

Article

Macrobenthos of the Tortoli Lagoon: A Peculiar Case of High Benthic Biodiversity among Mediterranean Lagoons

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Abstract: Coastal lagoons and brackish ponds are extremely dynamic and temporary ecosystems that follow natural changes throughout their geological history. The correct management of the lagoons ensures their integrity and proper functioning. For this reason, their ecological status should be surveyed for assessing the most appropriate strategies of use. In the present study, historical datasets collected in 2003–2004 are used to investigate the spatiotemporal variation in the species composition and community structure of the macrobenthos of the Tortoli Lagoon (Sardinia, Italy) and to assess their relationship with key environmental variables. Owing to the presence of a riverine runoff at a site and confined areas at some distance from the sea inlet, we hypothesize the marked spatiotemporal changes of the macrobenthic community consistent with the high environmental variability typical of coastal lagoons. The results show a surprisingly high benthic biodiversity for a medium-sized lagoon (250 ha), with 101 species unevenly distributed across the lagoon. The environmental variables did not explain the zonation of the macrobenthic community as that typically found along a lagoonal gradient, due to a marked marine influence. The sampling sites were in fact discriminated by the species distribution according to their ecological affinity; in particular, the most distinctive characteristics of the Tortoli Lagoon emerged from the strictly marine species that represented the most abundant group, consistently with the high marinization of the lagoon. Our results show that the Tortoli Lagoon constitutes a peculiar ecosystem within Mediterranean lagoons, departing from the classic confinement theory.

Keywords: benthic macroinvertebrates; species richness; community structure; lagoon ecosystems; brackish ponds; oyster culture

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1. Introduction

Transitional waters, including coastal lagoons, brackish ponds, and estuaries, are important and fragile ecosystems in the coastal landscape, and the scientific community and worldwide legislations (e.g., the US Clean Water Act, European Water Framework Directive, and Marine Strategy Framework Directive) recognize the necessities to assess their health status and ensure the proper management of their resources. Within the Mediterranean Sea, there are numerous transitional water ecosystems that are exploited for productive purposes, such as aquaculture and fisheries [1,2], and are interesting conservation sites for flora and fauna [3]. Coastal lagoons and brackish ponds are especially extremely dynamic and temporary ecosystems [4], which follow natural changes from their formation, evolution, and subsequent decline, throughout their geological history. Typically, their fate is closely connected to the presence of barriers enclosing them and cutting them off partially from the sea; on the other hand, the lagoons may be largely influenced by freshwater inflows from the continental system. Meteorological and climatic factors,

e.g., winds, waves, and currents, further influence the history of the lagoons and determine their shape. This involves the great diversity of lagoonal environments, both in time and space [5,6], which is also reflected on the peculiarity of their flora and fauna [7–13].

Human activities are also increasingly contributing to the fate of the lagoons by reclamation works, regulating sea and freshwater inflows, and modifying the hydrographic regime, based on the intended use of the lagoons by human beings [14,15]. Their use depends on the key ecosystem services they provide for both productive and conservation purposes, such as water quality improvement, fisheries resources, habitat and food for migratory and resident animals, and recreational areas for human populations [16–20]. By contrast, the lagoonal ecosystems are under various pressures due to anthropogenic impacts that endanger them and may cause the reduction in or even loss of their services and functions [21–24]. Consequently, the scientific communities and stakeholders have taken care to manage lagoons in order to maintain their integrity and functioning, which contrasts with the natural fate of lagoons, in order to ensure the numerous ecosystem services that lagoons provide. In this context, it is worthy of attention to detect changes to see if they are part of natural variability or if they presage a system malfunction [25,26].

A useful tool to understand environmental changes is the analysis of historical data, when available, to help us distinguish periodical fluctuations from sudden/short-term variations [27–29]. The lack of knowledge about past conditions, in parallel with the gradual change in the human perception of environmental conditions, often results in a growing tolerance to environmental degradation, which leads to harmful consequences on environmental and cultural heritage sites and their conservation [30–34]. In this context, the composition and abundance of benthic invertebrate fauna are one of the main biological elements used to assess ecological quality status, and it is also known to be one of the best effective indicators of pollution stress, as it shows predictive responses to different levels of anthropogenic impacts [35–38]. In coastal lagoons, macrobenthic assemblages show a typical zonation, with the marine species more abundant at the seaward sites and brackish and opportunistic species in the confined zone [11,12].

From these general concepts, we use historical datasets collected in the Tortoli Lagoon (Sardinia, Italy) to investigate the species composition and community structure of the macrobenthos and to assess their relationship with key environmental variables. As is typical of coastal lagoons, we hypothesize that the marked spatiotemporal changes in the macrobenthos are driven by the environmental variability typical of these systems. In particular, we aim (i) to analyze the variations in macrobenthic community structure and diversity in order to detect a possible spatial zonation; (ii) to investigate the consistency between the spatial pattern of benthos and that based on the environmental features of the lagoon; and (iii) to evaluate the possible causes influencing the species composition, diversity, and distribution of the macrobenthos within the investigated lagoon.

2. Materials and Methods

2.1. Study Area

The Tortoli Lagoon, located in the central-east coast of Sardinia, has a total area of approximately 250 ha and a perimeter of 15.1 Km (Figure 1); the average depth of the water is 1.5 m. It is composed of an ovoid basin connected to the sea through two channels in its central and southern areas, while the freshwater inputs enter the lagoon from Rio Mannu through a bulkhead system in its northern area and a small canal in the southwest area. Bottoms are sandy–muddy and large areas are covered with seagrasses, mainly *Zostera noltei*. The lagoon hosts a flourishing fish and shellfish traditional fishery, and aquaculture activities have been practiced for more than 30 years [39].

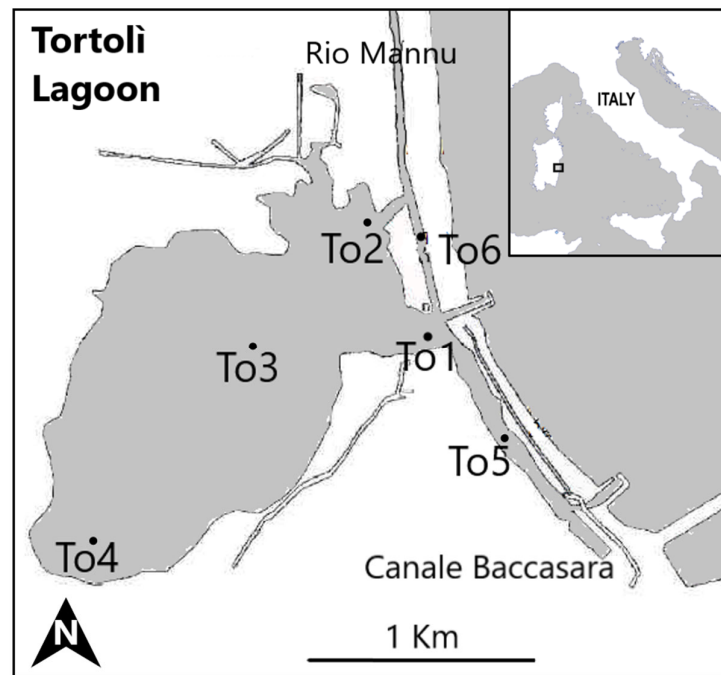


Figure 1. Study area (Tortoli Lagoon, east coast of Sardinia, Italy) and sampling sites (To1, To2, To3, To4, To5, To6).

For the present study, six sites (Figure 1) assumed to be representative of different environmental conditions according to the confinement theory (e.g., salinity, sediment grain-size, etc.) were selected. Three sites (To2, To3, To4) were located in the internal area of the lagoon and had sandy sediments; To1 and To5 were located, respectively, near the central and southern parts of the seaward channel, and both had muddy–sandy sediments; and To6 was located in Rio Mannu and had sandy–muddy sediments.

2.2. Sampling Methods and Taxonomical Analysis

The macrozoobenthos and water samples were collected at the six sites (Figure 1) in July and November 2003 and in February and June 2004; two replicates of macrozoobenthos were collected at each site to obtain a total of 48 samples. From the water samples that were collected on the same dates, the nitrates, total phosphorous, and chlorophyll-*a* levels were measured in the laboratory according to the method described by Parson et al. (1984) [40]. Salinity, temperature, and dissolved oxygen (mg/L) were measured monthly from July 2003 to June 2004 at each site using a multi-parametric probe (OxyGuard Handy Gamma).

The macrozoobenthos samples, collected with a Van Veen grab (sampling area: 500 cm²), were sieved using a 0.5 mm mesh-size sieve and fixed with a 10% buffered formaldehyde solution; when necessary, Rose Bengal was used to better highlight the organisms. In the laboratory, the animals were identified to the lowest possible taxonomic level, counted, and then preserved in 70% ethanol. The updated taxonomic nomenclature was checked by the World Register of Marine Species.

2.3. Data Analysis

Both abiotic and biotic data were analyzed by univariate and multivariate techniques. Principal component analysis (PCA) was performed on log-transformed and normalized abiotic data in order to highlight the variations among sites and sampling periods. Univariate diversity measures, such as average species richness (*S*), abundance (*A*), Shannon index (*H'*), and Evenness (*J*), were calculated to analyze the community structure and

species composition. The non-parametric permutational analysis of variance (two-way PERMANOVA) was conducted to test the significant differences in all the abiotic data (i.e., temperature, salinity, dissolved oxygen, NO_3 , chlorophyll-a, and P_{TOT}) and the biotic univariate measures (i.e., number of species, total macrofaunal abundance, Shannon diversity, and evenness). Macrozoobenthic data were analyzed by means of the multivariate non-metric multidimensional scaling (nMDS) procedure, using mean abundance values in the cumulative matrix of all the sites and months, based on the Bray–Curtis (dis)similarity measure [41]. Similarity, percentage (SIMPER) analysis [41] with a cut-off value of 95% was used to determine the contribution of each species to the (dis)similarity between sampling sites. The analysis of similarities (ANOSIM) was performed to test significant variations in the macrozoobenthos structure between sites [42]. Univariate and multivariate analyses were performed using PAST 4.05 and PRIMER v.6 software.

3. Results

3.1. Water Variables

Temperature and dissolved oxygen (DO) showed similar mean values and ranges at all sites, with maximum values of temperature in July and August and minimum values in December and January, while the lowest values of DO were recorded from June to September and the highest values from February to May (Figure 2). Salinity showed relatively higher mean values at the innermost site (To4) and at those closest to the sea (To1 and To5), while the site influenced by the Rio Mannu (To6) showed the widest range of variation in salinity, from 9‰ in winter–spring to 37‰ in summer–autumn.

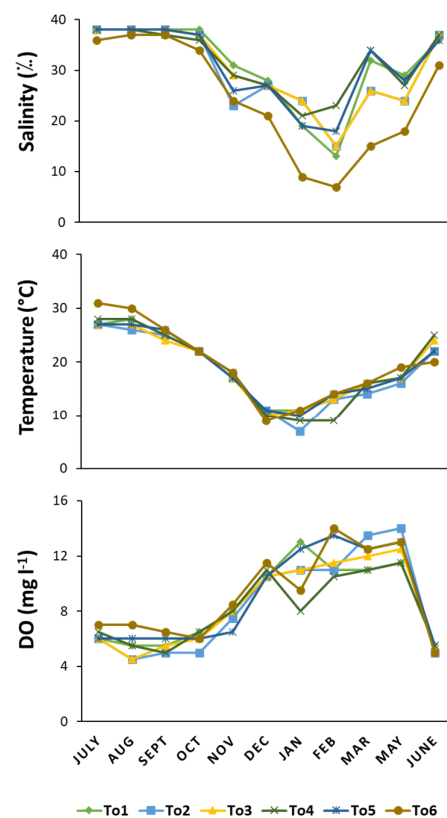


Figure 2. Line graph of water column variables related to the six sampling sites for each month: salinity, temperature, dissolved oxygen (DO).

The box plots in Figure 3 show relatively limited variations in the nutrient concentrations, being most apparent for nitrates at To6 and for total phosphorous at To4; the

smallest variations were found at To5 for nitrates and at To1, To2, and To3 for total phosphorous. Chlorophyll-a content varied between sites and showed the lowest mean values at site To1 close to the sea and at To2, and in the latter, the greatest range of chlorophyll-a was also recorded; the highest mean value was achieved for in the innermost site at To4.

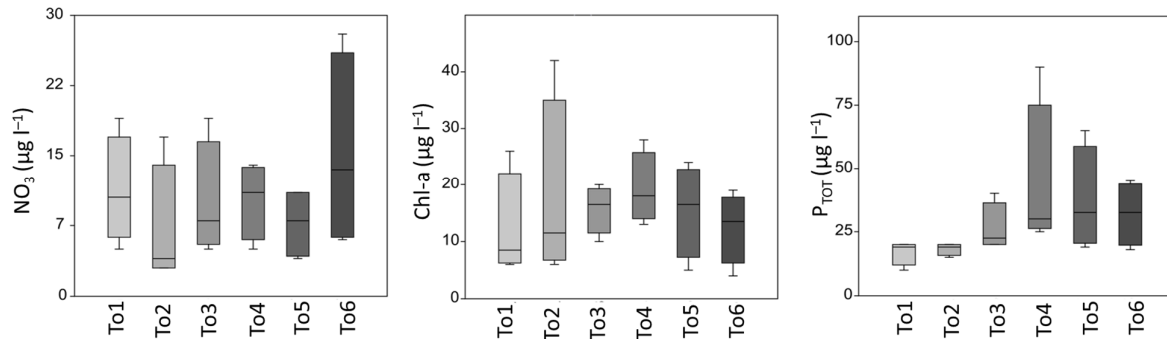


Figure 3. Box plot of water column nutrients related to the six sampling sites: nitrates (NO_3), chlorophyll-a (Chl-a), and total phosphorous (P_{TOT}); maximum value, minimum value, and median line.

The PCA based on the environmental variables showed a clear separation between different dates (Figure 4). The sampling points for the months of June and July were grouped on the right side of the plot, as opposed to those of February, while the sampling-points of November were located in the intermediate position. At each month, no particular arrangement separated the site points that remained close together within each group, with the exception of To6 in June and November.

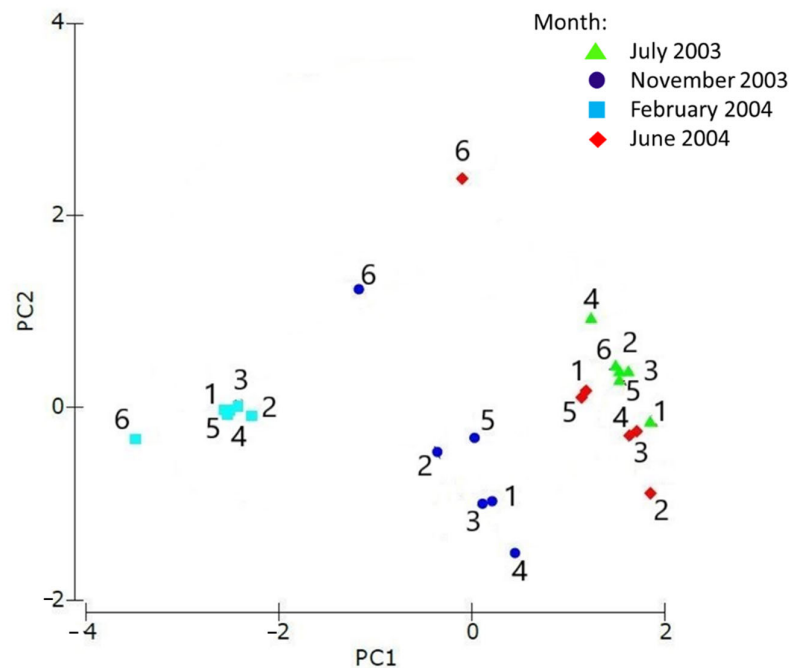


Figure 4. Principal component analysis (PCA) for environmental variables; cumulative variance (95.8%), PC1 (76.3%), PC2 (15.6%); 1, 2, 3, 4, 5, 6: number of sampling sites.

PERMANOVA showed no significant differences among the sampling sites for all the abiotic variables (data not shown).

3.2. Macrozoobenthic Community

The macrobenthic fauna found in the Tortoli Lagoon was composed of 101 species, for a total of 2839 individuals. Polychaetes were the richest in number of species (49.5%) and dominant in terms of number of individuals (42.7%), followed by crustaceans (28.4% of species and 34.9% of number of individuals) and mollusks (13.7%). The most abundant polychaetes were the marine species *Nephtys hombergii*, *Myriochele heeri*, and *Spiochaetopterus costarum* reaching the highest densities at To1 and the opportunistic species *Polydora ciliata* at To2 and To5 and *Capitella capitata* at To4. Among the crustaceans, the most abundant species were the amphipods with the brackish species *Monocorophium insidiosum*, which occurred at all the sites, except To1 and To5, but mostly at To4 and To6, and marine *Apocorophium acutum* recorded throughout the lagoon and *Elasmopus pocillimanus* especially at To3. The dominant mollusk was the bivalve *Abra segmentum*, a typical inhabitant of coastal shallow areas, which was found throughout the lagoon, and the brackish species *Cerastoderma glaucum*, recorded at all the sites, but only occasionally at To1 and To5.

The results of the biotic synthetic variables are shown in Figure 5. The highest values for all four variables (i.e., number of species and individuals, and H' and J indices) were found at To1; the lowest ones occurred at To2 (number of species), To5 (number of individuals), and To4 (and H' and J indices).

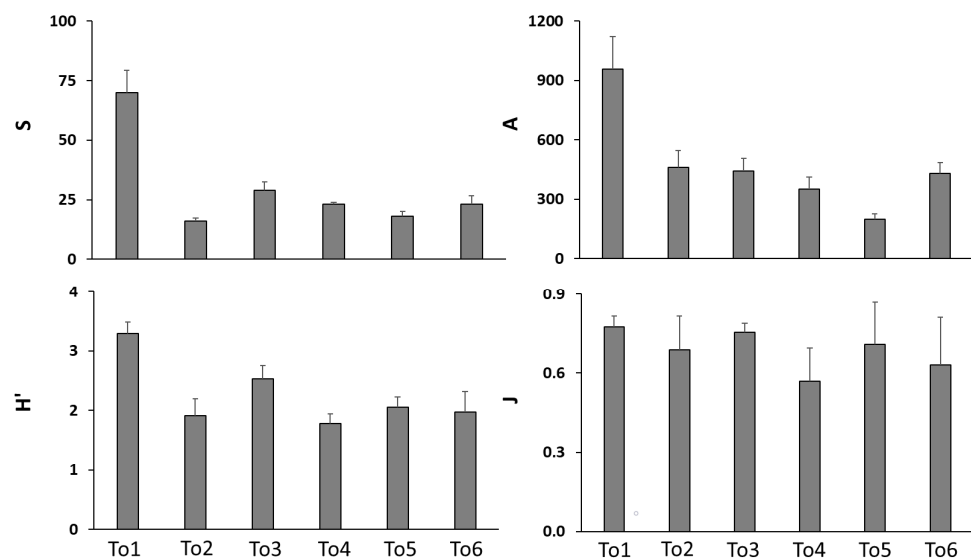


Figure 5. Mean values for the whole period of study ($n = 8$, \pm SE standard error) of macrofaunal community synthetic variables at the sampling sites (To1, To2, To3, To4, To5, and To6); S: number of species; A: number of individuals (ind 0.1 m^{-2}); H': Shannon index; J: Evenness.

The two-way PERMANOVA conducted for each biotic measure showed significant differences ($p < 0.001$) among sites and months in the species number, total abundance, evenness, and diversity index (Table 1).

Table 1. Results of two-way PERMANOVA testing differences among sites for the total macrofaunal abundance, number of taxa, Shannon diversity, and evenness.

| Variable | Factors | Total Sum of Squares | df | Mean Square | Pseudo-F | p |
|----------|---------|----------------------|----|-------------|----------|--------|
| Species | Sites | 1.31 | 5 | 0.26 | 8.96 | 0.0001 |
| | Months | 0.49 | 3 | 0.16 | 5.66 | 0.0006 |

| | | | | | | |
|-----------|----------------|------|----|------|-------|--------|
| | Sites × Months | 1.9 | 15 | 0.13 | 4.34 | 0.0001 |
| | Residual | 0.7 | 24 | 0.03 | | |
| | Total | 4.4 | 47 | | | |
| | Sites | 0.78 | 5 | 0.16 | 3.86 | 0.0008 |
| | Months | 3.45 | 3 | 1.15 | 28.49 | 0.0001 |
| Abundance | Sites × Months | 4.29 | 15 | 0.29 | 7.07 | 0.0001 |
| | Residual | 0.97 | 24 | 0.04 | | |
| | Total | 9.49 | 47 | | | |
| | Sites | 1.1 | 5 | 0.22 | 3.57 | 0.0011 |
| | Months | 0.42 | 3 | 0.14 | 2.27 | 0.0249 |
| Diversity | Sites × Months | 1.83 | 15 | 0.12 | 1.98 | 0.02 |
| | Residual | 1.48 | 24 | 0.06 | | |
| | Total | 4.83 | 47 | | | |
| | Sites | 0.38 | 5 | 0.08 | 7.28 | 0.001 |
| | Months | 0.53 | 3 | 0.18 | 17.15 | 0.0001 |
| Evenness | Sites × Months | 0.75 | 15 | 0.05 | 4.81 | 0.0024 |
| | Residual | 0.25 | 24 | 0.01 | | |
| | Total | 1.9 | 47 | | | |

The nMDS plot (Figure 6) shows the distinction of the sampling sites divided into three groups, based on the macrobenthic community structure. Two-way ANOSIM analysis confirmed significant differences among the sites ($R = 0.93$; $p < 0.0001$) and times ($R = 0.96$; $p < 0.0001$). The first group of sampling sites included To4 and To6 located at the opposite sides of the lagoon; the second group consisted of the sites To2 and To3 situated in the central area of the lagoon; and the third group consisted of To1 and To5, which were located at the sites closest to the sea.

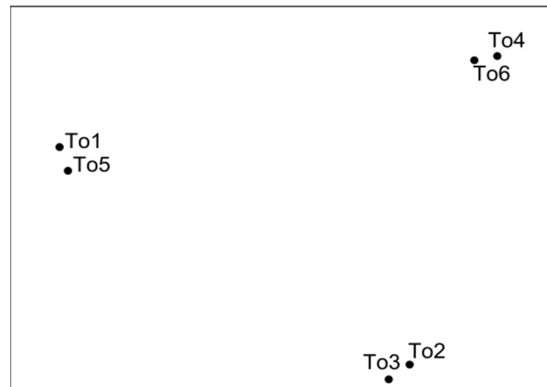


Figure 6. nMDS on average values of abundance data for the whole period of study (stress = 0.04) based on Bray–Curtis (dis)similarity.

Table 2 shows the list of the top discriminating species contributing to the 95% by SIMPER analysis at the investigated sites and their ecological affinity. The species were ordered according to their occurrence, and only four species (*A. segmentum*, *A. acutum*, *C. glaucum*, and *Heteromastus filiformis*) were found at all sites, most species occurring only at two or one site. The marine species group was the most abundant, followed by coastal, opportunistic, and brackish species.

Table 2. List of the top discriminating taxa contributing to the 95% in SIMPER analysis, ordered by occurrence (species occur.); higher taxon: A (ascidian), B (bivalve), C (crustacean), Ch (chironomid), Cn (cnidarian), E (echinoderm), G (gastropod), P (polychaete), Ph (Phoronid); ecological affinity: Br (brackish), Cs (coastal sheltered), Mr (marine), Op (opportunistic); contrib%: percentage of contribution of each species.

| Species | Higher Ecological | | Species Occur. | Contrib. % | To1 | To2 | To3 | To4 | To5 | To6 |
|--|-------------------|----------|----------------|------------|-----|-----|-----|-----|-----|-----|
| | Taxon | Affinity | | | | | | | | |
| <i>Abra segmentum</i> (Récluz, 1843) | B | Cs | 6 | 5.19 | ⊙ | ⊙ | ⊙ | ⊙ | ⊙ | ⊙ |
| <i>Apocorophium acutum</i> (Chevreux, 1908) | C | Mr | 6 | 4.22 | ⊙ | ⊙ | ⊙ | ⊙ | ⊙ | ⊙ |
| <i>Cerastoderma glaucum</i> (Bruguière, 1789) | B | Br | 6 | 2.63 | ⊙ | ⊙ | ⊙ | ⊙ | ⊙ | ⊙ |
| <i>Heteromastus filiformis</i> (Claparède, 1864) | P | Op | 6 | 2.21 | ⊙ | ⊙ | ⊙ | ⊙ | ⊙ | ⊙ |
| <i>Capitella capitata</i> (Fabricius, 1780) | P | Op | 5 | 7.69 | ⊙ | ⊙ | ⊙ | ⊙ | | ⊙ |
| <i>Microdeutopus gryllotalpa</i> Costa, 1853 | C | Cs | 5 | 3.60 | ⊙ | ⊙ | ⊙ | | ⊙ | ⊙ |
| <i>Monocorophium insidiosum</i> (Crawford, 1937) | C | Br | 5 | 13.27 | ⊙ | ⊙ | ⊙ | ⊙ | | ⊙ |
| <i>Nephtys hombergii</i> Savigny in Lamarck, 1818 | P | Mr | 5 | 4.51 | ⊙ | ⊙ | ⊙ | | ⊙ | ⊙ |
| <i>Phoronis psammophila</i> Cori, 1889 | Ph | Mr | 5 | 0.86 | ⊙ | ⊙ | ⊙ | ⊙ | ⊙ | |
| <i>Prionospio cirrifera</i> Wirén, 1883 | P | Op | 5 | 0.63 | ⊙ | ⊙ | ⊙ | ⊙ | | ⊙ |
| <i>Iphinoe trispinosa</i> (Goodsir, 1843) | C | Mr | 4 | 0.30 | ⊙ | ⊙ | ⊙ | | ⊙ | |
| <i>Melita palmata</i> (Montagu, 1804) | C | Cs | 4 | 0.57 | ⊙ | | ⊙ | ⊙ | | ⊙ |
| Chironomidae | Ch | Op | 3 | 4.59 | ⊙ | ⊙ | | ⊙ | | |
| <i>Venerupis corrugata</i> (Gmelin, 1791) | B | Mr | 3 | 1.68 | ⊙ | | | ⊙ | | ⊙ |
| <i>Aphelochaeta marioni</i> (Saint-Joseph, 1894) | P | Mr | 2 | 1.05 | ⊙ | | | | ⊙ | |
| <i>Chaetozone setosa</i> Malmgren, 1867 | P | Mr | 2 | 0.26 | ⊙ | | | | | ⊙ |
| <i>Diopatra neapolitana</i> Delle Chiaje, 1841 | P | Mr | 2 | 0.26 | ⊙ | | | | | ⊙ |
| <i>Elasmopus pocillimanus</i> (Spence Bate, 1862) | C | Mr | 2 | 4.30 | | | ⊙ | | ⊙ | |
| <i>Erichthonius brasiliensis</i> (Dana, 1853) | C | Mr | 2 | 0.25 | | | ⊙ | | | ⊙ |
| <i>Gammarus insensibilis</i> Stock, 1966 | C | Cs | 2 | 0.39 | ⊙ | | | | | ⊙ |
| <i>Loripes orbiculatus</i> Poli, 1795 | B | Cs | 2 | 0.45 | ⊙ | | | ⊙ | | |
| <i>Malacoceros fuliginosus</i> (Claparède, 1868) | P | Op | 2 | 1.62 | | | | ⊙ | | ⊙ |
| <i>Microdeutopus algicola</i> Della Valle, 1893 | C | Mr | 2 | 2.14 | ⊙ | | | | | ⊙ |
| <i>Neanthes acuminata</i> (Ehlers, 1868) | P | Cs | 2 | 1.12 | ⊙ | | | ⊙ | | |
| Oligochaeta | O | | 2 | 0.41 | ⊙ | | | ⊙ | | |
| <i>Paranemonia cinerea</i> (Contarini, 1844) | Cn | Cs | 2 | 0.46 | | | ⊙ | | | ⊙ |
| <i>Parvicardium exiguum</i> (Gmelin, 1791) | B | Mr | 2 | 0.38 | ⊙ | | ⊙ | | | |
| <i>Polydora ciliata</i> (Johnston, 1838) | P | Op | 2 | 8.64 | ⊙ | | | | ⊙ | |
| <i>Protodorvillea kefersteini</i> (McIntosh, 1869) | P | Mr | 2 | 0.58 | ⊙ | | | ⊙ | | |
| <i>Styela plicata</i> (Lesueur, 1823) | A | Cs | 2 | 1.53 | | | ⊙ | | | ⊙ |
| <i>Tanais dulongii</i> (Audouin, 1826) | C | Op | 2 | 0.29 | ⊙ | | ⊙ | | | |
| <i>Amphibalanus amphitrite</i> (Darwin, 1854) | C | Cs | 1 | 1.60 | | | ⊙ | | | |
| <i>Amphibalanus eburneus</i> (Gould, 1841) | C | Br | 1 | 2.71 | | | ⊙ | | | |
| <i>Amphipholis squamata</i> (Delle Chiaje, 1828) | E | Mr | 1 | 0.82 | ⊙ | | | | | |
| <i>Caecum clarkii</i> P. P. Carpenter, 1859 | G | Mr | 1 | 0.47 | ⊙ | | | | | |
| <i>Hilbigneris gracilis</i> (Ehlers, 1868) | P | Mr | 1 | 0.25 | ⊙ | | | | | |
| <i>Lagis koreni</i> Malmgren, 1866 | P | Mr | 1 | 0.50 | ⊙ | | | | | |
| <i>Lumbrineris latreilli</i> Audouin & Milne Edwards, 1833 | P | Cs | 1 | 0.50 | ⊙ | | | | | |
| <i>Myriochele heeri</i> Malmgren, 1867 | P | Mr | 1 | 4.50 | ⊙ | | | | | |
| <i>Pseudolirius kroyeri</i> (Haller, 1879) | C | Mr | 1 | 0.66 | ⊙ | | | | | |
| <i>Sphaerosyllis taylori</i> Perkins, 1981 | P | Mr | 1 | 0.28 | ⊙ | | | | | |
| <i>Spiochaetopterus costarum</i> (Claparède, 1869) | P | Mr | 1 | 4.75 | ⊙ | | | | | |

Some distinction in terms of species composition emerged between the sites, the highest number of species being found at To1, the majority of which were typically marine (*M. heeri*, *S. costarum*, *Aphelochaeta marioni*, *Microdeutopus algicola*, *Amphipholis squamata*, *Phoronis psammophila*) or common inhabitants of shallow coastal waters (*A. segmentum*, *Neanthes caudata*, *Microdeutopus gryllotalpa*), while strictly opportunistic species were lacking, save *H. filiformis* and very few individuals of *C. capitata*, which occasionally occurred. Some of these species, both marine and common in shallow coastal waters, were shared with the benthic assemblage of To5 (i.e., *A. marioni*, *P. psammophila*, *M. gryllotalpa*, *A. segmentum*), as well as the opportunistic species *H. filiformis*, which occurred in To5 with the highest abundance. Many marine and shallow coastal waters species, e.g., *N. hombergii*, *A. acutum*, *P. psammophila*, *A. segmentum*, together with the opportunistic species *Prionospio cirrifer*, characterized the benthos at both To2 and To3. Finally, few marine species occurred at To4 and To6, which, instead, shared some brackish-water (i.e., *M. insidiosum*, *C. glaucum*) and opportunistic (i.e., *C. capitata*, *Malacoceros fuliginosus*, *P. cirrifer*) species between their benthic assemblages. No typical freshwater elements were recorded in the lagoon, not even at To6 located next to the Rio Mannu freshwater input.

4. Discussion

The present study highlighted a limited range of spatial variations in the environmental features of the Tortoli Lagoon, contrary to a natural gradient typically found in coastal lagoons, i.e., from marine-influenced towards confined areas [12,43]. In particular, water temperature, dissolved oxygen, and salinity showed no significant differences among the sites, even though site To6 was affected by freshwater runoff from the Rio Mannu in the cooler season. Moreover, the other measured water variables only partially contributed to arrange the sampling sites along a trophic gradient, with chlorophyll-*a* showing slightly higher values and smaller variations at the sites of To3, To4, To5, and To6; total phosphorus at To4, To5, and To6; and nitrate at To6. The absence of confinement and trophic gradients was reflected in the macrobenthos community structure and species composition that did not show a clear zonation. Notwithstanding, PERMANOVA highlighted significant differences in species richness, abundance, diversity, and evenness, both in space and time. These latter factors were attributable to the seasonal cycle of macrozoobenthos assemblages in lagoon ecosystems [44–46]. Based on the macrozoobenthos structure data, distinct differences among sites emerged from the nMDS analysis and were supported by the ANOSIM results; however, the measured environmental variables were inconsistent to explain the different groupings of communities. We therefore hypothesized that the causes of these distinctions and spatial heterogeneity lie in the biological factors. Indeed, species of different ecological affinities occurred unevenly at different sites, save the only two brackish species, *M. insidiosum* and *C. glaucum*, found all over the lagoon. Half of the opportunistic species were distributed throughout the lagoon, while the other opportunistic ones characterized only two sites, as *M. fuliginosus* To4 and To6, *P. ciliate* To1 and To5, and *T. dulongii* To1 and To2. A similar pattern was revealed with regard to coastal-sheltered and strictly marine species. Of the ten coastal-sheltered species, only three (*A. segmentum*, *M. gryllotalpa*, *M. palmata*) were distributed over the large part of the lagoon, unlike the other species that distinguished two sites or a single site. Most distinctions emerged within the group of strictly marine species, which was also the most species-rich group. Of these, only four species (*M. acutum*, *N. hombergii*, *P. psammofila*, *I. trispinosa*) were able to entirely colonize the lagoon, while half of the remaining species characterized two sites and the other half a single site. These results suggest, on the one hand, the high biodiversity in the Tortoli Lagoon and, on the other, the marked degree of marinization that characterizes it.

Such peculiarity makes the Tortoli Lagoon a peculiar ecosystem among the Mediterranean transitional water environments, particularly located those along the Sardinian coast [12]. As a result of its physiographic features that characterize it as a medium-sized lagoon (surface of 2.5 km² and volume of 4 Mm³) and the efficient connection with the sea,

the Tortoli Lagoon appeared to be strongly influenced by the sea, except for the sector of the lagoon in close proximity to the main freshwater tributary (Rio Mannu). This observation was confirmed by the composition of the macrozoobenthos assemblages, which included a large number of marine species at each site. Most of the species, typical inhabitants of strictly marine and sheltered coastal areas, mostly characterized the marine site (To1), with some of them, e.g., Oweniidae *Myriochele heeri* and Chaetopteridae *Spiochaetopterus costarum*, presenting dense populations as result of their gregarious behavior [47,48]. At the same time, the presence of several marine species, also at the other sites, verified the strong marine influence throughout the lagoon. The very high number of species (101) recorded in the Tortoli Lagoon, despite its limited size, is a unique feature among the Italian brackish-water ecosystems. As an example, in the Santa Giusta Lagoon, with a similar salinity range and shape, and in the Mistras Lagoon, with a similar surface but higher salinity, both located in the same transitional district of Oristano in the central-west coast of Sardinia [49], a total of 59 and 39 species have been recorded, respectively [3,50]. Moreover, in the two lagoons of Varano and Alimini, which are located in the Adriatic district and are similarly influenced by the adjacent sea, a total of 52 and 33 were recorded against a larger extension of the Varano Lagoon and a similar salinity range of the Alimini Lagoon compared to the Tortoli Lagoon [51]. We hypothesized that the peculiarity of the Tortoli Lagoon was attributable to its physiographic features and the marked connection with the sea, which make it suitable for the entry of a large number of marine species. In fact, these species find environmental conditions suitable for their settlement heterogeneously across the whole lagoon basin, producing a scattered distribution instead of a distribution along the typical confinement gradient. Moreover, thanks to its physiographic and hydrological peculiarities, the Tortoli Lagoon has been exploited for aquaculture purposes, particularly the experimental oyster farming that started in the early 1990s after the decline in lagoonal fish production since the 1980s [52]. During these years, salinity has increased as a result of various interventions to improve the water circulation, and the changed environmental conditions resulted in conditions suitable for oyster farming [53]. In fact, such production continued successfully for the next twenty years, until the time of the present study (2003), when the oyster production yields, added to those of fish, reached the levels found before the decline in fish production (the author's unpublished data). These results demonstrate that the macrozoobenthos community in the Tortoli Lagoon has not been adversely affected by high-quality bivalve culture.

5. Conclusions

The present study showed the absence of zonation of the macrobenthic community driven by confinement and trophic gradients, as is typically found in Mediterranean lagoons. This was due to a marked marine influence and the dominance of strictly marine species, which contributed to an unusually high benthic biodiversity level. The peculiarity of the Tortoli Lagoon, among the Mediterranean lagoons, and the macrobenthic community analyzed here may represent a useful baseline for the future assessment and comparison of past and present environmental conditions in this and other lagoon systems.

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