same decreasing trend as for meiofauna:  $10.6 \pm 4.1 \text{ ind.}10 \text{ cm}^{-2}$  (BS),  $7.6 \pm 3.0 \text{ ind.}10 \text{ cm}^{-2}$  (LMF),  $2.7 \pm 0.8 \text{ ind.}10 \text{ cm}^{-2}$  (CS) and  $2.7 \pm 0.8 \text{ ind.}10 \text{ cm}^{-2}$  (SMF) (Figure 2A). In terms of copepod

densities, all four cored habitats were significantly different (one-way ANOVA,  $F(3,8) = 6.7$ ,  $P = 0.0141$ ). The Tukey test comparison revealed that only BS vs CS and BS vs SMF were significantly different from each other (Tukey,  $P < 0.05$ ). Standardization against dry weight generated the following decreasing trend:  $19.5 \pm 1.3 \text{ ind.}g^{-1} \text{ DW}$  (LMF),  $7.0 \pm 0.70 \text{ ind.}g^{-1} \text{ DW}$  (LL) and  $6.2 \pm 1.9 \text{ ind.}g^{-1} \text{ DW}$  (SMF) (Figure 2B). In terms of copepod densities, all three seagrass material habitats were significantly different (one-way ANOVA,  $F(2,6) = 87.95$ ,  $P < 0.0001$ ). As observed for meiofauna, the Tukey test revealed that only SMF and LL were not significantly different (Tukey,  $P > 0.05$ ).

In total, four copepod orders and 16 harpacticoid families were found in 1500 identified copepod specimens. The majority of the copepods ( $90.6 \pm 3.0\%$ ) belonged to the order Harpacticoida. The remaining copepods were

**Table 1.** Meiofauna and harpacticoid copepods diversity indices ( $S$  = number of harpacticoid families,  $N_{inf}$ , dominance index;  $J'$ , Pielou's evenness index;  $H'$ , Shannon – Wiener index). Sediment and leaf regrouping were based on the harpacticoid copepod cluster analysis (Figure 3). Values are mean  $\pm$  standard deviation.

	$S$	$N_{inf}$	$J'$	$H'$
<b>Meiofauna taxa</b>				
BS	12.00 $\pm$ 0.00	2.02 $\pm$ 0.11	0.60 $\pm$ 0.02	1.49 $\pm$ 0.04
CS	11.33 $\pm$ 0.58	2.13 $\pm$ 0.42	0.61 $\pm$ 0.04	1.47 $\pm$ 0.04
SMF	13.33 $\pm$ 2.52	2.02 $\pm$ 0.21	0.53 $\pm$ 0.07	1.37 $\pm$ 0.11
LMF	13.67 $\pm$ 3.06	2.02 $\pm$ 0.21	0.43 $\pm$ 0.08	1.36 $\pm$ 0.13
LL	15.00 $\pm$ 2.65	1.89 $\pm$ 0.20	0.51 $\pm$ 0.04	1.22 $\pm$ 0.02
	$S$	$N_{inf}$	$J'$	$H'$
<b>Copepod families</b>				
BS	10.00 $\pm$ 0.00	2.68 $\pm$ 0.41	0.73 $\pm$ 0.05	1.68 $\pm$ 0.10
CS	9.00 $\pm$ 1.00	2.20 $\pm$ 0.22	0.70 $\pm$ 0.01	1.53 $\pm$ 0.10
SMF	5.00 $\pm$ 1.00	1.32 $\pm$ 0.05	0.53 $\pm$ 0.06	0.84 $\pm$ 0.08
LMF	8.67 $\pm$ 1.53	2.57 $\pm$ 0.56	0.79 $\pm$ 0.14	1.70 $\pm$ 0.24
LL	10.33 $\pm$ 1.15	2.47 $\pm$ 0.43	0.74 $\pm$ 0.05	1.73 $\pm$ 0.13
			Sediment (Cluster 1)	
			8.00 $\pm$ 2.40	2.07 $\pm$ 0.64
				0.71 $\pm$ 0.03
			1.35 $\pm$ 0.40	
			Leaf (Cluster 2)	
			9.50 $\pm$ 1.52	2.52 $\pm$ 0.45
				0.69 $\pm$ 0.13
				1.72 $\pm$ 0.45

BS, bare sand; CS, covered sand; SMF, small macrophytodebris fragments; LMF, large macrophytodebris fragments; LL, living leaves.

copepodites ( $2.9 \pm 2.8\%$ ), representatives of the Cyclopoida order ( $6.1 \pm 2.8\%$ ) or belonged to the orders Calanoida and Misophrioida ( $0.4 \pm 0.3\%$  together). Since only a minority (few %) of the collected copepods did not belong to the Harpacticoida order, further analysis focused only on the latter. The harpacticoid families found, in decreasing order according to their overall relative abundance, were, Tisbidae, Thalestridae, Miraciidae, Laophontidae, Ameiridae, Longipediidae, Ectinosomatidae, Tetragonicepsidae, Harpacticidae, Porcellidiidae Ancorabolidae, Peltidiidae, Canuellidae, Tegastidae, Cletodidae and Cylindropsyllidae.

The harpacticoid copepods showed a significant difference among the habitats in terms of assemblage structure (ANOSIM,  $R = 0.92$ ,  $P = 0.001$ ), with an overall dissimilarity of 53% (SIMPER). ANOSIM habitat type pairwise comparisons test separated well all groups ( $R > 0.75$ ) except for BS&CS and LMF&LL showing overlap but still yielding a difference of  $R = 0.70$  and  $R = 0.63$ , respectively. Cluster analysis (Figure 3) revealed two major clusters: cluster 1 with an overall similarity of 62.6% and cluster 2 with an overall similarity of 52.9%. In the first cluster (cluster 1) a clear distinction was found among two habitats: the large macrophytodebris fragments (cluster 1A, 71.7% similarity) and the living leaves (cluster 1B, 68.7% similarity). The second cluster (cluster 2) consisted of: two replicates of covered sand (cluster 2A, 81.0% similarity) and a cluster (2B, 62.6% similarity) of small macrophytodebris fragments, bare sand and a single replicate of covered sand.

The two main clusters were significantly different (ANOSIM,  $R = 90$ ,  $P = 0.001$ ), showing an average dissimilarity of 61.7% (SIMPER). Cluster 1 had an overall average similarity percentage of 67.4% and four harpacticoid families were abundant with a cumulative contribution to the similarity of 86.8%. According to SIMPER analysis, the families primarily responsible for the similarity were, in decreasing order: Thalestridae (48.2%), Laophontidae (20.4%), Miraciidae (8.5%) and Tisbidae (8.7%). Cluster 2 had an average overall similarity percentage of 63.3% and was mainly characterised by three families with a cumulative contribution of 89.4% (SIMPER). A different decreasing contribution order was seen in comparison to cluster 1: Tisbidae (57.1%), Miraciidae (21.9%) and Thalestridae (10.4%) (Figure 4).

No significant differences were found in number of families ( $t$ -test,  $t(13) = 1.4$ ,  $P = 0.199$ ) between cluster 1 ( $S = 9.5 \pm 1.5$ ) and cluster 2 ( $S = 8.0 \pm 2.4$ ). In contrast to the significant difference among all habitats (one-way ANOVA,  $F(4,10) = 12.0$ ,  $P = 0.0008$ ), there was no significant difference among both clusters in terms of dominance index and Shannon–Wiener index ( $t$ -test,  $t(19) = 1.0$ ,  $P = 0.333$  and  $t(13) = 2.1$ ,  $P = 0.056$ , respectively). The Pielou's evenness index showed a significant difference between the two clusters ( $t$ -test,  $t(13) = 2.6$ ,  $P = 0.023$ ) (Table 1).

**Environmental data**

Total organic carbon values showed significant differences among the habitats (one-way ANOVA,  $F(2,3) = 179.7$ ,  $P = 0.0008$ ) except for SMF and LMF comparison (Tukey,  $P > 0.05$ ). Following TOC content were found in decreasing order: LL ( $31.0 \pm 0.5\%$ ), LFM ( $20.6 \pm 0.3\%$ ), SFM ( $19.7 \pm 1.0\%$ ) and the sand habitats ( $<0.1\%$ ).

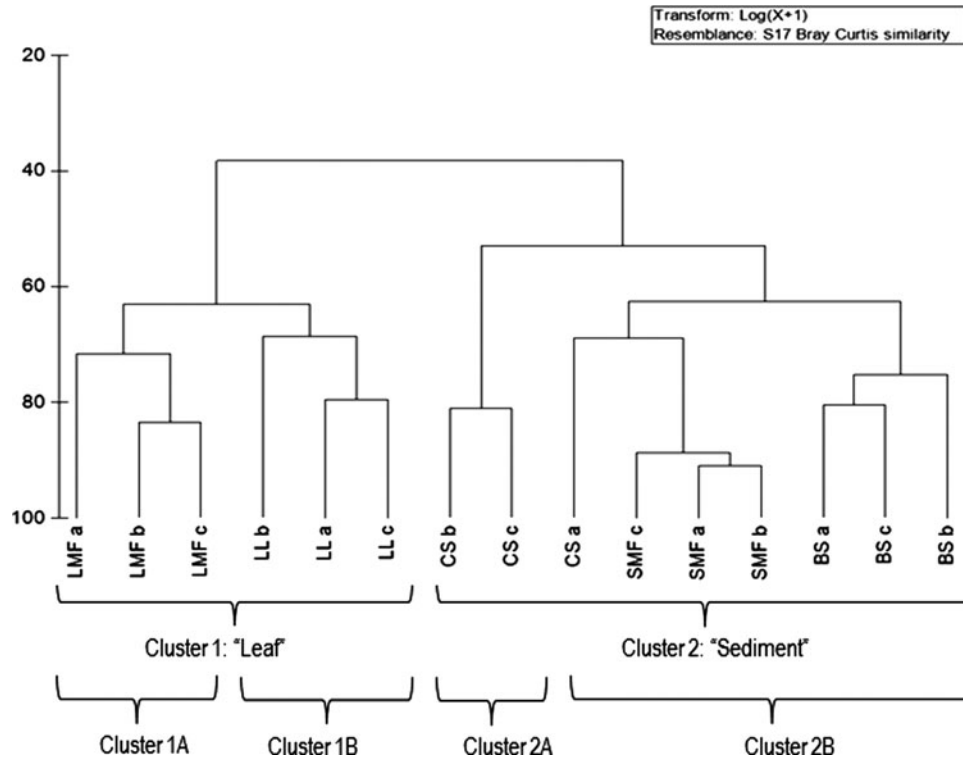


Fig. 3. Cluster analysis of relative harpacticoid copepod densities. LL, living leaves; LMF, large macrophytodebris fragments; SMF, small macrophytodebris fragments; CS, covered sediments; BS, bare sand. similarity coefficient in % on y-axis and a, b, c refer to the replicates.

### Trophic interactions by means of stable isotopes

Harpacticoid copepods from the different seagrass material habitats showed slightly different, but analogous  $\delta^{13}\text{C}$  values:  $-16.6 \pm 1.1\text{‰}$  (LL),  $-18.5 \pm 1.3\text{‰}$  (LMF) and  $-16.8 \pm 1.1\text{‰}$  (SMF) (Figure 5). Leaves with epiphytes were the most enriched  $^{13}\text{C}$  sources:  $\delta^{13}\text{C} = -9.1 \pm 1.5\text{‰}$  (LL) and  $\delta^{13}\text{C} = -14.5 \pm 1.5\text{‰}$  (LMF), however collection of epiphytes from SMF could not be achieved due to the

high fragmentation and fragility of the macrophytodebris material. Therefore only SMF with associated epiphytes could be analysed ( $\delta^{13}\text{C} = -13.7 \pm 1.1\text{‰}$ ), which ranged within the values of LMF without epiphytes. The epiphytes present on the LL and on the LMF material (Figure 5) were by far the most depleted ( $\delta^{13}\text{C} = -19.5 \pm 2.2\text{‰}$  and  $-20.0 \pm 1.0\text{‰}$ , respectively) in the three seagrass material habitats. The combination of living leaves and macrophytodebris with their attached epiphytes ranged between the values

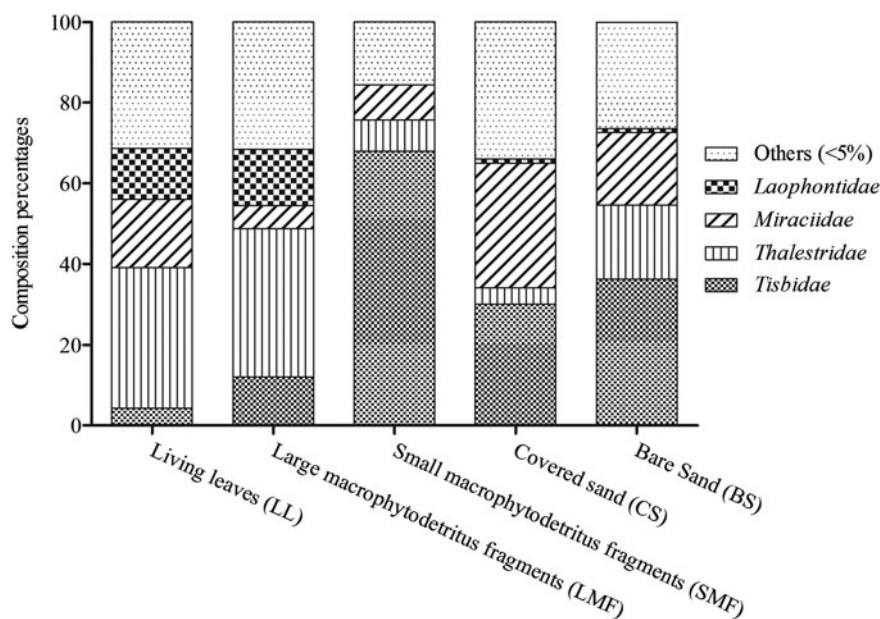


Fig. 4. Mean relative composition (%) of the harpacticoid copepod families. Families shown represent a total contribution of more than 5% over all samples.

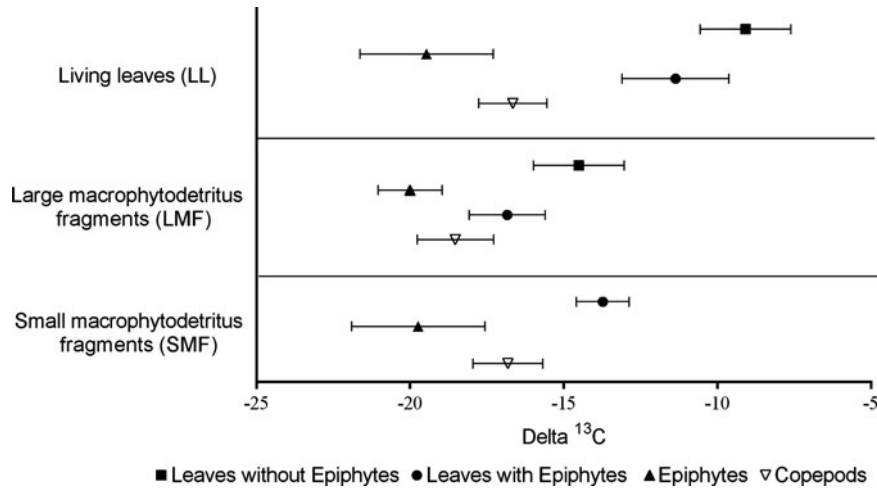


Fig. 5.  $\delta^{13}\text{C}$  values (‰) of plant material as potential food sources and copepods (mean  $\pm$  SD,  $N = 3$ ). The full symbols are potential sources: leaves (living or macrophytodebris) without epiphytes (squares), the removed epiphytes (triangles) and the leaves (living or macrophytodebris) with their epiphytes (rounds). The open symbols are the harpacticoid copepods, primary consumers (reversed triangles).

of the two latter separately with  $\delta^{13}\text{C} = -11.4 \pm 1.8\text{‰}$  and  $-16.9 \pm 1.2\text{‰}$  for the LL and the LMF, respectively (Figure 5).

Mixing model computation showed higher contribution of epiphytes than leaf material as carbon source for copepods in LL and LMF. For the LL habitat, epiphytes 0.95 confidence interval (CI) ranged from 42% to 97% (mode 70%) and LL without epiphytes 0.95 CI was 2–57% (mode 30%). For LMF, epiphytes 0.95 CI ranged from 37% to 99% (mode 72%) and for LMF without epiphytes 0.95 CI was 0–63% (mode 28%). For SMF habitat, epiphytes 0.95 CI ranged from 23% to 81% (mode 51%) and SMF with epiphytes 0.95 CI ranged from 18% to 76% (mode 49%) (Figure 6).

DISCUSSION

In the present study, it was remarkable to see that harpacticoid copepods numerically dominated the meiofauna samples in all habitats. Half of the meiofaunal organisms were harpacticoid copepods and only a quarter were nematodes. This is in contrast with most studies on meiofauna in seagrass meadows sediments (e.g. Fonseca *et al.*, 2011; Losi *et al.*, 2012) where nematodes dominate numerically. Nevertheless, dominance

of copepods is often documented for seagrass meadow canopy leaves (Hall & Bell, 1993; De Troch *et al.*, 2001; Hooper & Davenport, 2006).

The analysis of meiofauna at taxon level did not show any significant differences among the different habitats either in terms of assemblage composition or diversity. Indeed, the five habitats presented a high similarity, i.e. more than 84% (SIMPER). The LMF had the highest meiofaunal abundance from the seagrass material habitats which could indicate that the potential food quality/quantity or protection from predation was the highest in these habitats. A potential increase in complexity can be a reason for this, however concrete measurements (e.g. compactibility of the accumulation) to prove the possible rise in complexity were not part of this study. It could also be caused by an increase of biofilm quantity or quality as dead leaves are colonized by degrading microbes and generally lie on the sediment, exposed to sun light, in contrast to living leaves which are vertically disposed and often over-shaded.

Within the core sampled habitats, a significant difference in abundance between bare sand and covered sand was observed. This could be explained by the possible anoxia created by the layer of macrophytodebris above the covered sand. We expect that the oxygen does not penetrate deep enough

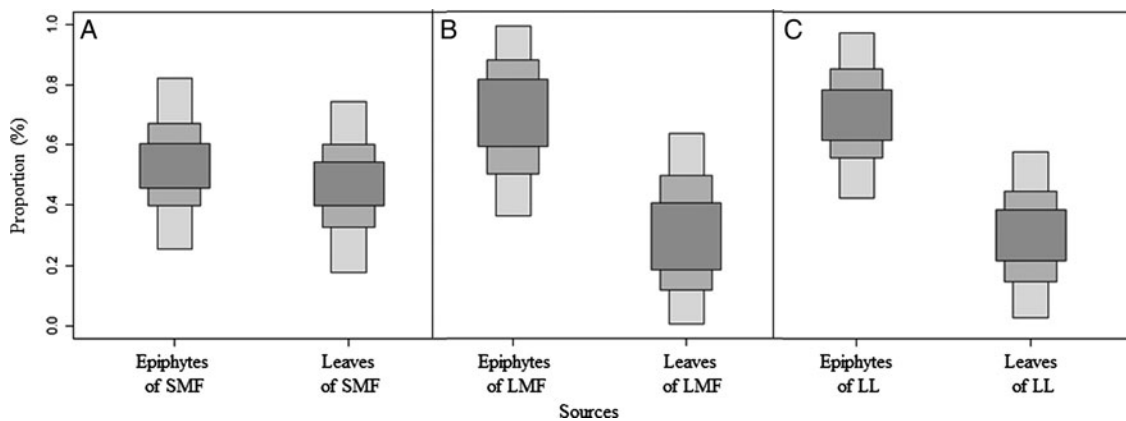


Fig. 6. SIAR boxplots show the proportional contribution (%) of different sources to the diet of harpacticoid copepods in (A) the small macrophytodebris fragments habitat (SMF), (B) the large macrophytodebris fragments habitat (LMF) and (C) the living leaves habitat (LL) with 95% (darkest grey), 75% and 25% (lightest grey) credibility intervals.

through the macrophytodebris to reach the sand and thus oxygen levels can become limiting. As a result, meiofauna could migrate upwards from the sand towards the macrophytodebris. In the present study, no measurements of oxygen were available, but it could be definitely interesting to include them in future research.

In terms of harpacticoid copepod density, the same higher abundance trend for bare sand and large macrophytodebris fragments compared to covered sand and small macrophytodebris fragments was found, similar to the meiofauna results. We could assume that bare sand includes most of the copepods and when covered by macrophytodebris these then migrate/emerge into large macrophytodebris fragments. Nevertheless, in terms of harpacticoid copepod family composition, two main significantly different clusters with a similarity of approximately 38.3% were displayed. The low similarity indicates that the small macrophytodebris fragments habitat behaves like a sediment habitat (CS and BS) and that the large macrophytodebris fragments habitat was similar to the living leaves habitat for copepod family composition. Therefore, cluster 1 (LL and LMF) and cluster 2 (SMF, CS and BS) will further be referred to as 'leaf' and 'sediment', respectively. Thus we can hypothesize that bare sand and large macrophytodebris fragments attract harpacticoid copepods adapted to different habitat. Harpacticoid copepods are morphologically diverse and well-adapted group occurring in numerous environments (Hicks & Coull, 1983; Huys & Boxshall, 1991; Boxshall & Hasley, 2004). The phytal living leaves environment is exposed to waves and currents. Organisms living in that habitat developed attachment capabilities such as prehensile grasping legs (e.g. copepod families Thalestridae and Laophontidae) or body flattening (Porcellididae and Peltitidae). Macrophytodebris accumulations on sandy patches are temporary, which implies that all meiofauna could be transported passively on the senescent leaves or immigrate actively from the surrounding habitat. High vagility of the phytal meiofauna was demonstrated by Bell & Hicks (1991) and the active emergence and colonization abilities of copepods to richer or easier accessible food resources was proven by Armonies (1988) and Thistle & Sedlacek (2004). Experiments with artificial substrates (Mirto & Danovaro, 2004) emphasize the good swimming and colonization abilities of copepods, which partially explains the higher abundance of copepods in the large macrophytodebris fragment. As such, the good colonization abilities of harpacticoid copepods could explain the high resemblance in terms of copepod assemblage structure between large macrophytodebris fragments and living leaves on the one hand and between small macrophytodebris fragments, bare sand and covered sand on the other hand. Novak (1984) stated that epiphytic cover increases from young to mature leaves. Large macrophytodebris fragments which are senescent mature leaves exhibit a lower total organic carbon content than living leaves. Nonetheless, large macrophytodebris fragments displays by far the highest number of individuals per gram dry weight. Therefore we can hypothesize that the content of the potential food sources does not seem to be the determining factor, but rather, the accessibility of the food source. It has been demonstrated that harpacticoid copepods occur primarily in function of resource availability (Webb, 1990), followed by hydrodynamic exposure, surface area colonizable by epiphytes (De Troch *et al.*, 2005) and food accessibility. Well-developed and accessible epiphytic

biofilms could thus enhance the species richness and density of the meiofauna (Hall & Bell, 1993; Peachey & Bell, 1997). This was congruent with some morphological adaptations found among the meiofaunal taxa. Only a small fraction of the phytal meiofauna (some nematodes, tardigrads and halacarids) can feed directly from the plant tissue, whereas the majority of meiofauna graze on the organic biofilm present on the leaves (e.g. Giere, 2009). Macrophytodebris accumulations function thus as refuge from predators and provide ample food supply (Bonsdorff, 1992; Norkko *et al.*, 2000).

Stable isotope analysis was used to identify trophic interactions and dietary relationships between the harpacticoid copepods and their potential food sources. The recorded stable isotope data of *Posidonia oceanica* leaves showed a range in  $\delta^{13}\text{C}$  values between  $-13\text{‰}$  and  $-8\text{‰}$ , however most delta values varied around  $-12\text{‰}$  (Hemminga & Mateo, 1996). These relatively high  $\delta^{13}\text{C}$  values compared to other potential source materials, like epiphytes ( $\delta^{13}\text{C}$  value around  $-20\text{‰}$ ) make it possible to trace seagrass material in fauna diet. In our present study harpacticoid copepods were more  $^{13}\text{C}$  depleted than the *P. oceanica* leaves or macrophytodebris and more  $^{13}\text{C}$  enriched than the attached epiphytic biofilm. The analogous harpacticoid copepod signatures in all three seagrass material habitats suggest that they feed on similar sources, independent of the habitat where they occur. The SIAR mixing model revealed that epiphytes contribute more to the carbon resource for harpacticoid copepods than plant material, living or macrophytodebris, do. This was congruent with the conclusion of Fry *et al.* (1987) on the basis that epiphytic algae can have an equal or greater nutritional importance than seagrasses for consumers in seagrass meadows. Since the outcome of the mixing model for SMF was biased due to the non-separation of the epiphytes from the leaves, no clear conclusion can be drawn for this particular habitat.

Harpacticoid copepods are known to feed on a variety of food sources (Hicks & Coull, 1983) and they can colonize plastic seagrass mimics (De Troch *et al.*, 2005). It was known that the epiphytic biofilm consists of different food sources ranging from cyanobacteria to diatoms and fungi and consequently represents a very variable food quality (Novak, 1984; Lepoint *et al.*, 2006). The macrophytodebris epiphytic biofilm compared to the seagrass epiphytic biofilm was composed of a higher number of detrital organisms, such as fungi and bacteria (Lepoint *et al.*, 2006). Therefore we can hypothesize that the main reason why epiphytes contribute primarily to the food supply of harpacticoid copepods was due to the richer organic content in comparison to the poor macrophytodebris material. Nevertheless, the isotopic composition did not exclude the occurrence of seagrass and macrophytodebris in the diet of copepods. The question arose as to whether harpacticoid copepods actively graze on plant material or accidentally ingest and assimilate it during epiphytic biofilm grazing. The isotopic signatures of *P. oceanica* macrophytodebris (LMF and SMF) differ from living leaves (LL) by  $3.9 \pm 1.1\text{‰}$ . This can be explained by the fractionation during decomposition. Nutrients are resorbed in senescing leaves before abscission and labile nutrients are quickly mobilized by bacterial degradation (Mateo & Romero, 1997). Next to the decomposition fractionation, the origin of the macrophytodebris leaves could play a major role. Macrophytodebris found on the studied sand patch does not necessarily come from the adjacent meadow but may be from deeper meadows which exhibit a lower isotopic signature



due to the light constraint on photosynthesis rate (Lepoint *et al.*, 2003).

## CONCLUSIONS

Meiofauna community assemblages were similar in the five habitats analysed in the present study. Meiofauna densities were the highest in the bare sand, followed by large macrophytodetritrus fragments compared to the other core sampled habitats. Harpacticoid copepods were found to be the most abundant taxa and had the highest density in large macrophytodetritrus fragments compared to the other seagrass material habitats. On the basis of harpacticoid copepod assemblage structure, the five different habitats were divided in two main clusters: a sediment group and a leaf habitat group. The small macrophytodetritrus fragments showed a higher similarity with both sand habitats in harpacticoid copepod composition and therefore can thus be considered to be more similar to sediment habitats than to phytal habitats. Copepod stable isotope signatures were similar, which indicates they feed on analogous food sources in the different habitats. As epiphytes contribute for 70% to the copepods' carbon signature in living leaves and large macrophytodetritrus fragments, they appear to be the preferential carbon source for harpacticoid copepods (SIAR mixing model).

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