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Potentially combined effect of the invasive seaweed *Caulerpa cylindracea* (Sonder) and sediment deposition rates on organic matter and meiofaunal assemblages

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Abstract

The seaweed *Caulerpa cylindracea* (Sonder) is one of the most successful marine bioinvaders worldwide. *Caulerpa cylindracea* can influence the quantity and biochemical composition of sedimentary organic matter (OM). However, it is still unknown if the effects of *C. cylindracea* on both OM and small metazoans (i.e. meiofauna) can change according to different sediment deposition rates.

To provide insights on this, we investigated the biochemical composition of sediments along with the abundance and composition of meiofaunal assemblages in sediments colonized and not-colonized by the seaweed *C. cylindracea* under different regimes of sediment deposition.

Our results show that the presence of the invasive alga *C. cylindracea* could alter quantity, biochemical composition, and nutritional quality of organic detritus and influence the overall functioning of the benthic system, but also that the observed effects could be context-dependent. In particular, we show that the presence of *C. cylindracea* could have a positive effect on meiofaunal abundance wherever the sediment deposition rates are low, whereas the contextual presence of high to medium sedimentation rates can provoke an accumulation of sedimentary organic matter, less favourable bioavailability of food for the benthos, and consequent negative effects on meiofauna.

Keywords: bioinvasions, NIS, interactive effects, organic matter quantity and biochemical composition, benthic assemblage’s response, Mediterranean Sea

1. Introduction

Understanding the mechanisms underlying marine bioinvasions' success is straightaway needed and represents a major challenge for the conservation of natural resources and of the goods and services they provide (Thomsen et al., 2011). Effects of bioinvasions on biological diversity are often equivocal (Gribben et al., 2018) with positive and negative impacts on native assemblages depending on the geographical context and on temporal and spatial scales of observation (Rilov and Crooks, 2009; Tamburello et al., 2015; Balestri et al., 2018).

The Mediterranean basin is considered a hotspot of biodiversity (Coll et al., 2010) affected by multiple anthropogenic stressors, climate change, and bionvasions (Zenetos et al., 2012). As a consequence, new effective management strategies, based on a multispecies perspective reflecting the complexity of interactions among stressors, are definitely needed (Mačić et al., 2018; Rockmann et al., 2018). Among the most successful bioinvaders that entered the Mediterranean Sea, the tropical alga *Caulerpa cylindracea* (Sonder) (Belton et al., 2014) is featured by a high adaptability to physical and biotic factors and its spread is apparently not limited by sedimentation, which, instead, severely affects indigenous seaweeds (Airoldi and Cinelli, 1997; Airoldi, 2003; Piazzi et al., 2005), in agreement with studies showing that stressed environments can be easily invaded by invasive allochthonous species (Occhipinti-Ambrogi and Savini, 2003; Zerebecki and Sorte, 2011). The synergistic effect of *C. cylindracea* and sedimentation on a rocky subtidal substrate has been explored by Piazzi et al. (2005) through a manipulative experiment. The authors concluded that native macroalgal communities, and especially erect species, decreased strongly in percent cover when affected by both sediment deposition and *C. cylindracea* (Piazzi et al., 2005).

Recent efforts recognized sedimentary and microbial processes as key drivers of the success of this opportunistic invader (Pusceddu et al., 2016; Rizzo et al., 2017; Gribben et al., 2018). High sedimentation rates (Bulleri et al., 2010; Balata et al., 2015) as well as microbial communities associated with introduced seaweeds could increase its invasion ability (Aires et al.,2013; Aires et al., 2015; Rizzo et al., 2016 a,b; Stabili et al., 2017), with important relations with the colonized sediment and, hence, benthic habitats. Moreover, *C. cylindracea* can promote the formation of up to 15-cm thick sediment layers, which modify hydrodynamics near the seabed (Piazzi et al., 2007; Hendricks et al., 2010), support the algal turf and, consequently, a biotic homogenization (Olden et al., 2004; Bulleri and Benedetti-Cecchi, 2008; Bulleri et al., 2011; Balata et al., 2015). For these reasons, *C. cylindracea* is considered an ecosystem engineer able to affect subtidal habitats of the Mediterranean Sea, acting with other human-driven threats (Bulleri et al., 2011; Bulleri et al., 2016).

The role of *C. cylindracea* in changing biogeochemical processes and associated ecosystem functions at several sediment deposition rates is far less known. The understanding of the underlying mechanisms of *C. cylindracea* success and its impacts on the biogeochemistry of the sediments was the focus of recent studies (Piazzi et al., 2007; Holmer et al., 2009; Hendricks et al., 2010; Matijevic et al., 2013; Pusceddu et al., 2016; Rizzo et al., 2017; Gribben et al., 2018). It is known that sediments colonized by *C. cylindracea* exhibited associated sulphide pools (Holmer et al., 2009; Casu et al., 2009), increased organic matter (OM), total protein and carbohydrate contents and, organic C, N, and P contents, while decreased C turnover rates (Matijevic et al., 2013; Pusceddu et al., 2016). Independently from the environmental conditions, interactions of this invader with native species, microbial processes and hosting sediments may play key roles in its invasion dynamics (Gribben et al., 2018; Bulleri et al., 2018).

Some studies have demonstrated either negative (Gianguzza et al., 2002; Vazquez-Luis et al., 2008; Byers et al., 2010) or positive (Argyrou et al., 1999; Box et al., 2010) effects on native assemblages. Detritivores species can benefit by the presence of the alien algae, which can increase the amount of labile food (Pusceddu et al., 2016); in turn, the presence of *C. cylindracea* can modify the feeding habits of herbivorous and, consequently, their trophic strategy (Vázquez-Luis et al., 2013). The complex structure of the *C. cylindracea* thalli and related rhizoids can increase habitat heterogeneity; on the one hand, this can support communities characterized by species richness levels as high as those observed in not colonized grounds, but with totally different compositions (Vazquez-Luis et al., 2008). Such idiosyncratic responses of the benthos to the presence of *C. cylindracea* suggest that the effects of this alga on the abundance of small metazoans (i.e. meiofauna) living on and into sediments, and on organic matter can vary across sites characterized by different environmental assets. In such a context, we contend that the effects of *C. cylindracea* on meiofauna and sedimentary organic matter attributes can vary under different sediment deposition regimes. To date, interactions between *C. cylindracea* and sedimentation rates were assessed on native macroalgal assemblages by manipulative experiments (Piazzi et al., 2005), but, the combined effects of *C. cylindracea* invasion and sedimentation rates have been neglected, so far.

As natural and anthropogenic sediment deposition can deeply influence the bioavailability of sedimentary organic matter for the benthos and their responses (Albertelli et al., 1999; Pusceddu et al., 2007; Pusceddu and Danovaro, 2009; Mirto et al., 2010), we tested the hypothesis by which the differences in the biochemical composition of sediments along with the abundance and composition of meiofaunal assemblages in sediments colonized and not-colonized by the seaweed *C. cylindracea* vary under different regimes of sediment deposition. Finally, we discuss the potential contribution of sediment deposition rates in the success of the invasive seaweed *C. cylindracea*.

2. Material and Methods

2.1. Study area and sampling strategy

Sampling was carried out within the Marine Protected Area (MPA) of Torre Guaceto (Southern Adriatic Sea, Italy, 40°42′N; 17°48′E, Fig. 1). In coastal dynamics, sediment accumulation depends upon wave action, wave-induced currents, tide-induced or wind-induced currents (Rijn et al., 2013).

To examine the local sedimentary rates, we individuated 3 sites within the MPA of Torre Guaceto (approximately at a distance of 2 km far apart each other) and, in each site, 3 cylindrical PVC sediment traps (height = 45 cm; diameter = 3.5 cm) were deployed over a period of 2 months (24 Jule-26 September 2013) at 5-6 m of depth. The sampling period, corresponding to the months characterized by the vegetative growth of *C. cylindracea*, typically comprised between June and November, was chosen well apart from the period of vegetative rest (a quasi-complete withdrawal), typically from December to May (Piazzi et al., 2001; Ruitton et al., 2005).

Upon their retrieval, the trap samples were placed upright in racks and transported to the laboratory for further processing and analysis. Particle-trapping rates were calculated as mass of particles trapped per unit area (cm^{-2}) per unit time (d^{-1}). All visible organisms were removed from the sand fraction remaining atop the sieve. Fractions were dried in an oven.

To determine mean grain size of the sand fraction, only one sample of the three sediment traps from each sampling site was analyzed. The content of a replicate sediment trap was shaken for 15 min and was sieved successively over 2000 and 63 μm stainless steel mesh sieves to determine the distribution of the <63 μm (silt-clay) and 63–2000 μm (sand) fractions of the trapped sediment (Botwe et al., 2017). Then, each of the sieved fractions was weighed.

Within each site, two habitat conditions were identified: soft bottom with and without *C. cylindracea*. Sampling on soft bottom with *C. cylindracea* has been carried out where algal cover of the invasive alga overcame 50% of a surface of 50x50 cm (0.25 m^2). For each condition, two areas were randomly chosen at a distance of tens of meters. Within each area, six replicated sediment cores were randomly sampled at a distance of few meters by scuba divers using plexiglass corers (4.7 cm internal diameter). Three of them were dedicated to the analysis of sediment organic matter and three to the analysis of meiofauna. Sampling was carried out in September 2013. The morphological identification of *C. cylindracea* was performed through analysis of different parts of the thalli (Belton et al., 2014).

Samples were immediately brought to the laboratory for preservation and/or processing. The cores were preserved with buffered 4% formaldehyde solution and stained with Rose Bengal (0.5 g L^{-1}) for meiofaunal counts. For the biochemical composition of organic matter the top 1 cm layer of the replicate sediment cores were immediately frozen and stored at -20°C until analysis.

2.2. DNA extraction, amplification and sequencing

The morphological identification of the seaweed was confirmed after DNA extraction, amplification and sequencing. More in details, genomic DNA was isolated by a CTAB DNA extraction method (Varela-Álvarez et al., 2006). Amplification by PCR was performed in a master mix of volume 25 µL containing 5 pmol of each primer; 200 µM of each dNTP; 1X assay buffer; and 1.25 units of Taq DNA polymerase. The reactions were exposed to the following PCR profile using the specificprimers TufA-F (TGAAACAGAAMAWCGTCATTATGC) and TufA-R (CCTTCNCGAATMGCRAAWCGC) (Famà et al., 2002): 35 cycles of denaturation (94 °C for 1 min), primer annealing (50 °C for 1 min), and extension (72 °C for 2 min). A 5-min final extension cycle at 72 °C followed the 40th cycle to ensure the completion of all novel strands. PCR products were purified and sequenced. Sequences were made available on GenBank database with the accession number KY773571.

2.3. Quantity and biochemical composition of sedimentary organic matter

Protein, carbohydrate and lipid contents were analysed spectrophotometrically (Danovaro, 2009), and expressed as albumin, glucose and tripalmitine equivalents, respectively. For each biochemical assay, blanks were obtained using pre-combusted sediments (450 °C for 4 h), and analyses were performed on triplicate superficial (0-1cm) samples. Carbohydrate, protein, and lipid contents were converted into carbon equivalents using the conversion factors 0.40, 0.49, and 0.75, respectively, and their sum reported as biopolymeric C (Fabiano et al., 1995), assumed to represent the semi-labile fraction of sedimentary OM available to meiofauna as food (Pusceddu et al., 2009; Van Oevelen et al., 2011).

2.4. Meiofaunal abundance and composition

Each sediment sample (0–1 cm) was fixed with 4% buffered formaldehyde (in filtered seawater solution) and, once in the laboratory, was sieved through 1000 µm (to retain macrobenthos and macroalgae) and 32 µm (to retain smaller meiofauna) sieves. The sample fraction retained by a 32 µm mesh net was added to Ludox HS 40 (density arranged to 1.18 g cm^{-3}), for density centrifugation extraction (10 min, 800 × g, for 3 times) from the sediment. All metazoans, after staining with Rose Bengal (0.5 g L^{-1}), were counted and classified per taxon under a stereomicroscope (Danovaro, 2009).

2.5. Statistical analyses

Permutational analyses of variance were used to assess differences in sediment deposition rates among sites: i) in meiofaunal abundance and taxonomic composition and ii) in sedimentary OM quantity and biochemical composition, between colonized and not-colonized grounds across sites.

To assess differences in the meiofaunal assemblages among colonized (CS) and not-colonized (NCS) sediments the design consisted of three factors: Site (S, as random factor with 3 levels) *Caulerpa* (C, as fixed factor with 2 levels), and Area (Ar as random factor with 2 levels, nested in C and S) with n = 3 for each combination of factors. The same design was applied to detect differences in the composition of organic matter between sediments colonized and not-colonized by *C. cylindracea*. Multivariate analyses of variance (PERMANOVA) were based on Bray Curtis dissimilarities on untransformed data for meiofaunal assemblages, using 9,999 random permutations of the appropriate units (McArdle and Anderson, 2001). Furthermore, permutational analyses of multivariate dispersion (PERMDISP) on the basis of Bray-Curtis dissimilarity were also performed to test the heterogeneity of multivariate dispersions among sites and among areas (Anderson, 2006; Anderson et al., 2006). PERMANOVA analysis was based on Euclidean distances of previously normalized data for organic matter and sediment deposition rates, using 9,999 random permutations of the appropriate units (McArdle and Anderson, 2001).

When significant differences were encountered ($p< 0.05$), post-hoc pairwise tests for the fixed factor were carried out, to ascertain the consistency of the differences between colonized and not-colonized grounds across sites. Because of the restricted number of unique permutations in the pairwise tests, p values were obtained from Monte Carlo samplings. Non-metric multi-dimensional scaling (MDS) plots were used to show patterns of the detected differences.

To determine whether the sedimentary features influenced meiofaunal assemblages, we carried out multivariate multiple regression analyses (DistLM forward, McArdle and Anderson, 2001) and performed distance-based Redundancy Analysis (db-RDA) plots.

The analyses were performed using the software PRIMER v. 6 (Clarke and Gorley, 2006).

3. Results

3.1. Sediment deposition rates and biochemical composition of sediments organic matter

All of the three sampling sites were characterized by the dominance of the 63-2000 μm fraction (Fig. 2). PERMANOVA on sediment deposition rates exhibited significant differences among the three sites (Table 1). Although the three sites were originally chosen randomly and so treated as a random factor in the PERMANOVA analyses, the comparison of the 3 sites showed that sediment deposition rates significantly decreased from north to south.

Sedimentary protein, carbohydrate, lipid, and biopolymeric C contents along with chlorophyll-a, phaeopigments, and phytopigments are reported in Tables S1. PERMANOVA on organic matter composition as well as on protein, carbohydrate, lipid, biopolymeric C, chlorophyll-a, phaeopigment, and phytopigment contents showed the significant C×S and A(S×C) interactions, indicating a different effect of the invasive seaweed at the scale of both sites and areas (Table 2). The results of the pairwise comparisons indicate that differences in sedimentary OM composition and in carbohydrate and lipid contents between sediments colonized and not-colonized by the seaweed were statistically significant at all sites, except for the site characterized by low sediment deposition rates (Table 3), while pairwise comparisons do not indicate significant differences in chlorophyll-a, phaeopigment, and phytopigment contents. Significant differences in protein and biopolymeric C contents are observed only at one out three sites. The MDS plot shows a segregation of colonized sediments exposed to high and mid sediment deposition rates (Fig. 3), where OM contents are significantly higher than those exposed to low sedimentation rates (Fig. 4, Table S1).

3.2. Meiofaunal abundance and taxonomic composition

Abundance data for each meiofaunal taxon, and for the whole meiofaunal abundance, are reported in Table S2. Overall, meiofauna were dominated by Nematoda representing the 42-94% of the total abundance, followed by Copepoda (5-55%), Polychaeta (0-4%), Ostracoda (0-7%) and other less abundant taxa (Fig. 5).

PERMANOVA on meiofauna assemblages' composition and total abundance showed the significant S×C and A(S×C) interactions, indicating that both composition and abundance varied not consistently in presence/absence of the invasive alga across sites and areas (Table 4). Accordingly, pairwise tests show significant differences between colonized and not-colonized sediments only in one out of three sites (Table 5). The MDS suggests that at low sediment deposition rates, the meiofaunal taxonomic composition shows a higher variability than the meiofauna exposed to high and medium sediment deposition rate (Fig. 6), both in not-colonized and colonized sediments. Vectors proportional to correlations between taxonomic abundances and ordination axes over-imposed to the MDS ordination show that most of the taxonomical groups but Bivalvia are related to colonized areas exposed to low sediment deposition rates (Fig. 6). However, results of PERMDISP showed no differences in multivariate dispersion of assemblages across areas (F = 2.0597 [p = 0.859]) and sites (F = 1.5004 [p = 0.4321]), revealing the absence of a significantly different spatial heterogeneity in the multivariate structure based on taxa relative abundance.

The results of the multivariate multiple regression analyses (DistLM forward) reveal that only sedimentation rates and lipid sedimentary contents explained significantly variations of meiofaunal assemblages, and that sediment features altogether explained cumulatively ca. 38% of meiofaunal assemblages variance. The results of the dbRDA analysis indicate that the sediment characteristics explained, cumulatively for the first 2 axes, 37% of meiofaunal taxonomic composition variance (Fig. 7).

4. Discussion

In this study, we focussed on the potential effects of interactions between the seaweed *C. cylindracea* and different regimes of sediment deposition on the biochemical composition of sediments and the abundance and composition of meiofaunal assemblages. In presence of *C. cylindracea*, our results show an increase in the quantity of sedimentary OM (especially of carbohydrates and lipids) together with changes in organic OM composition, only in sites with either high or medium sediment deposition rates. These results are consistent with previous studies underlining that the presence of *C. cylindracea* can be associated with changes in either the quantity and biochemical composition of sedimentary organic matter (Pusceddu et al., 2016; Rizzo et al., 2017) and, though with contrasting results, meiofaunal abundance and assemblage composition (Sandulli et al., 2004; Pusceddu et al., 2016). On the one hand, sediment deposition, whatever the source, can contribute to progressively trap nutritional resources providing the benthos with bioavailable food, but only within certain thresholds (Manini et al., 2003; Dell'Anno et al., 2008). Once these thresholds are exceeded, as observed for example in presence of the alga *C. taxifolia* (Bishop et al., 2010; Bishop et al., 2013), communities experiencing high loads of algal detritus are exposed to benthic eutrophication and sediment hypoxia and, thus, decrease in abundance and diversity. Analogously, the presence of *C. cylindracea* could increase the trophic status of colonized sediments by releasing its organic compounds to support benthic heterotrophs nutrition (Pusceddu et al., 2016), but depending on different regimes of sediment deposition. Indeed, the nutritional quality of sedimentary organic matter for the benthos is a combination of quantity and bioavailability, so that, according to the optimal foraging theory (Stephens and Krebs, 1986), the higher the organic matter content the lower its bioavailability (Pusceddu et al., 2009). In brief, we can anticipate that, as sedimentation increases, the high-quality algal remains are increasingly diluted within an inorganic matrix, which, overall, decreases its nutritional availability for the benthos. Accordingly, we observed a significant positive effect of *C. cylindracea* on meiofaunal assemblages only in areas characterized by low sediment deposition rates, where the meiofaunal abundance increased in presence of the invasive seaweed.

The presence of *C. cylindracea* can lead to the development of microbial communities specifically adapted to degrade the remains of the algae (Rizzo et al., 2017), whose bioavailability, however, can depend upon interactions with other abiotic factors, including sedimentation, as well as upon the rates of organic matter decomposition (Windham, 2001; Lawson et al., 2012; Hu and Juan, 2014; Pusceddu et al., 2016). Indeed, numerous studies concluded that the effects of bioinvaders on resident communities can vary among different benthic components, also being context-dependent (MacDougall and Turkington, 2005; Piazzi et al., 2005; Bulleri et al., 2010; Heiman and Micheli, 2010; Bulleri and Piazzi, 2015).

According to our hypothesis, our results show that the presence of the invasive alga *C. cylindracea* could alter quantity, biochemical composition, and nutritional quality of organic detritus and influence the overall functioning of the benthic system, but also suggest that the observed effects could be context-dependent. In particular, we have shown that the presence of *C. cylindracea* could have a positive effect on meiofauna wherever the sediment deposition rates are low, whereas the contextual presence of high to medium sedimentation rates can provoke an accumulation of sedimentary organic matter, less favourable bioavailability of food for the benthos, and consequent negative effects on meiofauna. However, the lack of replication in time and of manipulative experiments in our study limit the possibility to infer purely cause-effect relationships between *C. cylindracea* and each of sediment properties and meiofaunal communities, so that other factors could be invoked as responsible for the observed patterns. For example, intraspecific variations in the traits of *C. cylindracea* could also influence associated meiofaunal communities, as recently underlined by a meta-analysis examining the ecological effects of intraspecific variation (Des Roches et al., 2018). This analysis, indeed, concluded that when community composition is altered by indirect interactions, the role of the variation within species becomes relevant influencing, in turn, the surrounding environment (Des Roches et al., 2018). Again, the same factors that led to patchiness in the colonization of *C. cylindracea* might also led to patchiness in other environmental variables, so that sedimentary and meiofaunal variables, while being statistically correlated with *C. cylindracea* presence, could be not directly determined by the alga. Despite these limits, the results of our study represent a further step improving our comprehension of the interactions between bioinvaders and their effects on the biogeochemistry of coastal sedimentary systems and pinpoint that local environmental factors, including sedimentation rates, could interfere with those effects.

Although Marine Protected Areas (MPAs), like our study site, are fundamental operational options for marine conservation, at present, they are considered incapable to face biological invasions (Montefalcone et al., 2015; Caselle et al., 2018; Sala and Giakoumi, 2018). A recent study aimed at prioritizing management actions to decision-makers for the control of marine invasive species (Giakoumi et al., 2019), suggested that the implementation of targeted removal and commercial utilization of *C. cylindracea* could be even an appropriate tool to develop biotechnological and pharmacological applications (Stabili et al., 2016; D'Aniello et al., 2019).

However, the still incomplete knowledge of the complex interactions between bioinvasions and local environmental factors, eventually enforcing their impacts, could limit the efficacy of targeted removal actions, which could succeed under certain local environmental assets and fail in others.

Based on our results, we contend that a better knowledge of the dynamics of sedimentation in coastal systems could be crucial to predict in which conditions the invader could become a potential driver of change of benthic ecosystems', thus providing clues to improve the distribution of management and restoration actions of MPAs invaded by *C. cylindracea* over the local scale.

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Additional information

Competing financial interests: The authors declare no competing financial interests.

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Table 1 Results of multivariate permutational analyses (PERMANOVA) on sedimentary rates across the three investigated sites. df = degrees of freedom; MS = mean sum of squares; Pseudo-F = F value by permutation. P(perm) = probability level; ** = P< 0.01.

Source	df	MS	Pseudo-F	P(perm)
Site	2	1663.80	102.05	**
Residuals	6	16.30		
Total	8			

Table 2 Results of multivariate permutational analyses (PERMANOVA) on the quantity and biochemical composition of sedimentary OM. S= site; C = *Caulerpa* (present vs. absent); A= area. df = degrees of freedom; MS = mean sum of squares; Pseudo-F = F value by permutation; P = permutational level of probability. * = p<0.05; *** = p<0.001; ns = not significant. Only tests relevant to the hypotheses are reported.

		OM composition			**Protein**			**Carbohydrate**			**Lipid**		
Source	**df**	**MS**	**Pseudo-F**	**P**	**MS**	**Pseudo-F**	**P**	**MS**	**Pseudo-F**	**P**	**MS**	**Pseudo-F**	**P**
Site (S)	2	11.32	5.31		2.55	5.88		3.62	8.92		0.99	2.43	
Caulerpa (C)	1	45.76	1.82		12.34	1.97		9.39	1.38		21.01	5.88	
S x C	2	25.13	11.78	***	6.26	14.44	***	6.81	16.77	***	3.58	8.81	*
Area (SxC)	6	2.13	5.99	***	0.43	4.27	***	0.41	4.23	***	0.41	3.99	***
Residuals	24	0.36			0.10			0.10			0.10		
Total	35												

		Biopolymeric C			**Phytopigment**			**Chlorophyll-a**			**Phaeopigment**		
Source	**df**	**MS**	**Pseudo-F**	**P**	**MS**	**Pseudo-F**	**P**	**MS**	**Pseudo-F**	**P**	**MS**	**Pseudo-F**	**P**
Site (S)	2	2.86	8.63		4.17	4.69		7.36	6.73		3.47	4.22	
Caulerpa (C)	1	12.9	1.97		3.01	0.36		1.19	0.25		3.44	0.38	
S x C	2	6.54	19.73	**	8.48	9.55	*	4.79	4.38	*	9.11	11.08	**
Area (SxC)	6	0.33	6.10	***	0.89	15.6	***	1.09	8.93	***	0.82	13.66	***
Residuals	24	0.05			0.06			0.12			0.06		
Total	35												

Table 3 Results of the pairwise tests contrasting OM composition, protein, carbohydrate and lipid contents between colonized (CS) and not-colonized (NCS) sediments across the three sites. T = T value, P(MC) = probability level after Monte Carlo simulations. * = p<0.05; ** = p<0.01; *** = p<0.001; ns = not significant.

	OM composition		Protein		Carbohydrate		Lipid	
	NCS vs CS		NCS vs CS		NCS vs CS		NCS vs CS	
Sites	t	P(MC)	t	P(MC)	t	P(MC)	t	P(MC)
S1	3.61	*	2.33	ns	5.39	*	4.53	*
S2	7.1	**	12.7	**	4.92	*	36.33	***
S3	0.94	ns	1.13	ns	0.81	ns	0.89	ns

	Biopolymeric C		Phytopigment		Chlorophyll-a		Phaeopigment	
	NCS vs CS		NCS vs CS		NCS vs CS		NCS vs CS	
Sites	t	P(MC)	t	P(MC)	t	P(MC)	t	P(MC)
S1	3.22	ns	0.45	ns	0.18	ns	0.49	ns
S2	7.93	*	3.42	ns	1.82	ns	4.07	ns
S3	0.81	ns	2.09	ns	3.51	ns	1.76	ns

Table 4 Results of the PERMANOVAs ascertaining differences in the composition and abundance of the meiofaunal assemblages. S= site; C = *Caulerpa* (present vs. absent); A= area. df = degrees of freedom; MS = mean sum of squares; F = statistic F. P(perm) = probability level; * = p<0.05; ** = p<0.01; *** = p<0.001; ns = not significant.

		Taxonomic composition			Abundance		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Site (S)	2	4285.30	5.67	**	$3.6*10^6$	4.33	ns
Caulerpa (C)	1	2053.30	0.39	ns	$2.6*10^6$	0.34	ns
SxC	2	5267.80	6.98	*	$7.9*10^6$	9.40	*
Area (SxC)	6	755.16	3.87	***	$8.4*10^5$	4.58	**
Residual	24	195.20			$1.8*10^5$		
Total	35						

Table 5 Results of the pairwise tests contrasting composition and abundance of the meiofaunal assemblages between colonized (CS) and not-colonized (NCS) sediments across the three sites. T = T value, P(MC) = probability level after Monte Carlo simulations. * = P < 0.05; ns = not significant.

	Taxonomic composition		Abundance	
	NCS vs CS		NCS vs CS	
Groups	t	P(MC)	t	P(MC)
S1	0.89	ns	0.75	ns
S2	1.12	ns	1.15	ns
S3	3.37	*	4.06	*

Table 6 DISTLM analyses estimating the proportion of meiofaunal assemblages variation explained singularly (marginal tests) and cumulatively (sequential tests) by sediment features (proteins, carbohydrates, lipids and sedimentation rates). P < 0.001=***, P < 0.01=**, P < 0.05=*, ns=not significant. Prop. = proportion of explained variance.

MARGINAL TESTS			
Variable	P	Prop.	
Proteins	**	0.13	
Carbohydrates	ns	0.08	
Lipids	ns	0.01	
Sedimentation	***	0.18	
SEQUENTIAL TESTS			
Variable	P	Prop.	Cumul.
Sedimentation	***	0.18	0.18
Proteins	*	0.09	0.28
Carbohydrates	ns	0.05	0.33
Lipids	ns	0.05	0.38

Fig. 1. Map of the Apulian Region (Italy, Mediterranean Sea) showing the sampling sites (S1, S2, S3) of *C. cylindracea*.

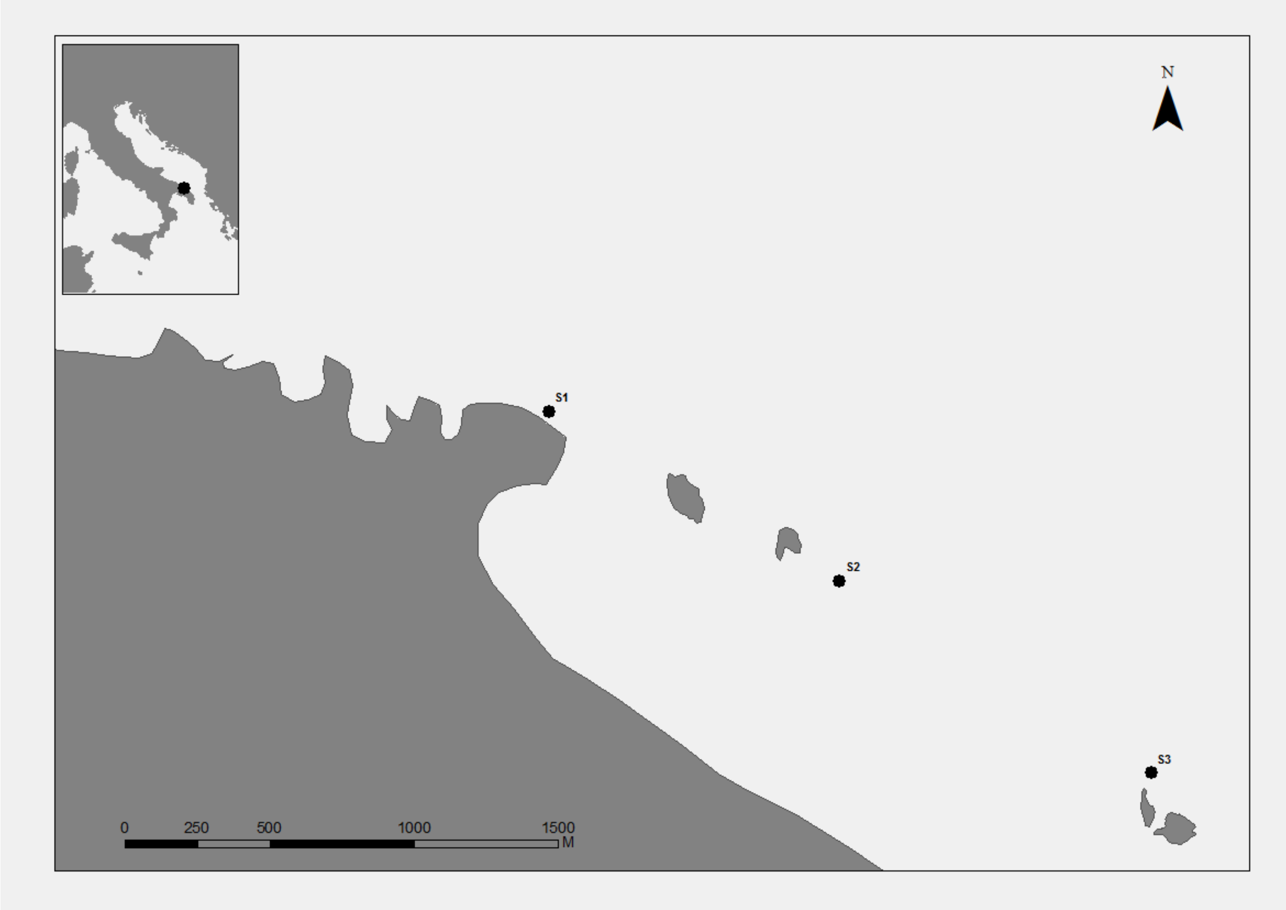


Fig. 2. Particle-trapping rates (mean±standard error) at three sampling sites based on accumulated dry mass in sediment traps. The weight fraction of the trapped sediment samples (> 2000, 2000-63 and <63 µm) and the results of the pairwise tests contrasting sedimentary rates across the three investigated sites are showed. * = p<0.05; *** = p<0.001.

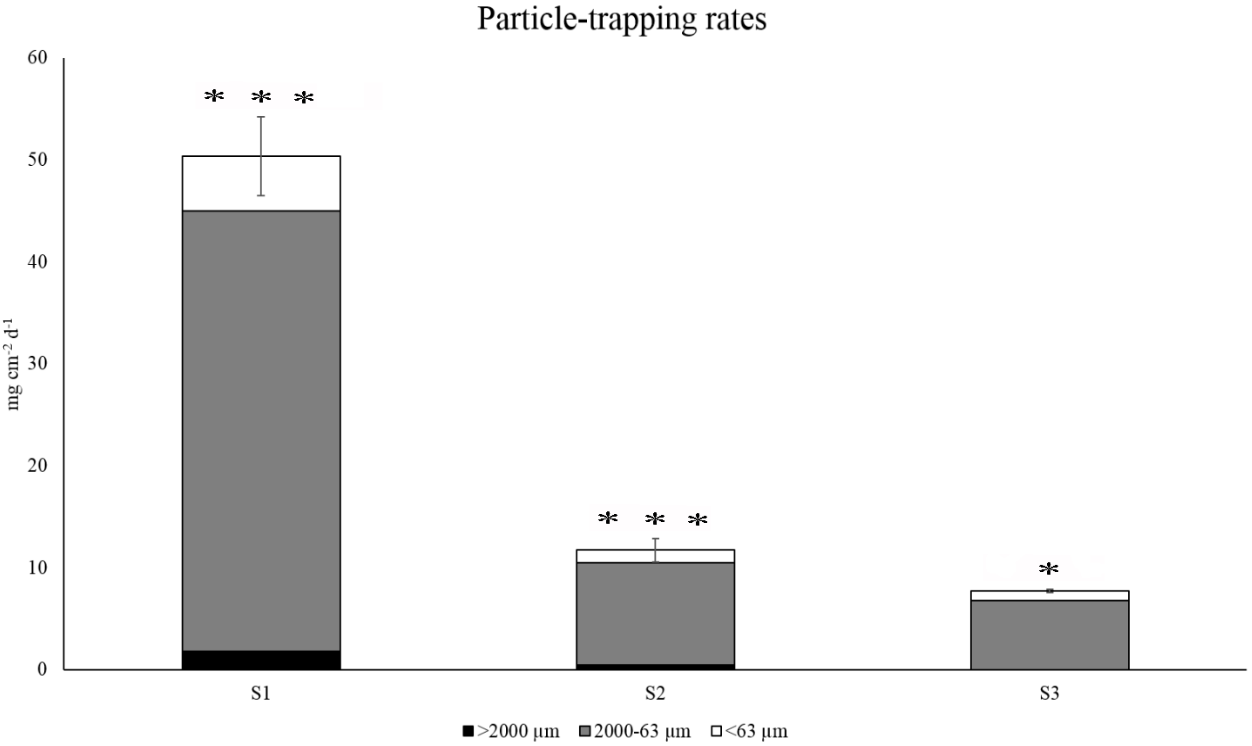


Fig. 3. Multi-dimensional scaling (MDS) plots based on a Euclidian distance resemblance matrix on normalized data of organic matter, across the three sites; CS = Presence of *C. cylindracea*. NCS = Absence of *C. cylindracea*.

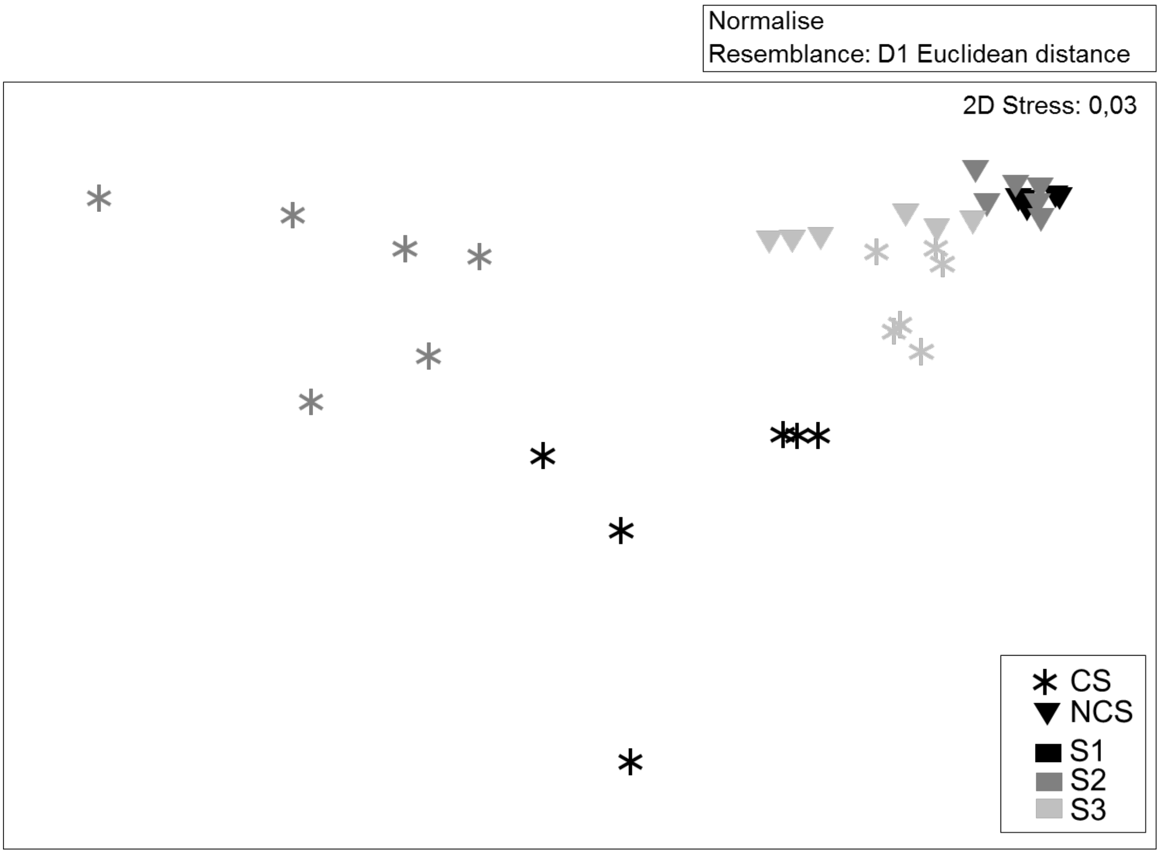


Fig. 4. Protein, carbohydrate lipid and biopolymeric carbon contents in the sediments of the three sampling sites (error bars indicate standard error; n = 6); CS = Presence of *C. cylindracea*. NCS = Absence of *C. cylindracea*.

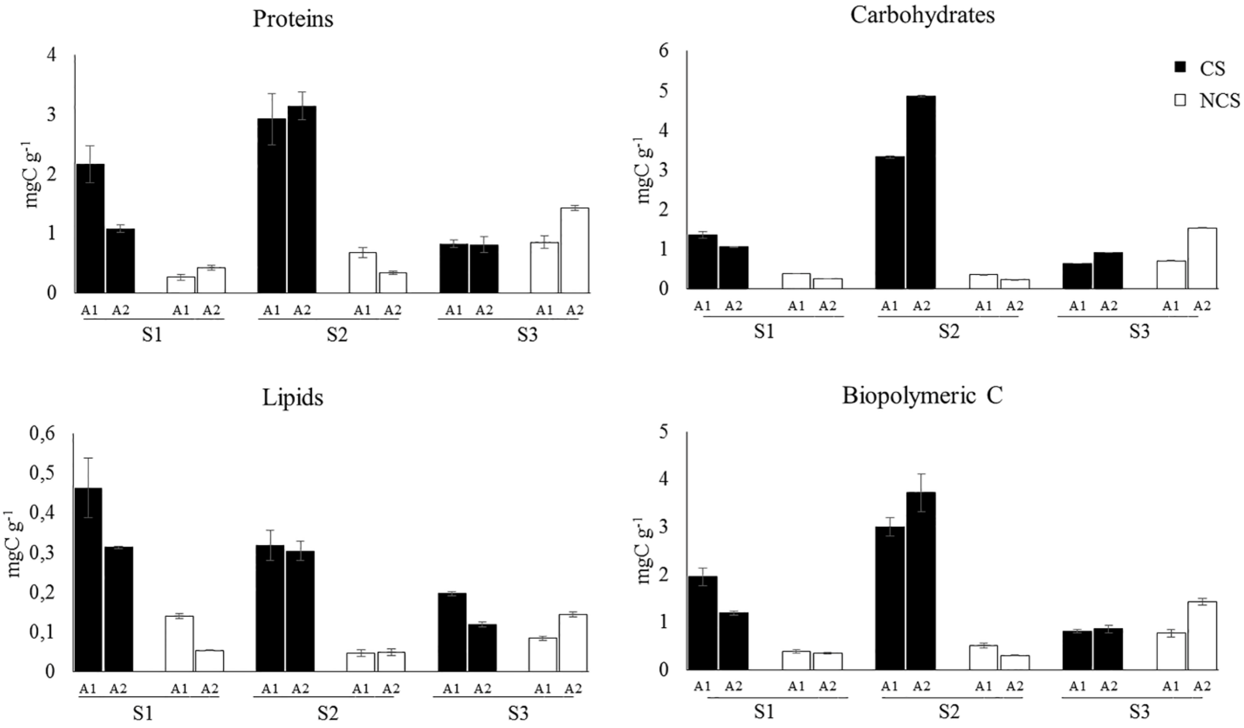


Fig. 5. Percentages of taxonomic composition in the sediments of the three sampling sites.
CS = Presence of *C. cylindracea*. NCS = Absence of *C. cylindracea*.

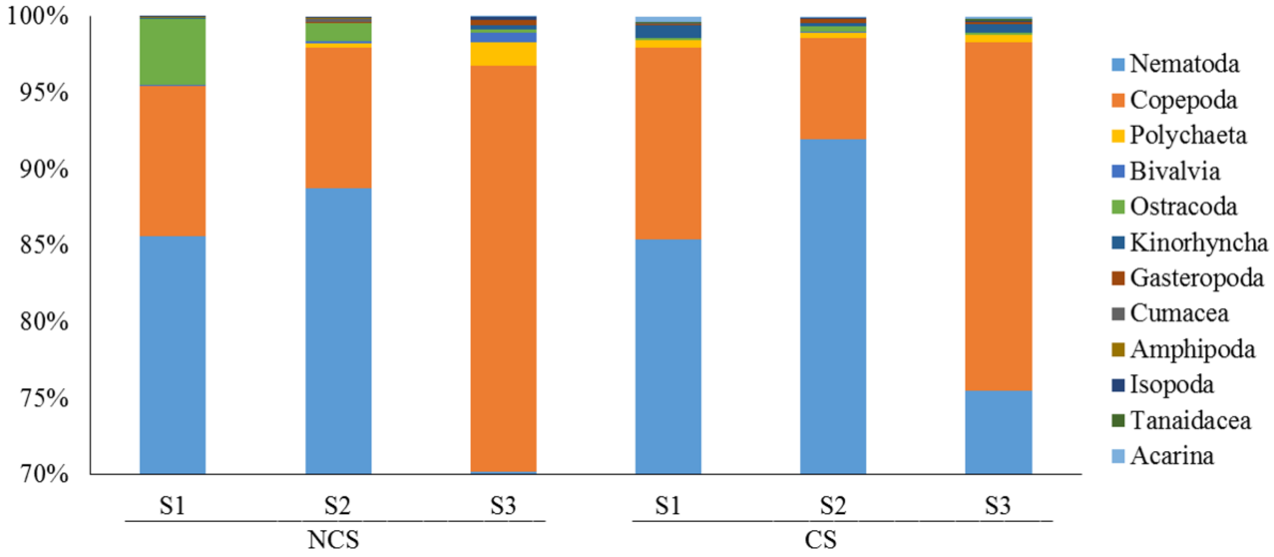


Fig. 6. Multi-dimensional scaling (MDS) plots based on Bray–Curtis similarity resemblance matrix on untransformed data of meiofauna composition across the three sites and in presence (CS) or absence (NCS) of *C. cylindracea*. Vectors are proportional to the Pearson correlations between the taxonomic abundances and ordination axes.

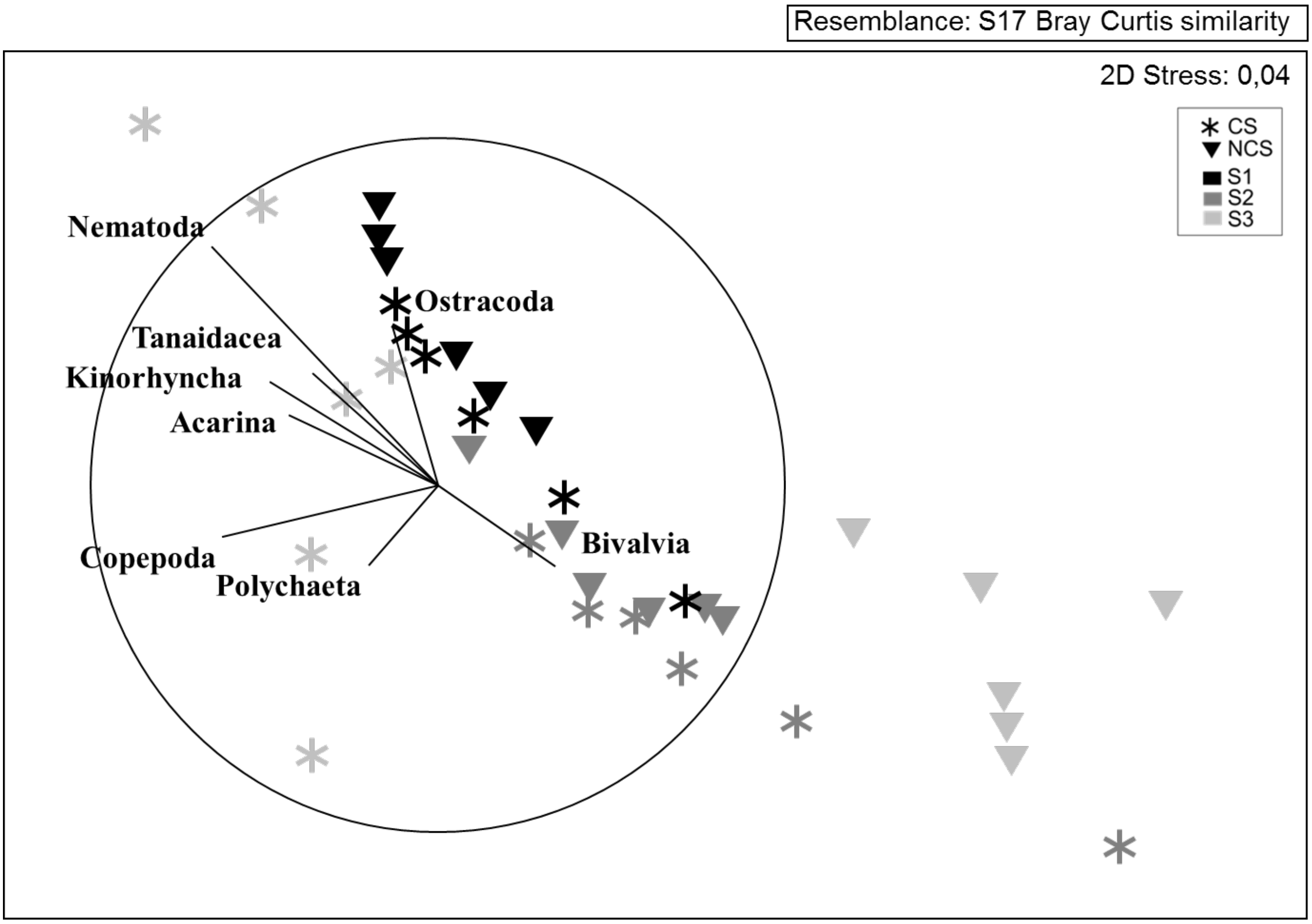
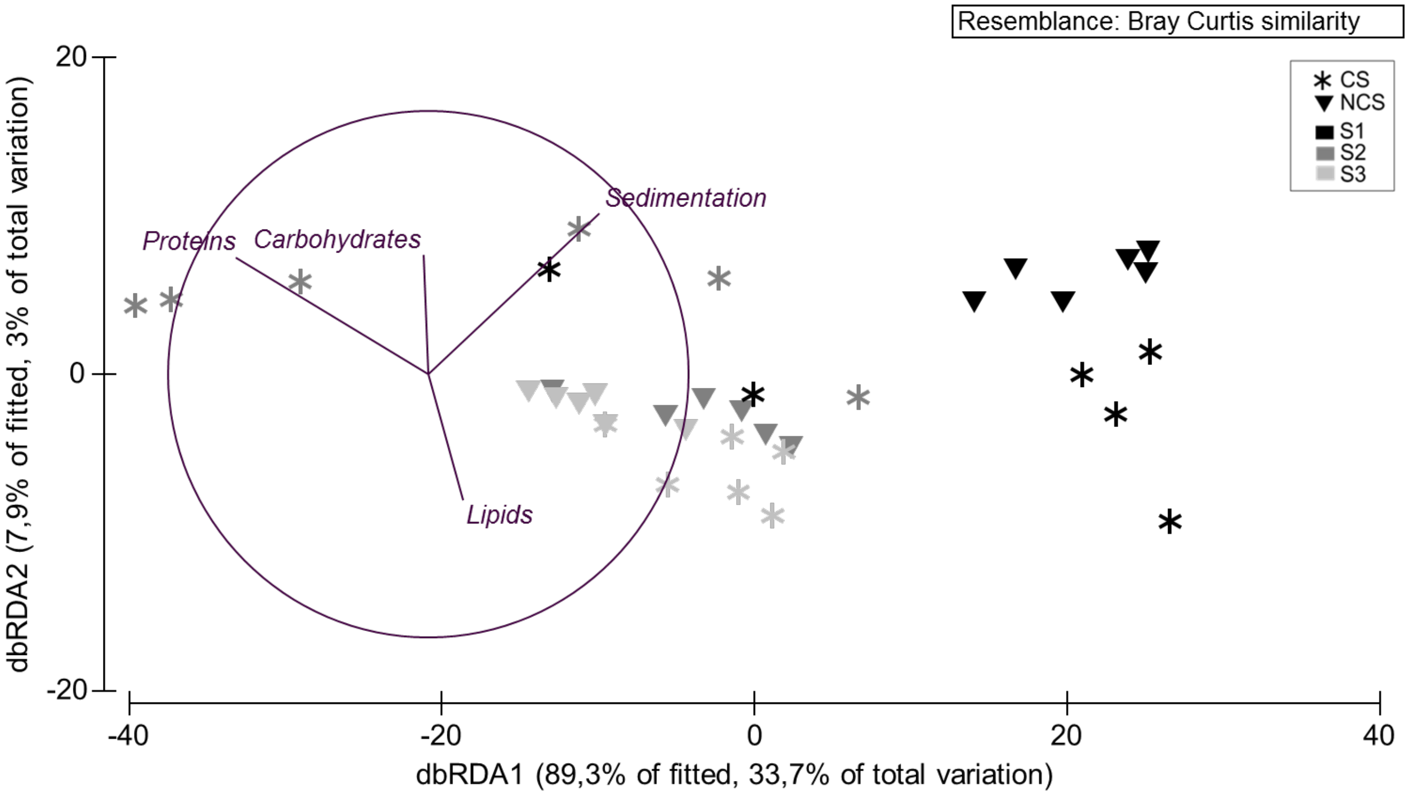


Fig. 7. dbRDA ordination after DistLM forward analysis, showing the relationships between the sediment characteristics and meiofaunal taxonomic composition.



Supplementary Material

Table S1 Organic matter content in the investigated sediments (mean ± SE).

	Protein	Carbohydrate	Lipid	Biopolymeric C	Chlorophyll-a	Phaeopigments	Phytopigments
	mgC g^{-1}	mgC g^{-1}	mgC g^{-1}	mgC g^{-1}	µgC g^{-1}	µgC g^{-1}	µgC g^{-1}
				Colonized sediments			
S1	1.62±0.28	1.21±0.12	0.39±0.05	1.57±0.19	6.76±0.4	12.75±0.92	19.51±1.2
S2	3.03±0.23	4.10±0.51	0.31±0.02	3.36±0.26	9.17±1.02	31.68±3.11	40.85±4.05
S3	0.82±0.07	0.78±0.07	0.16±0.02	0.83±0.04	2.52±0.23	6.83±0.46	9.35±0.61
				Not-Colonized sediments			
S1	0.35±0.05	0.33±0.03	0.05±0.004	0.34±0.02	6.91±0.69	15.37±2.33	22.28±2.79
S2	0.51±0.08	0.30±0.03	0.05±0.005	0.41±0.05	4.56±0.58	6.92±0.93	11.48±1.5
S3	1.14±0.14	1.13±0.20	0.11±0.01	1.1±0.16	4.17±0.25	11.49±1.37	15.66±1.51

Table S2 Abundance of meiofaunal taxa (number of individual in 10 cm^2) in the investigated sediments (mean ± S.E.).

	Nematoda	**Copepoda**	**Polychaeta**	**Bivalvia**	**Ostracoda**	**Kinorhyncha**
			Colonized sediments			
S1	1645.03±205.6	241.89±22.54	9.34±1.5	0±0	2.46±0.83	16.47±4.72
S2	864.31±139.69	62.19±8.76	3.44±1.04	0.74±0.17	3.2±0.64	1.97±0.46
S3	2265±494.5	683.87±146.88	15.49±2.66	1.23±0.44	3.44±0.71	16.96±2.49
			Not-Colonized sediments			
S1	2065.88±210.68	236.97±13.47	0.74±0.35	0.74±0.3	104.97±8.25	0.98±0.67
S2	1097.1±124.39	114.06±9.54	2.95±0.72	1.72±0.3	15.49±1.46	0±0
S3	415.93±44.65	157.57±29.35	8.85±2.02	3.69±1.35	1.47±0.47	1.47±0.47

	Gasteropodi	**Cumacea**	**Amphiopoda**	**Isopoda**	**Tanaidacea**	**Acarina**	**Total abundance**
				Colonized sediments			
S1	1.97±0.68	0.74±0.5	0.25±0.17	0.49±0.34	0.49±0.34	7.13±1.46	1926.25±232.26
S2	2.7±0.3	0±0	0±0	0.49±0.34	0±0	0.98±0.46	940.02±146.33
S3	4.18±1.15	0.49±0.18	0±0	0.74±0.35	4.18±2.15	4.92±1.14	3000.49±415.44
				Not-Colonized sediments			
S1	0±0	0.98±0.36	0.74±0.35	0.49±0.18	0±0	0±0	2412.49±216.3
S2	0.25±0.17	2.46±0.87	0.98±0.67	1.23±0.84	0±0	0±0	1236.23±117.43
S3	1.97±0.57	0.25±0.17	0±0	0.98±0.67	0±0	0.25±0.17	592.43±68.19