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Sessile macrobenthos (Ochrophyta) drives seasonal change of meiofaunal community structure on temperate rocky reefs

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ABSTRACT

Unlike the soft bottom meiofauna, meiofauna associated to hard substrata is poorly studied, despite its ecological relevance. Since communities of hard substrata are usually characterized by species with different life cycles and strategies from those of soft bottom assemblages, information on hard substrata meiofauna is still needed. In this study, sessile macrobenthos and the associated meiofaunal assemblages of two sites of Portofino (NW Mediterranean) were investigated in two seasons at three different depths on both sub-vertical and inclined reefs. The study aimed to assess the abundance, diversity and composition of the meiofauna and the factors structuring its assemblages. Moreover, as meiofauna is known to be dependent upon the substrate characteristics, the study investigated whether the meiofaunal patterns could be related to the sessile macrobenthos structure and composition, and to which extent. Macroalgae dominated the sessile macrobenthic assemblages, while Nematoda and Copepoda were the main meiofaunal groups. Meiofaunal higher-taxa richness and diversity resulted very high, due to the large number of different microhabitats offered by macroalgae. Macrobenthic assemblages were dominated by Rodophyta and Ochrophyta in summer, the latter dramatically collapsing in winter. The meiofaunal abundance and composition changed significantly with the season, consistently with the sessile macrobenthic assemblages, and resulted strongly correlated with Ochrophyta. Shaping the meiofaunal assemblages, macroalgae appeared to act as ecosystem engineer for the meiofauna.

1. Introduction

Rocky coastal substrates (i.e., hard bottoms) are heterogeneous habitats representing a great biodiversity reservoir (Bianchi et al., 2004). They show a high number of important ecological processes, such as spatial competition, trophic cascades, habitat structure, succession, oriented growth, differential utilisation of exposed versus hidden substrate surfaces (Taylor and Wilson, 2003). Rocky coastal substrates host a high density and variety of marine organisms that display multifarious adaptive strategies, often exclusive to those habitats. Hard bottoms are characterized by sessile organisms with a modular structure (i.e. algae, sponges, cnidarians, bryozoans, and tunicates), which have no equal in other environments (Bianchi et al., 2004). Those organisms may act as foundation species (Bruno et al., 2003), shaping the seascape and generating habitats for the associated mobile invertebrates and fish (Turner et al., 1999; Chemello and Milazzo, 2002; Guidetti et al., 2004). Thus, the sessile macrobenthos

generate a “biological conditioning” of the substrate for many other organisms, modifying physical factors such as light, water flow and sedimentation (Abbiati et al., 1987, 1991; Simboura et al., 1995; Bustamante et al., 2014; Casoli et al., 2016). Macrobenthic organisms may act as “ecosystem engineers” (Jones et al., 1994; Largaespada et al., 2012) for other smaller metazoans especially in soft-bottoms (Passarelli et al., 2012, 2014; Lacoste et al., 2018), but they may arguably exert the same function for the meiofauna living on hard bottoms. A large amount of information on the sessile macrobenthos associated to rocky reefs exists, but meiofauna is poorly investigated, despite its important ecological role in most marine ecosystems (Danovaro and Fraschetti, 2002).

Meiofauna is an abundant, taxonomically diversified and ubiquitous component of benthic ecosystems from the supralittoral zone to the deepest bottoms of the oceans (Giery, 2009; Sandulli et al., 2014; Semprucci et al., 2016). It affects the biodiversity-ecosystem functioning relationship and plays a dominant role in the turnover of

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organic matter as part of the “small food web”; at the same time, it supports a great diversity of higher trophic levels (Gièrè, 2009; Piot et al., 2014). Meiofauna is a potentially relevant food resource for macrofauna, small fishes, juveniles of larger fishes and other epibenthic predators (Chardy and Dauvin, 1992). An abundant and rich meiofauna is known to inhabit hard substrates (Gièrè, 2009). For instance, in rocky shores meiofauna exceeds numerically macrofauna and accounts for 25% of the total secondary production (Gibbons and Griffiths, 1986); it is essential for ensuring a continuous nutrient cycle in hard bottoms, maintaining the bacterial populations in a continued state of growth by means of its grazing activity (Gibbons and Griffiths, 1986), and making detritus available to macroconsumers either by enhancing microbial activity or through ingestion of the meiofauna itself (Coull, 1988).

Most previous studies on hard bottom meiofauna focused on the phytal meiofauna, and especially to the fraction living on macroalgae, while the meiofauna associated with the surfaces beneath the algal canopy or to other sessile organisms has received little attention (Gibbons and Griffiths, 1986, 1988; Gibbons, 1988a, 1988b; Arroyo et al., 2004; Frascchetti et al., 2006; Danovaro et al., 2007; Logan et al., 2008; Russo et al., 2015; Ape et al., 2018). Moreover, most studies have been conducted in the intertidal and upper sublittoral zones (e.g. Coull et al., 1983; Johnson and Scheibling, 1987; Prathep et al., 2003; Hooper and Davenport, 2006; Frame et al., 2007; Smith et al., 2014; Veiga et al., 2016) that are subjected to a wide range of environmental extremes (i.e. temperature, salinity, desiccation during tidal emersion, wave exposure), while only few studies investigated the meiofaunal community of the infralittoral zone especially in the Mediterranean Sea (Danovaro and Frascchetti, 2002; Frascchetti et al., 2006; Danovaro et al., 2007).

The present study contributes to reduce this gap of knowledge by investigating the meiofauna associated with the sessile macrobenthic assemblages of infralittoral hard substrata of Mediterranean reefs, between 5 m and 20 m depth. The aim of the study was twofold: (i) assessing possible changes of abundance, diversity and community structure of the meiofauna considering different seasons, sites, slopes and depths; (ii) investigating whether the meiofaunal patterns could be related to the structure and composition of the sessile macrobenthos, and to which extent. We analysed the sessile macrobenthos and the associated meiofauna along two rocky reefs located within the Portofino Marine Protected Area (Ligurian Sea). Sampling was performed in summer and in winter, at two different sites, at two different slopes of the reefs, and at three different depths.

Physico-chemical characteristics of the seawater in close vicinity to the rocky indicated general conditions of oligotrophy, with relative peaks of nutrients in spring at shallow depths; both water movement and light usually show little seasonal variation, whereas temperature ranged between 13 °C and 22 °C at about 20 m depth.

2. Materials and methods

2.1. Study area and sampling routine

The study area (Fig. 1) is located along the eastern side of the Portofino Promontory, in the Ligurian Sea (NW Mediterranean Sea). It is characterized by precipitous rocky cliffs made of Oligocene conglomerate.

Within this area, located within the buffer zone (C zone) of the Portofino Marine Protected Area, two sampling sites were identified: Paraggi (P), close to a beach highly frequented during summer, and Aurora (A), close to the village of Portofino at the south-eastern tip of the promontory (Fig. 1). In each site, two slopes were selected: sub-vertical (> 70°) (1) and inclined (30°–60°) (2). For each site, sampling stations were located at 5 m (a) and 10 m (b) depth on both sub-vertical and inclined slopes, and at 20 m (c) depth only on inclined slopes. This unbalanced design is due to the geomorphological constraints of the study sites, where sub-vertical walls are absent at depths higher than

15 m. Sampling activities were carried out during summer 2012 (S) and winter 2013 (W). Station codes are reported in Table 1.

The sessile macrobenthos composition and cover was assessed through visual census, using quadrats: a 50 × 50 cm square frame, divided into 25 sub-squares of 10 × 10 cm each, was employed. The percent cover of the sessile macrobenthic organisms was quantified by giving each species a score ranging from 0 (absence) to 4 (100% cover), and then adding up scores for all the sub-squares where the species was present; organisms filling less than ¼ sub-square were assigned an arbitrary score of 0.5 (Dethier et al., 1993). Only conspicuous species, easily recognizable underwater (Hiscock, 1987), were considered and identified at the lowest taxonomic level possible. For each station, three replicate quadrats were assessed.

The meiofaunal assemblages were sampled using a suction sampler (air-lift) specifically designed for hard bottoms (Bianchi et al., 2004). It consists of a PVC tube with a terminal spout, about one meter long and 10 cm in diameter, connected through a plastic hose and a pressure reducer to a devoted diving tank with compressed air. A faucet allows regulating the flux of the air, which flows and expands towards the surface creating a depression, and a consequent vertical traction of the small motile organisms. Opposite to the sucking end, the sampler is equipped with 38-µm mesh filters, adequate to trap the meiofauna. The sampled surface was delimited by a 20 × 20 cm square frame. In order to collect also the sessile meiofauna, the spout was repeatedly passed over the rocky substrate, scraping the surface delimited by the square frame. For each station, three replicates were collected after the visual assessment of the sessile macrobenthos over the same sampling surface.

2.2. Sessile macrobenthos

Sessile macrobenthos percent cover was analysed at both: (a) high detail in terms of “biotic and abiotic elements”, as we named the sessile macrophytobenthic and macrozoobenthic species (or higher taxa for those organisms not identified at species level) and the abiotic components (sediment, bare rock, and coarse detritus), and (b) low detail in “groups”, obtained grouping the species in higher taxonomic levels and the various abiotic components in a unique group, namely “Abiotic”.

2.3. Meiofaunal community

Meiofaunal samples were treated with 7% MgCl₂ to promote specimens tissue relaxation, fixed with 4% buffered formaldehyde and stained with Bengal Rose (Danovaro et al., 2004). In the laboratory, all meiofaunal samples were sonicated to better detach organisms from macroalgae (TRANSONIC LABOR 2000, 3 times for 1 min with 30 s intervals). Then samples were rinsed with a gentle jet of fresh water over a 1.0 mm sieve to exclude macrobenthos, decanted over a 38 µm sieve ten times, centrifuged three times with Ludox HS40 (specific density 1.18 g cm⁻³; Heip et al., 1985), re-stained with Rose Bengal (0.5 g L⁻¹) and fixed with buffered formaldehyde (4% final volume in 0.4 µm prefiltered seawater solution) in Falcon tubes (50 ml) (Danovaro et al., 2004). Meiofaunal organisms were counted and identified at higher taxon level, using a stereomicroscope (Leica G26). The rare taxa were defined as the taxa that represented < 1% of the total meiofaunal abundance in all investigated samples. Higher-taxon diversity was evaluated in terms of richness (number of higher taxa), Shannon entropy (H', log₂), and Pielou equitability (J', log₂).

2.4. Statistical analyses

Effects of season, site, slope and depth on: (i) sessile macrobenthos (biotic and abiotic elements, and groups), (ii) meiofaunal higher-taxon composition (separately for the entire community and rare taxa), and (iii) meiofaunal abundances and diversity indices, were explored using multivariate analysis of variance based on permutations (PERMANOVA, Anderson, 2001). PERMANOVA is applicable to datasets with

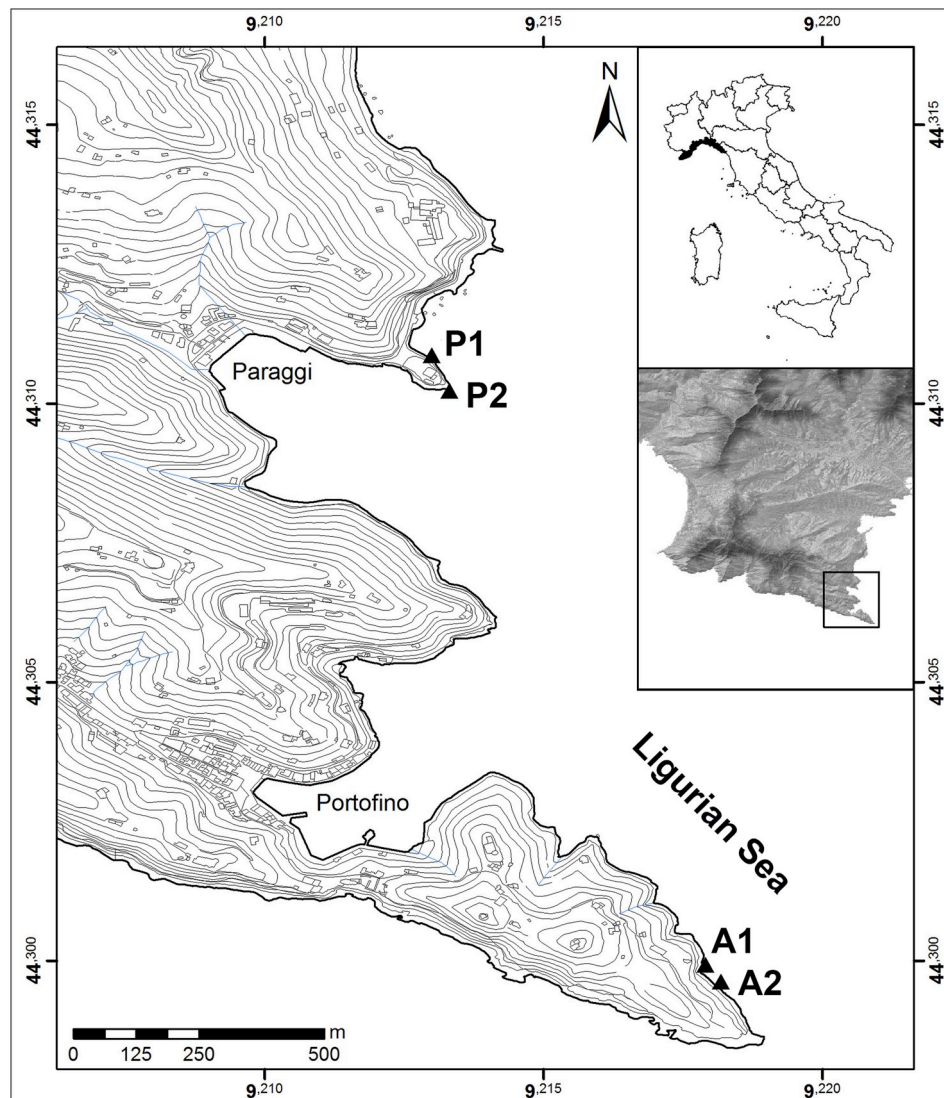


Fig. 1. Map of the study area: eastern Portofino Promontory, Ligurian Sea (NW Mediterranean Sea). Sampling sites and slopes are indicated by their code: P = Paraggi; A = Aurora; 1 = sub-vertical slope; 2 = inclined slope.

many zeros, and allows testing interactions in complex multifactorial designs with multivariate or univariate data. It makes no assumptions about underlying data distributions, and is robust to unbalanced designs (Walters and Coen, 2006). The design was a four-way crossed: factor 1 was Season (summer and winter), factor 2 was Site (Paraggi and Aurora), factor 3 was Slope (sub-vertical and inclined), factor 4 was Depth (5 m, 10 m and 20 m). The analyses were performed on Bray–Curtis distances.

A SIMPER (Similarity Percentages-species contributions) analysis (50% cut-off), based on the Bray–Curtis dissimilarity matrix, was performed to reveal which components of sessile macrobenthos and meiofaunal taxa mostly contributed to the observed dissimilarities among sampling stations.

Principal components analysis (PCA) was carried out on sessile macrobenthic groups to identify the most important variables in structuring the habitat and to simplify the variables (many of which were highly correlated) down to a few dimensions. The PCA biplot provides information regarding the correlation of each variable with principal component axes. Variables with the highest correlations to axes (longest arrows) are the most important in describing variation along the gradient identified by the PC axes. PCA was computed on log-transformed data, after checking the homogeneity of the data (Lepš;

Šmilauer, 2003). Prior to the PCA, draftsman plot and correlation matrices were produced to assess the distribution of each variable and to identify co-correlating variables (a 0.95 cut-off was applied). The draftsman plot didn't detected strongly co-correlating variables, therefore all variables were entered into the analysis.

The extent to which differences in meiofaunal assemblages could be explained by habitat characteristics (i.e., groups of the sessile macrobenthos) was explored by distance-based linear models (DistLM). The Akaike Information Criteria for small samples (AIC) was used to select the “best” models from all the possible combinations of predictor variables (Anderson et al., 2008). AIC selection was chosen as the method to create the most parsimonious model, as it adds a ‘penalty’ for increases in the number of predictor variables (Anderson et al., 2008). Predicting environmental variables used in the model were those detected by the PCA as the main important in structuring the habitat.

Distance-based redundancy analysis (dbrDA) plots were used to provide the best possible two-dimensional visualisation of DISTLM results.

Spearman's Rank Correlation Analysis was conducted to explore the relationships between sessile macrobenthos (either biotic and abiotic elements or groups) and meiofaunal taxa, abundance and diversity indices.

Table 1

Sampling station identification codes, composed by: the sampling site (P = Paraggi; A = Aurora), the slope of the substratum (1 = sub-vertical; 2 = inclined), the depth of the station (a = 5 m; b = 10 m; c = 20 m) and the season (S = summer; W = winter).

Station Code	Site	Slope	Depth (m)	Season
P1a S	Paraggi (P)	Sub-vertical (1)	5 (a)	Summer (S)
P2a S	Paraggi (P)	Inclined (2)	5 (a)	Summer (S)
P1b S	Paraggi (P)	Sub-vertical (1)	10 (b)	Summer (S)
P2b S	Paraggi (P)	Inclined (2)	10 (b)	Summer (S)
P2c S	Paraggi (P)	Inclined (2)	20 (c)	Summer (S)
A1a S	Aurora (A)	Sub-vertical (1)	5 (a)	Summer (S)
A2a S	Aurora (A)	Inclined (2)	5 (a)	Summer (S)
A1b S	Aurora (A)	Sub-vertical (1)	10 (b)	Summer (S)
A2b S	Aurora (A)	Inclined (2)	10 (b)	Summer (S)
A2c S	Aurora (A)	Inclined (2)	20 (c)	Summer (S)
P1a W	Paraggi (P)	Sub-vertical (1)	5 (a)	Winter (W)
P2a W	Paraggi (P)	Inclined (2)	5 (a)	Winter (W)
P1b W	Paraggi (P)	Sub-vertical (1)	10 (b)	Winter (W)
P2b W	Paraggi (P)	Inclined (2)	10 (b)	Winter (W)
P2c W	Paraggi (P)	Inclined (2)	20 (c)	Winter (W)
A1a W	Aurora (A)	Sub-vertical (1)	5 (a)	Winter (W)
A2a W	Aurora (A)	Inclined (2)	5 (a)	Winter (W)
A1b W	Aurora (A)	Sub-vertical (1)	10 (b)	Winter (W)
A2b W	Aurora (A)	Inclined (2)	10 (b)	Winter (W)
A2c W	Aurora (A)	Inclined (2)	20 (c)	Winter (W)

All statistical tests were performed using PRIMER 6 with PERMANOVA + add-on software package (Clarke and Gorley, 2006; Anderson et al., 2008).

3. Results

3.1. Sessile macrobenthos

A total of 50 biotic elements were identified (Supplementary material TS1). Sessile macrobenthic assemblages resulted mainly to be characterized by macroalgae belonging to Rhodophyta (36.5%, mainly *Lithophyllum/Mesophyllum* spp. and *Peyssonnelia squamaria*) and Ochrophyta (19.8%, mainly *Dictyota dichotoma*, *Halopteris scoparia* and *Padina pavonica*), and Turf (multispecific agglomerates of filamentous algae < 10 mm, 14.3%), while about 12.6% of substratum resulted to be abiotic (mainly sediment) (Fig. 2a and b). All the other biotic elements represented less than 10% of the substrate cover. Macroalgal cover accounted for 63.5%.

Considering the biotic and abiotic elements, the composition of the sessile macrobenthos showed significant differences between summer and winter ($p < 0.01$), between Aurora and Paraggi ($p < 0.05$), between sub-vertical walls and inclined surfaces ($p < 0.05$), among depths ($p < 0.01$), and a significant interaction Season \times Site ($p < 0.01$) (Table 2). According to pair-wise tests, the composition between summer and winter differed in both sites ($p < 0.01$), and in winter resulted different between Aurora and Paraggi ($p < 0.05$) (Table 2).

Considering the groups, the composition of the sessile macrobenthos exhibited significant differences between seasons ($p < 0.05$), and a significant interaction Season \times Site ($p < 0.05$) (Table 2). According to Pair-Wise tests, the composition between summer and winter differed in both sites (Table 2).

SIMPER analysis revealed that the significant dissimilarities found were mainly due to seasonal Ochrophyta algae as *D. dichotoma* and *P. pavonica*, perennial Rhodophyta (especially *Lithophyllum/Mesophyllum* spp. and *P. squamaria*), Turf and Sediment (see Table 3 and Supplementary material FS1 for more details).

3.2. Meiofauna

A total of 30 meiofaunal higher taxa were found (Supplementary

material TS2). The higher-taxa richness showed the lowest values (15) at Stations P1a and P1b in summer and at Station A1a in winter, while the highest values (20) were observed at Station A2b in summer and at Station P2b in both seasons (Fig. 3a). The higher-taxa richness exhibited a decrease from summer to winter at Aurora, while at Paraggi no temporal differences were found; however, no significant differences in the investigated factors were detected (Table 4). Station A1b in winter showed the lowest values of H' (1.86 ± 1.41) and J' (0.52 ± 0.27), while Station A2a in winter showed the maximum values of H' (2.86 ± 0.35) and J' (0.76 ± 0.08) (Fig. 3b and c). No significant differences in H' and J' in the investigated factors were detected (Table 4).

Total meiofaunal abundance reached the lowest mean value at Station A2a in winter (18.15 ± 7.71 ind. 10 cm^{-2}), whilst the highest mean value was recorded at Station A1b in summer (227.20 ± 61.99 ind. 10 cm^{-2}) (Fig. 3d). Meiofaunal abundances were significantly higher in summer than in winter ($p < 0.05$) (Table 4), with mean values of 151.31 ± 57.15 ind. 10 cm^{-2} and 66.35 ± 37.84 ind. 10 cm^{-2} , respectively.

Nematoda (34.9%) and Copepoda Harpacticoida (29.5%) were the dominant taxa, followed by Polychaeta (12.3%), Tanaidacea (3.5%), Bivalvia (3.3%), Amphipoda (3.2%), Ostracoda (3.0%), Gastropoda (2.7%), Cumacea (2.6%), and Halacaroida (2.3%) (Fig. 4, Table 5). All the other taxa represented less than 1% of the entire community. Crustacea together accounted for 42.6% of the total meiofauna.

The taxonomic composition of the meiofaunal community showed significant differences between summer and winter ($p < 0.01$) (Table 6). SIMPER analysis revealed that the dissimilarity between the two seasons (33.7%) was mainly due to Nematoda, Copepoda, Cumacea, Polychaeta, and Tanaidacea, all more abundant in summer (Table 7), and that the similarity within summer (79.0%) was higher than within winter (70.7%).

Differences between the two seasons were detected also considering only meiofaunal rare taxa, ($p < 0.05$) (Table 6). SIMPER dissimilarity between summer and winter (53.9%) was mostly explained by Chaetognata, Isopoda, Turbellaria and Gastrotricha (Table 7), and similarity within summer (59.7%) was higher than within winter (45.4%). Chaetognata and Isopoda resulted more abundant in summer, while Turbellaria and Gastrotricha were more abundant in winter. Some rare taxa were found only in one season: Syncarida and Euphasiacea in summer, Gnathostomulida, Nemertea, Polyplacophora, Ophiuroidea, Holothuroidea and Ascidiacea in winter (Supplementary material TS2).

3.3. Relationships between meiofauna and sessile macrobenthos

The results of the PCA ordination are showed in Fig. 5. The first two PC axes explained 63.4% of the variation (42.3 and 21.1 for PC1 and PC2, respectively). The main contributors were Ochrophyta (-0.711), Abiotic (0.535) and Cnidaria (0.374) for PC1 axis, and Turf (-0.791) and Chlorophyta (0.351) for PC2 axis.

According to DistLM, the only significant predictor variable resulted Ochrophyta ($p < 0.01$), which alone explained 27% of the variance in meiofaunal assemblage structure. Ochrophyta resulted in all the models selected by the BEST procedure, alone or in combinations with other variables. In particular, the combination of Ochrophyta, Chlorophyta, and Turf resulted as the best model, explaining 40% of the variance in meiofaunal assemblage structure (Table 8).

The model is illustrated in Fig. 6, where the dbRDA ordination of the meiobenthic community is superimposed by habitat explanatory variables. The resulting pattern shows two gradient in the community structure of the meiofauna. The first distinguishes among winter and summer stations and is driven largely by Ochrophyta. The second one identifies variability among groups of winter and summer stations: the differences here are mostly driven by differences in Chlorophyta and Turf.

These results are consistent with the correlations found between

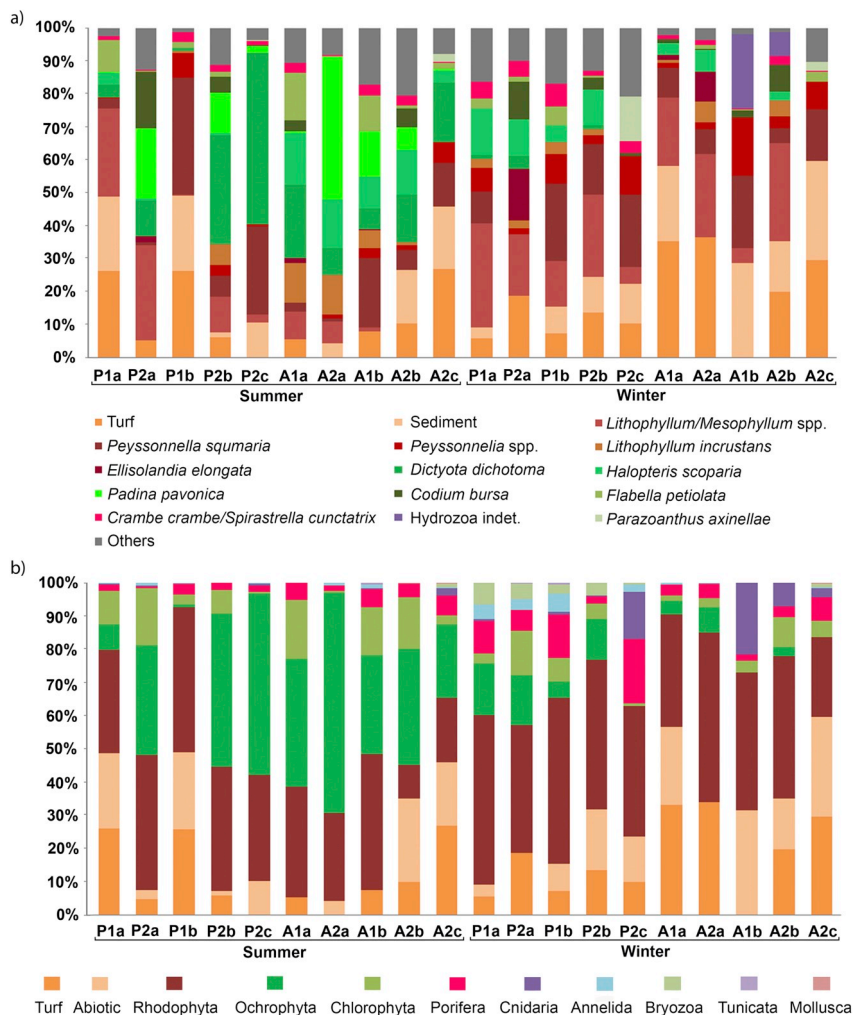


Fig. 2. Relative cover (%) of the sessile macrobenthos at the investigated stations: (a) biotic and abiotic elements; (b) groups. “Others” includes the biotic and abiotic elements with average abundances lower than 1%. Refer to Table 1 for station codes.

Table 2

Results of four-way PERMANOVA on sessile macrobenthos: (a) biotic and abiotic elements, (b) groups. Refer to Section 2.2 for details on the definition of biotic and abiotic elements and groups * = $p < 0.05$; ** = $p < 0.01$; n.s. = not significant.

	df	a) Biotic and abiotic elements			b) Groups		
		MS	Pseudo-F	p	MS	Pseudo-F	p
Season (Se)	1	2931.1	8.6714	**	1913.2	10.361	*
Site (Si)	1	1500.8	4.4399	*	374.01	2.0254	n.s.
Slope (Slo)	1	1791.9	5.301	**	563.82	3.0533	n.s.
Depth (De)	2	3282.9	9.7122	** ^a	1080.3	5.8502	n.s.
SexSi	1	2020.2	5.9765	** ^b	1247.1	6.7536	* ^c
SexSlo	1	814.49	2.4096	n.s.	654.86	3.5464	n.s.
SexDe	2	503.14	1.4885	n.s.	272.61	1.4763	n.s.
SixSlo	1	1030.7	3.0491	n.s.	132.66	0.71842	n.s.
SixDe	2	734.01	2.1715	n.s.	383.2	2.0752	n.s.
SloxDe	1	570	1.6863	n.s.	268.44	1.4537	n.s.
SexSixSlo	1	953.2	2.82	n.s.	1035.6	5.6083	n.s.
SexSixDe	2	527.32	1.56	n.s.	328.29	1.7778	n.s.
SexSloxDe	1	172.83	0.51131	n.s.	-95.557	Negative	
SixSloxDe	1	671.92	1.9878	n.s.	326.61	1.7688	n.s.
Res	1	338.02			184.66		
Total	19						
Transformation		Fourth root			Square root		

^a 5 m ≠ 10 m ($p < 0.01$); 5 m ≠ 20 m ($p < 0.001$); 10 m ≠ 20 m ($p < 0.001$).

^b Aurora: Summer ≠ Winter ($p < 0.01$); Paraggi: Summer ≠ Winter ($p < 0.01$); Summer: Aurora = Paraggi; Winter: Aurora ≠ Paraggi ($p < 0.05$).

^c Aurora: Summer ≠ Winter ($p < 0.01$); Paraggi: Summer ≠ Winter ($p < 0.01$); Summer: Aurora = Paraggi; Winter: Aurora = Paraggi.

Table 3
 3. SIMPER dissimilarity in sessile macrobenthos between the factors that resulted significant from PERMANOVA analysis. The biotic and abiotic elements/groups that mostly contributed to dissimilarity values are indicated. SIMPER analysis run with a 50% cut-off.

Factor	Biotic and abiotic elements	cumulative dissimilarity explained	Groups	cumulative dissimilarity explained
Season	<i>Dictyota dichotoma</i> , <i>Padina pavonica</i> (> in summer), <i>Lithophyllum/Mesophyllum</i> spp., <i>Peysommelia squamaria</i> , Turf, Sediment (> in winter)	55.8%	Ochrophyta (> in summer), Turf, Abiotic (> in winter) (Supplementary material FS1a)	33.9%
Site	<i>D. dichotoma</i> , <i>Lithophyllum/Mesophyllum</i> spp., <i>P. squamaria</i> (> at Paraggi), Sediment, Turf (> at Aurora)	53%		
Slope	<i>D. dichotoma</i> , Turf, <i>P. pavonica</i> (> on inclined), Sediment, <i>Lithophyllum/Mesophyllum</i> spp., <i>P. squamaria</i> (> on sub-vertical)	52.4%		
Depth	Sediment, <i>P. squamaria</i> , <i>D. dichotoma</i> (> at 10 m), <i>Lithophyllum/Mesophyllum</i> spp., Turf, <i>P. pavonica</i> (> at 5 m)	51.7%		
Depth	<i>Lithophyllum/Mesophyllum</i> spp., <i>Halopteris scoparia</i> (> at 5 m), <i>D. dichotoma</i> , Sediment, <i>P. squamaria</i> , Turf (> at 20 m)	63.5%		
Depth	<i>D. dichotoma</i> , Turf, <i>Parazoanthus axinellae</i> (> at 20 m), <i>Lithophyllum/Mesophyllum</i> spp. (> at 10 m)	52.3%		
Season x Site	<i>D. dichotoma</i> , <i>P. pavonica</i> (absent in winter), Turf, <i>Lithophyllum/Mesophyllum</i> spp., Sediment (> in winter), <i>H.scoparia</i> (> in summer)	57.9%	Ochrophyta (> in summer), Turf, Abiotic (> in winter) (Supplementary material FS1e)	38.7%
Season x Site	<i>D. dichotoma</i> , <i>P. squamaria</i> , Sediment, Turf (> in summer), <i>H.scoparia</i> , <i>Lithophyllum/Mesophyllum</i> spp. (> in winter), <i>P. pavonica</i> (absent in winter)	46.4%	Ochrophyta (> in summer), Bryozoa (absent in summer) (Supplementary material FS1e)	31.4%
Paraggi				

individual meiofaunal taxa and particular macrobenthic groups, species and abiotic elements (Supplementary material TS3). According to Spearman's Rank Correlation Analysis, almost all crustaceans and Halacaroida resulted positively correlated with Ochrophyta and with the seasonal erect brown algae *D. dichotoma* and *P. pavonica*. Nematoda and Gastropoda showed a weak correlation with *P. pavonica*. Only a few taxa showed a correlation with total macroalgal cover (Ostracoda, Amphipoda and Copepoda). Polychaeta showed a weak positive correlation with Chlorophyta and Rock, while Bivalvia with Cnidaria and Detritus. Considering univariate measures, meiofaunal abundances and higher-taxa richness resulted positively correlated with Ochrophyta, *D. dichotoma*, *P. pavonica* and, to a lesser extent, total macroalgal cover (Supplementary material TS3).

4. Discussion

4.1. Sessile macrobenthos

Even if the composition of the sessile macrobenthos in terms of biotic and abiotic elements showed significant differences for all the factors investigated (i.e. season, site, slope and depth), season proved to be the main factor structuring the sessile macrobenthic groups. From summer to winter, a marked reduction of Ochrophyta, linked to the collapse of the seasonal erect brown algae *D. dichotoma* and *P. pavonica*, and a proportional increase in perennial red algae (mainly *Lithophyllum/Mesophyllum* spp.) and sessile macrofauna, were observed. Despite the presence of many different macrobenthic components (turf, sediment, detritus, bare rock and sessile macrofauna), the community resulted to be strongly dominated by macroalgae: Ochrophyta and Rhodophyta dominated in summer, while Rhodophyta prevailed in winter.

4.2. Diversity, abundance and composition of the meiofauna

Meiofaunal abundance resulted low and diversity high if compared with values of soft-bottom meiofauna documented in the Ligurian Sea at comparable depths (see Danovaro et al., 1995a, 1995b; Danovaro, 1996; Vezzulli et al., 2003; Moreno et al., 2008; Losi et al., 2012), consistently with findings from studies on hard bottom meiofauna in other areas of the Mediterranean Sea (Danovaro and Fraschetti, 2002; Fraschetti et al., 2006; Russo et al., 2015). The numerical dominance of nematodes, usual in soft bottoms, did not appear: Crustacea were the main group, as reported elsewhere for hard bottom meiofauna (Giere, 2009). Many representatives of Crustacea were found among both the main and the rare taxa. Nematoda and Copepoda Harpacticoida co-dominated the community, followed by Polychaeta, with relative contributions very similar to those found by Fraschetti et al. (2006) in SE Italy.

Macroalgae represented the main habitat, but there were also many other habitats, including turf, sediment, detritus, bare rock and sessile macrofauna, which are known to be suitable for meiofauna (Gibbons, 1991 and references therein; Russo et al., 2015).

The high number of Copepoda Harpacticoida detected is typical for phytal habitats, especially for macroalgae (Wieser, 1959; Lewis and Hollingworth, 1982; Coull et al., 1983; Bell et al., 1984; Hall and Bell, 1993; Jarvis and Seed, 1996). However, high percentages of Copepoda have been found also associated to hard substrata dominated by sessile macrofauna (Russo et al., 2015). Aside from the Copepoda, many of the other taxa found are reported as inhabitants of phytal and hard substrata. Ostracoda and Tanaidacea are frequent members of the phyton (Colman, 1940; Hagerman, 1966; Kangas, 1978; Hull, 1997; Arroyo et al., 2004; Giere, 2009), as well as Amphipoda (Hagerman, 1966; Mukai, 1971; McBane and Croker, 1983; Pederson and Capuzzo, 1984; D'Antonio, 1985; Gibbons, 1988b; Giere, 2009), Cumacea (Logan et al., 2008) and Isopoda (Mukai, 1971; Sarma and Ganapati, 1972; Giere, 2009). Amphipoda are also reported to live on sponges (Poore et al.,

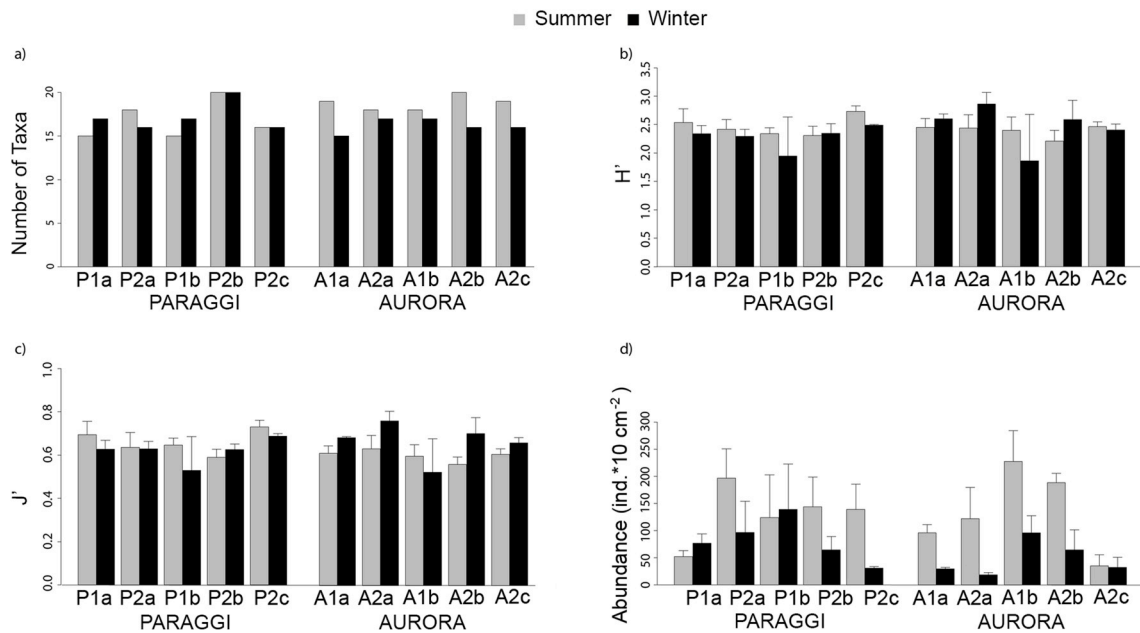


Fig. 3. Univariate measures of meiofauna: (a) number of taxa; (b) diversity (Shannon-Wiener Index, H'); (c) evenness (Pielou Index, J'); (d) abundance (ind. 10 cm^{-2}), at the each sampling station in each season (summer and winter). Refer to Table 1 for station codes.

Table 4

Results of four-way PERMANOVA on meiofauna: (a) number of taxa, (b) Shannon-Wiener Index (H'), (c) Pielou Index (J'), (d) abundance. * = $p < 0.05$; n.s. = not significant.

	df	a) Number of taxa			b) H'			c) J'			d) Abundance		
		MS	Pseudo-F	<i>p</i>	MS	Pseudo-F	<i>p</i>	MS	Pseudo-F	<i>p</i>	MS	Pseudo-F	<i>p</i>
Season (Se)	1	6.4126	0.76791	n.s.	10.422	14.329	n.s.	0.75658	1.4205	n.s.	1808.9	278.71	*
Site (Si)	1	8.5614	1.0252	n.s.	0.045008	0.06188	n.s.	4.6383	8.7083	n.s.	26.767	4.1243	n.s.
Slope (Slo)	1	18.404	2.2038	n.s.	7.4456	10.237	n.s.	5.0509	9.4829	n.s.	13.101	2.0186	n.s.
Depth (De)	2	8.867	1.0618	n.s.	15.137	20.812	n.s.	14.592	27.395	n.s.	376.72	58.044	n.s.
SexSi	1	26.669	3.1936	n.s.	3.2095	4.4125	n.s.	13.838	25.981	n.s.	357.58	55.095	n.s.
SexSlo	1	4.9065	0.58756	n.s.	21.279	29.256	n.s.	23.864	44.805	n.s.	263.44	40.59	n.s.
SexDe	2	0.37574	0.044995	n.s.	5.7924	7.9637	n.s.	3.1902	5.9894	n.s.	97.802	15.069	n.s.
SixSlo	1	8.1051	0.97058	n.s.	2.1895	3.0102	n.s.	5.5892	10.494	n.s.	77.169	11.89	n.s.
SixDe	2	4.2169	0.50497	n.s.	5.4203	7.4521	n.s.	6.9915	13.126	n.s.	246.71	38.012	n.s.
SloxDe	1	3.5893	0.42981	n.s.	6.2317	8.5677	n.s.	2.4002	4.5063	n.s.	254.4	39.197	n.s.
SexSixSlo	1	5.6893	0.68129	n.s.	3.0441	4.1851	n.s.	0.25114	0.47151	n.s.	81.183	12.508	n.s.
SexSixDe	2	0.64249	0.076938	n.s.	2.1216	2.9169	n.s.	0.65678	1.2331	n.s.	136.68	21.06	n.s.
SexSloxDe	1	2.011	0.24081	n.s.	9.2159	12.671	n.s.	8.1662	15.332	n.s.	15.107	2.3276	n.s.
SixSloxDe	1	4.9065	0.58756	n.s.	0.27604	0.37951	n.s.	0.22302	0.41871	n.s.	128.06	19.732	n.s.
Res	1	8.3508			0.72735			0.53263			6.4902		n.s.
Total	19												
Transformation		Square root			Square root			Square root			Square root		

2000), and in some cases to feed of them (Oshel and Steele, 1985).

Nematoda are other common inhabitants of the phytal, even if in lower numbers than in soft-sediments (Lewis and Hollingworth, 1982; Jarvis and Seed, 1996; Danovaro and Fraschetti, 2002; Semprucci and Balsamo, 2012; Semprucci et al., 2015), and with different community structure and composition (Da Rocha et al., 2006).

Polychaeta can be found on epiphytic algae and hard substrata (Giere, 2009) and were reported among the main community components in infralittoral hard substrata of the Mediterranean Sea (Fraschetti et al., 2006; Danovaro et al., 2007).

Halacaroida live preferably among plants and hard substrates: they feed on the soft parts of hydrozoan and bryozoan colonies or are phytophagous, piercing algal cells (Colman, 1940; Pugh and King, 1985; Somerfield and Jeal, 1995; Arroyo et al., 2004; Giere, 2009).

Bivalvia and Gastropoda have been documented in phytal meiofauna (Johnson and Scheibling, 1987). They usually belong to the

“temporary meiofauna”; however, there are numerous “microgastropods” and “microbivalves” which remain about 1–2 mm throughout their life, and therefore belong to the permanent meiofauna (Giere, 2009). The many representatives of temporary meiofauna found in this study could be related to the low disturbance, low predation pressure, and abundant food, typical for phytal substrata, which might favour a high number of larvae and juveniles.

The high values of meiofaunal higher-taxa richness and diversity found in the present study could be related to the substrate heterogeneity created by sessile macrobenthic organisms (Danovaro and Fraschetti, 2002). The various microhabitats and ecological niches offered by algae and the other substrata favour a highly diverse community with different adaptations and life styles. Moreover, sediments, the usually preferred habitat of Nematoda, are not the main environmental component here, thus leading to a lower dominance of nematodes, and an increase in the relative abundances of other taxa. Hard

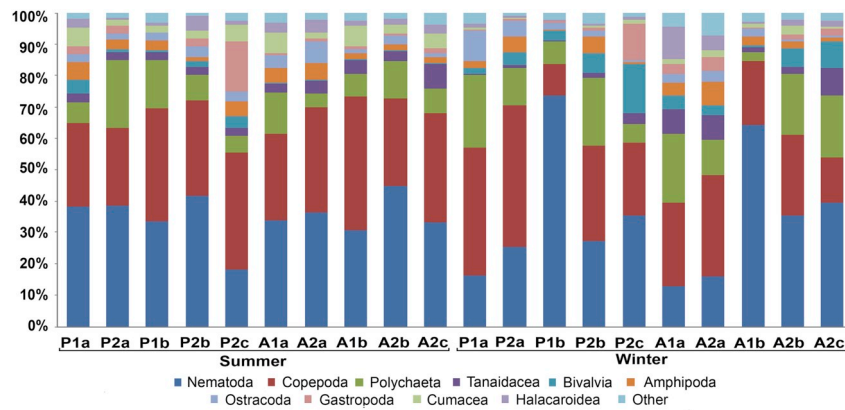


Fig. 4. Relative abundances (%) of meiofaunal taxa at each sampling station in each season (summer and winter). “Others” includes taxa that represented less than 1% of the total meiofaunal abundance of all samples investigated (i.e., rare taxa). Refer to Table 1 for station codes.

Table 5
Minimum and maximum average abundance of major meiofaunal taxa (ind 10 cm⁻²).

	Abundance min (ind 10 cm ⁻²)	Abundance max (ind 10 cm ⁻²)
Nematoda	2.95 ± 0.07	102.70 ± 149.02
Polychaeta	1.90 ± 0.95	42.43 ± 42.54
Bivalvia	0.03 ± 0.06	5.43 ± 4.19
Gastropoda	0.00 ± 0.00	22.17 ± 7.07
Halacaroida	0.17 ± 0.29	6.47 ± 3.64
Copepoda Harpacticoida	5.73 ± 5.17	96.63 ± 80.85
Ostracoda	0.20 ± 0.17	8.43 ± 11.35
Cumacea	0.13 ± 0.15	14.53 ± 15.12
Amphipoda	0.20 ± 0.10	6.53 ± 4.38
Tanaidacea	0.27 ± 0.06	17.67 ± 7.15

Table 6
Results of four-way PERMANOVA on assemblage composition of: (a) entire meiofaunal community, (b) rare taxa. * = p < 0.05; ** = p < 0.01; n.s. = not significant.

	df	a) Entire meiofaunal community			b) Rare taxa		
		MS	Pseudo-F	p	MS	Pseudo-F	p
Season (Se)	1	2727.1	11.129	**	8303.8	5.8551	*
Site (Si)	1	671.24	2.7393	n.s.	4642.4	3.2734	n.s.
Slope (Slo)	1	167.7	0.68437	n.s.	2743.1	1.9342	n.s.
Depth (De)	2	602.14	2.4573	n.s.	3013.3	2.1247	n.s.
SexSi	1	465.52	1.8998	n.s.	3091.9	2.1802	n.s.
SexSlo	1	484.49	1.9772	n.s.	2194.7	1.5475	n.s.
SexDe	2	270.61	1.1043	n.s.	1423.7	1.0038	n.s.
SixSlo	1	108.25	0.44174	n.s.	1069.4	0.75406	n.s.
SixDe	2	240.75	0.98248	n.s.	945.4	0.66662	n.s.
SloxDe	1	345.36	1.4094	n.s.	1600.7	1.1287	n.s.
SexSixSlo	1	84.785	0.346	n.s.	718.95	0.50694	n.s.
SexSixDe	2	342.84	1.3991	n.s.	1081	0.76226	n.s.
SexSloxDe	1	232.74	0.94981	n.s.	1616.1	1.1395	n.s.
SixSloxDe	1	192.51	0.78563	n.s.	290.72	0.20499	n.s.
Res	1	245.04			1418.2		
Total	19						

Transformation Square root Square root

substrata may provide refuge from predation (Coull and Wells, 1983). Predation at high intensity could result in competitive exclusion and thus in a heavily dominated community (Raes and Vanreusel, 2005). Therefore, the shelter from predation offered by the different microhabitats, together with the low disturbance and the high number of microniches could be responsible for the high values of evenness found. The low meiofaunal abundances observed are probably related to

Table 7
SIMPER dissimilarity in meiofaunal assemblage composition between seasons (summer vs winter) for the entire community (a) and rare taxa (b). Taxa that mostly contributed to dissimilarity values are indicated. SIMPER analysis run with a 50% cut-off.

(a) Entire meiofaunal community		(b) Rare taxa	
Dissimilarity (%)		Dissimilarity (%)	
Summer vs winter	33.7%	Summer vs winter	53.9%
Nematoda	17.2%	Chaetognatha	19.6%
Copepoda	16.1%	Isopoda	13.8%
Cumacea	8.2%	Turbellaria	9.2%
Polychaeta	7.7%	Gastrotricha	8.3%
Tanaidacea	5.9%		

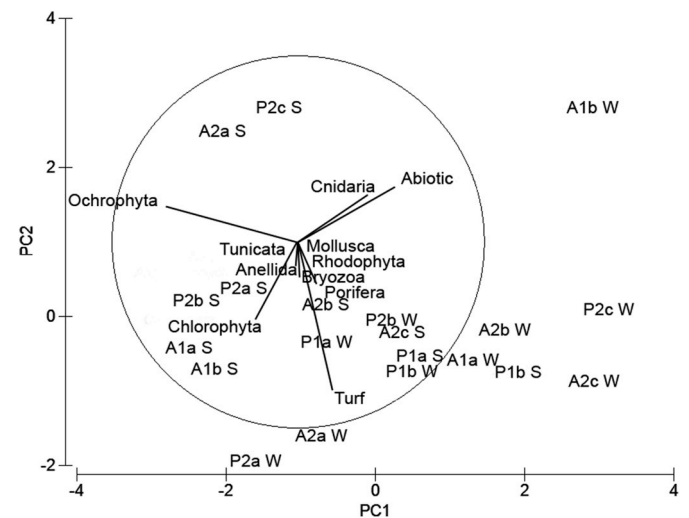


Fig. 5. Principal components analysis carried out on the sessile macrobenthic groups. Vectors indicate the direction and strength of each group contribution to the overall distribution. Refer to Table 1 for station codes.

the nature and structure of the primary substrate, poor of interstitial spaces (Danovaro and Fraschetti, 2002). This is particularly true for typical interstitial taxa, such as nematodes, which were comparatively scarce, thus affecting total meiofaunal abundance. Other typically interstitial taxa, such as Gastrotricha, Kinorhyncha and Tardigrada were present in low percentages (< 1%).

Our study is one of the first where Syncarida have been found in Mediterranean marine meiofauna (Baraldi et al., 2003). Syncarida have been usually reported as freshwater inhabitants, but a few species of the

Table 8

Results of the distance-based linear model (DistLM) of meiofaunal assemblage composition on habitat variables selected by the PCA: (a) marginal tests results; (b) results from the BEST model using the AIC criterion. (*P*, significance value; Prop., amount of explained variation).

	Variable	Pseudo-F	<i>P</i>	Prop.
(a) Marginal tests	Abiotic	0.3047	0.868	0.02
	Chlorophyta	2.0423	0.112	0.10
	Cnidaria	1.3866	0.223	0.07
	Ochrophyta	6.7034	0.002	0.27
	Turf	2.1947	0.091	0.11
	Model	AIC	R ²	RSS
(b) Best solution	Ochrophyta + Chlorophyta + Turf	118.97	0.39604	4494.8

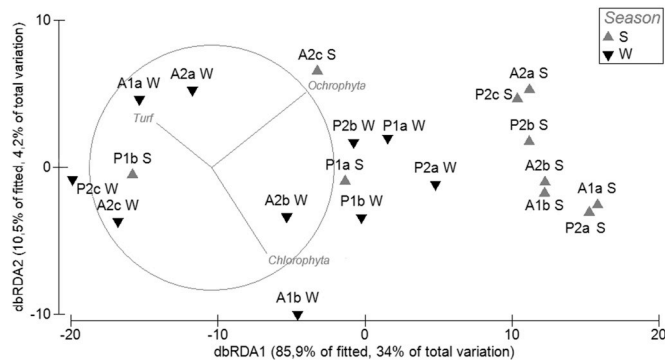


Fig. 6. Distance-based redundancy (dbRDA) illustrating the DistLM model based on meiofaunal assemblages and the fitted habitat variables (i.e., macrobenthic groups) as vectors.

genus *Hexabathynella* occur also in coastal waters; within this genus, the species with the most plesiomorphic characters occur in salt or brackish water, supporting a marine origin for the genus (Camacho, 2003; De Troch et al., 2008).

4.3. Meiofaunal patterns and relation with the sessile macrobenthos

Meiofaunal abundance and assemblage composition highlighted significant seasonal changes, while no significant differences were found for the other factors investigated. Seasonal variation in abundances and composition of phytal and hard bottom meiofauna has been previously documented (e.g., Edgar, 1983; Gunnill, 1983; Gibbons and Griffiths, 1986; Johnson and Scheibling, 1987; Prathep et al., 2003). Variations in meiofaunal abundances and composition reflect population dynamics, which are driven by a complex interplay of physical and biological factors (Johnson and Scheibling, 1987).

The results of the present study underline a major importance of seasonality as a driver of the meiofaunal pattern observed. While the single meiofaunal taxa had differing preferences, the communities as a whole likely responds to the significant seasonal change occurring in the sessile macrobenthos, and especially in the cover of brown algae (Ochrophyta). Given the links between the phytal meiofauna and the algae where they live, the seasonal meiofaunal variations observed could depend on the cycles of growth and decay of the algal stocks. Many seasonally reproducing species may be strongly influenced by variations in algal and epiphyte growth (Gibbons, 1991), and related food resources (Mukai, 1971; Kito, 1982; Johnson and Scheibling, 1987), rather than by temperature and season *per se* (Hicks, 1985).

Macroalgal cover has been reported as one of the main factors influencing the structure of hard bottom meiofaunal assemblages (Danovaro and Fraschetti, 2002). However, only a component of the macroalgal cover (i.e., Ochrophyta) appeared as the main factor influencing meiofauna in the present study, while the total macroalgal cover resulted correlated only with a few taxa.

Those taxa resulting associated with Ochrophyta and Chlorophyta are all common phytal inhabitants and their abundances resulted higher in summer. Other taxa, such as Bivalvia and Gastropoda, did not show any particular difference from summer to winter, and appeared to be related to other factors. In particular, the association of Bivalvia with Detritus could be explained with their feeding habit: many microbivalves are reported as detritivorous (Giere, 2009).

The reasons of the association of the meiofaunal community with Ochrophyta could be various. Meiofaunal trends observed in this study could not be explained by differences in palatability among the macroalgae: Ochrophyta would not be considered as a food source *per se*. In fact, the feeding strategies of phytal meiofauna are very different and only a few nematodes, halacarids, copepods (including some obligate endophagous in *D. dichotoma*), amphipods and ostracods feed directly on the macroalgae (Poore et al., 2000; Shimono et al., 2004, 2007; Giere, 2009). Some phytal organisms feed on diatoms on the macroalgae, other few meiofaunal organisms may take up exudates secreted by the macroalgae, however the majority of the phytal meiofauna feed on detritus and microorganisms accumulated on the macroalgae (Giere, 2009).

Detritus is not indiscriminately ingested by the meiofauna: brown algae debris seems to be preferred over red algae (Giere, 1975; Rieper-Kirchner, 1989), which could be a possible explanation of the preference for Ochrophyta. This seems supported by the correlation of a great number of meiofaunal taxa with *D. dichotoma* and *P. pavonica*, while the weak correlation showed by *H. scoparia* with all meiofauna may be explained by its texture, much more tough than *D. dichotoma* and *P. pavonica*.

Another possible explanation is that the amount of microflora, microorganisms and detritus associated with macroalgae could differ among species, thus influencing differently the phytal meiofauna (Frame et al., 2007). Moreover, differences in macroalgal complexity could explain differences in meiofaunal community (Gibbons, 1988; Gee and Warwick, 1994a, 1994b): more complex macroalgae increase meiofaunal abundance and diversity by offering a large number of habitats where to feed and live, a high variety of food resources, facilitating the amount of trapped sediment and detritus, and providing effective shelter against predation (Whatley and Wall, 1975; Coull and Wells, 1983; Hicks, 1980, 1985; Hull, 1997; Frame et al., 2007). The macroalgal size is another factor that influences the structure of meiofaunal assemblages (Hicks, 1980; Gunnill, 1982), but its effect seems to be dependent on macroalgal identity; this in turn may be attributable to differences of complexity between macroalgae (Veiga et al., 2016; Ape et al., 2018). The three-dimensionally shaped erect macroalgae belonging to Ochrophyta found in the present study showed a higher complexity compared to that of Rhodophyta, which were composed by a great number of encrusting algae, with a more bidimensional shape.

Worth considering is also the chemical defense produced by some macroalgae against marine herbivores. For example, the Ochrophyta *D. dichotoma*, produces secondary metabolites compounds which deter

feeding by macro-grazers, such as fishes and sea urchins, but not by some meso-grazers belonging to Amphipoda and Polychaeta (Hay et al., 1987, 1988). Thus, the capacity of living or feeding on algae unpalatable for macro-grazers, due to a higher resistance to their chemical defences, could be an advantage for small, sedentary meiofaunal animals, representing a possible explanation for the observed preferences.

Further investigations are needed in order to clarify the observed relationships between meiofauna and Ochrophyta. However, the role of infralittoral sessile macrobenthic groups, and in particular of some algal components, in shaping the meiofaunal assemblages resulted obvious. Similarly to sessile macrobenthos groups, meiofauna changed significantly with the season, while it did not show any significant variation with slope or depth, consistently with findings by other authors (Arroyo et al., 2004).

The sessile macrobenthic groups illustrated a different effect of the season in the two sites, which meiofauna did not detect. This can be explained by the close relation of meiofauna with Ochrophyta: even if a different trend in Turf and Sediment was observed, both sites recorded a strong decrease of these brown algae from summer to winter.

In conclusion, our study, one of the few performed in the infralittoral zone, provide suggestive evidence that some sessile macrobenthic groups act as ecosystem engineers for the meiofauna, influencing its abundances, higher-taxa diversity and community structure. Indeed, the macroalgal component showed a strong influence on the associated meiofaunal communities, paralleling what has already been seen for the motile macrobenthos (Abbiati et al., 1987, 1991; Bustamante et al., 2014).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2018.10.016>.

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