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Seasonal variability of meiofauna, especially harpacticoid copepods, in *Posidonia oceanica* macrophytodetritus accumulations

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ABSTRACT

The overall aim of this study was (1) to assess the diversity and density of meiofauna taxa, especially harpacticoid copepod species, present within accumulated seagrass macrophytodetritus on unvegetated sand patches and (2) to elucidate the community structure of detritus-associated harpacticoid copepods in relation to natural temporal variability of physico-chemical characteristics of accumulations. This was investigated in a *Posidonia oceanica* (L.) Delile seagrass ecosystem in the northwest Mediterranean Sea (Bay of Calvi, Corsica, 42°35′N, 8°43′E) using a triplicate macrophytodetritus core field sampling in two contrasting sites over the four seasons of 2011. Meiofauna higher taxa consisted of 50% Copepoda, of which 87% belonged to the Harpacticoida order. Nematoda was the second most abundant taxa. The copepod community displayed a wide variety of morphologically similar and ecologically different species (*i.e.* mesopsammic, phytal, phytal-swimmers, planktonic and parasitic). The harpacticoid copepod community followed a strong seasonal pattern with highest abundances and species diversity in May–August, revealing a link with the leaf litter epiphyte primary production cycle. Aside from the important role in sheltering, housing and feeding potential of macrophytodetritus, a harpacticoid community BEST analysis demonstrated a positive correlation with habitat complexity and a negative correlation with water movements and *P. oceanica* leaf litter accumulation.

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1. Introduction

In the Mediterranean Sea, seagrass meadows of *Posidonia oceanica* (L.) Delile cover vast areas of sea bottom. Yearly at the end of summer, the seagrass losses a major part of its leaf biomass after senescence. The fate of these *P. oceanica* dead leaves, also called leaf litter, varies (Pergent et al., 1997): a part of the leaf litter decays slowly or is buried within the meadow, while another part is exported to other adjacent habitats where it may represent a considerable organic material input (Cebrian et al., 1997; Duarte and Cebrian, 1996; Pergent et al., 1994; Romero et al., 1994). Such exported leaf litter mixes with drift epilithic macroalgae, uprooted living seagrass shoots with rhizomes, other seagrass litter, seeds, dead macrofauna and fine sediment to form detritus. The exported detritus form dense accumulations, especially on adjacent unvegetated sand patches, in relation to local hydrodynamics and sand patch morphology (Vetter and Dayton, 1999). The macrophytodetritus host many organisms which can participate in the degradation of this organic material, such as bacteria, fungi, diatom microalgae and invertebrates (Danovaro, 1996; Danovaro et al., 2002; Gallmetzer et al., 2005; Graca, 2001; Mancinelli and Rossi, 2002). Especially motile macro- (>1 mm) and meiofauna (38 μm–1 mm) invertebrates were revealed to be important in the shredding, degrading and decomposing of the organic wrack (Hyndes and Lavery, 2005; Lillebo et al., 2007; Mancinelli and Rossi, 2002; Vetter, 1995; Wittman et al., 1981).

Several studies in coastal ecosystems compared motile invertebrate communities in living seagrass habitats with communities present in directly adjacent habitats (unvegetated sand, root-rhizome matte and macrophytodetritus accumulations). Unvegetated sand showed a lower abundance of associated motile macro- and meiofauna than the foliar substrata of living seagrasses (Bostrom and Bonsdorff, 1997; Connolly, 1997; Edgar et al., 1994; Fonseca et al., 2011; Sanchez-Jerez et al., 1999). In the *P. oceanica* ecosystem, the root–rhizome layer mat supports diverse macro-invertebrate assemblages (Harmelin, 1964). These mats occur with live rhizomes or naturally dead rhizomes. The comparison between the dead and the living habitat yielded a higher total number of species and abundance in the dead detrital mat (Borg et al., 2006). However, certain randomness in the species assemblages was present depending on subliminal parameters such as the substrate compactness, bacterial growth, and depth (Abada Guerroui and Willise, 1984; Harmelin, 1964). Macrofaunal communities in macrophytodetritus accumulations on unvegetated sand patches were, in terms of diversity low, but in terms of total abundance equal to or higher than living seagrasses (Como et al., 2008; Dimech et al., 2006; Gallmetzer et al., 2005; Mancinelli and Rossi, 2002). Consequently, dead habitats and especially macrophytodetritus accumulations seem to support a unique macro-invertebrate assemblage.

Meiofauna are said to play an important role in the degradation of leaf litter (Hyndes and Lavery, 2005; Lillebo et al., 2007). In some habitats, studies were made and clear associations between detritus and meiofauna assemblages were established, such as in mangrove leaf litter (Gee and Somerfield, 1997; Gwyther, 2003; Torres-Pratts and Schizas, 2007) or in terrestrial forest (Dumont and Maas, 1988; Fiers and Ghenne, 2000). In seagrass ecosystems, food webs are mainly seen as detrital (Duarte and Cebrian, 1996; Mateo and Romero, 1997; Pergent et al., 1994), but many potential food sources coexist (Lepoint et al., 2000). No study, to our current knowledge, was ever performed on the harpacticoid copepod assemblage associated with seagrass macrophytodetritus. Mascart et al. (2013) compared *P. oceanica* meadows, sediment and two types of macrophytodetritus accumulations. The macrophytodetritus accumulations showed higher meiofauna abundances than living seagrasses, without expressing a higher diversity. Consequently, do macrophytodetritus accumulations support a unique meiofauna community, in particular harpacticoid copepods and what is the origin and variability of this community?

The overall aim of this study was to assess the diversity and density of meiofauna taxa, especially harpacticoid copepod species, present within macrophytodetritus wrack accumulations on unvegetated sand patches. A second aim was to elucidate the community structure of associated meiofauna and harpacticoid copepods to natural temporal variability of physico-chemical characteristics of macrophytodetritus accumulations. We investigated this by collecting triplicate macrophytodetritus core samples in the four seasons of the year in two contrasting sites. We addressed the following specific questions: (1) Do wind gusts act as a proxy for near bottom currents that control the dynamics of the macrophytodetritus? (2) Does the temporal dynamics have an effect on the meiofauna and copepod community composition and density in two contrasting sites? (3) What are the ecological groups of copepods present in the litter accumulation (*i.e.* planktonic, phytal or mesopsammic)?

2. Materials and methods

2.1. Sampling sites and strategy

Samples were collected in the Revellata Bay in the Gulf of Calvi, Corsica, northwest Mediterranean (42°35′N, 8°43′E). 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 amongst the most productive *P. oceanica* beds in the north west Mediterranean (Pergent-Martini et al., 1994). Annual surface temperatures have a classical summer maximum (26 °C in August) and winter minimum (13 °C in March). Currents are weak (≤ 5 cm·s^{-1}) and the salinity is 38 and stable throughout the year. The dominant winds on the Bay originate from the South-West (Libeccio, 200–250°) and North (Mistral and Tramontane, 320–60°) sectors (Bay, 1984; Dauby et al., 1995).

Samples were taken seasonally, *i.e.* in the months of February, May, August and October of 2011 representing winter, spring, summer and autumn, respectively. Sampling was carried out at a depth of 10 m by scuba divers during day time and calm sea conditions. Two contrasting sampling sites at about 1 km from each other were selected. Both sampling sites offered sandy patches with different local hydrodynamic conditions and variable shapes and patch sizes. The first sampling site was located in front of the harbour of the STARESO research facility and was referred to as PORT. The second sampling site was situated in front of the Punta Oscellucia peninsula and was referred to as OSCE. In each site, triplicate PVC cores were randomly pushed into the macrophytodetritus accumulation (inner diameter = 20 cm, surface = 0.0314 m^2). All detritus contained in the tube was gently scooped off the seafloor bed by hand and put into 6 L sealed plastic jars. Sediment was not taken. In order to ensure no loss of material or contamination, all jars were closed under water. In order to separate meiofauna from the macrophytodetritus, an 8% $MgCl_2$-solution was added (Hulings and Gray, 1971) and fresh water rinsing was used to stun the organisms. The samples were rinsed twice over a 1 mm mesh sieve to exclude detritus. Meiofauna was retained on a 38 μm mesh sieve and preserved in a 4% formaldehyde seawater solution. The defaunated detritus was stored frozen (−18 °C).

2.2. Abiotic factors

Meteorological data were recorded during the entire year in order to map the effect of the weather on the local hydrodynamics. Previous studies stated that currents in the study site are weak (≤ 5 cm·s^{-1}) and circulation mainly consists of a local residual gyre (Dauby et al., 1995). According to ocean surface mixed layer models (see Cushman-Roisin and Beckers, 2011 and references therein) it is generally accepted that the surface winds, next to other factors like off-shore generated swell, have a direct influence on the bottom currents. Shallow regions (typically with a depth of 10 m) are considered to be dominated by shear turbulence and friction (Cushman-Roisin and Beckers, 2011).

Therefore the surface wind can be used as proxy for the near bottom currents. For the purpose of this study, only wind gusts, *i.e.* maximum wind speed over a two-second period at any time during 20 min, higher than 3.06 $m \cdot s^{-1}$ were taken into account. Due to the geographical location and orientation of the bay, east-southerly to westerly winds are sheltered and thus have almost no effect on the local sea surface of the sampling sites. Therefore only wind gusts blowing from the 1st quadrant (0–90°), coming from North to East, were selected. In order to characterise and relate the selected wind gusts, two factors were included in the analysis: (1) wind gust velocity, *i.e.* the median speed of the wind gusts during the time frame and (2) wind gust quantity, *i.e.* the percentage of time gusts blowing during the time frame. The selected timeframe relevant to the sampling scale was four weeks prior to sampling, to map the long-term effects of the wind.

For each sample collection site at each season ($N = 24$), water was sampled using a 60 ml direct-suction filter sampler from Gobert et al. (2006) at different positions: the water column (WC), the water just above the detritus (WJA), the water inside the detritus (WI) and the interstitial water of the underlying sediments (IW). Nutrient concentrations, nitrogen (NH_4^+ and $NO_3 + NO_2$, hereafter NO_x) and phosphate (HPO_4^{2-}) were analysed with an autoanalyser (SKALAR San + continuous flow analyser) based on the method of Grasshoff et al. (2007) adapted for oligotrophic (low nutrient content) seawater (detection limits: 0.1, 0.04 and 0.05 μM for ammonium, NOx and phosphates, respectively). Oxygen concentrations were measured using the Winkler method with 13 ml biological oxygen demand (BOD) bottles. The Winkler method titration of iodine with a thiosulfate solution was adapted for microvolumes (Strickland and Parsons, 1968). Oxygen concentration was not measured in interstitial water of the underlying sediments. Oxygen values under 63 μM were defined as hypoxic (Middelburg and Levin, 2009).

2.3. Macrophytodetritus characterisation

During sampling, the macrophytodetritus accumulation height (Detritus height) was measured with a ruler stick pushed through the detritus alongside the core. The detritus accumulation was constituted of heterogeneous material, therefore after thawing, the defaunated macrophytodetritus was sorted in three categories: (1) the dead *P. oceanica* leaf litter fragments, (2) the drift epilithic macroalgae (Drift macroalgae) and (3) the living shoots of *P. oceanica* comprising rhizomes and living leaves (Living *P. oceanica*). In order to display the different contributions, all categories were dried at 60 °C for 96 h. Prior to dry weighting of the leaf litter category, the 25 first fragments were scraped according to Dauby and Poulicek (1995) to remove the epiphytes which would bias the weight of the leaf litter fragments. Afterwards, for calculation purposes, the total epiphyte dry weight (Leaf litter epiphytes DW) and net leaf litter dry weight (Leaf litter DW) were extrapolated from the measurements of the first 25 fragments. Standardisation of dry weight was done towards $gDW \cdot m^{-2}$ extrapolated from the core surface. An extra detritus characterisation factor (Epi/Lit ratio) was mathematically added for the BEST analysis (see further). The leaf litter epiphytes DW/leaf litter DW ratio was created (Epi/Lit ratio), since the seasonal fluctuation of the epiphytic primary production (read: leaf litter epiphytes DW) and the *P. oceanica* leaf senescence (read: leaf litter DW) don't follow the same pattern.

2.4. Meiofauna community characterisation

In the lab, the 38 μm–1 mm fraction of each replicate was centrifuged three times with Ludox HS40 (specific density of 1.18 $g \cdot dm^{-3}$) in order to extract meiofauna from the macrophytodetritus derived organic material. Meiofauna was stained with Rose Bengal before being sorted and enumerated at a higher taxon level based on Higgins and Thiel (1988). Harpacticoid copepods were picked out and stored in 75% ethanol. Due to time-consuming identification we restricted ourselves to the first one hundred twenty adult harpacticoid copepods (De Troch et al., 2001), representing 15 to 95% of the total adult copepod amount. Copepods were mounted *in toto* on glycerine slides for identification at species level using the identification keys and reference books by Boxshall and Hasley (2004) and Lang (1948, 1965). The number of individuals was standardised by area m^2 and towards dry weight g extrapolated from the core surface and leaf litter dry weight, respectively.

2.5. Data analysis

A fully crossed 2-factor design was performed in PERMANOVA with fixed factors month and site for the multivariate harpacticoid copepod species composition and univariate diversity indices and environmental variables (excluding nutrients and oxygen). A fully crossed 3-factor design was performed in PERMANOVA with fixed factors month, site and position for the environmental variables nutrients and oxygen. A Bray–Curtis and Euclidean distance based resemblance matrix was used for untransformed multivariate and normalised univariate measures, respectively. Significant differences between groups can be shown by PERMANOVA, but no difference due to location (factor effect) or due to dispersion (variance) can be distinguished. Therefore, homogeneity of dispersion was tested with a PERMDISP, using distances amongst centroids calculated on the lowest level (Quinn and Keough, 2002). For univariate Euclidian distance the PERMDISP test is equivalent to the traditional univariate Levene's test (Anderson et al., 2008). Post-hoc comparisons were performed using Pair-wise tests type III. Copepoda species diversity was measured as species richness and Hill's diversity indices (Hill, 1973): S = number of different species; $N_1 = \exp(H')$, where H' is the Shannon–Wiener diversity index based on the natural logarithm (ln); $N_2 = 1/\lambda$, where λ is Simpson's index.

Within the multivariate analysis, a SIMPER (similarity percentages) analysis was done to identify the main harpacticoid copepod species primarily providing the discrimination between the groups. A principal coordinate analysis (PCO) based on a Bray–Curtis similarity resemblance matrix of untransformed relative data of meiofauna taxa or harpacticoid copepod species was performed to visualise the community structure amongst the different months and sites (Anderson et al., 2008). In order to find the best explanatory environmental variable for the meiofauna and harpacticoid copepod community structure, a multivariate BEST analysis with the BIOENV algorithm based on the Spearman rank correlation coefficient was performed (Clarke and Gorley, 2006). The same BEST analysis was performed on the univariate data of the five most dominant harpacticoid copepods, representing each more than 5% of the total relative densities, to reveal the best explanatory variable of their distributions and abundances. After a skewness check through a Draftsman plot, the variables NO_x and PO_4 were log-transformed prior to the analysis. Several significant Spearman correlations were found: accumulation height and leaf litter DW ($r_s = 0.81$, $N = 24$, $P = 0.022$) and wind gust velocity and wind gust quantity ($r_s = 0.96$, $N = 24$, $P < 0.001$). Therefore accumulation height and wind gust quantity were excluded from the BEST analysis.

All the above mentioned analysis were performed with the Primer 6.1.11 software (Clarke and Gorley, 2006) with PERMANOVA add-on software (Anderson et al., 2008). A significance level of $P < 0.05$ was used for univariate analysis and $P < 0.001$ for multivariate analysis, due to the numerous comparisons in the multiple analyses of variance. Graphs were constructed in GraphPad 5.03 for Windows (GraphPad Software, San Diego California USA).

3. Results

3.1. Environmental data: macrophytodetritus characterisation

The month of October had the highest detritus accumulation height of 27 ± 4.6 cm (average ± standard deviation, henceforth used as notation) in OSCE compared to 5.0 ± 0.0 cm at the same site in August

(Fig. 1). Detritus accumulation height differed significantly over months (Table 1). Pair-wise post-hoc tests for detritus accumulation height revealed that October differed significantly from all other months and that May and August also significantly differed (Table 1).

The leaf litter dry weight showed a maximum average dry weight in October of 2287.6 ± 617.9 gDW·m^{-2} for OSCE (representing 90.7% of macrophytodetritus) and 1994.7 ± 860.1 gDW·m^{-2} for PORT (representing 66.1% of macrophytodetritus). The lowest leaf litter dry weight was found in August with 452.1 ± 295.9 gDW·m^{-2} (representing 73.1% of macrophytodetritus) and 452.5 ± 98.8 gDW·m^{-2} g (representing 48.2% of macrophytodetritus) for OSCE and PORT, respectively (Fig. 1). The factor month showed to be significant especially for October compared to May and August (pair-wise post-hoc test).

The leaf litter epiphyte DW was the highest in October with 233.6 ± 18.2 gDW·m^{-2} for OSCE and 336.9 ± 158.2 gDW·m^{-2} for PORT, representing 9.3% and 11.2% of the total macrophytodetritus. Regarding the macrophytodetritus composition, the highest leaf litter epiphyte DW contribution was found in August for PORT (representing 19.2% of macrophytodetritus) and for OSCE (representing 10.7% of macrophytodetritus). Both month and site factors showed a significant effect (Table 1). The pair-wise post-hoc test revealed that October differed significantly from the other months. There was a significant difference in site for the month of February.

The living *P. oceanica* DW was the highest in October in site PORT with 623.5 ± 284.9 gDW·m^{-2} and May in site PORT with 262.2 ± 111.8 gDW·m^{-2}, representing respectively 20.6% and 22.4% of the total macrophytodetritus (Fig. 1). The lowest biomass was observed in February in site OSCE with 12.5 ± 10.9 gDW·m^{-2} expressing 1.4% of the total macrophytodetritus biomass. No living *P. oceanica* DW was found in October OSCE (Fig. 1). All time, site and interaction factors had significant effects. The PERMDISP analysis of the lowest interaction factor was not revealed to be significant.

Drift macroalgae were absent in both sites in February and in the OSCE site in October. The highest drift macroalgae DW was found in May in the PORT site (106.5 ± 40.5 gDW·m^{-2}) representing 9.1% of the total macrophytodetritus biomass. As for living *P. oceanica* DW, all factors were found to be significant except the lowest interaction factor (Table 1).

3.2. Environmental data: abiotic factors

Median wind gust velocity reached a maximum during February (24.5 m·s^{-1}) and October (22.4 m·s^{-1}) (Fig. 2). The median wind gust velocity varied amongst months in decreasing order (OSCE, PORT): February (12.1 m·s^{-1}, 12.4 m·s^{-1}) > October (9.6 m·s^{-1}, 9.6 m·s^{-1}) > May (6.8 m·s^{-1}, 6.5 m·s^{-1}) > August (4.4 m·s^{-1}, 4.4 m·s^{-1}) (Fig. 2). The wind gust quantity varied with the same decreasing trend (OSCE, PORT): February (43.2%, 41.4%) > October (39.2%, 39.4%) > May (23.8%, 23.6%) > August (15.2%, 11.6%) (Fig. 2). Both median wind gust velocity and wind gust quantity showed a significant effect with the factor month but not for the site and interaction factors (Table 1).

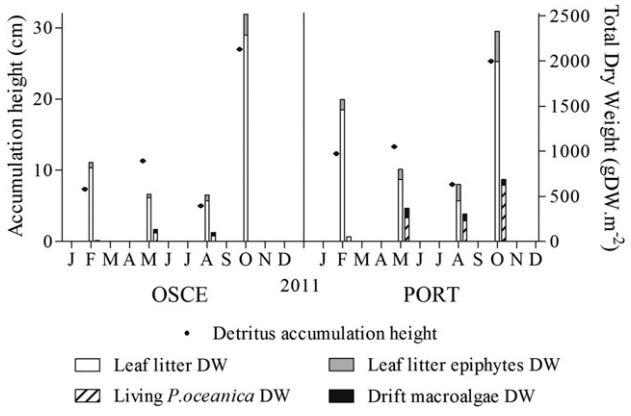

Fig. 1. Macrophytodetritus accumulation height represented in cm above the sea floor on the left y-axis. Dry weights (DW) of leaf litter, leaf litter epiphytes, living *P. oceanica* and drift macroalgae are represented on the right y-axis. $N = 3$.

The oxygen concentration of the water inside the macrophytodetritus (WI) was always lower than the concentration in the water column (WC) and the water just above the macrophytodetritus (WJA). The latter two were always in the same range between 190 and 250 μM (Fig. 3A). For the litter values at least one replicate of each sample was always under the hypoxia limit, defined by Middelburg and Levin (2009), explaining why the averaged O_2 concentrations were two to ten times lower than those of the water column and the water just above the litter. NO_x concentrations showed a high variability (Fig. 3B). Nevertheless in February a noticeable increase of the water column NO_x concentration is visible next to a decrease in interstitial water content from May onwards. NH_4 concentrations were at least ten times higher in the interstitial water (IW) than all other positions, except for the February OSCE sample where a measurement error might have occurred (Fig. 3C). The PO_4 concentrations showed no distinct trend apart from the higher concentration in the interstitial water with the exception of the February samples (Fig. 3D).

The 3-way PERMANOVA with all nutrient and oxygen concentrations was significant for all factors and interactions except for the month–site–position interaction factor with NO_x, the site–position interaction factor with oxygen and NO_x and month–position with oxygen (Table 2). PERMDISP's for all the lowest interaction factors turned out to be significantly different, indicating that the variation within all factors and interactions was due to the dispersion effect and perhaps the location effect as well. All pair-wise correlations between abiotic factors were non-significant, except for wind gust velocity with WI O_2 concentration ($r_s = 0.74$, $N = 24$, $P = 0.046$) and with leaf litter DW ($r_s = 0.77$, $N = 24$, $P = 0.028$).

3.3. Meiofauna communities

At a higher taxon level, relative meiofauna composition revealed a clear dominance of Copepoda. Over all months, copepods represented 46.5 ± 14.6% (OSCE) and 49.4 ± 22.2% (PORT) of the meiofauna with a minimum in February and a maximum in August. The second most abundant taxon was Nematoda with 20.3 ± 10.1% in OSCE and 14.8 ± 4.9% in PORT. The lowest relative abundance was present in August and the highest was in October for the OSCE site and May for the PORT site. The Copepoda/Nematoda ratio was high in August (8.6) and relatively equal throughout the other seasons: October (2.3), February (2.0) and May (1.8). The remaining taxa encountered in decreasing order, were nauplius larvae (15.7%), Amphipoda (4.9%), Turbellaria (4.5%), copepodites (3.7%), Polychaeta (<3%), Ostracoda, Isopoda, Halacaroidea, Tardigrada, Gastropoda, Kinorincha, Leptostraca, Cumacea, Gastrotricha, Oligochaeta, Tanaidacea, Cnidaria, Chaetognatha, Decapoda larvae and Pycnogonida.

The multivariate analysis showed no effect of the site factor or its interaction, and only showed an effect of month (2-way PERMANOVA, $F'_{(3,16)} = 6.7$, $P < 0.001$) on the meiofauna assemblage. The principal coordinate analysis (PCO) of meiofauna taxa composition showed a vague temporal separation (Fig. 4A).

The total number of individuals reached their maximum in May for the OSCE site (60,564 indiv. m^{-2}) and in August for the PORT site (78,062 indiv. m^{-2}). In October for OSCE (34,462 indiv. m^{-2}) and in February for PORT (31,025 indiv. m^{-2}) a minimum total meiofauna amount was reached (Fig. 5A). Meiofaunal standardisation towards gram leaf litter dry weight yielded the same maxima. The month of October returned low numbers of organisms per gram leaf litter in both sites (Fig. 5B). The univariate 2-way PERMANOVA on total meiofauna per m^2 displayed no significant differences in either factors (month, site) or interactions. In terms of total meiofaunal abundance

Table 1
Two-way factorial PERMANOVA of environmental variables: detritus and wind descriptors; F' = pseudo-F value. DW = dry weight.

Factors and interaction	Leaf litter DW	Leaf litter epiphytes DW	Drift macroalgae DW	Living *P. oceanica* DW
Month	$F'_{(3,16)} = 12.30\ P < 0.001^{***}$	$F'_{(3,16)} = 8.96\ P < 0.001^{***}$	$F'_{(3,16)} = 15.14\ P < 0.001^{***}$	$F'_{(3,16)} = 6.21\ P = 0.008^{**}$
Site	$F'_{(1,16)} = 0.40\ P = 0.532$	$F'_{(1,16)} = 6.41\ P = 0.021^{*}$	$F'_{(1,16)} = 28.68\ P < 0.001^{***}$	$F'_{(1,16)} = 28.93\ P < 0.001^{***}$
Month × site	$F'_{(3,16)} = 0.80\ P = 0.525$	$F'_{(3,16)} = 0.39\ P = 0.783$	$F'_{(3,16)} = 3.59\ P = 0.043^{*}$	$F'_{(3,16)} = 7.71\ P = 0.002^{**}$

Factors and interaction	Detritus accumulation height	Wind gust velocity	Wind gust quantity
Month	$F'_{(3,16)} = 28.30\ P < 0.001^{***}$	$F'_{(3,16)} = 372.63\ P < 0.001^{***}$	$F'_{(3,16)} = 435.65\ P < 0.001^{***}$
Site	$F'_{(1,16)} = 1.64\ P = 0.220$	$F'_{(1,16)} = 0.01\ P = 1.000$	$F'_{(1,16)} = 3.90\ P = 0.068$
Month × site	$F'_{(3,16)} = 0.74\ P = 0.543$	$F'_{(3,16)} = 0.05\ P = 0.666$	$F'_{(3,16)} = 1.76\ P = 0.192$

* = $0.05 < P < 0.01$ = significant.
** = $0.01 < P < 0.001$ = highly significant.
*** = $P < 0.001$ = very highly significant.

per gram dry weight, the factor site had no significant effect, but the factor month (2-way PERMANOVA, $F'_{(3,16)} = 12.1$, $P < 0.001$) and the interaction factor (2-way PERMANOVA, $F'_{(3,16)} = 4.8$, $P < 0.001$) had a highly significant effect. The PERMDISP for the interaction factor was not significant and the pair-wise post-hoc test revealed that only May and August were not significantly different.

The global multivariate BEST analysis revealed that wind gust velocity was the best explanatory variable (rho = 0.669) for the meiofaunal taxa assemblage, followed by its combination with the WI NO_x concentrations (rho = 0.587). The tertiary best explanatory correlation was the combination of wind gust velocity and WI NH_4 concentration (rho = 0.535). Oxygen concentration (WI O_2) correlation with all taxa abundances gave only one significant outcome (Amphipoda, $r_s = -0.809$, $N = 24$, $P = 0.015$). Correlating wind gust velocity with the different taxa abundances gave no significant Spearman correlation, with the exception of the Copepoda taxa ($r_s = -0.74$, $N = 24$, $P = 0.046$). The copepodite correlation was not significant, nonetheless the p-value was close to the significance threshold level ($r_s = -0.69$, $N = 24$, $P = 0.069$).

3.4. Harpacticoid copepod species composition

In total 44 different species belonging to four copepod orders were identified in the macrophytodetritus accumulations under study (Table 3). The majority of species (41) belonged to the order of the Harpacticoida, representing 87.2 ± 10.0%, while three species belonged to the orders Calanoida, Cyclopoida and Syphonostomatoida. Within those three orders, species other than those given in Table 3 were found only in a juvenile state and therefore were not included in the species list. The most diverse harpacticoid families were Miraciidae and Tisbidae that were represented by four and five different species, respectively. The family Tisbidae was present in the highest absolute densities.

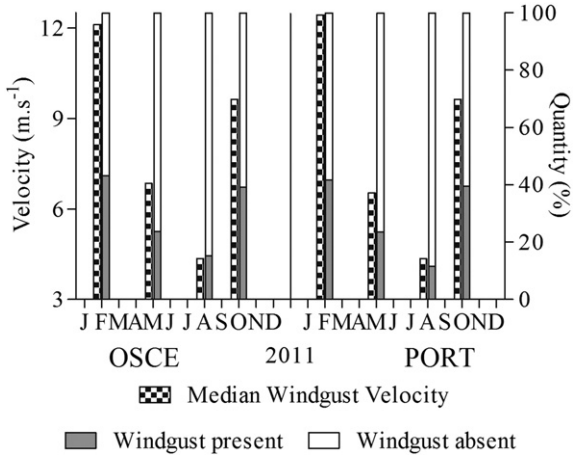

Fig. 2. Wind gusts (selected as winds from North to East, with a velocity > 3.06 $m \cdot s^{-1}$) represented by their median velocity (during the 4 week's timeframe prior to sampling) on the left y-axis and the quantity of the wind gusts compared to all winds measured in percentages on the right y-axis.

Principal coordinate analysis (PCO) of harpacticoid copepod species showed a strong seasonal separation (Fig. 4B). In each month, clusters per site could be detected except for February and October. The separation by months was supported by a multivariate PERMANOVA ($P < 0.001$; Table 4).

SIMPER results comparing months showed that one species (*Tisbe furcata*) was always amongst the top five similarity contributors. *Ectinosoma* cf. *dentatum* was ranked important in all months except in May. *Diosaccus tenuicornis*, *Idyella exigua*, *Tisbe ensifer* and *Ameira longipes* were ranked as important contributors in at least two months (Table 4). In May (53.6% similarity) both sites showed the lowest cumulative contribution of the first five contributors (50.7%; Table 4). The highest dissimilarity (75.4% dissimilarity) was found between May and October. The two lowest dissimilarities were found between February and October with a dissimilarity of 38.9%. The multivariate PERMANOVA analysis showed no separation per site ($P = 0.014$; Table 4). Over all months, four of the five most contributing species (SIMPER) were found in both sites. *A. longipes*, *Ectinosoma* cf. *dentatum*, *T. ensifer* and *T. furcata* accounted together for 64.3% in OSCE and 65.0% in PORT (Table 4).

The samples from the month of May harboured the highest species richness (S) in terms of harpacticoid copepod species in OSCE (24.7 ± 2.1) and in PORT (20.0 ± 4.6). The lowest S value was noted in October for OSCE (9.0 ± 1.0) and in February for PORT (12.3 ± 0.6). Species richness differed significantly for every factor and interaction (Table 5), with a non-significant PERMDISP of the interaction factor ($P = 0.324$). The heterogeneity of N_1 (more sensitive to the number of abundant species) and N_2 (giving more weight to the dominant species) differed significantly for the factor month (PERMANOVA) (Table 5).

Standardisation of harpacticoid copepod abundances towards gram dry weight leaf litter was significantly affected by the factor month and its interaction with the factor site. The interaction had a non-significant PERMDISP ($P = 0.360$). However, when copepod densities were standardised by square metre, only the factor month showed an effect (Table 5). A pair-wise test revealed that only February–May and May–October were not significantly different from other months.

The global multivariate BEST analysis found wind gust velocity to be the best explanatory variable for the harpacticoid copepod assemblage (rho = 0.510), followed by wind gust velocity combined with leaf litter DW (rho = 0.425). The tertiary explanatory variable was the combination of the latter two and the drift macroalgae DW

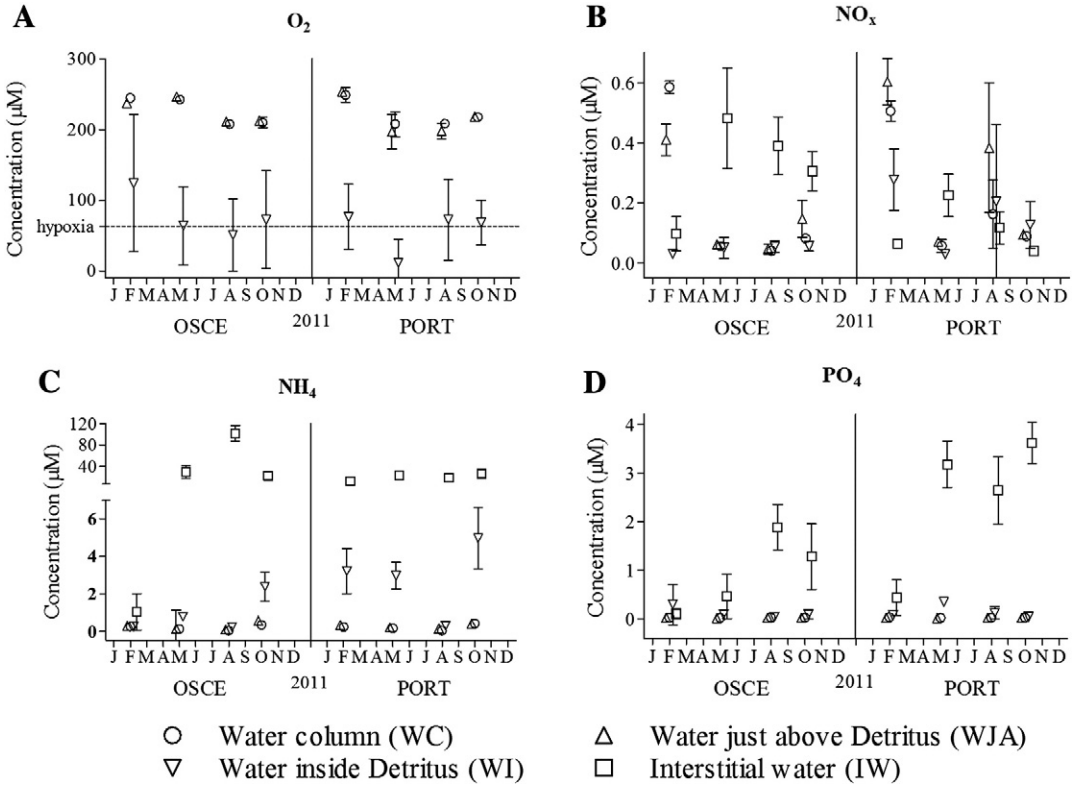

Fig. 3. Oxygen and nutrient concentration measurements in µM on the y-axis, A: oxygen, B: nitrates, C: ammonium and D: phosphates. $N = 6$ and error bars represent the standard deviation.

(rho = 0.409). Harpacticoid S and environmental factors yielded a significant correlation for leaf litter DW ($r_s = -0.82$, $N = 24$, $P = 0.011$).

The five univariate BEST analyses of the five most dominant harpacticoids yielded different best explanatory variables. The *T. furcata* (19.0% of all harpacticoids) test revealed primary variables that were a combination of leaf litter DW, wind velocity and Epi/Lit ratio (rho = 0.503). The *Ectinosoma* cf. *dentatum* (8.9% of all harpacticoids) test revealed primary variables that were a combination of leaf litter epiphytes DW and living *P. oceanica* DW (rho = 0.149). The *T. ensifer* (8.6% of all harpacticoids) and *A. longipes* (8.4% of all harpacticoids) test displayed combinations of drift macroalgae DW and wind velocity as the best explanatory variables (rho = 0.480 and rho = 0.305, respectively). The *Diosaccus tenuicornis* (4.5% of all harpacticoids) test found a combination of leaf litter epiphytes DW, WI O_2 concentration and Epi/Lit ratio (rho = 0.144) as the best explanatory variables.

4. Discussion

4.1. Harpacticoid copepod species assemblage in detritus

According to Hicks and Coull (1983), harpacticoid copepods are regularly encountered as the most dominant and diverse meiobenthic taxon in phytal substrata. The comparison between macrophytodetritus accumulations and seagrass canopy revealed similar trends of the harpacticoid copepod community. The macrophytodetritus accumulations harboured the same density in order of magnitude (10^4–10^5 indiv. m^{-2}) as *P. oceanica* meadows (Mascart et al., 2013; Novak, 1982). The diversity, around 30 to 50 harpacticoid species, was similar to other phytal ecosystems (De Troch et al., 2008; Heip et al., 1983; Hicks, 1977; Johnson and Scheibling, 1987; Steinarsdóttir et al., 2003). In this study, five abundant harpacticoid species were found belonging to different ecological and morphological groups. Two of them belonged to the phytal-swimmers group (Tisbidae family, genus *Tisbe*), known as

Table 2
Three-way factorial PERMANOVA of nutrients and oxygen environmental variables; F' = pseudo-F value.

Factors and interaction	NH_4	NO_x	PO_4	O_2
Month (Mo)	$F'_{(3,160)} = 83.8$ $P < 0.001$*	$F'_{(3,160)} = 38.9$ $P < 0.001$*	$F'_{(3,160)} = 46.9$ $P < 0.001$*	$F'_{(3,120)} = 16.6$ $P < 0.001$*
Site (Si)	$F'_{(1,160)} = 50.5$ $P < 0.001$*	$F'_{(1,160)} = 18.5$ $P < 0.001$*	$F'_{(1,160)} = 120.6$ $P < 0.001$*	$F'_{(1,120)} = 17.4$ $P < 0.001$*
Position (Po)	$F'_{(3,160)} = 584.9$ $P < 0.001$*	$F'_{(3,160)} = 3.5$ $P < 0.015$	$F'_{(3,160)} = 572.2$ $P < 0.001$*	$F'_{(2,120)} = 312.3$ $P < 0.001$*
Mo × Si	$F'_{(3,160)} = 89.3$ $P < 0.001$*	$F'_{(3,160)} = 18.5$ $P < 0.001$*	$F'_{(3,160)} = 26.6$ $P < 0.001$*	$F'_{(3,120)} = 15.6$ $P < 0.001$*
Mo × Po	$F'_{(9,160)} = 94.5$ $P < 0.001$*	$F'_{(9,160)} = 3.5$ $P < 0.001$*	$F'_{(9,160)} = 53.6$ $P < 0.001$*	$F'_{(6,120)} = 2.3$ $P = 0.038$
Si × Po	$F'_{(3,160)} = 68.3$ $P < 0.001$*	$F'_{(3,160)} = 1.1$ $P = 0.367$	$F'_{(3,160)} = 117.1$ $P < 0.001$*	$F'_{(2,120)} = 2.7$ $P = 0.074$
Mo × Si × Po	$F'_{(9,160)} = 82.7$ $P < 0.001$*	$F'_{(9,160)} = 1.1$ $P = 0.367$	$F'_{(9,160)} = 21.2$ $P < 0.001$*	$F'_{(6,120)} = 4.7$ $P < 0.001$*

* = $P < 0.001$ = significant.

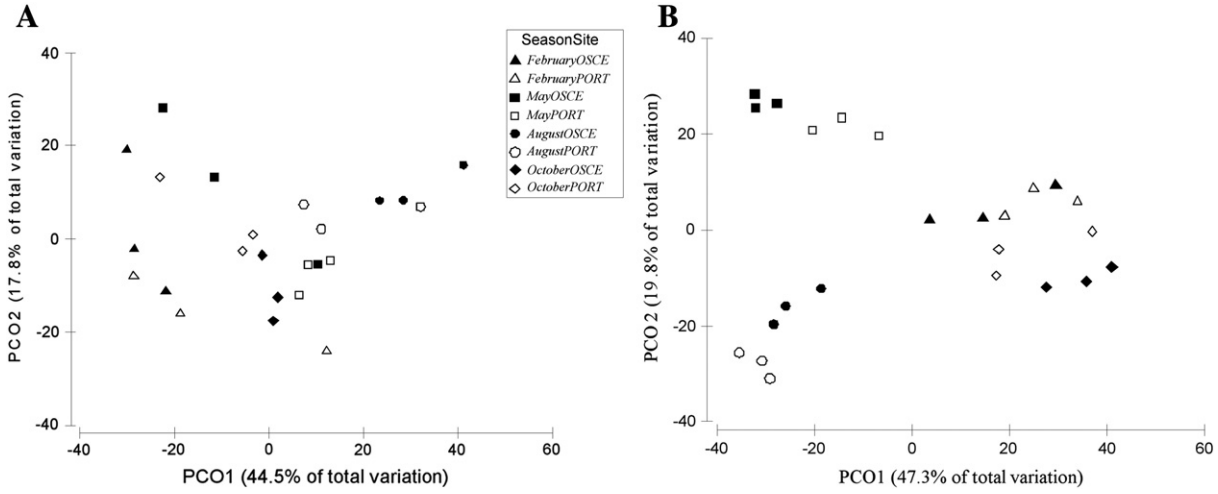

Fig. 4. Principal coordinate analysis (PCO) based on a Bray–Curtis similarity resemblance matrix on untransformed data of A: relative meiofauna taxon composition and B: relative harpacticoid copepod species composition. Filled symbols represent the Oscelluccia site (OSCE) and the un-filled symbols the harbour site (PORT). *Triangles*: February; *squares*: May; *circles*: August and *diamonds*: October.

very good swimmers. Two belonged to the phytal group *sensu strictu* (*A. longipes* and *Diosaccus tenuicornis*) and one was a typical mesopsammic species (Giere, 2009) of the Ectinosomatidae family (*Ectinosoma* cf. *dentatum*). The abundant species found in the macrophytodetritus are cosmopolitan and are recorded in other habitats as well (Bell et al., 1987; Colangelo et al., 1996; Giere, 2009; Steinarsdóttir et al., 2003; Walters, 1991). During the calmest and lowest accumulation months of May and August, harpacticoid species were abundant and diverse. This rise coincides with the rise in primary production and increase in densities of mostly phytal harpacticoids such as *A. longipes*, *Diosaccus tenuicornis*, *Sarsamphiascus tenuiremis*, *Dactylopusia tisboides* and *Porcellidium ovatum*. In months with high leaf litter biomass (February and October), *T. furcata* and *T. ensifer* dominated the community. Both species are phytal-swimmers and seemed more adapted to the higher hydrodynamic disturbance. The distribution of the mesopsammic *Ectinosoma* cf. *dentatum* on the other hand seemed to be linked, although with little strength (low rho), to the amount of leaf litter epiphytes and living *P. oceanica* present. Henceforth, we could assume that *Ectinosoma* cf. *dentatum* migrated into the macrophytodetritus accumulation to avoid low oxygen levels in the sediment underneath or to search for more accessible food. Harpacticoids are known to feed on a wide variety of food sources (Hicks and Coull, 1983; Lee et al., 1977), displaying species-specific food preferences (Buffan-Dubau and Carman, 2000; De Troch et al., 2012; Decho and Castenholz, 1986; Pace and Carman, 1996; Wyckmans et al., 2007). Hicks and Coull (1983) stated that the existence of a wide variety of morphologically similar species in one habitat is allowed as a consequence of harpacticoids' selective feeding. This all points to the possibility that the harpacticoid community is mainly associated with the macrophytodetritus for food availability and shelter (Coull and Wells, 1983).

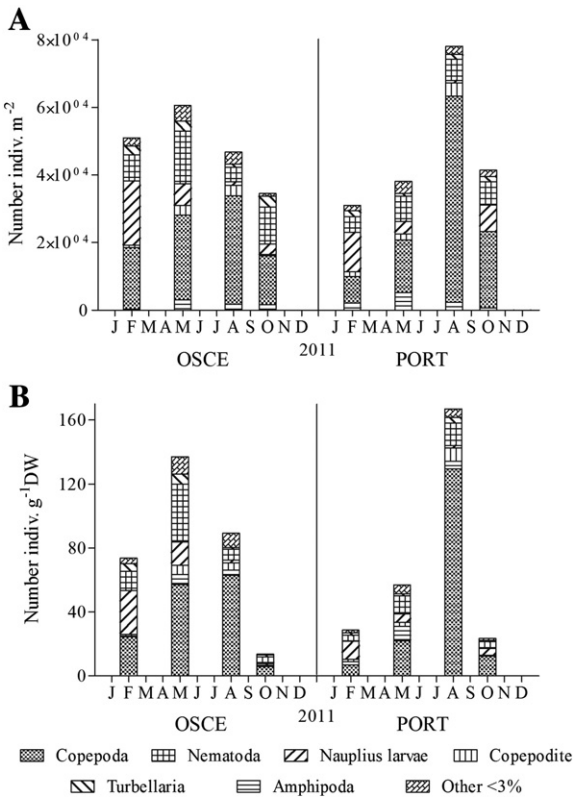

Fig. 5. Main meiofauna taxa densities per sampled month and site with left, Oscelluccia (OSCE) and right, harbour (PORT). A: abundance per m^2 and B: abundance per g dry weight (DW) leaf litter.

Leaf litter has been recognised as a food source for harpacticoid copepods (Meyer and Bell, 1989) since detrital forms of organic material were more palatable and more accessible than fresh material for consumers (Edgar et al., 1994; Enriquez et al., 1993; Harrison and Mann, 1975). It is thus possible that macrophytodetritus accumulations yield a more readily available food for harpacticoids in contrast to other habitats and this will attract them (Norkko and Bonsdorff, 1996). However, laboratory and field studies stated that the meiofaunal detritus-feeders primarily rely on the micro-epiphytes associated with the leaf litter surface (Carman and Thistle, 1985; Hicks and Coull, 1983; Ustach, 1982). In this study site, the leaf litter epiphytes consisted of an abundant community of micro-epiphytic organisms such as bacteria, marine fungi, protozoa, micro- and detrital-algae (Lepoint et al., 2006). This complex community of leaf litter epiphytes created micro-scale variability in resources and shelter for the associated fauna. However, no difference in terms of epiphytic members was found in the present study and consequently we can state that the leaf litter epiphytes represent a bulk of macro- and micro-epiphytes. In order to obtain more information on the species-specific feeding preference of harpacticoid copepods additional investigations (*e.g.* food source tracing experiment) are certainly required.

Table 3
List of relative abundances (%) of Copepoda species based on subsamples of 120 individuals averaged over three replicates (Avg.) ± standard deviation (SD). PORT = harbour and OSCE = Oscelluccia. Species with bold font are the five dominant harpacticoids.

	February		May		August		October	
	OSCE	PORT	OSCE	PORT	OSCE	PORT	OSCE	PORT
	Avg. ± SD	Avg. ± SD	Avg. ± SD	Avg. ± SD	Avg. ± SD	Avg. ± SD	Avg. ± SD	Avg. ± SD
Harpacticoida	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Ameiridae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
***Ameira longipes* (Boeck, 1865)**	2.2 ± 0.9	8.4 ± 1.8	2.2 ± 1.4	8.5 ± 1.5	0 ± 0	0 ± 0	0 ± 0	0.8 ± 1.3
Ancorabolidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Laophontodes bicornis (Scott A., 1896)	0.8 ± 0.7	0 ± 0	1.8 ± 1.2	0.8 ± 0.7	1.4 ± 1.5	1 ± 0.9	0 ± 0	1.2 ± 1.2
Laophontodes typicus (Scott T., 1894)	0.8 ± 1.4	0 ± 0	0 ± 0	0.3 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Canuelidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Canuella furcigera (Sars G.O., 1903)	1.8 ± 0.9	0.4 ± 0.7	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Cletodidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Cletodes limicola (Brady, 1872)	0 ± 0	0.4 ± 0.7	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Cylindropsyliidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Cylindropsyllus laevis (Brady, 1880)	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.4 ± 0.7	0 ± 0
Dactylopusiidae								
Dactylopusia tisboides (Claus, 1863)	2.1 ± 1.4	1.4 ± 2.4	12.9 ± 4.4	3.9 ± 4.3	6.7 ± 5.6	5.9 ± 1.7	0 ± 0	0 ± 0
Diarthrodes minutus (Claus, 1863)	2.1 ± 0.6	1.3 ± 0	2.2 ± 1.4	1.5 ± 1.5	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Paradactylopodia brevicornis (Claus, 1866)	2.1 ± 1.4	0.9 ± 0.8	1 ± 0.9	0.8 ± 0.7	1.4 ± 1.2	1.4 ± 1.4	0 ± 0	0 ± 0
Ectinosomatidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
***Ectinosoma* cf. *dentatum* (Steuer, 1940)**	12.8 ± 4.8	10.7 ± 1.7	2.2 ± 0.4	9.9 ± 2.7	12.5 ± 0.5	18.7 ± 5.2	10.2 ± 4	4.6 ± 0.6
Ectinosoma sp.	0 ± 0	0.9 ± 0.8	0 ± 0	0.5 ± 0.8	0.3 ± 0.6	1 ± 1.8	0 ± 0	0.4 ± 0.7
Microsetella norvegica (Boeck, 1865)	0.8 ± 1.4	0.4 ± 0.8	0 ± 0	0.3 ± 0.6	0.7 ± 0.6	0.5 ± 0.9	1.1 ± 1.9	0.9 ± 1.5
Euterpinidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Euterpina acutifrons (Dana, 1847)	0 ± 0	0 ± 0	0.3 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Hamondiidae								
Ambunguipes rufocincta (Norman in Brady, 1880)	0 ± 0	0 ± 0	3.1 ± 2.3	0.8 ± 0.7	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Harpacticiidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Harpacticus littoralis (Sars G.O., 1910)	3.5 ± 0.5	0 ± 0	0.9 ± 1.5	4.6 ± 3.5	5.9 ± 4	3.4 ± 0.9	1.1 ± 2	1.2 ± 2
Laophontidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Esola longicauda (Edwards, 1891)	0 ± 0	0 ± 0	0.6 ± 1.1	0 ± 0	2.7 ± 2	3 ± 2.6	0 ± 0	0 ± 0
Laophonte cornuta (Philippi, 1840)	0 ± 0	0.9 ± 1.5	2.4 ± 1.2	8.3 ± 1.6	1.4 ± 1.2	1 ± 0.8	0 ± 0	0 ± 0
Paralaophonte brevirostris (Claus, 1863)	1.2 ± 2.1	0 ± 0	6.9 ± 1.9	3.2 ± 1.9	4.2 ± 2.2	2.9 ± 1.3	0 ± 0	2.2 ± 2
Longipediidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Longipedia minor (Scott T. & A., 1893)	0 ± 0	0 ± 0	1.4 ± 0.6	1.1 ± 1	0.4 ± 0.6	0.5 ± 0.9	0 ± 0	0 ± 0
Metidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Metis ignea (Philippi, 1843)	0 ± 0	0 ± 0	0 ± 0	0.3 ± 0.6	0 ± 0	0 ± 0	0.4 ± 0.7	0 ± 0
Miraciidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Amphiascoides debilis (Giesbrecht, 1881)	2.2 ± 0.9	8.4 ± 1.8	2.2 ± 1.4	8.5 ± 1.5	0 ± 0	0 ± 0	0 ± 0	0.8 ± 1.3
Amphiascus minutus (Claus, 1863)	0 ± 0	0 ± 0	9.2 ± 5.3	19.3 ± 2.2	3.1 ± 1.7	2.1 ± 3.6	0 ± 0	4.1 ± 2.5
Sarsamphiascus tenuiremis (Brady, 1880)	0 ± 0	0 ± 0	2.3 ± 2	1.5 ± 1.5	13.2 ± 3.2	13.5 ± 2.8	0 ± 0	3.8 ± 1.3
***Diosaccus tenuicornis* (Claus, 1863)**	2.5 ± 2.1	5.8 ± 2.9	4.3 ± 0.8	3.9 ± 2.3	3.2 ± 2.9	9.2 ± 2.9	8.4 ± 5	3.8 ± 3.4
Peltiidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Alteutha depressa (Claus, 1863)	2.2 ± 0.8	0 ± 0	1.3 ± 1.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Porcellidiidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Porcellidium ovatum (Haller, 1879)	4.4 ± 1.7	5.8 ± 2	7.6 ± 2.2	4.7 ± 2.9	2.4 ± 3.4	0 ± 0	0.5 ± 0.9	0 ± 0
Pseudotachidiidae								
Dactylopodella flava (Claus, 1866)	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.8 ± 1.6	1.9 ± 0.7	0 ± 0	0 ± 0
Xouthous laticaudatus (Thompson I.C. & Scott A., 1903)	1.2 ± 2.1	0 ± 0	0 ± 0	101 ± 172.3	6.7 ± 5.6	5.9 ± 1.7	0 ± 0	0 ± 0
Tegastidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Tegastes areolatus (Monard, 1935)	0 ± 0	0 ± 0	0.3 ± 0.5	0.9 ± 0.8	0.7 ± 0.6	0 ± 0	0.6 ± 1	1.3 ± 2.2
Tegastes falcatus (Norman, 1869)	1.8 ± 0.9	0.5 ± 0.8	1.4 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Tegastes satyrus (Claus, 1860)	0.5 ± 0.8	0 ± 0	0.7 ± 0.6	2.1 ± 2.1	2.5 ± 2.2	2 ± 1	0 ± 0	0 ± 0
Tetragonicepsidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Diagoniceps laevis (Willey, 1930)	0 ± 0	0 ± 0	13.2 ± 18.3	0 ± 0	0 ± 0	0 ± 0	0.6 ± 1	0.4 ± 0.7
Phyllopodopsyllus bradyi (Scott T., 1892)	0 ± 0	0 ± 0	2.2 ± 0.4	0 ± 0	2 ± 3.5	0 ± 0	0 ± 0	0.4 ± 0.7
Thalestridae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Parathalestris harpactoides (Claus, 1863)	1.2 ± 2.1	0 ± 0	0 ± 0	0.8 ± 0.7	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Rhynchothalestris helgolandica (Claus, 1863)	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.3 ± 2.2
Thalestris rufoviolascens (Claus, 1866)	0 ± 0	0 ± 0	1.1 ± 0.2	0.3 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Tisbidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Idyella exigua (Sars G.O., 1905)	0 ± 0	11.2 ± 4.8	0 ± 0	0 ± 0	1.4 ± 1.6	0 ± 0	7.1 ± 1.4	12.2 ± 2.6
Tisbe elegantula (Sars G.O., 1905)	0 ± 0	0 ± 0	0.3 ± 0.5	0 ± 0	0 ± 0	0 ± 0	6.9 ± 6.8	3.8 ± 1.5
***Tisbe ensifer* (Fischer, 1860)**	23.9 ± 1	10.6 ± 2.3	2.9 ± 1.6	3.6 ± 3	4.2 ± 1.9	2.4 ± 2.1	18.4 ± 10.1	12.5 ± 8
***Tisbe furcata* (Baird, 1837)**	27 ± 14.9	36.3 ± 6.9	5.1 ± 2.8	13.6 ± 2	10.5 ± 1.4	3.4 ± 0.9	40.3 ± 1.5	37.2 ± 7.8
Sacodiscus littoralis (Sars G.O., 1904)	0 ± 0	0 ± 0	2.4 ± 1.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Calanoida								
Clausocalanidae								
Pseudocalanus minutus (Krøyer, 1845)	0.4 ± 0.7	0.4 ± 0.8	0 ± 0	2.8 ± 4.8	0.4 ± 0.6	0 ± 0	0 ± 0	1.3 ± 1.3
Cyclopoida	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Cyclopinidae spp.	17.2 ± 12.9	9.6 ± 7.8	13.7 ± 15.4	26.7 ± 17.5	15.5 ± 9.5	21.3 ± 9.2	1.3 ± 1.2	4.2 ± 2.2
Siphonostomatoida								
Artotrogidae								
Cribropontius normani (Brady & Robertson D., 1876)	1.7 ± 1.9	0.4 ± 0.7	1.5 ± 1.6	1 ± 1.6	0 ± 0	0 ± 0	0.6 ± 1	

Table 4
Multivariate PERMANOVA and SIMPER results with factors *month* and *site* for harpacticoid copepod species contributions. First five contributing species are shown.

Across factor *Month* (PERMANOVA: $P < 0.001$)					
February (75.9% similarity)			May (53.6% similarity)		
Species	%	cum. %	Species	%	cum. %
Tisbe furcata	32.2	32.2	*Amphiascus minutus*	15.3	15.3
Tisbe ensifer	21.3	53.5	*Tisbe furcata*	10.2	25.5
Ectinosoma cf. *dentatum*	12.7	66.2	*Dactylopusia tisboides*	9.9	35.4
Amphiascoides debilis	5.9	72.0	*Porcellidium ovatum*	7.8	43.3
Idyella exigua	5.5	77.5	*Ameira longipes*	7.4	50.7
August (72.5% similarity)			October (72.4% similarity)		
Species	%	cum. %	Species	%	cum. %
Ameira longipes	24.3	24.3	*Tisbe furcata*	49.6	49.6
Ectinosoma cf. *dentatum*	18.0	42.3	*Tisbe ensifer*	13.6	63.2
Sarsamphiascus tenuiremis	14.9	57.1	*Idyella exigua*	11.6	74.8
Tisbe furcata	8.0	65.1	*Ectinosoma* cf. *dentatum*	8.2	83.3
Diosaccus tenuicornis	5.6	70.8	*Diosaccus tenuicornis*	4.7	87.7
Across factor *Site* (PERMANOVA: $P < 0.014$)					
Oscelluccia (OSCE, 69.7% similarity)			Harbour (PORT, 67.5% similarity)		
Species	%	cum. %	Species	%	cum. %
Tisbe furcata	24.6	24.6	*Tisbe furcata*	27.6	27.6
Tisbe ensifer	14.5	39.2	*Ectinosoma* cf. *dentatum*	12.4	40.0
Ectinosoma cf. *dentatum*	11.0	50.2	*Ameira longipes*	11.3	51.3
Ameira longipes	8.9	59.1	*Amphiascus minutus*	7.0	58.3
Dactylopusia tisboides	5.2	64.3	*Tisbe ensifer*	6.7	65.0

The most abundant species in the macrophytodetritus accumulations were also commonly found in adjacent habitats (Hicks and Coull, 1983; Mascart et al., 2013; Novak, 1982). Colonisation by invertebrates is rapid, however, it is limited in its extent and magnitude (Norkko and Bonsdorff, 1996; Palmer, 1988). For that reason active migration or passive dispersion towards macrophytodetritus accumulations was not sufficient to explain comparable quantities and diversities. Dimech et al. (2006) suggested that small accumulations that persisted during the year in depressions of the seabed, harboured some fauna living permanently in this detritus. This implies that some harpacticoid species (morphologically specialised to a certain habitat) also live permanently in macrophytodetritus accumulations.

4.2. Environmental factors

The macrophytodetritus showed the highest accumulations and leaf litter dry weights in October, which coincided with the annual leaf fall, starting in September (Bay, 1984). The peak could be explained by the annual senescence, though other factors presumably play a role in the variation of the litter amount during the rest of the year. Enhanced hydrodynamics and storms had been put forward to explain the rise in accumulations of dislodged seagrasses and drift algae. The accumulation of dislodged material was shown to enhance habitat function by increasing structural complexity and food availability (Kirkman and Kendrick, 1997; Lenanton et al., 1982; Ólafsson et al., 2013). However, during higher hydrodynamic periods, the relative contribution of drift macroalgae and living *P. oceanica* was low. Subsequently, the meiofauna community assemblage was not directly influenced by dislodged material (drift macroalgae and living *P. oceanica*) in the macrophytodetritus accumulation. However, drift macroalgae were a tertiary explanatory variable for the harpacticoid assemblage and a primary variable for the most abundant harpacticoid species, *T. ensifer* and *A. longipes*. This result, points at a possible species-specific effect regarding the presence of drift macroalgae and its associated micro-epiphytes.

The BEST analysis revealed the median wind gusts as the best explanatory variable for the meiofauna and harpacticoid assemblages in the macrophytodetritus accumulations. Dauby et al. (1995) conducted a sediment trap experiment in the Bay of Calvi that showed that Northerly winds peak from October to April, with maximum values from mid-January to early March, which would cause a bigger disturbance during those months. Vetter (1995) reported low diversities of macro-invertebrates in disturbed leaf litter patches and attributed it to the disturbance by currents. Hovel et al. (2002) stated that hydrodynamic differences between seasons and years could explain the variability in crustacean density by directly influencing larval settlement, feeding rates and/or locomotion of crustaceans. Nonetheless, the yearlong presence of planktonic adults and juveniles in macrophytodetritus accumulations could highlight species-specific adaptations. It is known that copepods have an ability to swim and to emerge from the bottom into the water column and back (Guidi-Guilvard et al., 2009; Teasdale et al., 2004). As a possible consequence some planktonic species could adapt to an epibenthic life (Giere, 2009; Huys et al., 1992). Although in general the orders Calanoida, Cyclopoida and Syphonostomatoida have a planktonic life cycle, feeding on suspended fine-particulate organic matter or they are parasitic on fish and invertebrates (Boxshall and Hasley, 2004). Since, Thistle (2003) concluded that high hydrodynamic flows suppressed emergence, it was thus highly probable that the non-harpacticoid adults and juveniles actively sought shelter in the macrophytodetritus from extensive hydrodynamic movements and predation. Consequently, we could conclude that benthic meiofauna and harpacticoid assemblages were negatively correlated with the wind gust induced water movements. Subsequently, planktonic copepods were to a lesser extent affected by the hydrodynamics, but sought shelter or adapted partially to the macrophytodetritus accumulations.

According to the accumulation and compaction of the detritus, a difference in oxygen penetration depth in the detritus accumulation could be expected. An oxygen gradient from the oxic water column and top layer of the detritus to the hypoxic bottom layer was present and directly influenced the vertical distribution and diversity of the meiobenthos (Higgins and Thiel, 1988). Highly active fauna, especially crustaceans who are usually highly sensitive to hypoxia will be impacted first (Tietjen, 1969). Since harpacticoid copepods are the most sensitive taxon to decreased oxygen (Moodley et al., 2000), they are typically limited to the top layer of the detritus package. Nematodes conversely are more tolerant to low oxygen levels (Murrell and Fleeger, 1989; Wetzel et al., 2001). The Copepoda/Nematoda ratio peaked in August, while the nematode abundance remained fairly constant through the year. This sudden rise in copepod abundances and diversity (especially in the harbour) coincided with the calmest wind period and lowest accumulation height and leaf litter dry weight. Thus we might expect a

Table 5
Two factorial PERMANOVA of harpacticoid copepod species diversity indices and abundance standardised per square metre (indiv. m^{-2}) and per gram dry weight leaf litter (indiv. g^{-1} DW). S = species richness, N1 and N2 = heterogeneity of diversity.

Factors and interaction	S	N_1	N_2	Harpacticoida indiv. m^{-2}	Harpacticoida indiv. g^{-1} DW
Month	$F'_{(3,16)} = 26.0$ $P < 0.001^{***}$	$F'_{(3,16)} = 5.7$ $P = 0.012^{*}$	$F'_{(3,16)} = 4.4$ $P = 0.016^{*}$	$F'_{(3,16)} = 4.3$ $P = 0.006^{**}$	$F'_{(3,16)} = 15.1$ $P < 0.001^{***}$
Site	$F'_{(1,16)} = 4.9$ $P = 0.044^{*}$	$F'_{(1,16)} = 3.0$ $P = 0.095$	$F'_{(1,16)} = 2.3$ $P = 0.156$	$F'_{(1,16)} = 1.3$ $P = 0.271$	$F'_{(1,16)} = 2.1$ $P = 0.106$
Month × site	$F'_{(3,16)} = 4.7$ $P = 0.019^{*}$	$F'_{(3,16)} = 1.9$ $P = 0.169$	$F'_{(3,16)} = 1.1$ $P = 0.411$	$F'_{(3,16)} = 2.0$ $P = 0.099$	$F'_{(3,16)} = 6.5$ $P < 0.001^{***}$

* = $0.05 < P < 0.01$ = significant.
** = $0.01 < P < 0.001$ = highly significant.
*** = $P < 0.001$ = very highly significant.

trade-off between harpacticoid copepods and nematode densities according to the oxygen levels present in the accumulation. In our study, no such correlation of oxygen level with the Copepoda/Nematoda ratio was found. This could indicate the patchiness of the oxygen distribution within the accumulation and the high mobility of copepods that could migrate vertically out of the accumulation towards the oxygen-rich water just above the detritus. It could furthermore indicate a species-specific behaviour of harpacticoids, like *Diosaccus tenuicornis*, which was the only dominant harpacticoid species influenced by the oxygen levels. Hence, no overall effect of oxygen concentrations on higher taxa was present, except for the Amphipoda. These abundances negatively correlated to the oxygen levels inside the macrophytodetritus. A possible explanation could be the species-specific behaviour of amphipods towards hypoxia (Gamenick et al., 1996). Another factor to be taken into account is that adults belong to the macrofauna and thus the organisms found are juveniles. These juveniles could possess physiological characteristics which allow them to use the hypoxic accumulation to shelter temporarily from predators that are not adapted to hypoxia.

Next to oxygen, other physico-chemical aspects were altered inside the macrophytodetritus accumulation. Meiofauna are not known to directly assimilate dissolved nutrients (Mitwally and Fleeger, 2013; Siebers, 1982), but physico-chemical fluctuations influence their potential food sources (Atilla et al., 2005; Hall and Bell, 1988; Hicks, 1977, 1980). Therefore, nutrient fluctuations would also presumably impact meiofauna indirectly by altering the habitat structure (Arroyo et al., 2013).

The present seasonal study demonstrated that meiofauna and harpacticoid copepod assemblages in macrophytodetritus accumulations reflect a seasonal cycle with a maximum abundance and diversity during spring–summer and a minimum during winter, coinciding with the epiphytic primary production cycle. These results are congruent with Hall and Bell (1988) and Johnson and Scheibling (1987) who showed that dominant motile invertebrates' abundances and diversities are positively correlated with the habitat complexity as measured by the biomass of seagrass epiphytic algae. As pointed out by several authors, *e.g.* Wieser (1959), Novak (1982) and Hicks and Coull (1983), abundances and diversity of meiofauna of marine vegetation are positively correlated with habitat complexity and negatively correlated with water movements, which is confirmed by this study.

5. Conclusions

Meiofauna was ubiquitously present in the macrophytodetritus accumulations and half is composed of the crustacean subclass Copepoda, of which 87% belonged to the order Harpacticoida. As a consequence of the harpacticoid copepod species-specific selective feeding, a wide variety of morphologically similar and ecologically different species was present. The macrophytodetritus played an important role in sheltering, housing and feeding possibilities for meiofauna and harpacticoid copepods. These communities' seasonal abundances follow the epiphytic primary production cycle. They were positively correlated with habitat complexity and negatively correlated with water movements and leaf litter accumulations. Migration and dispersion from other adjacent habitats seemed to promote faunal communities, however, a permanent population in the macrophytodetritus accumulations should not be excluded.

Three specific questions in this study were addressed and answered as follows: (1) The macrophytodetritus accumulation and associated communities were mainly determined by seasonal wind induced hydrodynamics and leaf litter biomass. (2) Meiofauna and harpacticoid copepod assemblages displayed a maximum abundance and diversity during May–August (site depending) and a minimum during February. (3) Several ecological groups of copepods, including planktonic, parasitic, mesopsammic, phytal and phytal-swimmer copepods were present.

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