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PRIMARY RESEARCH PAPER

Influence of environmental factors and biogenic habitats on intertidal meiofauna

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Abstract This study investigated the influence of physical and chemical conditions and biotic factors on the distribution and diversity of meiofauna in intertidal zone along a geographical gradient. At 11 sites along the Italian coast, we studied the concurring role of environmental variables, trophic resources and the presence of habitat-forming species (macroalgae vs. mussels) in controlling the meiofaunal communities. The increase of water temperature combined with local thermal conditions was associated with a decrease in nematodes and copepods, with a consequent decrease in meiofaunal abundance towards the south. However, the increase in salinity, as geographical gradient decreases, and local thermal conditions favoured the settlement of a greater number of taxa, influencing communities' composition. The presence of macroalgae or mussels differently influenced the community structure of meiofauna on intertidal substrates and their response to environmental factors. From our results, the presence of macroalgae coverage appeared to reduce the impact of thermal stress on meiofauna and was associated with higher levels of meiofaunal diversity with respect to mussels. This work highlighted the importance of considering the interplay among biotic and abiotic factors, resulting in local combinations of environmental conditions, in order to understand the pattern of diversity and distributions of marine organisms.

Keywords Intertidal environment · Meiofauna distribution · Community composition · Environmental factors · Habitat-forming species

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Introduction

The distribution and the occurrence of marine organisms at the coast change mainly through large-scale spatial-related abiotic factors such as temperature, salinity gradient, seasonality and organic carbon flux (Rohde, 1992; Ingole & Parulekar, 1998; Gaston, 2000; Yasuhara et al., 2012). At the coast, other abiotic and biotic factors, such as wave fetch, tidal amplitude, trophic resources and organisms' interactions, are critical at local level to structure marine communities (Gaston, 2000; Gartner et al., 2013; Kroeker et al., 2016). Also human disturbances, such as coastal transformation and eutrophication, and the effect caused by climate change, can act both on small and large scales, increasing the vulnerability of marine habitats (Airoldi & Beck, 2007; Brierley & Kingsford, 2009; Crain et al., 2009; Coll et al., 2010; Semprucci et al., 2015). Thus, to better understand the pattern of diversity and distributions of marine organisms, we need to consider this plethora of biotic and abiotic factors as interplaying among those that, acting at different scales, shape local diversity (Gaston, 2000; Menge et al., 2004; Kroeker et al., 2016). The marine intertidal zone is a perfect model to study the concurrence of different factors in shaping biodiversity; it is one of the most dynamic and challenging environments worldwide, but provides important ecosystem goods and services (Sarà et al., 2014). It represents a unique resource to explore hypotheses about patterns potentially driving organisms' distribution and diversity at different geographical scales (Hulings & Gray, 1976; Papageorgiou et al., 2007; Covazzi-Harriague et al., 2013; Sarà et al., 2014). Fluctuations in a wide array of physical forces, like wave exposure, tide amplitude and anthropogenic disturbance, are main determinants in driving the distribution of organisms (Papageorgiou et al., 2007, Helmuth, 2008, Covazzi-Harriague et al., 2013; Sarà et al., 2014; Kroeker et al., 2016). These factors may covary, affecting the intertidal substrate, and the occurrence and the characteristics of habitat-forming species, which in turn influence (both directly and indirectly) food and shelter availability for other organisms (Gartner et al., 2013) and strengthen the effect on local diversity further. Most research in intertidal zones has focused on macro-organisms such as macro-zoobenthos and algae (e.g. Benedetti-Cecchi et al., 2001; Bulleri et al., 2002; Covazzi-Harriague & Albertelli, 2007; Defeo & McLachlan, 2013), while only scant research has focused on meiofauna (Giere, 2009), paying more attention to sandy beach systems (e.g. Rodríguez et al., 2003; Kotwicki et al., 2005; Papageorgiou et al., 2007; Covazzi-Harriague et al., 2013). Meiofauna comprise the organisms that are amongst the most abundant and diverse metazoans on Earth (Balsamo et al., 2010); they play a key role in the functioning of the food webs and sustain critical ecological processes (Danovaro & Fraschetti, 2002). They provide a suitable model for the study of marine biodiversity and biogeographic patterns of benthic marine organisms (Kotwicki et al., 2005; Danovaro et al., 2008; Curini-Galletti et al., 2012; Carugati et al., 2015), potentially providing useful information for planning monitoring and conservation strategies (Sandulli et al., 2010; Zeppilli et al., 2012; Bianchelli et al., 2013; Zeppilli et al., 2013; Semprucci et al., 2016). Distribution and diversity of meiofauna are affected by several abiotic and biotic factors acting on different spatial scales, from the main geographical-related gradients (i.e. temperature, salinity) (Hulings & Gray, 1976; Soltwedel, 2000) to local physical–chemical variables, in particular in exposed and unstable environments, like intertidal zones (Albuquerque et al., 2007; Kotwicki et al., 2014). However, most of the studies on meiofaunal distribution did not show a clear latitudinal pattern (Kotwicki et al., 2005; Gobin & Warwick, 2006). In addition, biotic factors, such as the presence of intertidal rocky-shore-forming species like large macroalgae and sessile macrofauna (i.e. mussel beds and oysters, coral and vermetid reefs), increase the structural complexity of substrate and concur in physically and chemically structuring the intertidal, emerging as some of the most crucial determinants in structuring meiofaunal communities (Norkko et al., 2001; Danovaro & Fraschetti, 2002; Reise, 2002; Kostylev et al., 2005; Danovaro et al., 2007; Bianchelli et al., 2013). A lot of studies have shown the role of macroalgae in influencing meiofaunal settlement and distribution, trapping the sediment and providing detritus as useful food for grazers (Gibbons, 1988a; Arroyo et al., 2004; Urban-Malinga et al., 2008), refuges from predation and dislodgment, and ameliorating physical conditions by retaining water and offering protection from desiccation (Gibbons, 1988a, b; Danovaro & Fraschetti, 2002; Danovaro et al., 2007; Logan et al., 2008). The studies on meiofauna associated with oyster and mussel beds

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generally suggest that it is more related to functional trait organisms, such as biodeposition (Dittmann, 1990; Reise, 2002; Norling & Kautsky, 2007; Radziejewska et al., 2009). However, exploring how all these factors (biotic and abiotic) concur in shaping local meiofaunal community is complicated by a scale effect. Therefore, the need for substantial information still exists, to investigate their relationship and explain the pattern of distribution and diversity of intertidal meiofaunal organisms. Considering that meiofaunal communities of swash intertidal zone are mostly influenced by physical constraints of this zone (e.g. temperature variability, exposure to desiccation; Hulings & Gray, 1976), here we tested hypotheses about factors (chemical–physical conditions and trophic resources) potentially driving meiofaunal distribution and diversity, associated with two different habitat formers (macroalgae vs. mussels), on mediterranean scale. When we are aware that without community inventories it is not possible to identify accurate diversity patterns reflecting the finest community structure, here we present a coarse taxonomic analysis as we believe that also this kind of analysis can however bring us to have that correct and useful information when assessing the effects of abiotic and biotic factors on meiofaunal taxa distribution at large spatial scale. For our purpose, we planned a large survey along the Italian coast (1) to study environmental factors affecting meiofauna and their concurring role in controlling meiofaunal distribution and community composition along a geographical gradient; (2) how the occurrence of different habitat-forming species can affect the abundance and community composition of meiofauna, and (3) how the habitat formers can influence the relative control of environmental factors on meiofaunal distribution and diversity in intertidal habitats.

Materials and methods

Study area, sampling and environmental variables

Factors affecting meiofaunal distribution along a geographical gradient were studied in the Italian intertidal system by choosing 11 sites, not affected (pristine) by significant anthropogenic disturbance, which were chosen according to the proximity with areas under different levels of protection, characterised by rocky shores, spanning 9° north–south from Trieste, the northernmost site, down to Porto Palo, and 8° east–west from Livorno to Otranto (Fig. 1). In 2013, from the 22nd June to 24th July, we choose three plots per site (1 m^2 area) with the same inclination and at the same height ($\sim$ 0.35 m) above the mean lower low water (MLLW) level (Sarà et al., 2014), colonised by two habitat-forming species that, alternatively, were macroalgae (A) (Livorno, Orbetello, Palinuro, Taranto, Mazara del Vallo e Porto Empedocle; more than 80% of coverage) and generally characterised by the presence of *Cystoseira sp*., or mussels (M) (*Mytilus galloprovincialis* in Trieste, Ancona, Gaeta, Otranto, and/or *Mytilaster minimus* in Palermo; more than 50% of coverage). Although sampling was carried out in the intertidal, where sites are wave splashed, our target in all investigated sites was the small layer (not more than 1 cm thick) of fine sandy sediment deposited on the rock trapped in the middle of habitat formers. We did not perform specific analysis on the sediments' grain size, but it is known that both algae and mussels trap fine sandy sediment

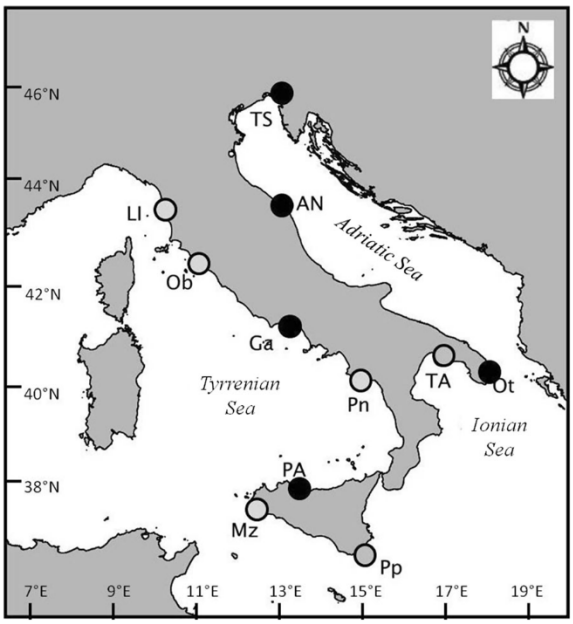


Fig. 1 Geographical position of the 11 intertidal study sites along the Italian coastline. *TS* Trieste, *AN* Ancona, *LI* Livorno, *Ob* Orbetello, *Ga* Gaeta, *Pn* Palinuro, *Ot* Otranto, *PA* Palermo, *Mz* Mazara del vallo, *Pp* Porto Empedocle (denoting by black dots the sites with mussel (M) coverage and by grey dots the algae (A) substrate coverage). Geographic coordinates of the sites are reported in Table 1. Map projection ETRS89

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(Arroyo et al., 2004; Cole, 2010; Du et al., 2012), and accordingly we found fine-grained sediments in all investigated sites. At each site, inside each plot, we collected sediment samples to extract meiofauna, scraping the sediment by means of a paint scraper within three randomly chosen quadrats (10 × 10 cm). Once collected, the sediment was fixed in 4% buffered formaldehyde in filtered (0.4 µm) seawater solution until laboratory meiofauna analyses could be performed. Moreover, in the same plots, we collected three randomly chosen replicates (~ 10 g) of sediment, which we stored at – 20 °C until laboratory analyses to estimate the concentrations of phytopigments and biochemical components (proteins carbohydrates, lipids and biopolymeric carbon) (Pusceddu et al., 2003). These variables are among the most effective trophic proxies in explaining the distribution of meiofauna. Thus, our main prediction was that meiofaunal distribution and diversity were affected by both biogenic habitat and environmental factors. Then, to disentangle the roles of each component, we measured both biotic and abiotic variables along a geographical gradient. We chose the habitat former coverage and trophic resources (sedimentary phytopigments, lipids, proteins, carbohydrates and biopolymeric carbon; see below for details) as the main biotic variable, while a large number of chemical and physical factors (water temperature, salinity, body temperature, emersion and immersion time and wave fetch) were chosen as a set of abiotic variables that can be easily used as a proxy for driving factors of meiofaunal distribution and diversity.

However, meiofauna, like most ectotherms, are mainly affected by body temperature (BT) experienced during life span (from some months to a few years; Giere, 2009). Body temperature is the main effector of metabolism and, with available food, drives main life history traits (Sarà et al., 2011, 2013; Kroeker et al., 2016). Thus, to investigate whether local thermal profiles along a geographical gradient were responsible for possible diversity differences in meiofaunal community, we estimated the role of changing conditions on BT of these invertebrate ectotherms. We know that in ectotherms BT more or less mirrors the same temperature of the mean environment: (Lima et al., 1985) even more so if they live under intertidal conditions where BT results from the biophysical combinations of many factors, as shown by Helmuth (1998). While for larger organisms, such as mussels, algae or crabs, obtaining good estimates of BT is facilitated by sensors (e.g. Helmuth, 1998), in small organisms like meiofauna it is not possible to get high-resolution series of BT due to their miniscule size. As a main consequence, we obtained the BT for these small organisms via a modelling approach, applying the Helmuth (1998, 1999) biophysical heat budget model (BE) (Kearney et al., 2010; Sarà et al., 2011, 2013). We know that many intertidal organisms live very close to their physiological limits, particularly in the intertidal zone, where they contend with both BT and food acquisition. In the intertidal, they cannot be simply estimated through rough water and air temperature and tidal range data (Helmuth, 1998), as they are not biologically relevant unless they are integrated into a BE to describe the climatic niche of intertidal organisms using large-scale weather and climate data archives. Such models capture the high complex interaction of factors, ultimately determining what an intertidal organism actually experiences in the field. This is achieved by deriving from the integration of aerial body temperature, submersed body temperature, desiccation and reduction in feeding time; all of these increase with increasing tidal elevation to affect the performance of intertidal organisms. The BE model was originally conceived, validated and later successfully applied to study mussel BT, and it has never been applied to study smaller organisms. Nevertheless, one of the most important assumptions of the original model was that heat budget should depend on body size and colour of target organisms. Thus, in our model, we set body size at 0.05 cm, to be as close as possible to the size of most meiofaunal animals (from 30 µm to 1 mm; Giere, 2009). The colour in our model was left black, as originally conceived by Helmuth (1998). While we are aware that this should be tested with appropriate experimental research in future, leaving the colour black should not affect the outcome of the model, as meiofauna live partially immersed in the sediment. Thus, there should be no effect on heat exchanges. Having set the body size, we informed BE models for every ECOTRIP site with hourly data (2nd January 2010–31st December 2013) of tidal amplitude (m), water and air temperature (°C), wind direction (°) and speed (m s^{-1}) for all sites, which were downloaded from the Italian Institute of Environmental Research (ISPRA) website (http://www.mareografico.it/). Irradiance (global sky) data ($W \times m^{-2}$), calculated on an hourly basis as an average for each month of the year

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under clear skies, were obtained from the European Joint Research Centre (http://sunbird.jrc.it/pvgis). Using a BE approach, we modelled, on an hourly basis, the aerial and aquatic body temperatures of an intertidal (mean lower low water [MLLW] + 0.35 m) standard animal not larger than 0.05 cm, at each site. The Mediterranean Sea is characterised by narrow tidal amplitude (not more than 30–50 cm; Sarà et al., 2011, 2014), so that the role of wave splash, which in turn is driven by wave height, can easily overwhelm the effects of the tide in driving patterns of aerial exposure (Helmuth et al., 2005). Because wave height data were not available for the sites investigated during the study period, hourly wind data from the ISPRA website were used to scale sea conditions according to the empirical Beaufort scale. We then converted Beaufort scale scores into wave heights using the following empirical formula: Beaufort = cube root of wind velocity (km × h^{-1})/9 (Beer, 1997), assuming open-sea conditions. A Beaufort 3 (indicating a wave height of ~ 0.6–1.0 m) is the sea condition at which intertidal organisms positioned at MLLW + 0.35 m should experience wave splash when the still tide level is approximately at mean sea level. Using this approach, we estimated, on an hourly basis, for each site (1) the mean annual BT of intertidal (MLLW + 0.35 m) animals (OPTIMUM); (2) the amount of emersion (OFF) and immersion (ON) time as a proxy of feeding reduction; (3) the periods during which animals experienced Tb < 5 °C (COLD) and (4) the number of exposures with Tb > 35 °C (HOT, ~ 8 °C higher than the normal maximum summer water temperature). This was an assumption in our modelling approach, as there were no data on meiofauna thermal tolerances and we therefore set our model boundaries to those of the mussels above. These measures were expressed as a percentage of exposure time (%). Moreover, we calculated the average wave fetch using the method of Burrows et al. (2008) and reported this in km. The values of temperature and salinity used in this study were derived from the hourly seawater temperature measured about 1 m below the surface, in each site, by the Italian Oceanographic Buoy Network maintained at ISPRA (http://www.mareografico.it/) and satellite-derived Sea Surface Salinity (SSS) daily data, obtained from Copernicus Marine Service Products (marine.copernicus.eu). We considered the mean of values for 3 days before the sampling day.

Trophic variables: phytopigments and biochemical variables

Total phytopigments (CPE) were estimated as the sum of chlorophyll-a and phaeopigments (Pusceddu et al., 2003) from sediments collected from each plot per site. Phytopigments were extracted (12 h at 4°C in the dark) using 5 ml of 90% acetone, according to Lorenzen and Jeffrey (1980). Extracts were analysed spectrophotometrically (Shimadzu, UV spectrophotometer) to estimate chlorophyll-a and, after acidification by 200 µl 0.1 N HCl, to estimate phaeopigment concentrations. Phytopigment concentrations were normalised to sediment dry weight (60°C, 24 h) and reported as µg g^{-1}. Similarly, proteins (PRT), carbohydrates (CHO) and lipids (LIP), a biochemical proxy of quantity, quality and organic matter composition available to meiofauna, were collected from the same quadrats and analysed in triplicate on sediment samples using spectrophotometric methods (Pusceddu et al., 2003; Danovaro, 2010). The concentrations were expressed as bovine serum albumin, glucose and tripalmitine equivalents, respectively, and for each biochemical assay, blanks were obtained using precombusted sediments (450°C for 4 h). We estimated the total biopolymeric carbon (BPC; Pusceddu et al., 2003) as the sum of CHO, PRT and LIP, previously converted into carbon equivalent by 0.40, 0.49 and 0.75 mg C mg^{-1} factors, respectively. Furthermore, we used phytopigment contribution (CPE/BPC%)—having converted CPE concentration into carbon equivalents using a mean value of 40 µg C $µg^{-1}$ (Pusceddu et al., 2003)—and protein contribution (PRT/BPC%) to BPC concentrations and the values of the protein-to-carbohydrate ratio (PRT:CHO) as descriptors of the ageing and nutritional quality of sediment organic matter (Pusceddu et al., 2010).

Meiofauna analysis

Meiofaunal samples were sieved through a 37-µm mesh. The fraction retained on the sieve was resuspended and centrifuged three times with Ludox HS40 (diluted with water to a final density of 1.18 g cm^{-3}; Heip et al., 1985). The material collected was preserved in 50-ml tubes with 4% buffered formalin and staining with Rose Bengal (0.5 g l^{-1}). Meiobenthic organisms were counted and classified at the

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Table 1 Types of substrate coverage, latitude, longitude and values of all studied parameters (reported in % or mean ± standard deviation): temperature, salinity, exposure time to low (COLD), high (HOT) and optimal (OPTIMUM) temperature, immersion (ON) and emersion (OFF) time, wave fetch, concentrations of proteins (PRT), carbohydrates (CHO), lipids (LIP), biopolymeric carbon (BPC) and total phytopigments (CPE), contribution of CPE and PRT to BPC (CPE/BPC% and PRT/BPC%) and PRT-to-CHO ratio (PRT:CHO), meiofaunal abundance, meiofaunal taxa richness and Shannon–Wiener (H'), Pielou (J') and Margalef (D) diversity indexes of meiofauna

Variables	Trieste	Ancona	Livorno	Orbetello	Gaeta	Taranto	Otranto	Palinuro	Palermo	Mazara del Vallo	Porto Empedoclee
Coverage	M	M	A	A	M	A	M	A	M	A	A
Latitude (N)	45.74	43.57	43.48	42.44	41.22	40.37	40.03	40.02	38.03	37.61	36.69
Longitude (E)	13.67	13.59	10.33	11.15	13.50	17.31	18.45	15.29	13.59	12.62	15.14
Temperature (°C)	21.4 ± 1.1	22.8 ± 0.2	20.6 ± 1.6	20.4 ± 0.5	22.7 ± 0.2	24.4 ± 0.5	24.7 ± 0.5	23.9 ± 0.3	26.2 ± 0.0	25.8 ± 0.2	20.8 ± 0.2
Salinity (psu)	37.7 ± 0.0	34.9 ± 0.1	38.1 ± 0.0	38.2 ± 0.0	38.1 ± 0.0	39.2 ± 0.0	38.7 ± 0.0	38.1 ± 0.0	38.4 ± 0.0	37.9 ± 0.0	38.9 ± 0.0
COLD (%)	4.8	6.1	2.2	2.4	1.0	1.6	1.6	0.9	0.1	0.1	0.1
OPTIMUM (%)	89.9	83.9	90.2	88.9	92.8	82.2	82.2	77.7	83.6	83.5	91.5
HOT (%)	5.3	10.0	7.6	8.7	6.2	16.3	16.3	20.1	16.3	16.2	8.5
ON (%)	31.0	5.2	14.6	8.8	20.3	1.8	1.8	0.1	26.7	26.0	20.3
OFF (%)	69.0	94.8	85.4	91.3	79.8	98.2	98.2	98.2	73.2	73.7	79.8
Wave fetch (km)	1.75	3.67	3.73	1.26	3.98	2.80	3.45	2.54	3.95	4.21	3.37
PRT (mg g^{-1})	1.9 ± 0.5	0.4 ± 0.1	0.2 ± 0.0	0.3 ± 0.0	0.1 ± 0.0	0.3 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.3 ± 0.0	0.7 ± 0.2	0.1 ± 0.0
CHO (mg g^{-1})	0.9 ± 0.2	0.2 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.6 ± 0.2	0.2 ± 0.0
LIP (mg g^{-1})	0.3 ± 0.1	0.04 ± 0.0	0.03 ± 0.0	0.1 ± 0.0	0.03 ± 0.0	0.1 ± 0.0	0.3 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
BPC (mg g^{-1})	1.5 ± 0.3	0.3 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.1 ± 0.0	0.3 ± 0.0	0.4 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.6 ± 0.0	0.2 ± 0.0
CPE (μg g^{-1})	8.2 ± 0.9	1.3 ± 0.3	0.6 ± 0.2	2.2 ± 0.4	0.8 ± 0.1	2.7 ± 0.1	2.0 ± 0.2	0.7 ± 0.1	1.7 ± 0.4	1.0 ± 0.1	0.7 ± 0.2
CPE/BPC %	22.7	17.5	11.3	29.1	22.4	31.0	21.9	5.3	27.4	6.8	17.3
PRT/BPC %	61.4	65.2	40.2	46.1	37.1	47.7	28.6	41.2	50.3	53.7	33.8
PRT:CHO	2.1 ± 0.3	2.3 ± 0.4	0.7 ± 0.3	1.1 ± 0.2	0.7 ± 0.1	1.5 ± 0.3	1.6 ± 0.1	0.9 ± 0.1	1.7 ± 0.1	1.2 ± 0.3	0.8 ± 0.1
Total meiofauna (ind. 100 cm^{-2})	5862.0 ± 1464	1335.0 ± 247.8	4697.7 ± 799.4	3792.0 ± 570.1	7363.0 ± 1843.2	6634.3 ± 1255.2	2178.7 ± 114.6	2819.0 ± 594.1	2049.7 ± 414.0	2602.7 ± 517.5	8788.5 ± 79.5
Taxa Richness	9.67 ± 2.1	7.3 ± 2.5	10.0 ± 0.0	13.7 ± 1.5	13.3 ± 2.5	14.3 ± 0.6	13.3 ± 0.6	12.3 ± 0.6	9.0 ± 1.0	11.3 ± 2.1	11.7 ± 1.5
H'	0.9 ± 0.1	0.9 ± 0.2	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.1	1.1 ± 0.0	1.5 ± 0.1	1.2 ± 0.1	1.1 ± 0.0	0.9 ± 0.1	1.0 ± 0.0
J'	0.38 ± 0.0	0.44 ± 0.1	0.42 ± 0.0	0.40 ± 0.0	0.39 ± 0.0	0.40 ± 0.0	0.58 ± 0.0	0.46 ± 0.0	0.50 ± 0.0	0.37 ± 0.1	0.38 ± 0.0
D	1.5 ± 0.4	1.3 ± 0.4	1.5 ± 0.0	2.1 ± 0.3	1.9 ± 0.3	2.0 ± 0.1	2.3 ± 0.1	2.0 ± 0.2	1.5 ± 0.2	1.9 ± 0.3	1.6 ± 0.3

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Table 2 Results of regression analysis (Statistica 6.0, StatSoft) among the principal environmental variables: latitude, longitude, temperature, salinity, exposure time to low (COLD), high (HOT) and optimal (OPTIMUM) temperature, immersion (ON) and emersion (OFF) time, wave fetch, concentrations of biopolymeric carbon (BPC) and total phytopigments (CPE), contribution of CPE and PRT to BPC (CPE/BPC% and PRT/BPC%) and PRT-to-CHO ratio (PRT:CHO)

	Latitude	Longitude	Temperature	Salinity	Cold	Optimum	Hot	ON
Latitude	–							
Longitude	n.s.	–						
Temperature	− 0.51**	0.45**	–					
Salinity	− 0.47**	n.s.	n.s.	–				
Cold	0.83***	n.s	− 0.37*	− 0.73***	–			
Optimum	n.s.	− 0.47**	− 0.63***	n.s.	n.s.	–		
Hot	− 0.55***	0.50**	0.77***	n.s.	− 0.39*	− 0.79***	–	
ON	n.s.	− 0.40*	n.s.	n.s.	n.s.	0.56***	− 0.37*	–
OFF	n.s.	0.40*	n.s.	n.s.	n.s.	− 0.43*	0.44*	− 0.90***
Wave fetch	− 0.48**	n.s.	0.48**	n.s.	− 0.35*	n.s.	n.s.	n.s.
BPC	0.47**	n.s.	n.s.	n.s.	0.43*	n.s.	n.s.	0.48**
CPE	0.57***.	n.s.	n.s.	n.s.	0.48**	n.s.	n.s.	n.s.
PRT/BPC%	0.42*	n.s.	n.s.	-0.65***	0.58***	n.s.	n.s.	n.s.
CPE/BPC%	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
PRT:CHO	0.37*	n.s.	n.s.	-0.51**	0.61***	n.s.	n.s.	n.s.

	OFF	Fetch	BPC	CPE	PRT/BPC%	CPE/BPC%	PRT:CHO
Latitude							
Longitude							
Temperature							
Salinity							
Cold							
Optimum							
Hot							
ON							
OFF	–						
Wave fetch	n.s.	–					
BPC	− 0.47**	− 0.39*	–				
CPE	− 0.35*	− 0.58***	0.88***	–			
PRT/BPC%	n.s.	n.s.	0.51**	0.44*	–		
CPE/BPC%	n.s.	n.s.	n.s.	0.38*	n.s.	–	
PRT:CHO	n.s.	n.s.	0.52**	0.56***	0.71***	n.s.	–

We reported the values of R and P (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, *n.s.* not significant)

major taxa level of taxonomic discrimination using a stereomicroscope (LEICA M80) at 40× magnification. The abundance of total meiofauna and of single taxa was reported to the surface unit (10 × 10 cm area = 100 cm^2).

Statistical analyses

The relationships between geographical gradients and all measured variables (water temperature, salinity, body temperature, emersion and immersion time, wave fetch and trophic resources), and their correlation with abundance and diversity of meiofauna, were examined through linear regressions (Statistica 6.0, StatSoft). Univariate and Multivariate Permutational

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Analysis Of Variance (PERMANOVA; Anderson, 2001; McArdle & Anderson, 2001) was performed to test differences in biochemical components (quantity, quality and organic matter composition) and meiofauna (abundance, taxa richness, diversity indexes and community structure) between the two types of biogenic habitats (algae [A] and mussel [M]; 2 levels, fixed). PERMANOVAs were based on Euclidean distance matrices calculated on normalised data (for organic matter variables) or Bray–Curtis similarity matrices after square root transformation of the data (for meiofaunal parameters), using 9999 random permutations of the appropriate units (Anderson, 2001). Here, we expressed the diversity through taxa richness and a number of diversity indexes, such as the Margalef index (D), Shannon–Wiener index (H') and Pielou's evenness (J'), estimated by the DIVERSE routine (Clarke & Gorley, 2006). Spatial variation of meiofaunal community structure was displayed using a non-metric multidimensional scaling plot (n-MDS), based on the Bray–Curtis similarity matrix calculated from the square-root-transformed species abundance data. SIMPER analyses were performed to assess dissimilarity in meiofaunal community between A and M substrate coverage. Because the general dominance of nematodes and copepods in the meiobenthic communities may mask the changes in the relative importance of the other meiofaunal taxa (Pusceddu et al., 2011), we also considered the community without these two dominant taxa. The analysis, based on the square-root-transformed Bray–Curtis similarity matrix with a cut-off value restricted to 60%, was also performed to identify those taxa mostly contributed to the observed dissimilarity. To identify which were the principal drivers of meiofauna (abundance and community composition) in the presence of algae or mussels, we used distance-based redundancy analysis (dbRDA), based on the Bray–Curtis dissimilarities to obtain plots for each biogenic habitat (McArdle & Anderson, 2001). We performed a draftsman plot (Clarke & Gorley, 2006) to detect possible skewness and/or strong correlation ($R > 0.7$; see Results) among pairs of biotic and abiotic factors and we chose the following as predictor variables: temperature, salinity, OPTIMUM, OFF, fetch, BPC, PRT:CHO, CPE/BPC%. Statistical analyses were performed using the PRIMER v6+ software (Plymouth Marine Laboratory, Clarke & Gorley, 2006).

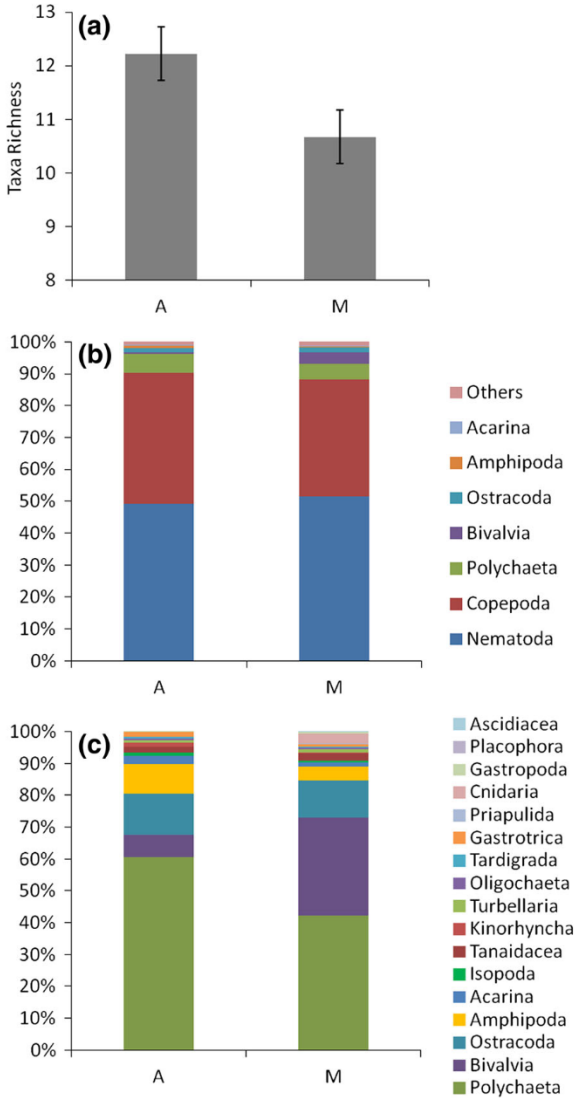


Fig. 2 Taxa richness (mean ± SE) (**a**) and the composition of whole meiofaunal (**b**) and rare taxa (**c**) assemblages in the sites with macroalgae (A) and mussel (M) substrate coverage. In (**b**), we pooled in a single category named 'others' the taxa with percentage lower than 0.5%, generally found in all sites

Results

Gradients of biotic and abiotic factors along intertidal coasts

All factors considered in this study are reported in Table 1. The regression analysis showed that environmental and trophic variables significantly varied along the geographical scale (in particular the north–south axis) (Table 2). Water temperature increased

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Table 3 Results of linear regression analysis (Statistica 6.0) between meiofaunal components (total abundance, abundance of the most abundant taxa and of "others" taxa, taxa richness (*S*), Shannon–Wiener (H'), Pielou (J') and Margalef (*D*) indexes) and latitude, longitude, temperature, salinity, exposure time to low (COLD), high (HOT) and optimal (OPTIMUM) temperature, immersion (ON) and emersion (OFF) time, wave fetch, concentrations of proteins (PRT), carbohydrates (CHO), lipids (LIP), biopolymeric carbon (BPC) and total phytopigments (CPE), contribution of CPE and PRT to BPC (CPE/BPC% and PRT/BPC%) and PRT-to-CHO ratio (PRT:CHO)

	Tot abund	Nematoda	Copepoda	Polychaeta	Bivalvia	Ostracoda	Amphipoda	Acari	Others	Taxa	H'	J'	*D*
Latitude	n.s.	n.s.	n.s.	n.s.	n.s.	–	− 0.37*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Longitude	n.s.	n.s.	n.s.	n.s.	0.40*	n.s.	n.s.	n.s.	0.48**	n.s.	0.58***	0.47**	n.s
Temperature	–0.48**	–	-0.35*	n.s.	n.s.	0.55***	n.s.	n.s.	n.s.	n.s.	n.s.	0.41*	n.s.
Salinity	0.48**	0.45**	0.38*	n.s.	n.s.	0.38*	n.s.	n.s.	n.s.	0.61***	0.38*	n.s.	0.45**
COLD	n.s.	n.s	n.s	n.s.	n.s.	–	n.s.	n.s.	n.s.	–	n.s.	n.s.	–
OPTIMUM	0.60***	0.65***	0.52**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	–	–	n.s.
HOT	–	–0.57***	− 0.39*	n.s.	n.s.	0.49**	n.s.	n.s.	n.s.	n.s.	0.46**	0.42*	0.38*
ON	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	–	–	–
OFF	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.46**	0.34*.	0.43*
Wave fetch	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
BPC	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.47**	n.s.	n.s.	n.s.	n.s.
CPE	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	− 0.40*	n.s.	0.38*	n.s.	n.s.	n.s.	n.s.
PRT/BPC%	n.s.	n.s.	n.s.	− 0.41*	–	n.s.	− 0.46**	n.s.	n.s	–	–	n.s.	–
CPE/BPC%	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.36*	n.s.	n.s.	n.s.	n.s.	n.s.
PRT:CHO	–	− 0.44*	n.s.	− 0.51**	n.s.	n.s.	− 0.44*	n.s.	n.s.	–	n.s.	n.s.	n.s.

We reported the values of *R* and *P* (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, *n.s.* not significant)

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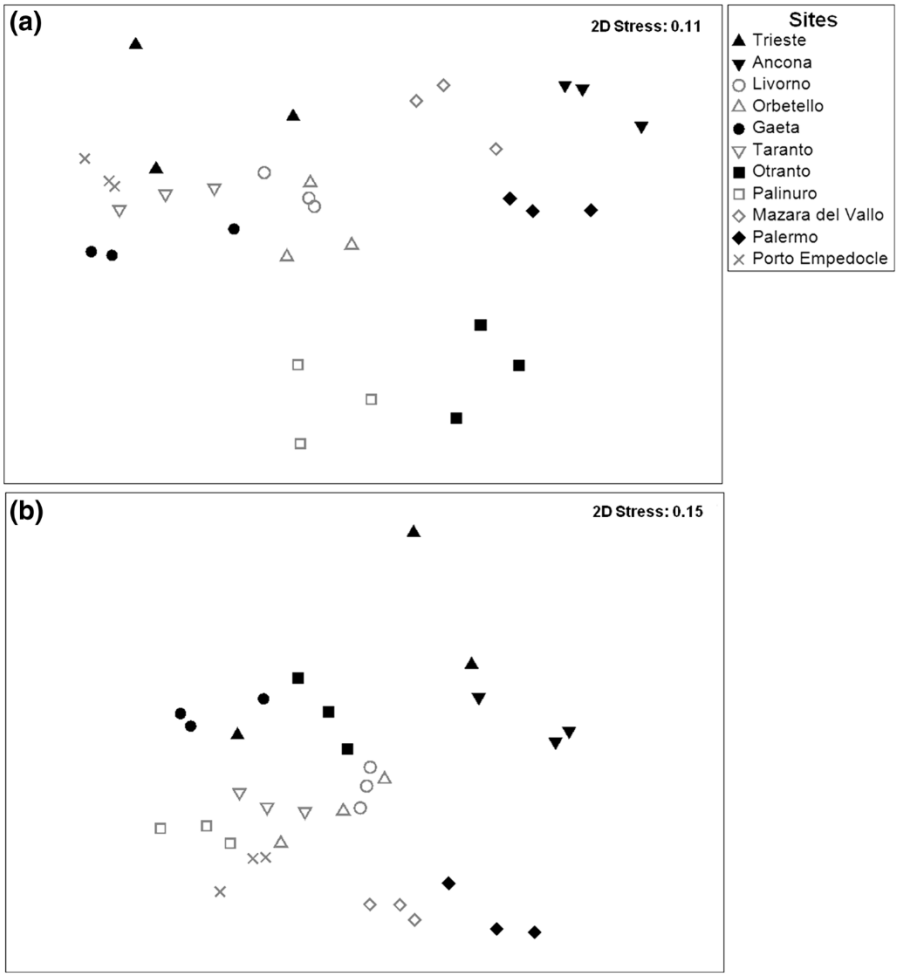


Fig. 3 Non-metric multidimensional scaling (n-MDS) plot, based on a Bray–Curtis distance matrix calculated from the square-root-transformed, of the whole meiofaunal (**a**) and rare taxa (**b**) assemblages, between macroalgae (grey empty symbols; A) and mussel (black filled symbols; M) substrate coverage, with dissimilarity (%) resulting from SIMPER analysis

towards the south and from the west to the east ($P < 0.01$; Table 2), influencing positively HOT and negatively COLD and OPTIMUM ($P < 0.001$, $P < 0.05$ and $P < 0.001$, respectively; Table 2); also, salinity and wave fetch increased from the north to the south ($P < 0.01$; Table 2). Emersion time (OFF) increased from the west to the east coast due to increased tidal range ($P < 0.05$; Table 2). Sedimentary organic matter descriptors (CPE and BPC concentrations, PRT:CHO ratio and PRT/BPC%) showed a significant increase towards north ($P < 0.05$; Table 2). CPE and BPC concentrations in the sediment displayed a correlation with local variables: positive with COLD ($P < 0.05$) and negative with wave fetch ($P < 0.01$) and OFF ($P < 0.05$). The shorter the fetch and the longer the immersion time, the higher the concentration of organic matter in intertidal habitats (Table 2). The nature of substrate cover affected both concentration and quality of trophic resources. We observed significantly higher concentration of sedimentary CPE (PERMANOVA, $P < 0.05$; Online Resource 1) and significantly higher values of PRT:CHO ratio (PERMANOVA, $P < 0.001$; Online Resource 1) in the sites characterised by M coverage than in those with A coverage, with a consequent significant difference in biochemical composition between the two biogenic habitats (PERMANOVA, $P < 0.05$; Online Resource 1).

Influence of environmental variables and biogenic habitat on intertidal meiofauna

Total meiofaunal abundance ranged from 1335.0 ± 247.8 (Ancona) to 8788.0 ± 79.5 ind. 100 cm^{-2} (Porto Empedocle; Table 1). In all investigated sites, meiofaunal communities were dominated

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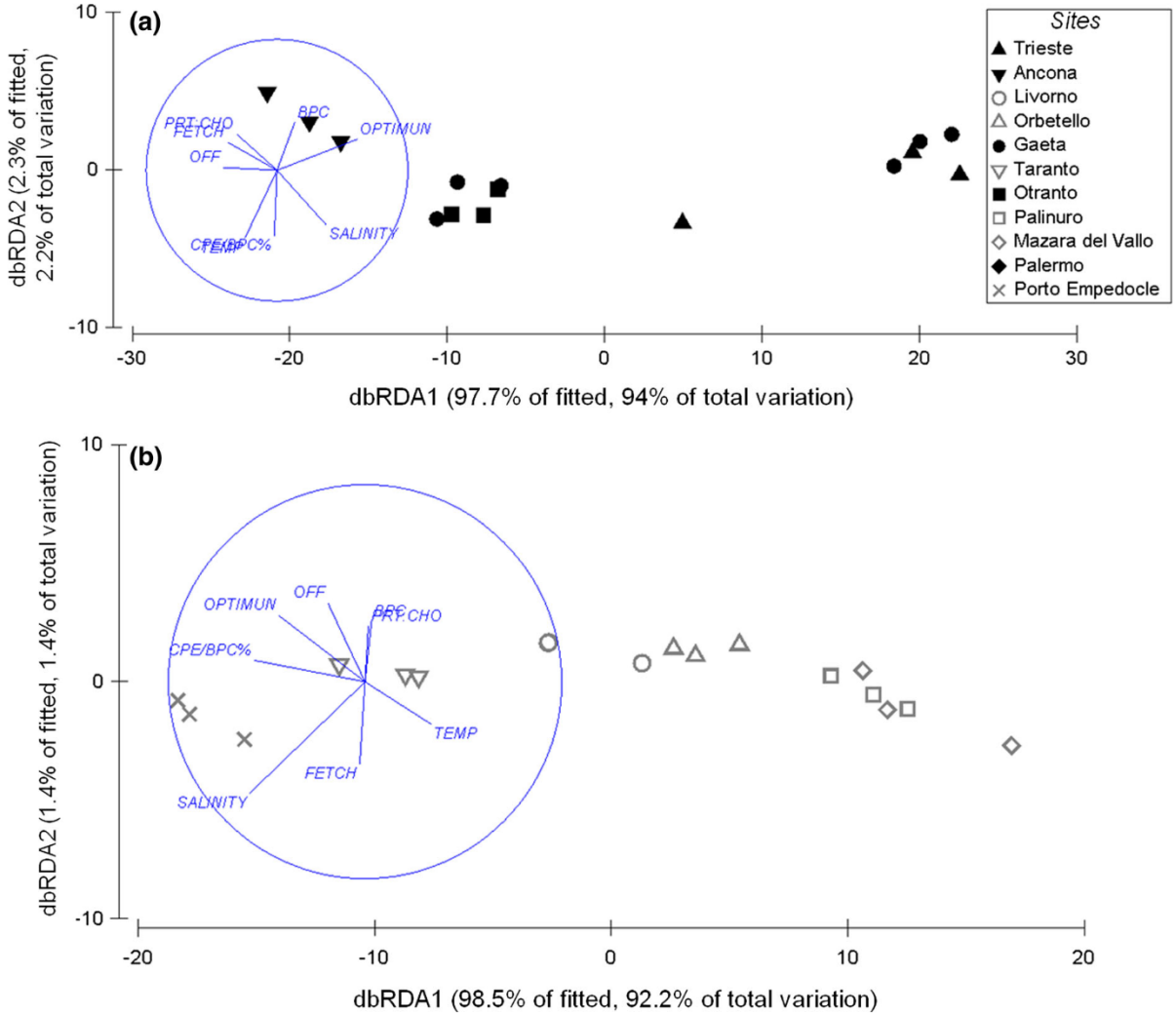


Fig. 4 Distance-based redundancy analysis (dbRDA) of (**a**) sites with mussel coverage (black filled symbols; M) and (**b**) the sites with macroalgae coverage (grey empty symbols; A) to investigate the relationships between meiofaunal abundance and temperature, salinity, exposure time to thermal optimum (OPTIMUM) emersion time (OFF), wave fetch, concentrations of biopolymeric carbon (BPC), contribution of CPE to BPC (CPE/BPC%) and PRT-to-CHO ratio (PRT:CHO)

by nematodes (25–61%) and copepods (18–68%), followed by polychaetes, bivalves, ostracods, amphipods and acarina (Fig. 2b). We pooled in a single category named 'others' the taxa with a percentage lower than 0.5%, generally found in all sites (isopoda, tanaidacea, kinorhyncha, turbellaria, oligochaeta, tardigrada, gastrotricha) and more rare taxa (priapulida, cnidaria, gastropoda, placophora, ascidiacea). The results of linear regression between meiofauna and environmental variables are reported in Table 3. A significant decrease in the abundance of total meiofauna and of nematodes and copepods was detected with the increase of water temperature and HOT. Conversely, meiofaunal abundances were significantly higher in the sites with higher OPTIMUM values. The abundance and diversity (in terms of taxa richness, H' and D indexes) of meiofauna increased with salinity. All diversity indexes were also positively correlated with HOT and OFF, but negatively with OPTIMUM. Both abundance—in particular that of polychaetes—and diversity (in terms of taxa richness, H' and D indexes) of meiofauna were negatively influenced by the quality of organic matter (PRT/BPC% and PRT:CHO). The group of "others"

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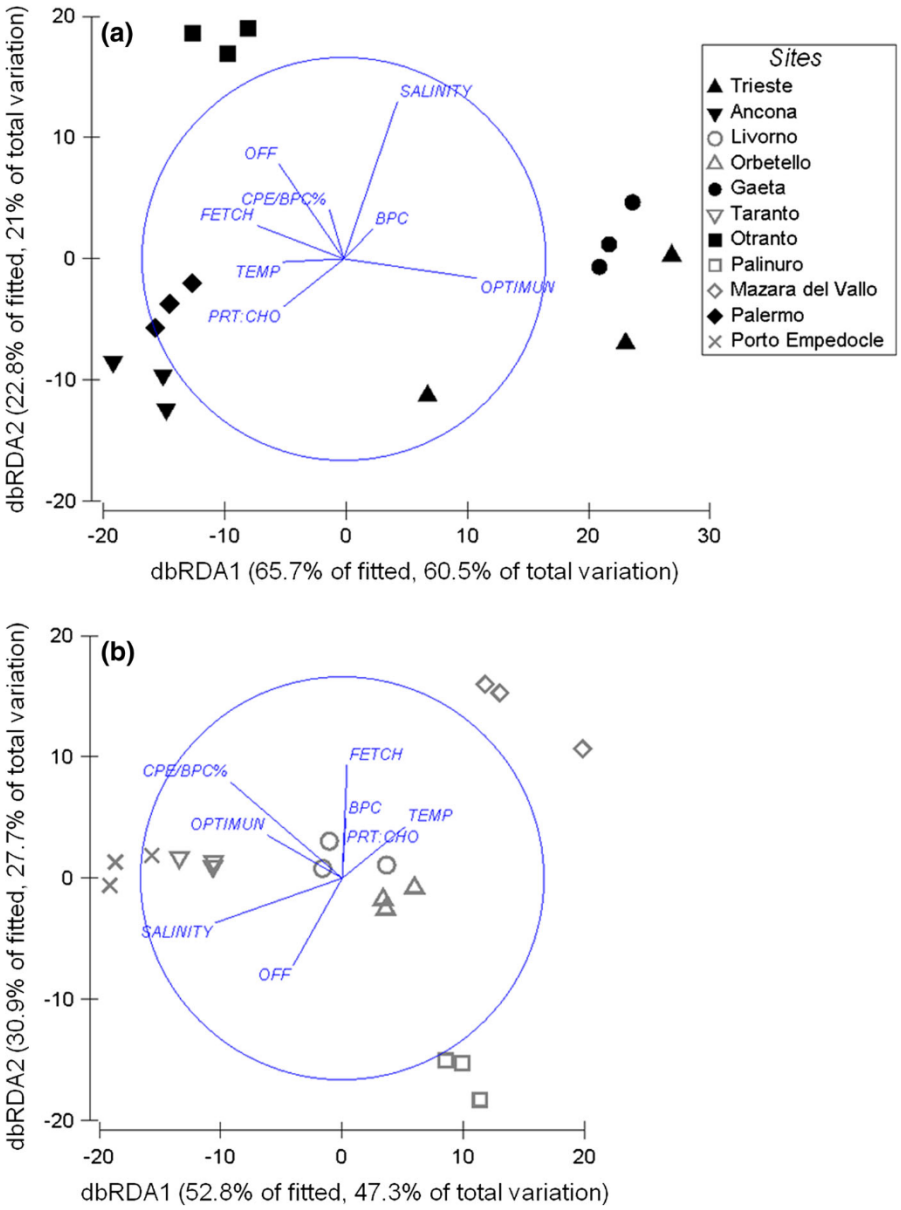


Fig. 5 Distance-based redundancy analysis (dbRDA) of (**a**) sites with mussel coverage (black filled symbols; M) and of (**b**) the sites with macroalgae coverage (grey empty symbols; A) to investigate the relationships between meiofaunal communities' composition and temperature, salinity, exposure time to thermal optimum (OPTIMUM) emersion time (OFF), wave fetch, concentrations of biopolymeric carbon (BPC), contribution of CPE to BPC (CPE/BPC%) and PRT-to-CHO ratio (PRT:CHO)

was correlated (positively) with organic matter concentration (BPC and CPE). PERMANOVA analysis ($P < 0.05$; Online Resources 2) showed that meiofaunal community significantly differed between habitat types (A vs. M) (Fig. 2b, c). SIMPER analyses revealed 31% of dissimilarity between A and M substrate coverage for all meiofaunal communities (MDS Fig. 3a). This difference became more evident without nematodes and copepods (dissimilarity of 49%), and was mostly explained by polychaetes and bivalves, followed by ostracods and amphipods (MDS Fig. 3b).

Polychaetes, amphipods and ostracods were significantly higher in terms of abundance and percentage contribution to total meiofaunal abundance in the sites characterised by A coverage (PERMANOVA, $P < 0.05$; Online Resources 2), where we also found significantly higher meiofaunal taxa richness (PERMANOVA, $P < 0.05$; Online Resources 2), than in those with M coverage (Table 1; Fig. 2a–c). Conversely, meiofaunal bivalves were significantly most

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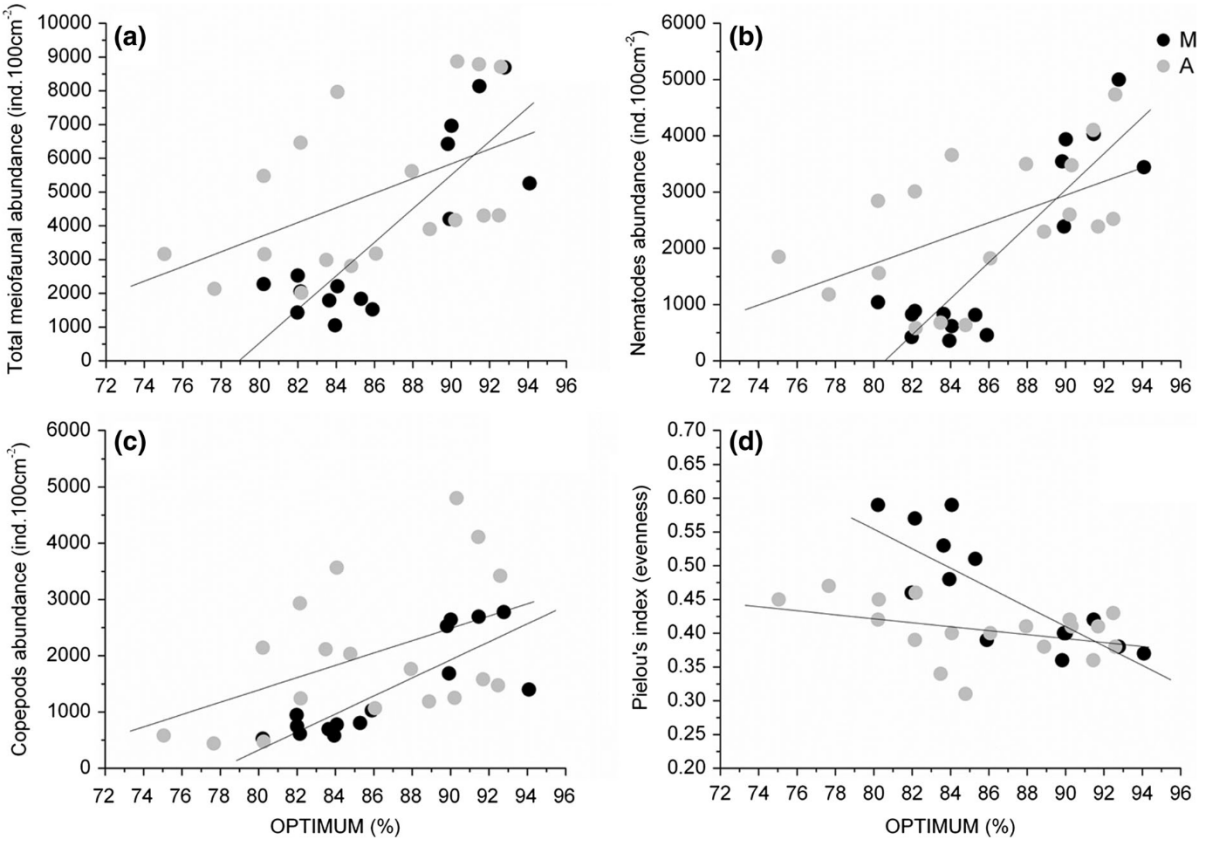


Fig. 6 Linear regressions between the values of OPTIMUM and abundance of (**a**) total meiofauna ($R = 0.84$; $P < 0.001$ in M, $R = 0.50$; $P < 0.05$ in A), (**b**) nematodes ($R = 0.88$; $P < 0.001$ in M, $R = 0.54$; $P < 0.05$ in A) and (**c**) copepods ($R = 0.82$; $P < 0.001$ in M, $R = 0.46$; $P =$ n.s. in A), (**d**) Pielou's index ($R = -0.79$; $P < 0.001$ in M, $R = -0.38$; $P =$ n.s. in A) in the sites with macroalgae (grey dots; A) and mussel (black dots; M) substrate coverage

abundant in the sites characterised by mussels (PERMANOVA; $P < 0.01$; Online resources 2). The abundance of each meiofaunal taxon was reported in Online Resources 3.

The dbRDA plot of the sites characterised by M coverage (Fig. 4a) showed that the first two axes were explaining up to 97.7 and 2.3% of the variation of the fitted model, and up to 94.0 and 2.2% of the total variation in total meiofaunal abundance. As regards the community composition (Fig. 5a), the first two axes explained up to 65.7 and 22.8% of the variation of the fitted model, and up to 60.5 and 21% of the total variation. In both plots, the vectors of the drivers showed the importance of the exposure time to thermal optimum (OPTIMUM), representing the most important predictor variable, followed by emersion time (OFF) for the abundance and fetch for community. In the sites characterised by A coverage (Fig. 4b), the first two axes of the dbRDA plot explained up to 98.5 and 1.4% of the variation of the fitted model, and up to 92.2 and 1.4% of the total variation in meiofaunal abundance. The dbRDA plot performed on community composition (Fig. 5b) showed that the first two axes were explaining up to 52.8 and 30.9% of the variation of the fitted model, and up to 47.3 and 27.7% of the total variation. In both plots, we observed that the variability among sites was based on salinity and CPE/BPC%, representing the most important predictor variables, followed by OPTIMUM.

Discussion

Here, we investigated the role of abiotic and biotic factors on the distribution and diversity of intertidal meiofauna along the Italian coast. What emerges from

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this study (although not specifically tested) is that the tangle of biotic and abiotic factors, rather than a single main driver, affected the distribution and diversity of intertidal meiofauna, for example at southern sites higher water temperature, combined with local thermal conditions (i.e. exposure time to temperatures higher than their thermal OPTIMUM), reducing the abundance of nematodes and copepods and consequently of total meiofaunal abundance. Higher salinity values in southern sites while interacting with site-specific factors, such as emersion time and thermal conditions, favoured the presence of a more diversified intertidal meiofaunal community. However, the presence of different habitat-forming species (macroalgae vs. mussels) differently influenced the community structure of meiofauna on intertidal substrate and their response to environmental factors, concurring with environmental variables to affect the distribution and diversity of meiofaunal organisms along the intertidal Italian coast.

Intertidal zones have been considered to be physically stressful environments, where meiofaunal communities are subjected to a complex array of environmental factors (Hulings & Gray, 1976; Kotwicki et al., 2005; Albuquerque et al., 2007; Covazzi-Harriague et al., 2013; Kotwicki et al., 2014). Temperature can affect the distribution of meiofauna either directly, e.g. in exposed rocky shores, where extreme thermal conditions and desiccation rate can affect the community structure (Hulings & Gray, 1976)) or, indirectly, promoting biological interactions such as predation and competition (Coull, 1999; Du et al., 2012). Nevertheless, our results showed that the higher water temperature in the southern Italian sites and the associated local thermal conditions, in particular the decrease in exposure time to thermal OPTIMUM of meiofaunal organisms and increase in exposure time to HOT, appeared to cause a reduction in the abundance of total meiofauna and in the dominant taxa, nematodes and copepods (Fig. 6). In fact, Wieser and Shiemer (1977) affirm that the distribution of meiofauna, in particular of some nematode species, in subtropical beach was not determined by temperatures at a given time but by the maximum temperature experienced in their habitats. Salinity was another significant factor affecting our meiofaunal organisms. Accordingly, the increase in salinity, towards the south, showed a positive correlation with abundance and diversity (in terms of taxa richness, H' and D indexes) of meiofauna, confirming the results of other studies (Chatterji et al., 1995; Ingole & Parulekar, 1998). The relationship between longitude-related factors, higher emersion time (OFF) and higher exposure time to HOT temperature (lower OPTIMUM) appeared to cause the major increase in meiofaunal diversity. This could be explained by the capacity of some meiofaunal taxa to endure a lack of water and high temperatures reducing their metabolism (i.e. tardigrades; De Zio & Grimaldi, 1966), or it could be due to their terrestrial origin (i.e. oligochaetes and some nematode orders; Jansson, 1968; Gheskiere et al., 2005). Local thermal conditions influenced the community evenness (J') especially, which showed higher values in sites where the meiofaunal organisms were exposed to lower thermal OPTIMUM (Fig. 6). This suggests the presence, in these sites, of communities with higher equitability of distribution, caused by the decrease of dominant taxa (nematodes and copepods) abundance as OPTIMUM decreases. Although data on higher taxa could not reflect the biodiversity patterns at species level, our findings can help better understand the influence of abiotic and biotic factors on meiofaunal taxa distribution at large spatial scale. Trophic resources also represent important factors in controlling meiofaunal communities (Soltwedel, 2000; Giere, 2009). We observed that trophic resources were influenced by wave energy and tidal amplitude: the higher the emersion time and wave fetch, the lower the concentration of sedimentary organic matter, probably due to a reduction in the amount of deposited organic matter (Semprucci et al 2011; Covazzi-Harriague et al., 2013).

However, the physical action is entangled with the exertion of fine sediment and organic matter trapping by habitat formers (both macroalgae and mussels; Arroyo et al., 2004; Cole, 2010; Du et al., 2012). In fact, biogenic habitat plays a key role in structuring the meiofaunal communities through provision of shelter and food (Gibbons, 1988a,b; Danovaro & Fraschetti, 2002; Arroyo et al., 2004; Danovaro et al., 2007; Logan et al., 2008; Urban-Malinga et al., 2008). While there are a few studies discussing the facilitation role of mussels on meiofauna—and most of the focus is on biodeposition effects, with sometime contrasting results—the general outcome is that organic matter emitted into mussel beds increases meiofaunal abundances (Norling & Kautsky, 2008). Some of our descriptors of quality and quantity confirmed this

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pattern: higher concentrations of CPE and PRT:CHO ratio in the sediment organic matter in the sites characterised by the presence of mussels more than in those with algae coverage. Despite the importance of quantity and quality of organic matter for meiofaunal organisms (Soltwedel, 2000; Pusceddu et al., 2011), some taxa (e.g. polychaetes) were more abundant when associated with algae, where the protein contribution was lower than in the substrates colonised by mussels. As a main consequence, our results lead us to hypothesise that the structural function of substrate coverage could be more important than its trophic rule. In fact, we found higher meiofaunal taxa richness associated with the presence of macroalgae. We also observed that differences in community compositions, tested between the two types of substrate coverage (algae and mussels), became more evident when we excluded dominant taxa (nematodes and copepods, Pusceddu et al., 2011). These differences were mostly explained by the abundance of polychaetes, amphipods, ostracods and bivalves. Habitat features could play a key role in the supply and settlement of the temporary meiofaunal taxa (Bianchelli et al., 2010); in fact some rare taxa, frequently encountered as temporary meiofauna, appeared to prefer a substrate colonised by algae (e.g. polychaeta, amphipoda, isopoda) and instead other taxa preferred the presence of mussels (e.g. bivalvia, priapulida, oligochaeta, gastropoda, cnidaria and ascidiacea). The higher abundance of crustaceans taxa (in particular ostracods and amphipods) associated with the presence of algae could be due to their biological cycle being closely related to macroalgae, which in turn offers them nutrition and refuge from predation (Danovaro & Fraschetti, 2002; Frame et al., 2007; Logan et al., 2008).

Macroalgae, in particular canopy algae such as Cystoseira sp., can reduce the impact of physical and biological factors, maintaining high levels of diversity in rocky shore habitats (Gibbons, 1988b; Benedetti-Cecchi et al., 2001; Crowe et al., 2013). Consistent with this, our results showed that the influence of thermal conditions (i.e. exposure time to thermal OPTIMUM) on the distribution of nematodes and copepods and, consequently, of total meiofauna and community composition, was lower in the sites characterised by the presence of macroalgae than in those with mussels (Figs. 5, 6). This could be the result of macroalgae's greater capacity to protect meiofaunal organisms from thermal stress with regard to mussels. The exposure time to thermal OPTIMUM negatively influenced the community evenness (J'), significantly only in the presence of mussels, that was probably caused by the higher abundance and dominance of nematode and copepods associated with this biogenic substrate coverage at higher values of OPTIMUM (as previously explained) (Fig. 6).

Conclusions

In conclusion, our results highlighted that the interplay among environmental factors and habitat-forming species results in sites with peculiar combinations of environmental conditions. This supported the current trend that the study of factors affecting the distribution of organisms needs to be tailored to the organism and recipient habitat, based on prior assessment of the relationship between drivers acting on multi-scales. While the main outcome of this study was based on a coarse level of taxonomic identification and we are aware that more details are needed, it can help in a context of conservation and could allow a better understanding of the mechanisms of recruitment of specific taxa in different habitats. Conservation measures could be tailored at local scale in order, for example, to preserve habitat-forming species (i.e. macroalgae), which act as ecological facilitators in harsh and stressful habitats such as the intertidal via their role as complexity and heterogeneity effectors. Indeed, they may be able to promote higher meiofaunal diversity, with important cascading effects on higher trophic levels. However, further studies are required to investigate the drivers of distribution and biodiversity of meiofauna that more carefully consider biotic interactions (i.e. predation) and anthropogenic impact and examine diversity in species and trophic roles of communities.

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