

Article

Meiofaunal Dynamics and Heterogeneity along Salinity and Trophic Gradients in a Mediterranean Transitional System

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Abstract: The spatiotemporal variation in meiofaunal assemblages were investigated for the first time in the Cabras Lagoon, the largest transitional system in the Sardinian Island (W-Mediterranean Sea). Two main environmental (salinity and trophic) gradients highlighted a significant separation of the three study sites across the lagoon, which were consistent through time. The environmental variability and habitat heterogeneity of the Cabras Lagoon influenced the meiofauna. In particular, salinity and dissolved oxygen, primarily, shaped the meiofaunal assemblage structure at the seaward site which was significantly different from both the riverine and the organically enriched sites. On the other hand, the trophic components (e.g., organic matter, Chlorophyll-*a*, and phaeopigments) and the different degrees of confinement and saprobity among sites were the secondary factors contributing mostly to the separation between the latter two sites. The lack of significant differences in the temporal comparison of the meiofaunal assemblage structure along with the very low contribution of temperature to the meiofaunal ordination indicated that this assemblage was more affected by spatial rather than by temporal variation. This pattern was also supported by significant differences between the three sites in several univariate measures, including total number of individuals, number of taxa, Pielou's evenness, and the ratio between nematodes and copepods. Thus, the present study corroborates the hypothesis that meiofaunal organisms are good indicators of the spatial heterogeneity in transitional waters (TWs) and could have a greater species richness than that expected. Indeed, the Cabras Lagoon overall showed one of the highest meiofaunal richness values found from both Mediterranean and European TWs.

Keywords: biodiversity; spatial variation; sediments; confinement; saprobity; organic enrichment; coastal lagoons; Mediterranean sea

1. Introduction

Transitional waters, being a continuum between continental and marine ecosystems, represent areas with high environmental heterogeneity. As such, there is a complex association between abiotic and biotic components that makes these water bodies ideal to study the distribution and dynamics of the benthic assemblages with the aim to further our understanding of the ecosystem functioning [1,2]. Lagoons have a historically relevant “social” value because they offer a high biological productivity [3]. For this reason, they host many human activities (i.e., fisheries, aquaculture, agriculture, industry,

and tourism [4]) that, on the other side, have endangered their integrity and ecological quality status as well [5,6]. Therefore, there is general agreement among the scientific community, which is also recognized by legislations worldwide (e.g., the US Clean Water Act, European Water Framework Directive, Marine Strategy Framework Directive, and the National Water Act in South Africa), about the need to assess their health status and ensure proper management of their resources [4,7].

Meiofauna are small benthic invertebrates that have a well-recognized role in the food webs of lagoon systems connecting microbial components to higher trophic levels that contributes to the overall carbon fluxes and organic matter mineralization [8,9]. Because of their high taxonomic diversity, rapid generation times, lack of larval stages, and various life strategies meiofaunal organisms are considered excellent bioindicators of natural or anthropogenic stressful conditions [10–12]. However, their role in ecosystems tends to be overlooked, mainly due to the lack of taxonomists and the small size of meiofauna, which require time and the appropriate techniques for their study [13].

In the Mediterranean basin, there are more than 100 coastal lagoons, half of which have available physico-chemical or ecological data in the scientific literature [4]. Among them, the largest amount of information on meiofaunal spatial pattern is available for the upper Adriatic Sea, including the Venice lagoon [14–20]. Meiofaunal diversity and assemblage structure are also well-documented in the southern part of the Adriatic Sea, including the Lesina and Varano lagoons [6,8,17,21–23]. Instead, meiofaunal studies in transitional environments along the Tyrrhenian coast, with the exception of the Stagnone of Marsala (Western Sicily), are largely lacking [17,24]. Furthermore, most of the available literature on meiofauna from coastal lagoons takes into consideration the spatial pattern of the assemblages, while only in a few cases their temporal dynamics is reported [2,8,24–26]. Finally, little is known on spatiotemporal dynamics of meiofauna in Mediterranean transitional systems characterized by different physico-chemical gradients related to the riverine inflow, the connection to the sea, and the organic matter (OM) enrichment of sediments.

Within the Tyrrhenian coast, the Sardinian Island is one of the richest Italian regions in number and extension of lagoons [27], yet knowledge on meiofaunal composition and distribution in these systems is absent. In the present study, we describe for the first time the spatiotemporal variation in meiofaunal assemblages in the Cabras Lagoon, the largest and most complex transitional system in the Sardinia Island. This lagoon is characterized by a large environmental heterogeneity, with an increasing salinity along its main longitudinal axis and varying degrees of trophic condition across the basin [28–30]. For these reasons, it represents a valuable case-study in which to test the general hypotheses on the meiofaunal dynamics in these highly variable systems. Our main objectives were to investigate the pattern of spatial variation in meiofaunal diversity and community structure in relation to the main environmental gradients, and to assess whether this pattern was consistent through time. In particular, we tested whether spatiotemporal variation could be identified in: (1) the whole meiofaunal assemblage of the three sites in terms of (i) total number of individuals, (ii) total number of taxa, and (iii) Shannon diversity (H') and Pielou's evenness (J) indices; and (2) the abundance of dominant taxa, including the ratio between nematodes and copepods. We anticipate that the response of meiofaunal assemblages to the environmental drivers (both in water and sediments) identified in the present study will provide one of the few evidences of the importance of meiofaunal studies to further our understanding of the functioning of Mediterranean lagoons.

2. Materials and Methods

2.1. Study Area and Sampling Sites

The Cabras Lagoon (central-western Sardinia; Figure 1) is the largest lagoon in the Sardinia island, with a surface area of 22 km² and a watershed of ~430 km² inhabited by approximately 38,000 people. Its main freshwater riverine source is the Rio Mare e Foghe located in the northern sector of the lagoon, with a minor contribution from the Rio Tanui, southward. The lagoon is connected to the adjacent Gulf of Oristano only via three narrow creeks that flow into a large channel ("scolmatore")

built in the late 70's, closed in proximity of the lagoon by a 30 cm high dam. In the last two decades, the Cabras Lagoon has been extensively investigated from various perspectives and using different approaches, including physical/modeling [31,32], biogeochemical [33,34], biological [35–38], and ecological [5,39,40]. However, while several studies have been conducted in the Cabras Lagoon on the macrozoobenthos [28–30,41,42], nothing is known regarding the spatiotemporal variation in meiofaunal assemblages. In fact, no such studies are available for transitional waters in the Sardinian Island, one of the richest Italian regions in number and extension of lagoons [27], with only few examples conducted in fully marine coastal waters [43,44].



Figure 1. Location of the study area (Cabras lagoon, western Sardinia, Italy) and sampling sites (C1, C2, and C3). Image source: Google Earth.

For the present study, three sites (C1, C2, and C3; Figure 1) were selected along the longitudinal axis of the Cabras Lagoon, being representative of different environmental (e.g., salinity, confinement, and sediment grain-size) and trophic (e.g., sediment OM and phytopigments) conditions. Site C1 was located in the northern sector of the lagoon, connected to the main freshwater tributary the Rio Mare e Foghe. This site was characterized by sandy sediments, low OM content of sediments, and the

presence of halophytic vegetation (*Phragmites* sp.) along the shore. Site C2, was located in the satellite pond of Sali e Pauli and surrounded by halophytic vegetation (*Salicornia* sp.). This site was highly confined and characterized by a high OM content of sediments [33]. Biofilm-forming cyanobacterial strains with extremely growth rates were also found here [45,46]. Site C3 was located in the southern sector of the lagoon, at the confluence of the three creeks connecting the Cabras Lagoon to the main channel. This site was characterized by muddy-sandy sediments, limited OM enrichment of sediments, abundant submerged vegetation (e.g., *Ruppia*), and a significantly higher hydrodynamics than at the other sites [47].

2.2. Field Surveys and Sample Treatment

The field surveys were carried out at sites C1, C2, and C3 on 6 July 2010 and 2 February 2011. At each site and date, water temperature, salinity, and dissolved oxygen (DO) were measured using portable probes (WTW LF 197 and WTW Oxil 197, respectively). Subsequently, sediment samples for the determination of the water content (Wc) and chemical analysis (OM, chlorophyll-a, and phaeopigment content) were collected using a manual core (40 cm long, 5.5 cm diameter) gently pushed by hand into the sediments. Procedural details of sediment collection and chemical analysis are given in the companion paper by [30].

For the analyses of the meiofauna, six replicates were collected at each site by means of plexiglas corers (diameter: 3.6 cm) inserted 5 cm in the sediment. These samples were pre-filtered with magnesium chloride (MgCl_2 ; 80 g L^{-1}) to allow organisms to relax before fixation and facilitate subsequent taxonomic identification [48]. This treatment appears important because the “soft-bodied” taxa (e.g., Gastrotricha, Plathelminthes, and Nemertina) usually undergo the major morphological alterations after fixation and they can remain in good conditions with magnesium chloride treatment. The sediment samples were then fixed in a solution of pre-filtered seawater containing formalin buffered with sodium tetraborate $\text{Na}_2\text{B}_4\text{O}_7$ to reach a pH of ca. 8.2 [49]. The amount of formalin to be added to the sample to obtain a final concentration of 4% was calculated based on the total volume of sediment and water present in the sample. A few drops of a Rose Bengal solution (0.5 g L^{-1}) were added to the sample in order to facilitate the identification of organisms in the sorting phase [50].

2.3. Meiofaunal Analysis

The samples were rinsed with a gentle jet of fresh water through a 0.5 mm sieve to separate the macrofauna from the meiofauna [48]. They were then decanted, sieved 10 times through a $42 \mu\text{m}$ mesh and centrifuged three times with Ludox HS30 (specific density 1.18 g/cm^3) [51]. The obtained animals were then transferred to a “Delfuss” Petri dish with a checkered bottom (200 squares, to make counting easier), sorted into their major taxa under a Leica G26 stereomicroscope, and counted.

All the values obtained was recalculated as abundance per 10 cm^2 . The richness (number of major taxa), Shannon’s diversity, Pielou’s evenness indices (\log_2) were calculated to describe the structure of the meiofaunal assemblage. The possible occurrence of anthropogenic impact on the meiofaunal community was also assessed by the total number of nematodes (Ne) and copepods (Co) computed in the Ne:Co ratio. This index was proposed by Raffaelli and Mason [52] for the pollution monitoring with meiofauna. The hypothesis was that the divergent auto-ecological characteristics of these two abundant and frequent meiofaunal components (the extreme tolerance of nematodes and the high sensitivity of copepods) might detect the occurrence of human stress in marine sediments.

2.4. Statistical Analysis

Both abiotic and biotic data were used for the data analysis. Water variables were temperature, salinity, and dissolved oxygen; sediment variables included water content, OM, chlorophyll-a, and phaeopigments. Biotic data consisted in the abundance of the meiofauna and were used to construct a taxa-by-site and period matrix. The environmental data variation was represented by means of box-plots for each variable and each site. The biotic parameters computed were the number

of taxa (S, taxon richness), the number of individuals per taxa (A, abundance), and the Shannon (H' , diversity) and Pielou (J, evenness) indices, as well as Ne/Co ratio. These biotic variables were computed for the three sampling sites C1, C2, and C3, for each replicate and date.

As for multivariate analysis, the non-parametric permutational analysis of variance (two way-PERMANOVA), based on Bray-Curtis (dis)similarity measures [53] was carried out to test significant differences of the structure of community among sites (three levels: C1, C2, and C3), periods (two levels: July and February), and site \times period interactions as fixed factors. The data were $\log(x+1)$ transformed before the analysis. The PERMANOVA, based on Euclidean distance, was also used to test the significant differences of all the biotic univariate measures (i.e., total meiofaunal abundance, number of taxa, Shannon-diversity, Pielou evenness, and Ne/Co ratio). A $\log(x+1)$ transformation of data was applied only for the total meiofaunal abundance. The significance was computed by permutation with 9999 replicates. The pairwise comparisons between all pairs of sites were computed as post-hoc test and the Bonferroni correction procedure was followed to account for multiple simultaneous correlations [54]. The principal component analysis (PCA), based on the correlation matrix, was used to explore the faunal variations within the lagoon and periods. The environmental variables were used to understand the key environmental variables accounting for the much % of variance affecting the meiofaunal distribution. The multivariate procedure non-metric multidimensional scaling (nMDS) was used to investigate the differences between the sites; the more informative environmental variables were added in the analysis to best explain the meiobenthos structure and they were superimposed in the graph [55]. The meiofaunal major taxa contributing most to (dis)similarities among the sites were identified using the similarity percentages (SIMPER) test.

3. Results

3.1. Environmental Variables

Among the water variables, both salinity and DO showed increasingly higher values from C1 to C3 (Figure 2), most variation found in salinity at C3 due to large differences between the summer (27 psu) and winter (3 psu) dates [30]. Differently from salinity, the median of DO was significantly higher at C3 than at both C1 and C2. Sediment variables had large within- and between-site variation. In particular, while C1 had low and homogeneous Wc, OM, chlorophyll-*a* (Chl-*a*), and phaeopigment values, C2 was most variable and had the highest peaks and outliers in OM, Chl-*a*, and phaeopigments among the three sites. C3 was in an intermediate position, with the medians of all sediment variables between C1 and C2 (Figure 2).

The PCA showed a clear separation of both sites and dates (Figure 3). C1 data-points were located on the left-hand side of the ordination model (second and third quadrants), while those of C2 were located on the right-hand side (first and fourth quadrants). C3 was in intermediate position, yet clearly separated from C1 and C2. The two sampling dates were also clearly distinguishable for each site, summer and winter data-point being positioned on the upper and lower portion of the model, respectively. Among the environmental variables, sediment Wc, OM, Chl-*a*, and phaeopigments were mostly correlated with PC1, while water temperature and salinity showed the highest correlation with PC2 (Table 1). This indicates that sites were discriminated on the *x*-axis by the sediment variables mostly affected by the trophic features, while on the *y*-axis they were distributed in relation to the confinement gradient as indicated by the water variables. The variance explained by the model was 46.1% and 23.5% for PC1 and PC2, respectively.

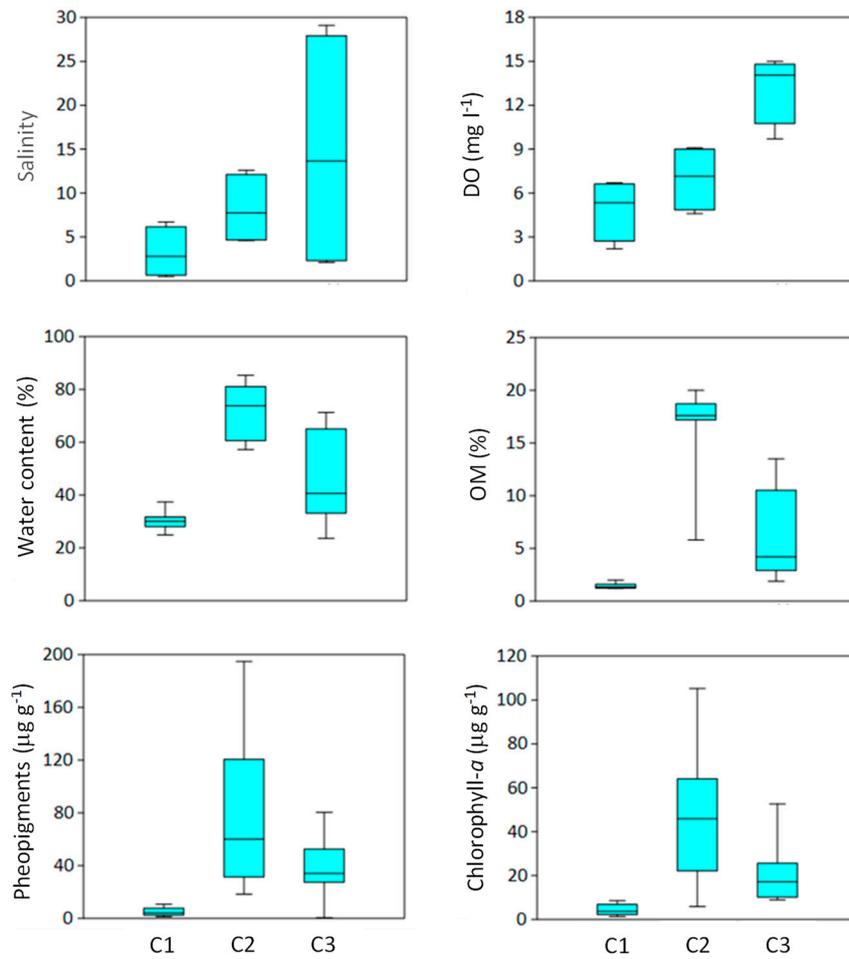


Figure 2. Mean values (n = 4, ±SE) of water salinity and dissolved oxygen (DO) concentration, and mean values (n = 12, ±SE) of sediment water (Wc), phaeopigment (Pha), organic matter (OM), and chlorophyll-a (Chl-a) contents at the sampling sites C1, C2, and C3 during the study period.

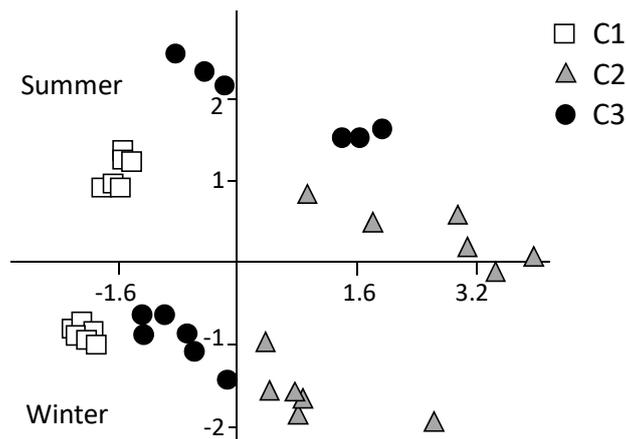


Figure 3. Principal component analysis (PCA) on environmental variables.

Table 1. Component correlation coefficients in the PCA of the environmental variables and the first two components. 69.6% of variance explained by Principal Components 1 (46.1%) and 2 (23.5%). In bold, the highest loadings.

Variable	PC 1	PC 2
Temperature	0.17	0.71
Salinity	0.24	0.59
Dissolved oxygen	0.004	−0.12
Water content	0.49	−0.27
OM	0.50	−0.22
Chlorophyll- <i>a</i>	0.47	0.06
Phaeopigments	0.45	−0.12

3.2. Meiofauna

A total of 16 meiofaunal taxa were found: Plathelminthes, Nemertina, Nematoda, Kinorhyncha, Bivalvia, Polychaeta (adults and nectochaetes), Oligochaeta, Copepoda (adults and juveniles), Ostracoda, Amphipoda, Cladocera, Isopoda, Tanaidacea, Insecta, Halacaroidea, and Pycnogonida. The dominant taxa were generally nematodes (from 41% at C2 in winter 2011 to 86% at C3 in summer 2010), copepods (from 4% at C3 in summer 2010 to 33% C3 in winter 2011), and ostracods (from 0% at C2 in summer 2010 to 12% at C3 in winter 2011).

The PERMANOVA carried out on the structure of the meiofaunal assemblage indicated highly significant differences only among sites ($p < 0.001$), while no significant differences emerged among periods or site \times period interactions (Table 2). In particular, pairwise comparisons highlighted significant differences between C3 and the other two sites (C1 and C2). The aforementioned variations were tested by means of the SIMPER analysis, which highlighted that five main groups, i.e., Nematoda, Copepoda, Ostracoda, Nauplii, and Halacaroidea, contributed up to the 95% of the cumulative similarity, with an individual contribution varying from 58% for Nematoda to 2.3% for Halacaroidea (Table 3; Figure 4). All the other taxa contributed to less than 2%.

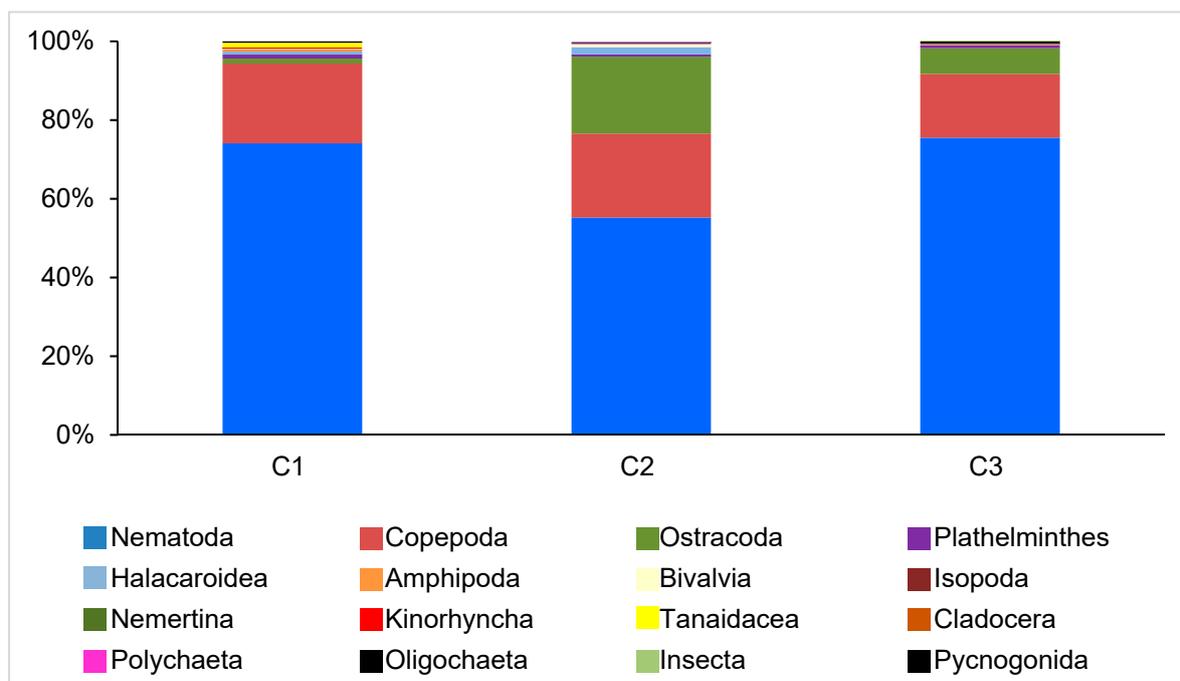


Figure 4. Meiofauna community structure in the sampling sites C1, C2, and C3.

Table 2. Results of two-way PERMANOVA (Bray Curtis (dis)similarity based) testing the differences among sites, periods and their interactions for the meiofaunal assemblage structure. Df = degrees of freedom. Significant *p* values are marked, ** for *p* < 0.001.

Factors	Total Sum of Squares	Df	Mean Square	Pseudo-F	<i>p</i>	Pairwise
Sites	2.72	2	1.36	6.36	0.0001 **	C1 vs. C3 <i>p</i> = 0.0003 **; C2 vs. C3 <i>p</i> = 0.0006 **
Periods	0.20	1	0.20	0.94	0.44	
Sites × Periods	0.66	2	0.33	1.55	0.12	
Residual	6.41	30	0.21			
Total	9.99	35				

Table 3. Results of the Similarity Percentage (SIMPER) analysis showing the average dissimilarity (Av. Dissim.), % contribution of each taxon (Cont. %), % cumulative for the pair comparisons (Cum. %), and average abundances of each sites (Av. ab.). The overall average dissimilarity is 70.9, 76.0, and 82.6 for C1 vs. C2, C1 vs. C3, and C2 vs. C3, respectively.

C1 vs. C2	Av. Dissim.	Cont. %	Cum. %	Av.ab. C1	Av.ab. C2	C1 vs. C3	Av. Dissim.	Cont. %	Cum. %	Av.ab. C1	Av.ab. C3	C2 vs. C3	Av. Dissim.	Cont. %	Cum. %	Av.ab. C2	Av.ab. C3
Nematoda	41.2	58.1	58.1	73.1	54.8	Nematoda	52.8	69.4	69.4	73.1	619	Nematoda	58.0	70.2	70.2	54.8	619
Copepoda	13.4	18.9	77.0	17.5	20.3	Copepoda	12.5	16.4	85.8	17.5	89.8	Copepoda	13.0	15.8	85.9	20.3	89.8
Ostracoda	9.4	13.2	90.3	1.3	19.4	Ostracoda	4.9	6.5	92.3	1.3	53.4	Ostracoda	5.6	6.8	92.8	19.4	53.4
Nauplii	2.4	3.4	93.6	2.5	0.9	Nauplii	3.7	4.8	97.1	2.5	43.3	Nauplii	3.8	4.6	97.3	0.9	43.3
Halacaroida	1.7	2.3	96.0	0.8	1.8	Plathelminthes	0.9	1.2	98.3	1.0	6.3	Plathelminthes	0.9	1.0	98.4	0.6	6.3
Tanaidacea	0.8	1.1	97.1	1.2	0.0	Oligochaeta	0.3	0.4	98.7	0.3	4.3	Halacaroida	0.3	0.4	98.8	1.8	0.6
Plathelminthes	0.5	0.8	97.9	1.0	0.6	Tanaidacea	0.2	0.3	99.0	1.2	0.1	Oligochaeta	0.3	0.4	99.2	0.3	4.3
Amphipoda	0.3	0.5	98.3	0.7	0.0	Amphipoda	0.2	0.2	99.2	0.7	1.2	Polychaeta	0.2	0.2	99.4	0.4	2.1
Bivalvia	0.3	0.4	98.8	0.1	0.7	Polychaeta	0.2	0.2	99.5	0.0	2.1	Bivalvia	0.2	0.2	99.6	0.7	0.5
Cladocera	0.3	0.4	99.2	0.1	0.1	Halacaroida	0.1	0.2	99.6	0.8	0.6	Amphipoda	0.1	0.1	99.8	0.0	1.2
Pycnogonida	0.2	0.2	99.4	0.0	0.3	Bivalvia	0.1	0.2	99.8	0.1	0.5	Insecta	0.1	0.1	99.9	0.0	0.4
Oligochaeta	0.2	0.2	99.6	0.8	0.3	Insecta	0.1	0.1	99.9	0.0	0.4	Pycnogonida	0.0	0.1	99.9	0.3	0.0
Kinorhyncha	0.1	0.2	99.8	0.1	0.0	nectochaetes	0.0	0.0	99.9	0.0	0.3	nectochaetes	0.0	0.0	100.0	0.0	0.3
Isopoda	0.1	0.1	99.9	0.2	0.0	Isopoda	0.0	0.0	99.9	0.2	0.0	Cladocera	0.0	0.0	100.0	0.1	0.0
Polychaeta	0.1	0.1	100.0	0.0	0.4	Cladocera	0.0	0.0	100.0	0.1	0.0	Nemertina	0.0	0.0	100.0	0.0	0.1
Nemertina	0.0	0.0	100.0	0.0	0.0	Kinorhyncha	0.0	0.0	100.0	0.1	0.0	Tanaidacea	0.0	0.0	100.0	0.0	0.1
Insecta	0.0	0.0	100.0	0.0	0.0	Nemertina	0.0	0.0	100.0	0.0	0.1	Kinorhyncha	0.0	0.0	100.0	0.0	0.0
nectochaetes	0.0	0.0	100.0	0.0	0.0	Pycnogonida	0.0	0.0	100.0	0.0	0.0	Isopoda	0.0	0.0	100.0	0.0	0.0

Variation in the meiofaunal abundance, number of taxa, diversity, evenness, and the Ne/Co ratio are shown in Figure 5. While differences between sites in abundance, evenness, and the Ne/Co ratio were high, those in taxon number and diversity were not. In particular, abundance was the highest at C3, which also showed the most marked standard error, and consequently the lowest evenness. The Ne/Co ratio was higher in summer, but always lower in winter both at C2 and C3, which coincided with the drop in salinity. Finally, the most confined and organically enriched site C2 showed the most variation in the Ne/Co ratio up to various orders of magnitude, particularly in summer. The 2-way PERMANOVA conducted individually on each biotic measure showed significant differences among sites in the total abundance, taxon number, evenness and the Ne/Co ratio, while no difference was found for the diversity index (Table 4). The pairwise comparisons among the three sites are showed in Table 4 and highlighted higher and significant differences especially of C3. PERMANOVA did not reveal significant differences of meiofaunal abundance, taxon richness, Shannon diversity, and Ne/Co ratio among the periods investigated, while some differences of evenness ($p < 0.05$) were found (Table 4).

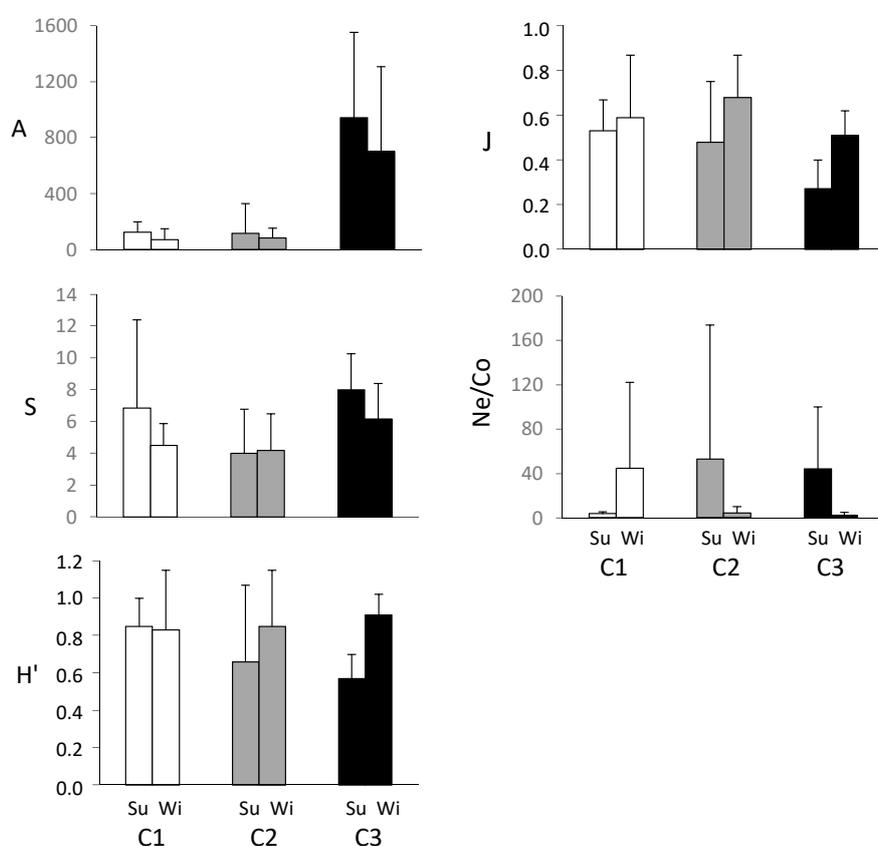


Figure 5. Mean values ($n = 6$, \pm SE standard error) of meiofaunal community synthetic measures at the sampling sites C1, C2, and C3 in summer (Su) and winter (Wi).

The nMDS on the structure of assemblage similarly highlighted three major groups corresponding to the three study sites, with a partial overlap between C1 and C2, and a major separation of C3 from both C1 and C2 (Figure 6). In this analysis, the environmental variables superimposed to the biotic data showed that salinity and DO were the main responsible factors for the separation of C3 from C1 and C2 (on the right-hand side) and that W_c , OM, Chl-*a*, and phaeopigments contributed mostly to the separation between C1 and C2 (Figure 6). These results demonstrated two main gradients influencing the spatiotemporal variation in the meiofaunal assemblages in the Cabras Lagoon. Temperature, on the contrary, did not make a relevant contribution to the ordination of the sites as indicated by its short segment.

Table 4. Results of two-way PERMANOVA testing differences among sites for the total meiofaunal abundance, number of taxa, diversity, evenness, and Ne/Co ratio (Euclidean distance based). Significant p values are marked, * for $p < 0.05$; ** for $p < 0.01$.

Variable	Factors	Total Sum of Squares	df	Mean Square	Pseudo-F	p	Pairwise
Total abundance	Sites	0.54	2	0.27	10.74	0.0003 **	C1 vs. C3 $p = 0.01$ *; C2 vs. C3 $p < 0.01$ **
	Periods	0.01	1	0.01	0.46	0.57	
	Sites \times Periods	0.11	2	0.06	2.2	0.11	
	Residual	0.75	30	0.03			
	Total	1.41	35				
number of taxa	Sites	0.49	2	0.24	6.15	0.0023 **	C2 vs. C3 $p < 0.05$ *
	Periods	0.03	1	0.03	0.76	0.42	
	Sites \times Periods	0.02	2	0.01	0.21	0.76	
	Residual	1.19	30	0.04			
	Total	1.73	35				
Shannon-diversity	Sites	0.08	2	0.04	0.64	0.8	-
	Periods	0.07	1	0.07	1.11	0.31	
	Sites \times Periods	0.16	2	0.08	1.29	0.22	
	Residual	1.9	30	0.06			
	Total	2.22	35				
Pielou-evenness	Sites	0.31	2	0.16	2.52	0.0166 *	C1 vs. C3 $p < 0.05$ *
	Periods	0.17	1	0.17	2.71	0.0356 *	
	Sites \times Periods	0.19	2	0.1	1.56	0.13	
	Residual	1.86	30	0.06			
	Total	2.53	35				
Ne/Co ratio	Sites	1.16	2	0.58	3	0.02 *	C1 vs. C3 $p < 0.01$ **
	Periods	0.24	1	0.24	1.25	0.28	
	Sites \times Periods	0.71	2	0.36	1.83	0.13	
	Residual	5.81	30	0.19			
	Total	7.92	35				

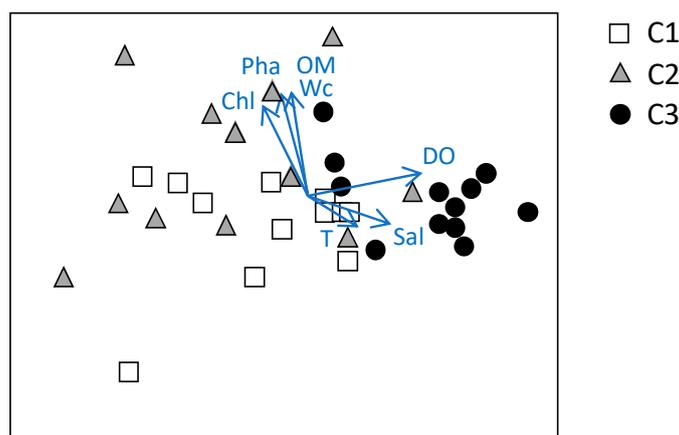


Figure 6. MDS on meiofaunal abundance (stress = 0.09) with superimposed environmental.

4. Discussion

The present study provides the first information of the spatiotemporal variation in lagoonal meiofaunal assemblages in one of the richest Italian regions in number and extension of lagoons within the Tyrrhenian coast, i.e., the Sardinian Island. We demonstrated significant changes in meiofaunal diversity and community structure in relation to the main environmental gradients which, in the studied lagoon, are driven by salinity and dissolved oxygen concentration in water, sediment organic enrichment, and different degrees of confinement and saprobity. Our results highlight the importance of meiofaunal studies often neglected, by ecologists and policy makers, to further our understanding of the functioning of Mediterranean lagoons.

From an abiotic point of view, the heterogeneity of the Cabras Lagoon can be related to two main interlinked environmental and ecological gradients. The first gradient is due to the marine influence seaward, the second one is related to spatial differences in the trophic status and saprobity condition across the lagoon. In particular, the most confined site C2 differed from the other two investigated sites as being characterized by muddy, organically enriched sediments, and due to its lack of connection and exchange with both continental and marine waters, mostly influencing C1 and C3, respectively. Differently, the northern site C1 was most directly affected by the riverine input of freshwater and had sandy sediments with a very low phytopigment and OM content. This is consistent with the high energy and the low water residence time found at C1, which helps explaining the resuspension and export of fine sediment particles from this site to the central sector of the lagoon [56,57]. Finally, the seaward site C3 located in one of the three creeks connecting the lagoon to the Gulf of Oristano was in terms of sediment features intermediate between C1 and C2. It is worthwhile noting that in this sector of the lagoon man-made structures constructed in proximity of the inlet have caused modifications in the sedimentary regime of the lagoon and the water exchange with the adjacent Gulf [41,56]. Yet, the largest variation in salinity was found at C3 due to a marked drop in salinity in the whole lagoon in the winter of the present study, nullifying temporarily the salinity gradient and further highlighting the high seasonal and interannual environmental variability of the Cabras Lagoon [35,36].

Overall, these results show that the environmental (dis)similarities between the three study sites were constant in the two periods investigated, although summer and winter data-points were most clumped at C1 and more widespread, but still clearly separated one another, at C2 and C3. Thus, temporal variation did not alter significantly the location of the site-points in the multivariate model ordination. This highlighted that the most relevant source of variation in the study area was not due to differences between summer and winter dates, but to differences between sampling sites.

Regarding the meiofaunal richness, our data can be compared only with a few studies because the complete list of meiofaunal taxa is rarely reported. However, an overall high number of richness (i.e., 16 taxa) was recorded in the present study showing levels higher than those documented from both Mediterranean and European transitional water bodies [17–19,22,58,59]. Nematodes were the dominant

taxon as frequently reported in lagoon systems worldwide [2,17,22,60,61]. This is likely related to their capacity to colonize the fine (suboxic or anoxic) sediments that generally characterize lagoons [19]. As reported in literature, the second most abundant group is represented by copepods [14,22,58,59]. Copepods are one of the most sensitive taxa to oxygen limitation and therefore they are confined to the oxic sediments [20,48], but they seem to take advantage of the high abundance of the microphytobenthos occurring in lagoon sediments and that are a primary food source for numerous copepod species [24].

The meiofaunal structure assemblage seemed to be very sensitive to the spatial environmental heterogeneity found in the Cabras Lagoon appearing a promising indicator of biotic changes in transitional water bodies. Indeed, the multivariate analysis (nMDS and PERMANOVA) applied on the assemblage structure clearly distinguished the three different sites in line with their environmental features with a partial overlap of the meiofaunal structure of C1 and C2, and a greater separation of C3 (Table 2, Figure 6). The latter site, characterized by “marine conditions”, had the highest abundance of all the meiofaunal taxa and in particular, it was distinguished by the greater abundances of Plathelminthes and Oligochaeta. These two taxa are often closely associated with each other and are among the primary components of transitional environment sediments [20,24]. Oligochaeta are regarded as taxa able to adapt to numerous environmental stress [18,48]. Plathelminthes are effective predators of many meiobenthic organisms such as copepods that could explain their higher abundance at C3 where the higher meiofaunal densities and copepods was found [14,62].

Instead, the high degree of confinement and consequent trophic load existing at site C2 was marked by a higher presence of Halacaroidea and Ostracoda. Ostracoda are generally recognized as sensitive taxon to environmental perturbations, but adaptive behaviors to numerous natural and anthropogenic environmental (e.g., organic load and trace element contamination) changes have been documented in several species [22,24,63]. In that site, there was also the only record of Pycnogonida that is generally recognized as a marine taxon. Pycnogonida have a few representatives in the meiofauna, but the *Anoplodactylus* genus has some species that ranges in the meiofaunal body size and are also tolerant to salinity variations until values comparable to those found in C2 (11 PSU) [64].

In C1, the site with the lowest salinity, Tanaidacea was one of the discriminating taxon. Noteworthy is that although many euryhaline species from Tanaidacea are found in transitional habitats, most occur only temporarily in these environments, appearing unable to form stable populations there [65]. Furthermore, Ateş et al. [66] reported that some species are particularly related to coarse grain size and low content of organic matter that were the conditions that distinguish C1.

The environmental variables that appeared to mainly affect the meiofaunal assemblage of the study area were salinity and DO that were the main responsible parameters for the separation of C3 and the other two sites. Salinity gradient is one of the primary factors that influence meiofauna in transitional environments [8,18] along with the oxygen availability that seems to influence all the meiofaunal taxa and not only the oxygen sensitive ones such as copepods (see above references). The quantity and quality of the organic matter (OM, Chl-*a*, and phaeopigments) and *W_c*, which is an indirect indication of the grain size of the substrates, were also important for the meiofaunal distribution as suggested by many authors [8,17,22] and contributed mostly to the separation between the other two sites (i.e., C1 and C2). Instead, temperature did not show a relevant contribution to the ordination of the meiofauna. This issue as well as the lack of significant differences in the comparison of the meiofaunal assemblage structure suggest that meiofauna was more affected by spatial than temporal variations. This pattern resembled the distribution patterns of the macrozoobenthos observed at the same study sites where spatial differences were greater than significant seasonal changes [30].

When the spatiotemporal variation in the univariate measures were statistically studied, the greatest differences were observed between the three sites further supporting the results revealed by the structure of the meiofaunal assemblage (Table 4). In particular, PERMANOVA showed significant differences of the total meiofaunal abundance, number of taxa, evenness and the *Ne/Co* ratio. Among them, the *Ne/Co* ratio showed a very temporal variable trend (i.e., it was higher in C1 in the winter and lower in C2 and C3 in the summer) which likely is why PERMANOVA did not reveal

significant differences between periods. However, the variation in the Ne/Co ratio did not highlight the presence of anthropogenic stress being the values lower than the thresholds reported by Raffaelli and Mason [52] for stressful conditions. Instead, the highest evenness at C1 was likely related to the coarser grain size of the sediments that generally host a more diversified meiofaunal assemblage [67,68].

5. Conclusions

The present study is one of the few investigations on the meiofaunal community structure, composition, and diversity conducted in transitional waters (TWs) in the Western Mediterranean Sea. The high environmental variability and habitat heterogeneity of the Cabras Lagoon, the largest TW in Sardinia, was reflected in significant differences in meiofauna among the study sites. Spatial differences in several faunal parameters (i.e., community structure, richness, Pielou-evenness, and Ne/co ratio) were stronger than temporal variation, suggesting that meiofaunal organisms are good indicators of the physical-chemical variation in TWs. Furthermore, the Cabras Lagoon showed high values of meiofaunal species richness further supporting the idea that TWs may be biodiversity hotspots and meiofauna is an important biotic component to understand their functioning.

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