

Macrobenthos of lagoon ecosystems: a comparison in vegetated and bare sediments

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ABSTRACT

The classic paradigm, not always unequivocal though, that seagrass macrobenthic abundance and diversity are greater than those in adjacent unvegetated areas, was tested in a Mediterranean lagoon for which evidence is lacking. We compared the community structure and species composition of macrobenthic assemblages in three distinct areas of the Mistras Lagoon (Sardinia, Italy) dominated by i) the seagrass *Cymodocea nodosa* (Cym), ii) mixed-macrophyte/detritus (Mix), and iii) unvegetated sediments (Unv). Samplings were conducted in each area twice in spring (April and May) and twice in autumn (October and November) 2010. Multivariate analyses showed significant differences among the three areas and a marked separation between the two vegetated (Cym and Mix) and the unvegetated (Unv) areas. The top discriminating species, indicated by SIMPER analysis, were characterized by direct development lacking free living larvae. They included marine species, e.g. *Cerithium lividulum*, *Microdeutopus gryllotalpa*, *Loripes orbiculatus* and *Gammarus aequicauda*, at Cym vs Mix, whereas the pair discrimination of the areas Cym vs Unv and Mix vs Unv mostly depended on the marine *Abra tenuis*, the opportunistic Chironomidae and *Capitella capitata*, and the brackish *Hydrobia acuta*. Both vegetated areas showed a higher species number than the unvegetated area. Differently, abundance was higher in Unv than in Cym and Mix in all sampling dates, most notably in spring likely because of reproductive events, due to both opportunistic (*C. capitata*, chironomids) and halolimnobic (*H. acuta*, *Cerastoderma glaucum*) species. Overall, the present study demonstrated the importance of biological factors in structuring the macrobenthic assemblages of the Mistras Lagoon. Habitat-forming phanerogams hosted species-rich assemblages, species-specific reproductive cycles and adaptive strategies contributed to drive species colonization and abundance distribution. Both vegetated and unvegetated patches were found to contribute greatly to the local-scale heterogeneity of the habitat, highlighting the importance of coastal lagoons as hotspots for benthic biodiversity. For these reasons, lagoons must be considered major targets for conservation measures.

Introduction

While in marked decline worldwide, seagrasses are important structural species considered to be “ecosystem engineers”, hosting rich and abundant benthic assemblages and often representing a source of biodiversity for adjacent habitats (e.g. Surugiu *et al.*, 2021; Barnes *et al.*, 2022; García-Gómez *et*

al., 2022). In intertidal and subtidal estuarine systems, several studies have been conducted on biodiversity differentials between seagrass and bare sediments, highlighting the prominent role of seagrass in enhancing the benthic biodiversity (Barnes and Barnes, 2012; Barnes, 2013a; Surugiu *et al.*, 2021). Other studies have compared macrobenthic assemblages in different seagrass species (Leopardas *et al.*, 2014; Barnes, 2020a, 2020b;), confirming the importance of the architectural complexity of seagrass meadows in supporting higher abundance, species richness and diversity. This said, it should also be acknowledged that the classic paradigm that seagrass supports macrobenthic assemblages with different composition and with greater abundance and diversity with respect to adjacent areas without this cover is not always unequivocal (see Nakaoka, 2005; Barnes, 2022 and references therein). For instance, departure from this paradigm is found in some intertidal and estuarine systems in relation to local environmental conditions and gradients, assemblage composition and biomass, predatory behaviour and ontogenetic diet shift, latitudinal gradients, rhizome biomass and seasonal cycle of macrophyte vegetation, etc. (see Barnes and Barnes, 2014; Włodarska-Kowalczyk *et al.*, 2014; Magni *et al.*, 2017 and references therein). These studies highlight the complexity of animal-plant interaction in seagrass ecology, which requires a detailed analysis of the local environmental peculiarities. Most importantly, this suggests that both vegetated and unvegetated areas need to be considered mutually for conservation purposes to prevent the potential loss of local biodiversity and to understand the ecological processes structuring the benthic assemblages in these complex habitats (Barnes, 2013b; Barnes and Hamylton, 2016; Barnes 2021).

It has been shown that in coastal lagoons continuous stands of seagrass offer stability to well structured and taxa-rich macrozoobenthic assemblages (Sfriso *et al.*, 2001; Tagliapietra *et al.*, 2016). This can also be due to a series of additional factors, such as the shading effect and protection of seagrass meadows from high temperature in summer, especially in shallow waters, and a better oxygenation of the water and sediments in the presence of the seagrass (Tagliapietra *et al.*, 2016). Moving away from the meadow to the bare sediment, the temporal fluctuations of the community structure become wider and the assemblages reduce their resistance and resilience, due to worsening or changing environmental conditions, such as increased sediment organic enrichment (Magni *et al.*, 2015; Leopardas *et al.*, 2016) or reduced structural complexity of the habitat (Bachelet *et al.*, 2000; Leopardas *et al.*, 2014), respectively. However, very few studies looking at seagrass vs bare sediment benthic biodiversity are available in coastal lagoons (Magni *et al.*, 2017; Barnes, 2022) and, to our knowledge, no studies have compared the community structure of macrobenthic assemblages in multiple habitats, including vegetated and non-vegetated areas, within a Mediterranean lagoon system.

The present study was carried out in one of these Mediterranean lagoons, the Mistras Lagoon, located along the western coast of Sardinia. We aimed to evaluate the differences in macrobenthic assemblages between seagrass-dominated and unvegetated seabeds by analyzing and comparing the community structure and species composition of macrobenthic assemblages in three distinct areas, within the same lagoon,

characterized by the dominance of i) the seagrass *Cymodocea nodosa*, ii) mixed-macrophyte/detritus, and iii) unvegetated sediments.

Materials and Methods

The Mistras Lagoon

The Mistras Lagoon is a semi-enclosed coastal barrier system (~4.5 km², mean depth <1 m) located on the western coast of Sardinia Island (Italy, Western Mediterranean Sea) (Figure 1). Connected to the Gulf of Oristano through its mouth, it is part of the so-called Oristano Lagoon-Gulf (OLG) system which comprises the Gulf of Oristano (150 km²; maximum depth 24 m), several salt marshes and the lagoons of Cabras, Santa Giusta, S'Ena Arrubia, Corru S'Ittiri and San Giovanni-Marceddi (Magni *et al.*, 2008a). These lagoons are characterized by eutrophic conditions, with the dominance of small sized phytoplankton species and the occurrence of harmful algal species (*e.g.* Cabras Lagoon) or the major presence of macrophyte (*e.g.* S'Ena Arrubia and Santa Giusta lagoons) (Padedda *et al.*, 2012; Satta *et al.*, 2014; Pulina *et al.*, 2018). Sediments are generally organically enriched, leading to impoverished benthic communities (Magni *et al.*, 2005; Brundu and Magni, 2021) and occasional dystrophic events (Murenu *et al.* 2004; Magni *et al.*, 2008b). On the contrary, the Mistras Lagoon is characterized by oligotrophic waters (Sechi, 1982; Specchiulli *et al.*, 2018) and sandy sediments with a low content of Organic Matter (OM), especially in the unvegetated areas, owing to negligible riverine discharge and low sediment supply (Pascucci *et al.*, 2018). Major pollution sources are absent, leading a low-pressure index compared to other Sardinian lagoons (Gravina *et al.*, 2020). During dry periods with high evaporation rates in summer, satellite ponds and natural salt flats are formed in shallower and confined areas where salinity can exceed 50 psu. Fishing activity in the Mistras Lagoon is carried extensively using a capture system made by workers and fish traps named “bertovelli”.

The Mistras Lagoon is listed in the Ramsar Convention on Wetlands (D.M. 04/03/82) and is a Special Protection Area under the Nature 2000 Network (ZPS ITB034006, SIC ITB030034), thus subjected to local protection measures. In the lagoon there are meadows of various species of aquatic phanerogams, including the dominant *C. nodosa* followed by *Zostera noltii* and *Ruppia maritima*, and several macroalgal species, such as *Gracilaria* sp., *Ulva* sp. and *Enteromorpha* sp., (Camarda, 1995). The lagoon is surrounded by luxuriant glasswort dominated by *Salicornia fruticosa*, with the presence of *Obione portulacoides*, *Salsola soda*, *Limonium vulgare*, *Aeluropus litoralis*, *Arthrocnemum glaucum*, *Atriplex* sp. and *Scirpus* sp. (Fenzi, 2013).

Study areas, sampling strategy and sample treatment

Three different sampling areas were selected based on the morphology of the lagoon and the presence and distribution of vegetation. In particular, the seagrass area (hereafter, Cym) was located in the southwest sector of the lagoon and was dominated by *C. nodosa* meadows, with scattered patches of *Z. noltii*. The

second vegetated area, named Mixed (hereafter, Mix), was located closer to the lagoon's mouth and was characterized by sparse patches of both *C. nodosa* and *Z. noltii*, the red alga *Gracilaria* sp. developing from autumn to spring, and vegetation-derived detritus. The third area was unvegetated (hereafter, Unv) and was located in the north-eastern and most confined sector of the lagoon. This area was characterized by sandy sediments and low OM content, without vegetation except sporadic patches of *R. maritima* and *Enteromorpha* sp. in spring (Figure 1).

Sampling was conducted in each of the three selected areas, *i.e.* Cym, Mix and Unv, twice in spring, *i.e.* April and May, and twice in autumn, *i.e.* October and November, 2010. In each area and each date, 3 stations were randomly selected 10's meters apart and at each station four replicate samples, meters apart, were randomly collected using a box-corer (170 cm², penetration depth 15 cm), for a total of 144 samples. Each sample was sieved on a 0.5 mm mesh-size and the residue was preserved in a 4% buffered formaldehyde solution for the determination of macrozoobenthos. In the laboratory, macrobenthic organisms from each sample were sorted, counted and identified to the species level whenever possible using a stereomicroscope.

Data analysis

Macrozoobenthic data were analyzed by means of ordination technique Non-Metric Multidimensional Scaling (nMDS) using the mean abundance of four replicates for each of the three stations in each area and each sampling date based

on (dis)similarity Bray-Curtis measure. Significance tests for differences among spatial and temporal replicates within and between areas were performed by means of the ANOSIM test. The SIMPER test was carried out in order to evaluate the taxa contributing most to (dis)similarity between and within temporal and spatial groups of replicates. In order to analyze spatiotemporal changes in the macrobenthic assemblages, the following biotic variables were computed: species richness (number of species), total abundance (N, number of individuals m⁻²), diversity (H'), calculated by the Shannon-Wiener index, and evenness by the Pielou index. Significance of the biotic variables was tested by means of a two-way PERMANOVA.

Results

Macrobenthic assemblages

In the present study, 6524 individuals belonging to 33 taxa were classified, of which 39.9 % were molluscs, followed by gastropods (16.1%), crustaceans (15.5%) and polychaetes (14.9%). The ten most abundant taxa, accounting for 88.8% of the total abundance, included the bivalves *Abra tenuis* (26.3%), *Cerastoderma glaucum* (6.6%) and *Loripes orbiculatus* (4.6%), the gastropods *Cerithium lividulum* (8.6%) and *Hydrobia acuta* (7.6%), the polychaetes *Capitella capitata* (7.7%) and *Perinereis rullieri* (3.9%), the amphipods *Microdeutopus gryllotalpa* (6.5%) and *Gammarus aequicauda* (4.4%), and Chironomidae (12.7%).

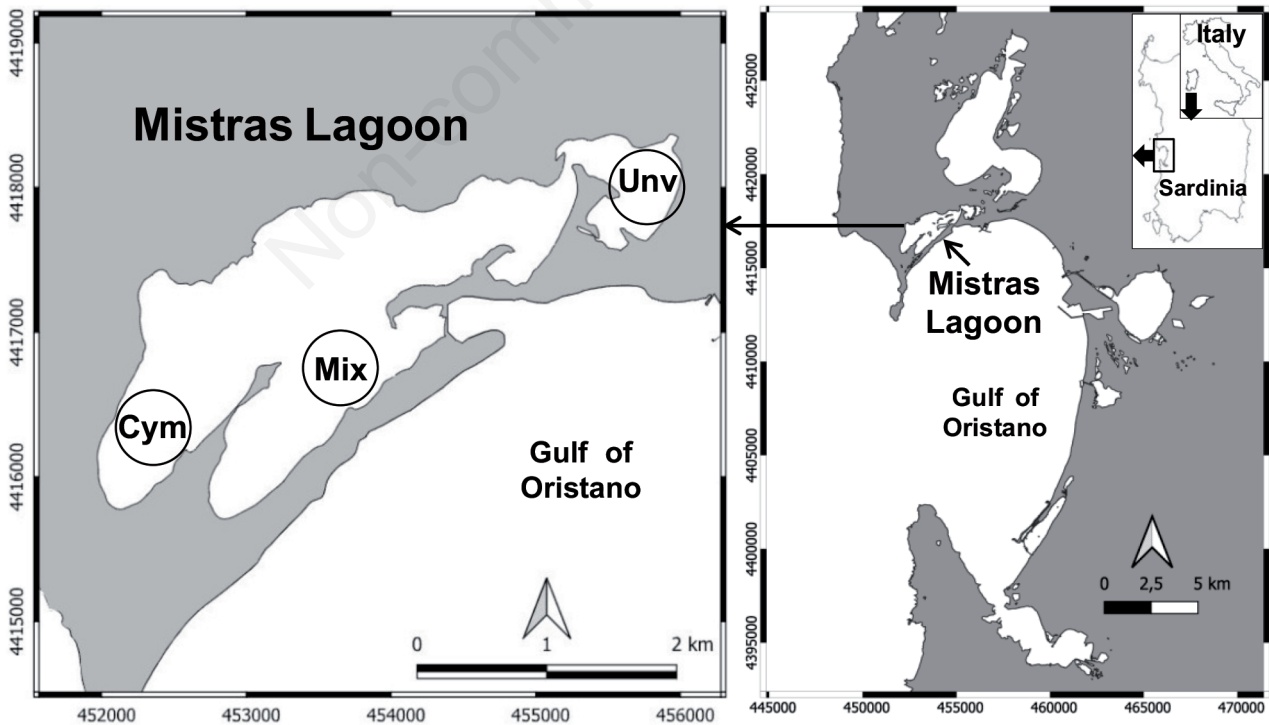


Figure 1. Location of the Mistras Lagoon and the three study areas: *Cymodocea nodosa*-dominated (Cym) area, mixed-macrophyte/detritus (Mix) area, and unvegetated sediment (Unv) area.

Multivariate analyses

The one-way ANOSIM test revealed significant differences among the three areas and a marked separation between the two vegetated (Cym and Mix) and the unvegetated (Unv) areas, with a global $R=0.74$, and a within and between mean ranks of 156.3 and 388.5 ($p=0.0001$), respectively. The nMDS ordination model confirmed this separation, with Unv being most isolated irrespective of seasonal changes. There was instead some overlap between Cym and Mix as a result of a high similarity between the two biocoenoses (Figure 2). Furthermore, on a seasonal basis, the two autumn samplings at Unv were more dispersed than those at Cym and Mix, due to a major reduction of both abundance and species richness and diversity.

The percentage contribution to the average dissimilarity between the sampling areas, measured by the SIMPER analysis, was reported for the top discriminating species accounting for up to 95% of the cumulative percentage (Table 1). These latter included marine species, e.g. *C. lividulum*, *M. gryllotalpa*, *L. orbiculatus* and *G. aequicauda*, at Cym vs Mix, whereas the pair discrimination of the areas Cym vs Unv, and Mix vs Unv mostly depended on the marine species *Abra tenuis*, the opportunistic taxa, e.g. Chironomidae and *C. capitata*, and the brackish species *H. acuta*.

Two-way PERMANOVA conducted on the biotic variables showed significant differences in the species richness, abundance, diversity and evenness between areas and months (Table 2).

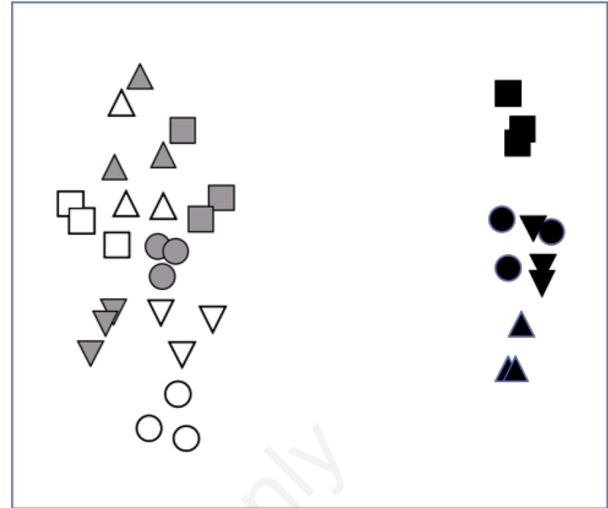


Figure 2. Non-Metric Multidimensional Scaling (nMDS) ordination plot of macrozoobenthic abundance data for the three investigated areas of the Mistras Lagoon: white symbols refer to Cym, gray to Mix and black to Unv. Circles indicate April, inverted triangles May, squares October and triangles November (each symbol represents the mean of 4 replicates, see M&M) (Stress=0.1).

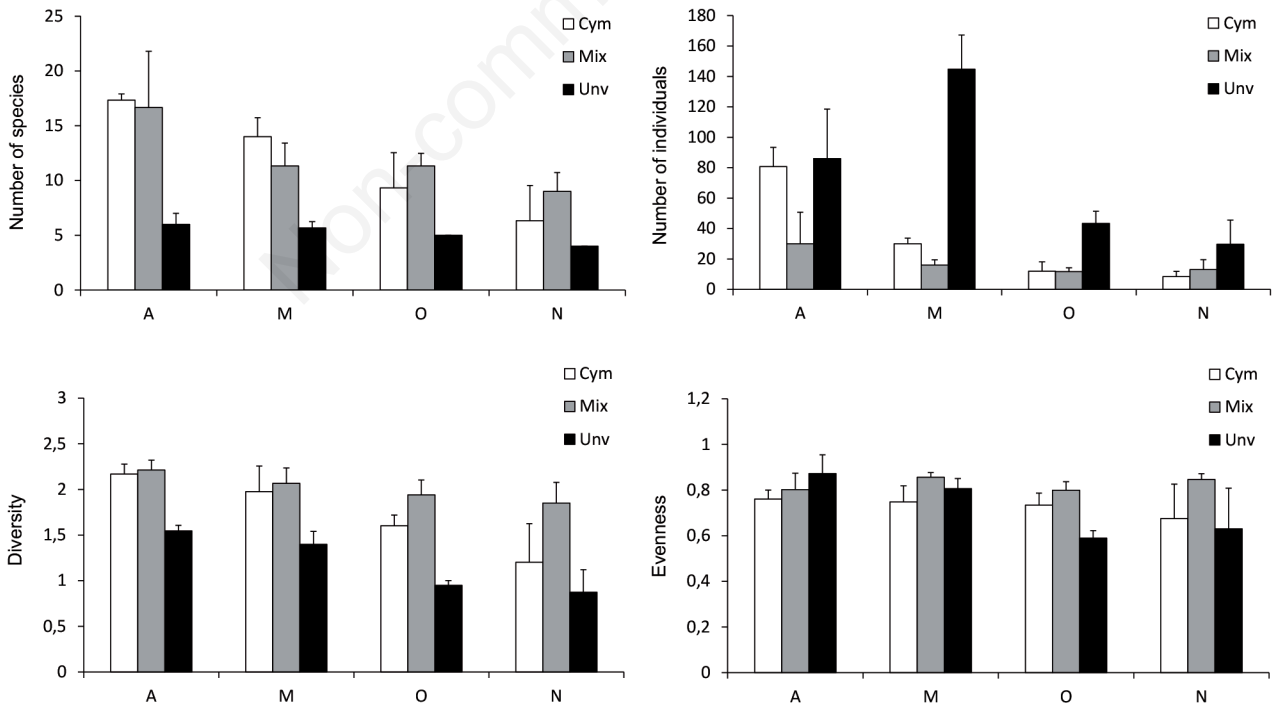


Figure 3. Mean values ($n=12 \pm$ standard error, SE) of the total abundance of individuals (N. ind. 170 cm^{-2}), species richness (S), Shannon-Wiener diversity index and Evenness Pielou index in the three study areas in the Mistras Lagoon. A, April; M, May; O, October; N, November.

Table 1. List of the top discriminating taxa with contribution more than 5% by SIMPER analysis at the three investigated areas, *C. nodosa*-dominated (Cym), mixed-macrophyte/detritus (Mix) and Unvegetated (Unv). Species category: O, opportunistic; C, common in coastal sheltered waters; B, brackish; M, properly marine.

Cym vs Mix		Average dissimilarity	Contribution %	Cumulative %	Average abundance Cym	Average abundance Mix
<i>Cerithium lividulum</i>	M	8.39	13.71	13.71	7.77	3.88
<i>Microdeutopus gryllotalpa</i>	C	8.36	13.67	27.37	6.46	2.23
<i>Loripes orbiculatus</i>	C	6.98	11.41	38.78	3.83	2.40
<i>Gammarus aequicauda</i>	C	6.50	10.62	49.41	3.50	2.33
<i>Abra tenuis</i>	M	4.74	7.74	57.15	1.63	1.67
<i>Sphaeroma serratum</i>	M	4.60	7.52	64.67	4.00	0.25
<i>Nainereis laevigata</i>	C	3.93	6.42	71.08	2.19	0.56
<i>Perinereis rullieri</i>	M	3.66	5.98	77.06	2.06	3.29
<i>Abra segmentum</i>	C	3.59	5.86	82.92	1.08	2.15
Chironomidae	O	2.11	3.45	86.37	0.19	1.04
<i>Tanais dulongii</i>	O	1.33	2.17	88.54	1.15	0.06
<i>Cyathura carinata</i>	B	0.94	1.53	90.07	0.73	0.00
<i>Gibbula adansoni</i>	M	0.85	1.39	91.46	0.08	0.42
<i>Cerastoderma glaucum</i>	B	0.79	1.30	92.76	0.23	0.35
<i>Phylo norvegicus</i>	C	0.61	1.00	93.76	0.65	0.02
<i>Dispio uncinata</i>	M	0.56	0.91	94.67	0.00	0.25
<i>Pirenella conica</i>	B	0.51	0.84	95.51	0.00	0.27
Cym vs Unv		Average dissimilarity	Contribution %	Cumulative %	Average abundance Cym	Average abundance Mix
<i>Abra tenuis</i>	M	26.91	27.93	27.93	1.63	32.40
Chironomidae	O	16.39	17.01	44.94	0.19	16.00
<i>Capitella capitata</i>	O	8.23	8.54	53.48	0.02	10.30
<i>Hydrobia acuta</i>	B	8.15	8.46	61.94	0.00	10.30
<i>Cerithium lividulum</i>	M	8.11	8.42	70.36	7.77	0.00
<i>Cerastoderma glaucum</i>	B	6.08	6.31	76.67	0.23	8.33
<i>Microdeutopus gryllotalpa</i>	C	5.50	5.71	82.38	6.46	0.13
<i>Loripes orbiculatus</i>	C	3.17	3.29	85.68	3.83	0.00
<i>Sphaeroma serratum</i>	M	2.95	3.06	88.74	4.00	0.00
<i>Gammarus aequicauda</i>	C	2.64	2.74	91.47	3.50	0.17
<i>Perinereis rullieri</i>	M	2.34	2.43	93.90	2.06	0.00
<i>Nainereis laevigata</i>	C	2.05	2.13	96.03	2.19	0.00
Mix vs Unv		Average dissimilarity	Contribution %	Cumulative %	Average abundance Cym	Average abundance Mix
<i>Abra tenuis</i>	M	28.62	30.90	30.90	1.67	32.40
Chironomidae	O	17.80	19.22	50.13	1.04	16.00
<i>Hydrobia acuta</i>	B	8.86	9.57	59.70	0.00	10.30
<i>Capitella capitata</i>	O	8.72	9.41	69.11	0.19	10.30
<i>Cerastoderma glaucum</i>	B	6.51	7.03	76.14	0.35	8.33
<i>Cerithium lividulum</i>	M	4.75	5.13	81.27	3.88	0.00
<i>Perinereis rullieri</i>	M	4.00	4.32	85.59	3.29	0.00
<i>Gammarus aequicauda</i>	C	2.81	3.03	88.62	2.33	0.17
<i>Abra segmentum</i>	C	2.72	2.94	91.56	2.15	0.00
<i>Microdeutopus gryllotalpa</i>	C	2.57	2.78	94.34	2.23	0.13
<i>Loripes orbiculatus</i>	C	2.32	2.51	96.85	2.40	0.00

Univariate analyses

The mean number of species was highest in Cym in April (17.3 ± 0.6) and lowest in Unv in November (4.0 ± 0.0) (Figure 3). Overall, both vegetated areas (Cym and Mix) showed a higher species richness than Unv, yet with a progressive reduction from April to November. In particular, species number was significantly higher in spring and autumn in Cym, and significantly higher in April than in the other three dates in Mix. Instead, species number was constantly lowest in Unv where it did not show significant differences between dates. Similarly, the diversity index H' was generally higher in Cym and Mix than in Unv which showed no significant differences between dates. Differently, the mean abundance was highest in Unv in May (144.7 ± 32.5) and lowest in Mix in October (11.7 ± 2.5), with a marked reduction in autumn especially in Unv. Overall, abundance was higher in Unv than in Cym and Mix in all sampling dates. Accordingly, evenness was lowest in Cym in April and May, and highest in Unv in April (0.87 ± 0.08), while Mix showed the highest evenness values in May, October and November (Figure 3).

Discussion

The present study demonstrated that both seagrass-dominated and mixed/detritus beds hosted a higher macrobenthic species richness and diversity than unvegetated sediments, the latter being characterized by very different assemblages in terms of community structure and species composition. On the contrary, the abundance was considerably higher in the bare sediments than in the vegetated areas. Peaks in the number of individuals in Unv were due to both opportunistic (*Capitella capitata*, chironomids) and halolimnobic (*Hydrobia acuta*, *Cerastoderma glaucum*) species, which most notably occurred in spring, likely as a result of reproductive events. Notwithstanding an overall decline from spring to autumn, the abundance remained higher in Unv than in Cym and Mix, indicating that the unvegetated areas sustain large populations. The lowest evenness values recorded in Unv in autumn indicated that variations in the community structure are mainly due to changes in the abundance rather than in the number of species which in turn remained similar over time. Similarly, Barnes (2021) found that in the Knysna estuarine bay (South Africa) the

endangered dwarf-eelgrass, *Zostera capensis*, supports fewer animals than adjacent unvegetated areas. This reportedly unusual situation was explained by a probable of lack of bioturbators in bare sediments, whose activity may cause a significant reduction of surface and near-surface animals. In the Mistras Lagoon, marked differences between areas were also indicated by the seasonal changes of the macrobenthic assemblages. As highlighted by the nMDS plot, both spring and autumn replicates in the two vegetated areas were spatially very close one another, with a marked distinction between the two seasons. The observed decline in the number of species and individuals at Cym and Mix over the months can be explained by the expected seasonal cycles of lagoonal environments (Magni *et al.*, 2005; 2015; Tagliapietra *et al.*, 2016), including the extent of algae and plant cover providing important food sources, especially in spring, for many benthic species (Magni *et al.*, 2008b; Como *et al.*, 2012; Zheng *et al.*, 2020). Differently, the autumn replicates of the unvegetated area appeared to be much more separated one another than the spring ones. The larger spread of the autumn replicates in Unv than in Cym and Mix can be related to a greater suffering and a slower recovery of the benthic assemblage in Unv from environmental stress occurring in the Mistras Lagoon in summer, when a significant increase in temperature and salinity is recorded (unpublished data). On the contrary, the function of seagrass meadows in offering protection from “natural stress” was clearly expressed by the benthic assemblage at Cym that displayed greater spatial and temporal stability of abundance and composition (Tagliapietra *et al.*, 2016; see also Barnes, 2023), and high levels of resilience to the harsh environmental conditions found in summer.

In the Mistras Lagoon, faunal differences in terms of species composition were especially due to several marine species and species typical of coastal sheltered waters (Gravina *et al.*, 2020), which were found much more numerous in the two vegetated areas. As indicated by the SIMPER analysis, most of the species that contributed up to the cumulative 95% were amphipods (*M. grylotalpa*, *G. aequicauda*), isopods (*S. serratum*, *C. carinata*), tanaids (*T. dulongii*) and two bivalves, *L. lacteus* and *A. tenuis* (see Currás and Mora, 1996; Holmes *et al.*, 2004), all being characterized by direct development lacking free living

Table 2. Results of two-way PERMANOVA among areas and dates (permutation N: 9999, df = Degrees of Freedom).

Source	Species Richness			Abundance			Diversity (H')			Evenness (Pielou)		
	Sum of squares	df	p	Sum of squares	df	p	Sum of squares	df	p	Sum of squares	df	p
Areas	1.00	2	0.0001	1.50	2	0.0001	0.43	2	0.0001	0.04	2	0.0001
Dates	0.43	3	0.0003	1.38	3	0.0001	0.26	3	0.0001	0.04	3	0.0001
Interaction	0.18	6	0.0386	1.08	6	0.0001	0.09	6	0.0001	0.05	6	0.0581
Residual	0.28	24	0.01	0.81	24	0.03	0.16	24	0.01	0.09	24	0.00
Total	1.89	35		4.76	35		0.93	35		0.22	35	

larvae. They also included the nonplanktotrophic gastropod *C. lividulum* which is able of crawling directly on the bottom after hatching (Garilli and Galletti, 2006; Evangelisti *et al.*, 2016). Only a few of the main discriminating species revealed by the SIMPER analysis were opportunistic and brackish/halolimnobic species which contributed to characterize the unvegetated area. They comprised chironomids, *C. capitata*, *H. acuta* and *C. glaucum*, the latter two species found >10 times more abundant in the unvegetated area. Marked differences between areas were also highlighted by the distribution of two congeneric species, *Abra segmentum* and *Abra tenuis*, which relates to their different biological cycles and larval phases. In particular, *A. segmentum*, characterized by a long-life pelagic larval phase typical of bivalves, was dominant and exclusive to the two vegetated areas. This suggests that the nearby marine environment can be a source of new recruits, while too confined unvegetated areas may be hardly colonisable by this bivalve. Differently, *A. tenuis* was dominant in very high numbers in the unvegetated area indicating its ability to maintain a considerable population in confined areas due to its direct development which does not require the marine environment as an external donor (Holmes *et al.*, 2004). A similar adaptive strategy was shown by opportunistic (*C. capitata*, chironomids) and halolimnobic (*H. acuta*, *C. glaucum*) species which were able to occupy very confined habitats due to their reproduction and adaptation modes. These results show that only a portion of marine species occurring in the Mistras Lagoon can be sustained by larval supply from the marine environment, while another pool of species lacking direct connectivity with the sea, but characterized by direct development, is able to self-sustain their populations.

The results of the present study add new knowledge to the spatial and temporal distribution of benthic assemblages in vegetated coastal environments, contributing to the understanding of differences (or similarities) between seagrass and bare sediments. It follows conspicuous research on macrobenthic seagrass ecology conducted in the intertidal zone (*e.g.*, Barnes and Barnes, 2012, 2014; Barnes, 2020a, 2020b), with fewer comparative studies carried out in coastal marine habitats (Włodarska-Kowalczyk *et al.*, 2014; Surugiu *et al.*, 2021) and coastal lagoons (Magni *et al.*, 2017; Barnes, 2022; Hu *et al.*, 2022). Furthermore, although several ecological studies have been carried out on macrophyte-derived detritus (*e.g.* see review by Lepoint and Hyndes, 2022), few works have examined the benthic assemblages in leaf litter and respective mother plants in the same environmental settings (Ólafsson *et al.*, 2013). One of these studies was conducted outside the Mistras Lagoon in the Gulf of Oristano (Como *et al.*, 2008). The authors found that two seagrasses, *Posidonia oceanica* and *Cymodocea nodosa*, had similar species composition and differed from a third habitat, *i.e.* leaf litter beds, for the exclusive presence of hard-bottom species, such as the tunicate *Phallusia fumigata*, and seagrass-associated species, such as the polychaete *Syllis garciai* and the decapod *Paguristes syrtensis*. In contrast, the leaf litter sediments were characterized by the bivalves *A. alba* and *C. glaucum*, not found in the seagrasses, and by the bivalves *L. lacteus* and *Ruditapes decussatus*, and the polychaete *Prionospio multibranchiata*, exclusive to leaf litter beds.

Conclusions

The present study demonstrated the importance of biological factors in structuring the macrobenthos of the Mistras Lagoon in both vegetated and non-vegetated areas. The presence of habitat-forming phanerogams, such as *C. nodosa*, *Z. noltii* and *Ruppia maritima*, sustained well-structured and diverse benthic assemblages that were lacking in bare sediments. Our results agree with those reported from other lagoons and sheltered coastal areas worldwide (Bachelet *et al.*, 2000; Sfriso *et al.* 2001; Blanchet *et al.*, 2005; Brito *et al.*, 2005; Yamada *et al.*, 2007; Barnes and Barnes, 2012; Magni *et al.*, 2015; Tagliapietra *et al.*, 2016; Magni *et al.*, 2017; Surugiu *et al.*, 2021). Furthermore, the life-history traits of the species, such as species-specific reproductive cycles and adaptive strategies (Nonnis Marzano *et al.*, 2010; Cardone *et al.*, 2014; Gravina *et al.*, 2020), were important drivers for the colonization of benthic species in the confined areas. We anticipate that, in addition to biological factors, environmental constraints, such as confinement, are also to be considered to fully explore the reasons for differences in the benthic community of the Mistras Lagoon. In particular, the marked isolation of the unvegetated area and the limited water exchange with the sea and other areas of the lagoon, may enhance the “natural stress” due to larger variations in abiotic variables, *e.g.* salinity. This could affect both the flora and the fauna of the lagoon and will be the focus of a subsequent study. Finally, the present study demonstrates that both vegetated and unvegetated patches contribute greatly to the local-scale heterogeneity of the lagoon ecosystems, highlighting the peculiarity and importance of these habitats as hotspots of benthic biodiversity. For these reasons, coastal lagoons must be considered major targets for conservation measures.

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