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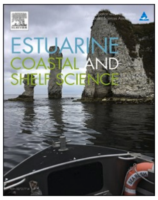

To change or not to change: Macrozoobenthic community variation versus persistence in Tortolì lagoon (Sardinia, Italy)

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ABSTRACT

In the framework of the complexity of transitional ecosystem dynamics, which strongly drive ecological processes and their effects on communities and ecosystem functioning, the seasonal changes in 2021 of macrobenthic community were analysed at four sites of the Tortolì lagoon (Sardinian, Italy), which were characterised in terms of temperature, salinity, organic matter content of sediment and dissolved oxygen. Two macrobenthic community conditions separated by 20 years, between 2003 and 2021, were also compared. Both the composition of the community in terms of species and the main functional traits, related to the relationship with the sediment, feeding mode and development type, were investigated. The objective was to identify which aspects (species composition/functional species traits) of the benthic community are most responsible for changes on an annual and multi-year scale, and which persist two decades later. The benthic assemblage was extraordinarily rich in species (86 species in 2021 and 124 species in total over the two years). Most of species were typical of coastal sheltered waters and properly marine, while opportunistic and brackish/halolimnobic species were scarce; two alien Isopods (*Paracerceis sculpta*, *Mesanthura* sp.) and the new record of Enteropneusta (*Glossobalanus minutus*) were also reported. Differences between seasons and sampling sites resulted significant sources of variation and marine species mainly contributed to discriminate sites closer to the sea, while the others were especially distributed in the confined sites. The comparison between 2003 and 2021 highlighted that the species richness remained high in the two periods, but significant changes in the species composition of the benthic community, explained in terms of a 50 % species turnover rate. This was attributed to different dispersal modes, which proved that new colonisers arrived in the lagoon from the adjacent marine area by active (via larvae) and passive (adult rafting, human-mediated activities) means. The persistence in terms of functional group composition and diversity of the macrobenthic community after twenty years was also evidenced. The considerable diversification of functional groups in the benthic food web, together with the high level of species richness and taxonomic diversity, is assumed to be indicative of an efficient degree of ecosystem functioning of the Tortolì lagoon 20 years later.

1. Introduction

In the context of coastal ecosystems, transitional waters (TWs), including lagoons, coastal lakes, brackish ponds, exhibit extreme dynamism from their formation to subsequent fate, being highly mutable over geological and historical time (Barnes, 1980; Pérez-Ruzafa et al., 2011). They do not persist for long time, in fact, on the one hand, their fate is determined by the persistence of barriers that enclose them and partially cut them off from the sea; on the other hand, modifications of freshwater inflows, hydrographic regimes and movements of sediments may direct their fate towards freshwater basins or continental swamps and marshlands. Their highly dynamic nature makes TWs particularly susceptible to further variations in climatic and meteorological factors (Tagliapietra et al., 2012). In addition, man also

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influences the fate, shape and extension of lagoons through reclamation works. The increasing pressure of human activities, such as urbanization and industrialization, also contribute to the fate of the lagoons, representing a possible threat of their integrity, ecological status and functioning often causing a reduction in their supply of goods and services (Barnes, 1991; Crooks and Turner, 1999; Magni et al., 2005; Panigrahi et al., 2007; Kolios and Stylios, 2013). The great diversity in temporal dynamics of lagoonal environments is also reflected in the remarkable changes of their flora and fauna (Cognetti and Maltagliati, 2008 Tagliapietra et al., 2016; Magni et al., 2017; Gravina et al., 2020a; Brundu and Magni, 2021). Whitin the latter, benthic invertebrates have proven to be one of the most effective indicators capable of responding to different levels of anthropogenic impacts and pollution stress (Magni, 2003; Nonnis Marzano et al., 2003; Basset et al., 2009; Giangrande and Gravina, 2015).

In the Mediterranean lagoons, seasonal or annual changes in benthic community have been the focus of a plethora of studies (e.g. Gravina et al., 1989; Kevrekidis et al., 2000; Koutsoubas et al., 2000; Mistri et al., 2000; Como et al., 2007; Nonnis Marzano et al., 2007; Reizopoulou and Nicolaidou, 2007; Afli et al., 2008; Specchiulli et al., 2008; Reizopoulou et al., 2014; Orro and Cabana, 2021; Como et al., 2024); emphasis has been also given to changes occurred in benthic communities after extreme events, such as dystrophic crisis (Perdicaro et al., 1980; Giangrande and Gambi, 1985; Lardicci et al., 2001; Munari et al., 2003; Magni et al., 2008) and flood events (Fabbrocini et al., 2008). However, a limited number of studies have dealt with the long-term analysis of macrozoobenthos changes, mainly because the availability of historical data, used as a baseline, is an essential prerequisite for the perception of change (see Gravina et al., 2020b and references therein). In this context, some studies have focused on individual taxonomic groups, such as molluscs (Macali et al., 2013), which compared the current fauna with historical traces based on bibliography and museum materials, and polychaetes, which have been reexplored in some Tyrrhenian coastal lakes (Nicoletti et al., 2006) and in Adriatic lagoons (Giangrande and Gravina, 2015; Bettoso et al., 2024) after nearly twenty years.

In the framework of the complexity of transitional ecosystem dynamics, which strongly drive ecological processes and their effects on communities and ecosystem functioning, it is particularly intriguing to investigate changes (Bellino et al., 2019). For example, it is interesting to address the manifold facets related to the variation in species abundance, species replacement and persistence in the community, processes that allow for the overcoming of the adverse conditions (i.e. dystrophic crises), the mechanisms that allow for the maintenance and/or recovery of the functional organization of the ecosystem. In particular, short-term changes deserve to be distinguished from long-term-ones. The former include periodic fluctuations, such as seasonal fluctuations, and are somehow predictable based on the activity and life-history traits of the species. The long-term changes include variations that may lead to a stable modification of the community that cannot be attributed to predictable variations (Boero, 1994); especially these latter requires special attention because they may even lead to the irreversible degradation of the environment.

Due to the confined nature of lagoons, the degree of connection with the neighbouring coastal areas plays a key role in modulate the intensity of exchanges with the sea and promotes the entry of new species and so may cause changes in species composition of the community structure (Magni and Gravina, 2023). In addition to the hydrological dynamics of marine area, the arrival of new species is mainly constrained by their life traits, such as the duration of larval stage, which depends on type of the development: planktotrophic development results in a long-life span of larvae in the water columns and thus favour their dispersal over long distance, in contrast to the lecithotrophic development that results in a short life span causing a reduced dispersal (Giangrande et al., 2017 and references within). Thus, the type of development is a considerable source of variation in the species composition of lagoon communities. On the other hand, the life-history traits of the species relating to their relationships with sediment and feeding patterns, since they describe the functional role of the species, are an expression of the functional structure of the community (Loreau et al., 2001; Paganelli et al., 2012). The composition in functional groups of the community structure has been showed to be an expression of the conservation aspects (persistence, resilience), rather than changes, of the transitional ecosystem food web (Lobry et al., 2008; Barnes and Hendy, 2015).

Here, we studied patterns of change in the macrobenthic community structure of the Tortolì lagoon (Sardinian, Italy), both in the short-term, between the 2021 seasons, and in the long-term, comparing two conditions (2003–2004 and 2021) separated by ca. 20 years. In particular, we analysed the macrobenthic community both in terms of composition of species and the main functional traits, for a comparison between the seasons of 2021 and between the two years under scrutiny. The objective was to identify which aspects (species composition/functional species traits) of the benthic community are most responsible for the changes on annual and multi-year scale and which persist over two decades.

2. Materials and methods

2.1. Study area

The Tortolì Lagoon, located on the central-east coast of Sardinia, has a total area of approximately 250 ha and a perimeter of 15.1 Km (Fig. 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. The lagoon hosts a flourishing fish and shellfish traditional fishery, and aquaculture activities have been practised for more than 30 years (Giampaoletti et al., 2023). In Table 1 we reported the physiographic and environmental features of the Tortolì lagoon and the range of salinity and temperature values measured in both years considered, 2003–2004 and 2021.

2.2. Sampling methods, sediment and taxonomical analysis

Four sampling stations were selected along a putative gradient of confinement, based on environmental variables, including salinity, dissolved oxygen, sediment grain-size, organic matter. The sampling design (Fig. 1) was consistent with that used for the 2003–2004 study (Giampaoletti et al., 2023), for comparison. Salinity, temperature and dissolved oxygen were measured both on the bottom and at the surface

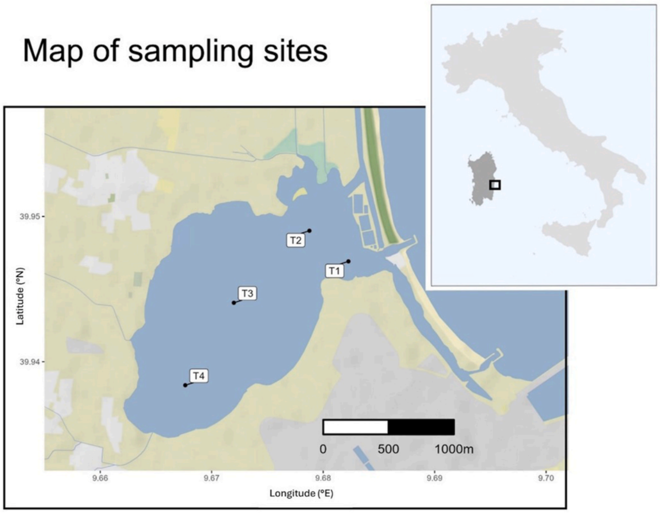

Fig. 1. Study area (Tortolì Lagoon, east coast of Sardinia, Italy) and sampling sites (T1, T2, T3, T4).

Table 1
Range of variation, minimum (Min), maximum (Max) and mean values, of salinity and temperature at each sampling station (T1, T2, T3, T4) in both years considered, 2003 and 2021, in the Tortolì lagoon.

		T1		T2		T3		T4	
		2003	2021	2003	2021	2003	2021	2003	2021
Salinity (‰)	Min	13	30	15	30	15	37	29	32
	Max	38	37	38	37	38	39	38	38
	Mean	30	35	28	35	30	37	32	37
Temperature (°C)	Min	13	15	13	16	13	17	9	17
	Max	27	25	27	25	27	25	28	25
	Mean	20	20	20	20	20	21	20	21

with a multi-parametric probe. Sediment samples were collected at each station with three replicates, meters apart as independent replicates, using a manual box-corer (sampling area: 255 cm^2), in May (spring) and November (autumn) 2021 for a total of 24 samples. Additional box-corer samples were collected at each station for the measurement of sediment total organic matter and mud content (0–2 cm and 2–5 cm layers). The total organic matter (OM) content in the sediment was determined from a subsample of about 1 g by loss on ignition (LOI) at 495 °C for 4 h and expressed as a percentage of the dry weight. Macrozoobenthos samples were collected by sieving with a 0.5 mm mesh, stained using Rose Bengal and fixed with 98% ethanol. In the laboratory, all specimens were identified to the lowest possible taxonomic level and counted. The updated taxonomic nomenclature was checked by the World Register of Marine Species (https://www.marinespecies.org; accessed 2024-09-20). To infer possible colonization and distribution patterns of the lagoon, we considered the main functional traits of the species and assigned the species to different functional groups and categories related to sediment relationship and larval development according to the current literature (Bremner et al., 2003; Jumars et al., 2015; Magni et al., 2023)

2.3. Data analysis

Both abiotic and biotic data were analysed by univariate and multivariate techniques. Water and sediment variables, i.e. temperature, dissolved oxygen (DO), salinity, organic matter (OM) content, were tested by means of two-way PERMANOVA (based on Euclidean distance) to explore differences between stations (four levels: T1, T2, T3 and T4) and seasons (two levels: May and November). Such four major environmental variables (log-transformed and normalized data) were analysed by means of Principal Component Analysis (PCA), based on the correlation matrix. In order to investigate changes in macrobenthic community between sites and periods, the following biotic variables

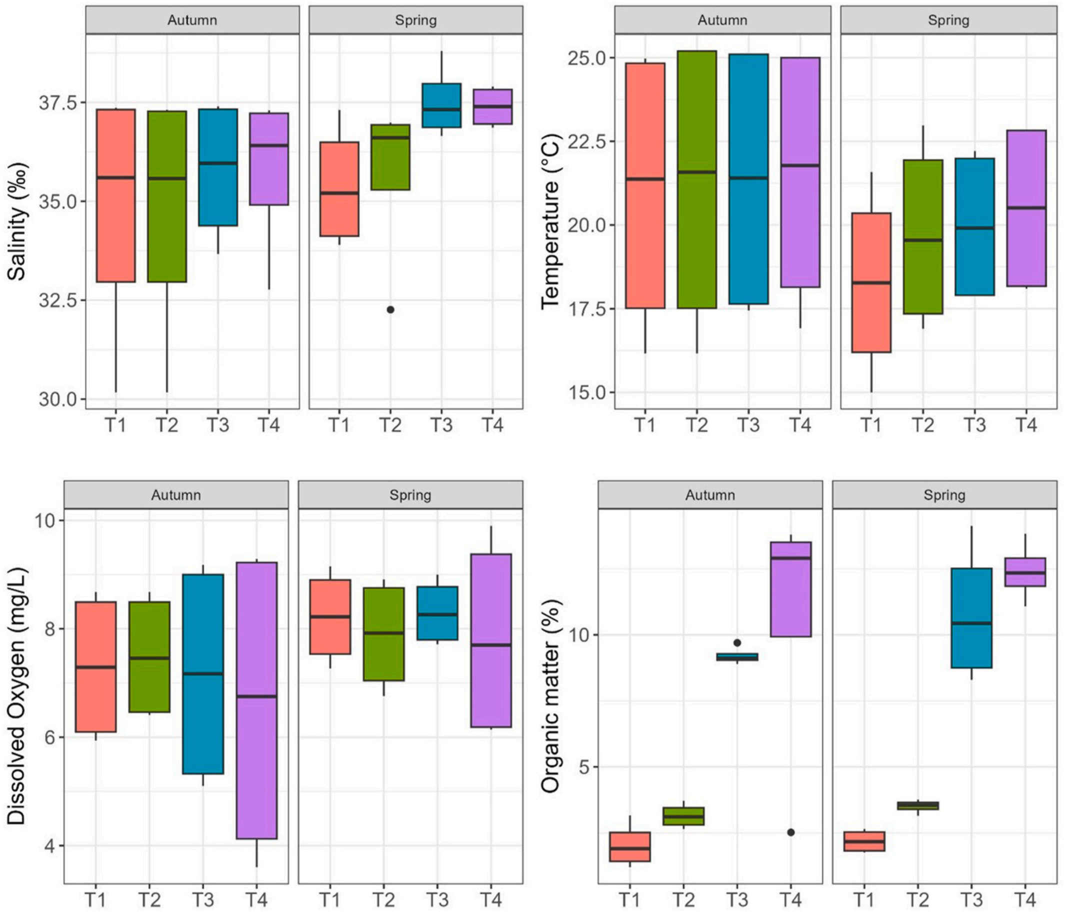

Fig. 2. Box plot of water and sediment variables related to the four sampling sites (T1, T2, T3, T4) in each season showing the maximum value, the minimum value, and the median line. Vertical lines are the upper whiskers and lower whiskers, respectively; isolated points are outliers. See Table 2 for significant differences.

Table 2
Results of two-way PERMANOVA testing differences in water and sediment parameters among Stations, Seasons and their interactions (St x Season). Significant *p* values are marked, * = significant at $p < 0.05$, ***p* < 0.01, ****p* < 0.001, ns = not significant.

	Factors	df	Sum of Squares	Mean Square	Pseudo - F	*p*
Temperarure	Station	3	3.89	1.30	1.49	ns
	Season	1	85.67	85.67	98.59	***
	St x Season	3	1.47	0.49	0.56	ns
	Res	8	6.95	0.87		
	Total	15	97.98			
Salinity	Station	3	15.38	5.13	1.20	ns
	Season	1	33.96	33.96	7.97	*
	St x Season	3	0.88	0.29	0.07	ns
	Res	8	34.08	4.26		
	Total	15	84.30			
Dissolved oxygen	Station	3	1.27	0.42	1.31	ns
	Season	1	12.51	12.51	83.04	**
	St x Season	3	2.40	0.80	7.06	*
	Res	8	0.24	0.03		
	Total	15	16.42			
Organic matter content	Station	3	257.67	85.89	10.19	**
	Season	1	15.29	15.29	1.81	ns
	St x Season	3	20.59	6.86	0.81	ns
	Res	8	67.45	8.43		
	Total	15	361.00			

were computed, i.e. species richness, abundance, Shannon index, and evenness. Non-parametric Kruskal–Wallis and Mann–Whitney tests were used to detect significant differences between these biotic variables. Macrozoobenthic data were analysed by means of the multivariate procedure non-metric multidimensional scaling (nMDS), using mean abundance values in the cumulative matrix of all the stations and months, based on Bray-Curtis (dis)similarity measure (Clarke and Warwick, 2001). Two-way ANOSIM permutation tests, based on Bray–Curtis similarity, were performed to test significant differences in community composition between sampling stations and seasons. Cluster analysis, based on UPGMA algorithm and Jaccard similarity index, was used to investigate changes in macrobenthic community between the years 2003–2004 and 2021. The SIMPER procedure was used to discriminate species contribution to the (dis)similarity between sampling stations (T1-T2 vs T3-T4) and periods (Spring and Autumn) in 2021 and for the comparison between the 2003–2004 and 2021 sampling periods. The measure of species turnover after a twenty-year period, from 2003 to 2021, was estimated using the Whittaker Index $\beta = (S/\bar{\alpha}) - 1$, being S the total number of species that results from merging the number of the two times and $\bar{\alpha}$ the average number of species per individual year sample (Whittaker, 1972; Koleff et al., 2003). Such measure was computed to evaluate the proportion by which the two years investigated differ from each other in species composition. Statistical analyses were conducted with R 4.0.4 (R Core Team, 2021), using vegan (Oksanen, 2020) package, and Past 4.17.

3. Results

3.1. Water and sediment variables

Box plots of water and sediment variables for each station and season are shown in Fig. 2. Temperature, salinity and dissolved oxygen (DO) showed significant differences among seasons, with higher values in autumn for temperature and in spring for DO and salinity, while there were no significant variations between stations (Table 2). In contrast, PERMANOVA analysis revealed significant differences in organic matter (OM) content between stations, but not between seasons (Table 2). In fact, organic matter in the sediment was lower in the stations near the seawater input (2.1% in T1, 3.3% in T2) and higher in the confined ones (10.0% in T3, 11.5% in T4).

The PCA based on the environmental variables showed a clear separation of stations and seasons (Fig. 3). Spring station-points were located along the right portion of the model (first and forth quadrants) and the autumn station-points along the left portion (second and third quadrants); station-points T1 and T2 and station-points T3 and T4 were positioned respectively at the top and at the bottom of the model. The environmental variables superimposed to the biotic data highlighted that temperature and DO were the main responsible factors for the separation of the spring (T1S, T2S, T3S, T4S) and autumn station-points (T1A, T2A, T3A, T4A) and that salinity and OM mainly contributed to distinguish the confined stations T3 and T4 from the stations T1 and T2 directly exposed to the sea.

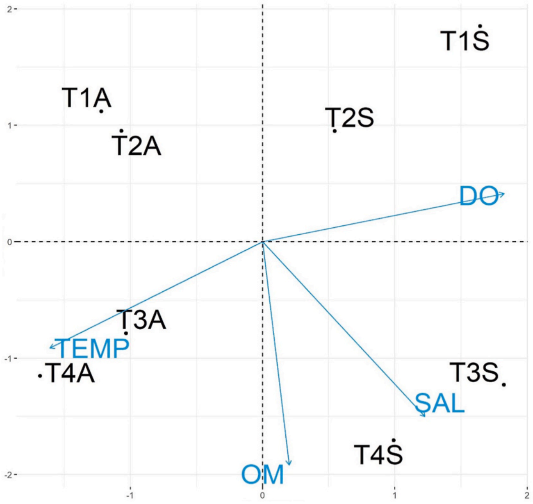

Fig. 3. Biplot obtained after a Principal Component Analysis carried out to illustrate multivariate differences between seasons (Spring and Autumn; S and A, respectively) and sampling stations (T1, T2, T3 and T4) in dissolved oxygen (DO), salinity (SAL), temperature (TEMP) and sedimentary organic matter (OM) contents. Percentage of explained variances: 49.4 % for PC1 and 45.9 % for PC2.

Table 3

List of the identified species (presence/absence) in the Tortolì lagoon in 2003/2004 and 2021 with indication of their life traits. **Functional group:** BMO, Burrower Motile Omnivorous; BMSubDF, Burrower Motile Subsurface Deposit feeder; BSSubDF, Burrower Sessile/Semi motile Subsurface Deposit feeder; BSTSubDF, Burrower Sessile Tubicolous Subsurface Deposit feeder; MDF, Motile Surface Deposit feeder; ME, Motile Herbivore; MF, Motile Filter feeder; MO, Motile Omnivorous; MP, Motile Predator; MTO, Motile Tubicolous Omnivorous; SDF, Sessile/Semi Motile Surface Deposit feeder; SF, Sessile/Semi Motile Filter feeder; SP, Sessile/Semi motile Predator; STF, Sessile/Semi motile Tubicolous Suspension/Filter feeder. **Sediment position:** Ep, epifauna; En, endofauna. **Larval development:** B, benthic; D, direct; Pl, planktotrophic; P, pelagic; L, lecithotrophic.

	Species	Functional group	Sediment position	Larval development	2003/2004	2021
Anthozoa	*Paranemonia cinerea*	SP	Ep	Pl	X	X
Nemertea			Ep	Pl		X
Polychaeta	*Abarenicola* sp.	SDF	En			X
Polychaeta	*Aonides oxycephala*	MDF	En	L	X	
Polychaeta	*Aphelochaeta marioni*	SDF	En		X	
Polychaeta	*Aphelochaeta multibranchiis*	SDF	En		X	
Polychaeta	*Aponuphis bilineata*	MTO	Ep	D	X	
Polychaeta	*Armandia cirrhosa*	BMSubDF	En	Pl	X	
Polychaeta	*Caulleriella* ind.	SDF	En			X
Polychaeta	*Capitella capitata*	BSSubDF	En	L	X	X
Polychaeta	*Chaetozone setosa*	SDF	En	L	X	
Polychaeta	*Cirriformia tentaculata*	SDF	En	L		X
Polychaeta	*Diopatra neapolitana*	MTO	Ep	L	X	X
Polychaeta	*Drilonereis filum*	BSSubDF	En			X
Polychaeta	*Glycera tridactyla*	MP	Ep	Pl	X	
Polychaeta	*Glycera unicornis*	MP	Ep			X
Polychaeta	*Heteromastus filiformis*	BSSubDF	En	Pl	X	X
Polychaeta	*Hilbigneris gracilis*	BMO	En		X	
Polychaeta	*Hydroides dianthus*	STF	Ep		X	X
Polychaeta	*Lagis koreni*	BSTSubDF	En	Pl	X	
Polychaeta	*Lumbrineris coccinea*	BMO	En		X	
Polychaeta	*Lumbrineris latreilli*	BMO	En	D	X	X
Polychaeta	*Malacoceros fuliginosus*	SDF	En	Pl	X	
Polychaeta	*Malmgrenia lunulata*	MP	Ep	Pl	X	
Polychaeta	*Myriochele heeri*	SDF	En		X	
Polychaeta	*Naineris laevigata*	BMSubDF	En	L	X	X
Polychaeta	*Neanthes acuminata*	MO	Ep		X	X
Polychaeta	*Nephtys hombergii*	MO	Ep	Pl	X	X
Polychaeta	Nereididae juv.	MO	Ep			X
Polychaeta	*Nereiphylla rubiginosa*	MO	Ep		X	X
Polychaeta	*Nereis pelagica*	MO	Ep	Pl		X
Polychaeta	*Notomastus* ind.	BSSubDF	En			X
Polychaeta	*Notomastus latericeus*	BSSubDF	En	L		X
Polychaeta	*Notomastus lineatus*	BSSubDF	En			X
Polychaeta	*Ophelina modesta*	BMSubDF	En		X	
Polychaeta	*Paradoneis lyra*	BSSubDF	En		X	X
Polychaeta	*Perinereis rullieri*	MO	Ep	Pl		X
Polychaeta	Phyllodocidae ind.	MP	Ep			X
Polychaeta	*Phylo foetida*	BSSubDF	En	D	X	X
Polychaeta	*Pista unibranchia*	SDF	En		X	X
Polychaeta	*Pista adriatica*	SDF	En			X
Polychaeta	*Podarkeopsis capensis*	MP	Ep			X
Polychaeta	*Polycirrus* sp.	SDF	En		X	X
Polychaeta	*Polydora ciliata*	SDF	En	Pl	X	
Polychaeta	*Prionospio cirrifera*	SDF	En	Pl	X	X
Polychaeta	*Prionospio malmgreni*	SDF	En	Pl	X	
Polychaeta	*Protodorvillea kefersteini*	MP	Ep	D	X	X
Polychaeta	*Pterocirrus macroceros*	MP	Ep			X
Polychaeta	*Ophiodromus pallidus*	MP	Ep			X
Polychaeta	Sabellidae gen. sp.	STF	Ep			X
Polychaeta	*Schistomeringos rudolphii*	MP	Ep	L		X
Polychaeta	*Scolelepis foliosa*	MDF	En	Pl		X
Polychaeta	*Sphaerosyllis taylori*	MP	Ep	D	X	X
Polychaeta	*Spio filicornis*	SDF	En	Pl	X	
Polychaeta	*Spiochaetopterus costarum*	STF	En	Pl	X	
Polychaeta	*Syllidia armata*	MP	Ep	Pl	X	
Polychaeta	*Syllis armillaris*	MP	Ep		X	X
Polychaeta	*Syllis garciai*	MP	Ep			X
Polychaeta	*Syllis gracilis*	MP	Ep			X
Polychaeta	*Syllis parapari*	MP	Ep			X
Polychaeta	*Syllis pulvinata*	MP	Ep			X
Polychaeta	*Terebella lapidaria*	SDF	En			X
Polychaeta	Terebellidae	SDF	En			X
Oligochaeta					X	X
Gastropoda	*Bittium latreillii*	ME	Ep	L		X
Gastropoda	*Caecum clarkii*	MDF/ME	Ep	P	X	
Gastropoda	*Crisilla semistriata*	MDF/ME	Ep			X
Gastropoda	*Haminoea hydatis*	MDF/ME	Ep	D	X	X
Gastropoda	*Nassarius nitidus*	MP/MDF	Ep	Pl		X

(*continued on next page*)

Table 3 (*continued*)

	Species	Functional group	Sediment position	Larval development	2003/2004	2021
Gastropoda	*Retusa minutissima*	MP	Ep	P		X
Gastropoda	*Rissoa membranacea*	MDF/ME	Ep	P		X
Gastropoda	*Steromphala umbilicaris*	ME	Ep		X	
Gastropoda	*Tritia neritea*	MP/MDF	Ep	D		X
Bivalvia	*Abra segmentum*	SDF	En	P/B	X	X
Bivalvia	*Cerastoderma glaucum*	SF	En	L	X	
Bivalvia	*Gastrana fragilis*	SF	En	Pl		X
Bivalvia	*Hemilepton nitidum*	SF	En			X
Bivalvia	*Loripes orbiculatus*	SF	En	Pl	X	X
Bivalvia	*Lucinoma borealis*	SF	En	Pl	X	X
Bivalvia	*Musculus costulatus*	SF	Ep	Pl	X	
Bivalvia	*Mytilaster marioni*	SF	Ep	Pl	X	
Bivalvia	*Parvicardium exiguum*	SF	En	Pl	X	X
Bivalvia	*Parvicardium papillosum*	SF	En	Pl		X
Bivalvia	*Polititapes aureus*	SF	En	Pl	X	X
Bivalvia	*Ruditapes decussatus*	SF	En	Pl	X	
Amphipoda	*Apocorophium acutum*	STF	Ep	D	X	X
Amphipoda	*Caprella equilibra*	MP	Ep	D		X
Amphipoda	*Dexamine spinosa*	ME	Ep	D	X	X
Amphipoda	*Elasmopus rapax*	MO	Ep	D	X	X
Amphipoda	*Ericthonius brasiliensis*	STF	Ep	D	X	X
Amphipoda	Gammaridae ind.	MO	Ep	D		X
Amphipoda	*Gammarella fucicola*	MO	Ep	D		X
Amphipoda	*Gammaus aequicauda*	MO	Ep	D		X
Amphipoda	*Gammarus crinicornis*	ME	Ep	D		X
Amphipoda	*Gammarus insensibilis*	MO	Ep	D	X	X
Amphipoda	*Maera grossimana*	MDF	Ep	D		X
Amphipoda	*Melita palmata*	MO	Ep	D	X	
Amphipoda	*Microdeutopus algicola*	MDF	Ep	D	X	
Amphipoda	*Microdeutopus gryllotalpa*	MDF	Ep	D	X	
Amphipoda	*Microdeutopus versiculatus*	MDF	Ep	D	X	
Amphipoda	*Microdeutopus* sp.	MDF	Ep	D		X
Amphipoda	*Monocorophium insidiosum*	STF	Ep	D	X	X
Amphipoda	*Pariambus typicus*	MDF	Ep	D	X	
Amphipoda	*Parvipalpus linea*	MP	Ep	D	X	
Amphipoda	*Phtisica marina*	MDF	Ep	D	X	X
Amphipoda	*Pseudolirius kroyeri*	MP	Ep	D	X	
Isopoda	*Cymodoce truncata*	MO	Ep	D		X
Isopoda	*Mesanthura* sp.		Ep	D		X
Isopoda	*Munna* sp.		Ep	D		X
Isopoda	*Paracerceis sculpta*	ME	Ep	D	X	X
Cumacea	Nannastacidae gen. sp.	MF	Ep	D		X
Cumacea	*Iphinoe trispinosa*	MF	Ep	D	X	
Mysidacea	*Diamysis bahirensis*	MF	Ep	D		X
Tanaidacea	*Apseudopsis latreillii*	MDF	Ep	D	X	
Tanaidacea	*Chondrochelia savignyi*	MDF	Ep	D	X	X
Tanaidacea	*Tanais dulongii*	MDF	Ep	D	X	
Decapoda	*Liocarcinus arcuatus*	MP	Ep	Pl	X	
Decapoda	*Upogebia pusilla*	SF	En	Pl		X
Insecta Diptera	Chironomidae gen. sp.			B		X
Phoronida	*Phoronis psammophila*	STF	Ep	Pl	X	X
Ophiuroidea	*Amphipholis squamata*	ME	Ep	Pl	X	X
Ascidiacea	*Ascidiella aspersa*	SF	Ep	Pl	X	
Ascidiacea	*Styela plicata*	SF	Ep	Pl	X	
Enteropneusta	*Glossobalanus minutus*	SF	En	Pl		X
Total number of species					**74**	**86**

3.2. *Macrozoobenthic community*

The benthic assemblage of the Tortolì lagoon amounted to 86 species (Table 3), represented by Polychaetes (42), Molluscs (15), Crustaceans (22), and other infrequent taxa, such as Phoronids and Enteropneusta, each represented by only one species; Anthozoans were also found with the unique species *Paranemonia cinerea* with many individuals (Table 3). Species typical of coastal sheltered waters and properly marine were dominant, e.g. Polychaetes *Naineris laevigata*, *Cirriformia tentaculata*, *Paradoneis lyra*, *Syllis parapari*, Molluscs *Crisilla semistriata*, *Parvicardium exiguum*, *Polititapes aureus*, Crustaceans *Elasmopus rapax*, *Cymodoce truncata*; by contrast, opportunistic species, e.g. Polychaetes *Capitella capitata*, *Heteromastus filiformis*, *Prionospio cirrifera*, and brackish/halolimnobic species, i.e. Crustacean *Monocorohium insidiosum*, were scarce. Two alien species were also recorded, i.e. the Isopods *Paracerceis sculpta*, found in high abundance, and *Mesanthura* sp. with only one specimen.

Comparison of species richness, abundance, diversity and evenness of macrobenthos in the four sampling stations and in the two seasons revealed significant differences only in spring for stations closer to the sea, whereas in autumn there were no significant differences between the stations (Fig. 4). In spring for both stations T1 and T2 (Kruskal-Wallis statistic $H = 11.4$, $p = 0.009$), the pairwise Mann-Whitney test showed significant differences in species richness compared to stations T3 and T4 respectively. Both in terms of abundance and diversity (Kruskal-Wallis statistic $H = 10.1$, $p = 0.02$ and $H = 10.8$, $p = 0.01$, respectively) the station T2 differed from other stations. In contrast, in term of evenness, no significant differences emerged either between stations or between seasons.

The nMDS plot (Fig. 5), based on the macrobenthos abundance data

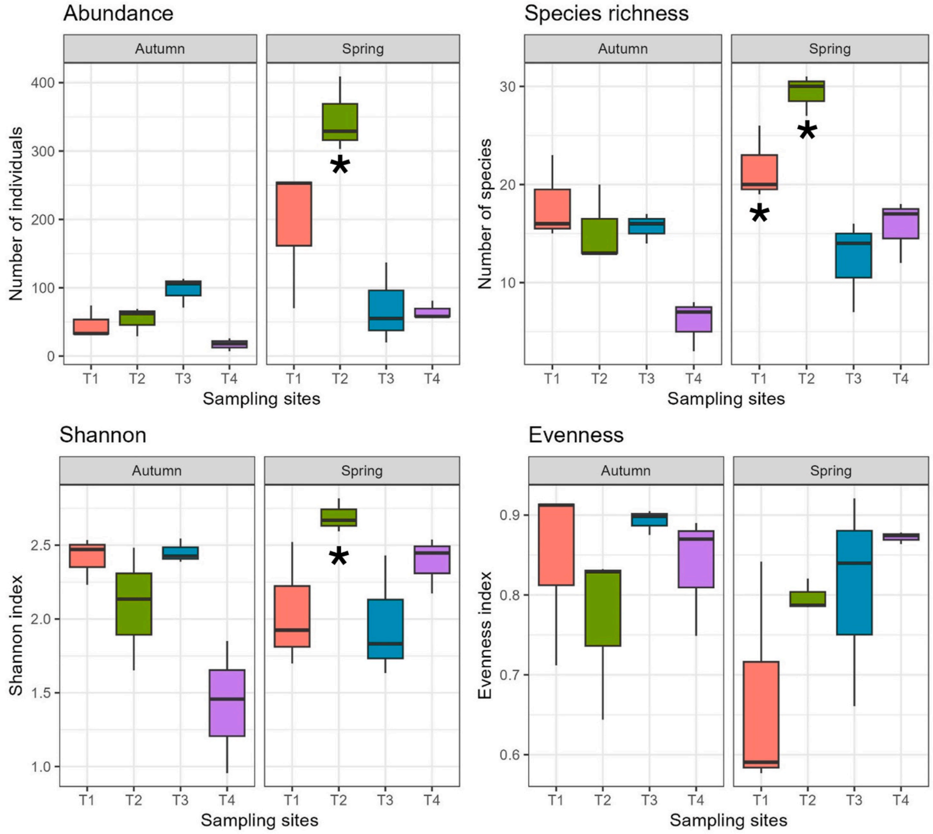

Fig. 4. Comparison of total abundance (n° ind. 255 cm^2), species richness, Shannon and Evenness indexes of macrobenthos in the four sampling stations in Spring and Autumn (2021) in the Tortolì Lagoon. Horizontal lines are medians; vertical lines are upper and lower whiskers, respectively. Asterisks mark significant differences ($p < 0.05$).

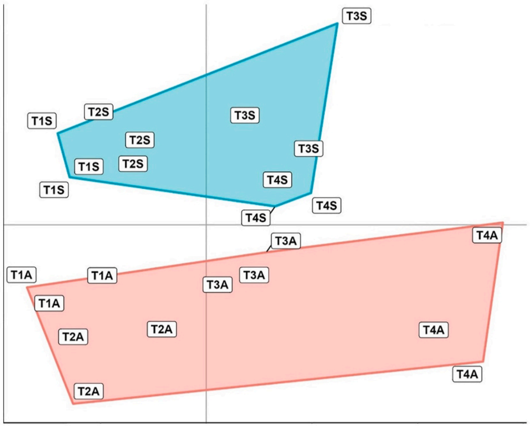

Fig. 5. Non-metric Multidimensional Scaling (nMDS) of abundance data of macrobenthic species across the four sampling stations (T1, T2, T3, T4) and the two sampling seasons (Spring and Autumn; S and A, respectively) in 2021. Stress: 0.14. Polygon definition was tested by ANOSIM.

for each site and date highlighted the separation of two groups of station points corresponding to the two seasons, spring and autumn, respectively. Differences on seasons and sampling sites were proved to be significant by two-way ANOSIM (global R for seasons = 0.78, p = 0.0001; global R for sites = 0.72, p = 0.0001). These results revealed that sources of variation were mainly related to differences between seasons and sampling sites. In fact, sampling dates of spring were included in the upper polygon and those of autumn were grouped in the lower polygon, as well as the sampling sites of the stations under direct marine influence (T1 and T2) are placed on the left side of the plot and those of the confined stations of the lagoon (T3 and T4) are located on the right side, in both the upper and lower polygons respectively. The SIMPER analysis revealed the top discriminating species responsible for the similarity/dissimilarity between the sampling sites for each season (Table 4). The discrimination of stations T1-T2 *vs* T3-T4 mostly depended on marine species (contribution more than 1%), such as *Parvicardium exiguum, Paradoneys lyra, Cymodoce truncata, Schistomeringos rudolphi*, and *Amphopholis squamata, Syllis garciai, Gammerella fucicola* and *Elasmopus rapax, Syllis parapari, Crisilla semistriata* as exclusive species in spring and in autumn, respectively. Other discriminating species, that are typical of sheltered coastal areas e.g. *Pareanemonia cinerea, Paracerceis sculpta, Cirriformia tentaculata, Haminoea hydatis*, were more abundant in the stations T3-T4. Table 3 provides the list of the species found in the lagoon and the indication of their life traits on terms of adult motility and feeding mode (included in the “functional group” category), relationship with the sediment and larval development mode. In terms of the first two categories, functional group and relationship with the sediment, most of the species (54) belonged to epifauna, while 30 species were ascribed to the endofauna. Many species were predators, e.g. the Polychates of the families Glyceridae and Syllidae; motile and sessile/semi-motile surface deposit feeders, e.g. Polychaetes, Gastropods and Crustaceans, were each composed by 9 species; other groups, such as filter feeders and omnivorous included 16 and 14 species respectively; less numerous were the motile and sessile/semi-motile subsurface deposit feeders and herbivores, which accounted for 9 and 7 species respectively. Most of Polychaetes and Molluscs, for a total of 28 species, showed a pelagic, both planktotrophic and lecithotrophic, larval development; while 29 species, most of Crustaceans except Decapods, showed direct development. The Mollusc *Abra segmentum* is known to have variable development, i.e. producing both

Table 4

List of the species identified by the SIMPER analysis (individual contribution >1.0%) responsible for 86% of the distinction between groups of sampling stations (T1-T2 and T3-T4) in the two sampling seasons (May and November). Ecological (Ecol.) affinity: O, opportunistic; C, common in coastal sheltered waters; B, brackish; M, properly marine.

T1-T2 vs T3-T4: May	Ecol. Affinity	Contrib. %	Cumulative %	Mean T1-T2	Mean T3-T4
Abra segmentum	C	18.77	18.77	52.20	1.50
Heteromastus filiformis	O	14.57	33.34	45.70	2.00
Parvicardium exiguum	M	6.40	39.74	17.30	13.90
Paradoneis lyra	M	5.25	44.99	18.00	0.25
Prionospio cirrifera	O	4.80	49.78	16.50	0.00
Amphipholis squamata	M	4.62	54.40	13.30	6.17
Protodorvillea kefersteini	M	4.39	58.78	14.00	1.08
Polititapes aureus	C	4.13	62.91	12.30	1.42
Paracerceis sculpta	C	3.80	66.71	8.67	6.33
Cymodoce truncata	M	3.48	70.19	5.17	9.25
Syllis garciai	M	3.38	73.57	9.83	0.00
Paranemonia cinerea	C	3.26	76.83	0.00	8.50
Schistomeringos rudolphii	M	2.70	79.53	8.83	0.92
Oligochaeta		2.09	81.62	6.00	0.00
Cirriformia tentaculata	C	1.53	83.14	0.17	3.67
Microdeutopus sp.	C	1.27	84.41	4.33	0.25
Podarkeopsis capensis	M	1.14	85.55	3.67	0.58
Gammarella fucicola	M	1.08	86.63	4.17	0.17

T1-T2 vs T3-T4: November	Ecol. Affinity	Contrib. %	Cumulative %	Mean T1-T2	Mean T3-T4
Heteromastus filiformis	O	19.61	19.61	16.80	1.50
Elasmopus rapax	M	6.52	26.13	0.33	8.67
Schistomeringos rudolphii	M	6.18	32.31	5.00	0.50
Paranemonia cinerea	C	6.00	38.31	0.33	6.33
Paracerceis sculpta	C	5.64	43.95	0.17	4.50
Parvicardium exiguum	M	5.42	49.36	3.83	3.92
Paradoneis lyra	M	4.88	54.24	2.67	4.08
Polititapes aureus	C	3.77	58.01	0.67	5.58
Syllis parapari	M	3.42	61.44	2.50	0.08
Naineris laevigata	C	3.42	64.85	0.83	4.58
Chironomidae		3.26	68.11	2.67	0.00
Cymodoce truncata	M	2.47	70.58	0.50	4.25
Crisilla semistriata	M	2.18	72.76	1.50	1.42
Diamysis bahirensis	B	1.89	74.65	0.83	2.08
Cirriformia tentaculata	C	1.80	76.45	0.00	1.50
Ericthonius brasiliensis	M	1.56	78.01	0.33	1.58
Haminoea hydatis	C	1.39	79.40	0.17	1.00
Condrochelia savignyi	M	1.38	80.77	0.67	0.92
Glossobalanus minutus	C	1.37	82.14	1.00	0.00
Loripes orbiculatus	C	1.32	83.46	0.33	0.75
Neanthes acuminata	C	1.21	84.67	0.83	0.08
Podarkeopsis capensis	M	1.17	85.84	0.67	0.25
Hemilepton nitidum	C	1.10	86.94	0.83	0.00

short pelagic and long benthic larvae (Reizopoulou and Nicolaidou, 2007), and this was confirmed by the finding of many juveniles of this species within the temporary meiofaunal community of the Cabras lagoon (western Sardinia) (Magni et al., 2022). Particularly, eight larval stages corresponding to the adult benthic invertebrates present in the benthos of the Tortolì lagoon were identified from plankton samples collected in the surrounding coastal marine area (personal observations) (Fig. 6). The planula was the oval shaped, uniformly ciliated larva of Anthozoa sea anemones and was recognised by its mouth and well-developed gastrovascular cavity. The typical pilidium larvae of Nemerteans, long-lived and uniformly ciliated, have been distinguished by their characteristic mitre-shaped and helmet-shaped episphere, which showed the juveniles developing internally (Maslakova and Hebert, 2014). The nectochaetae, different segmented polychaete larvae, have been identified by the gradual acquisition of the adult characteristics, i.e. two antennae on the prostomium and tentacular cirri in the Nereididae and a reduced, tapered prostomium with four small antennae in the Glyceridae. The veligers of Gastropods and Bivalves have been recognised due to the shape of the protoconcha, which was spirally coiled in the former and bivalve in the latter. The actinotrocha, typical larvae of Phoronids, have been recognised by its body divided in the anterior pre-oral hood, the collar bearing a ring of tentacles and the trunk ending with the telotroch and the anus. The ophioplutei of Ophiuroids of the family Amphiuridae have been distinguished by the presence of three pairs of arms, as they lack postero-dorsal arms (Tortonese, 1965). Three successive larval stages of the Enteropneusta tornaria have been identified: the early stage characterized by a ciliate band crossing the surface, the typical tornaria stage with the loops of the ciliate band extended over the surface and the metamorphic stage in which the proboscis, collar and trunk region were outlined (Nezlin and Yushin, 2004).

3.3. *Past and present condition: a comparison*

The total number of species has not changed considerably being 74 in 2003 and 86 in 2021, out of the overall total of 124 species (Table 3). The proportion by which the benthic communities differ from each other between the two years (2003 and 2021) in species composition was assessed with the turnover index β. Based on the entire benthic community, the overall turnover of species was $\beta = 0.5$ and it was quite similar in the cases of the different taxonomic groups, being 0.5 for the Crustaceans and 0.6 for the Polychaetes Molluscs. The two decadal changes between 2003 and 2021 in terms of community structure were revealed by the cluster analysis, that produced the separation of two groups of stations corresponding to the different years (Fig. 7). The PERMANOVA test confirmed significant differences between the two groups of stations identified by the cluster analysis (total sum of squares: 2.39; within-group sum of squares: 1.66; pseudo-F: 2.65; $p = 0.02$). Half of the 24 top discriminating species (contribution more than 1%) revealed by the SIMPER analysis were marine species (e.g. *Apocorophium acutum, Nephtys hombergii, Parvicardium exiguum, Paradoneis lyra*) and the other half comprised coastal (e.g. *Paracerceis sculpta, Microdeutopus gryllotalpa*), opportunistic and brackish species (e.g. *Polydora ciliata, Heteromastus filiformis, Monocorophium insidiosum*) (Table 5).

Six main functional groups were identified in the benthic community of the Tortolì lagoon: predator, herbivorous, omnivorous, surface deposit-feeder, subsurface deposit-feeder, filter-feeder (Table 3) and they were all represented with similar proportion in the two years, both in terms of number of species (Fig. 8) and of individuals. The PERMANOVA test confirmed this results, revealing no significant differences in either the abundance or species composition of the functional groups in the two years (data not shown).

4. Discussion

This study revealed both similarities and changes in the species

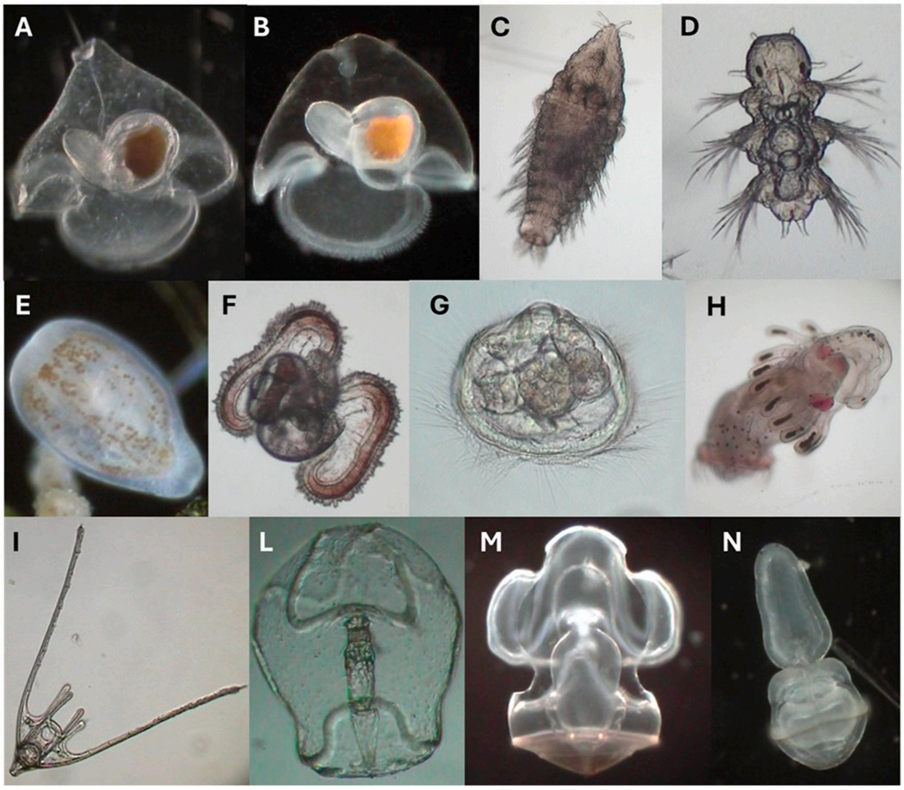

Fig. 6. Photos of the larvae from the Tyrrhenian Sea whose adults were found in the zoobenthic community of in the Tortolì lagoon; **A-B**: pilidium larvae of Nemertea, mitre-shaped episphere (A) and helmet-shaped episphere (B); **C-D**: nectochaete larvae of Polychaeta of the family Glyceridae at the stage of seven chaetigers (C) and Nereididae at the stage of three chaetigers (D); **E**: Anthozoan sea anemone planula; **F-G**: veliger larvae of Gastropoda Mollusca of the family Nassariidae (F) and Bivalvia (G); **H**: actinotroch larva of Phoronida; **I**: ophiopluteus of brittle stars of the family Amphiuridae with three pairs of arms; **L**: early tornaria stage of Enteropneusta of the family Ptycoderidae; **M-N**: tornaria larva of Enteropneusta of the family Ptycoderidae (M) and its metamorphic stage (N). (Photos by Marco Lucarelli, Rome).

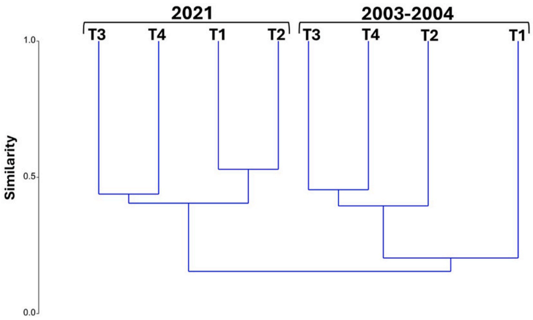

Fig. 7. Dendrogram illustrating the segregation in macrobenthos community composition in the years 2003–2004 and 2021. Sampling stations: T1, T2, T3, T4. The significance of segregation was assessed with the PERMANOVA.

composition of the zoobenthic community of Tortolì lagoon between the seasons of 2021 and the two years 2003 and 2021. Currently, the level of biodiversity was high as it was twenty years ago (Giampaoletti et al., 2023) and such a high number of macrobenthos species found (86) is an unusual record for the Mediterranean lagoons (Munari and Mistri, 2008). For example, in other Sardinian lagoons, the total number of species ranged from nearly 60 in the Santa Gilla lagoon to 25 in the Cabras lagoon, being about 6 and 10 times larger in size, respectively, than the Tortolì lagoon (Gravina et al., 2020a). Furthermore, the biological peculiarity of Tortolì lagoon was indicated by the composition of the benthic community, which consisted almost entirely of marine species, belonging to different benthic taxa, such as the Polychaetes *Diopatra neapolita*, *Drilonereis filum*, *Glycera unicornis*, *Nephtys hombergii*; the Molluscs *C. semistriata*, *Rissoa membranacea*, *Lucinoma borealis*, and most of Crustaceans, such as *Ericthonius brasiliensis*, *E. rapax*, *Dexamine spinosa*; the Ophiuroid *Amphipholis squamata*. The SIMPER analysis revealed that they were responsible for the significant differences between the two stations closest to the sea (T1 and T2) and the two confined stations (T3 and T4), as confirmed by the ANOSIM test. Other species, widely distributed in the lagoon, were common inhabitants of sheltered coastal areas including the Actinian *P. cinerea*, the Polychaetes *C. tentaculata*, *Lumbrineris latreilli*, *Neanthes acuminata*, *Nereiphylla rubiginosa*, *Podarkeopsis capensis*; the Molluscs *Tritia neritea*, *Haminoea hydatis*, *Nassarius nitidus*, the Crustaceans *Gammarus* spp., *Microdeutopus* spp. Particularly, species characteristic of the biocoenosis of the muddy sands in sheltered areas (sensu Pérès, 1967) included the infauna *Phylo foetida*, *H. filiformis*, *P. lyra*, *Loripes orbiculatus*, *P. exiguum*, *Polititapes aureus* and the borrower decapod *Upogebia pusilla*; the crawling epifauna *Aonides oxycephala*, *Schistomeringos rudolphi*, *S. parapari* (synonym for *Syllis cornuta*) and the sessile epifauna *Phoronis psammophila*. This biocoenosis has been reported some time ago for some unpolluted sites on the French Mediterranean coast, characterized by low hydrodynamic energy, fine sediment and freshwater contributions from the mouth of the Rhône River (de Gaillande, 1968; Massé, 1972) and constitutes the most marinized area of the well-known Paralic Domain (Guélorget and Perthuisot, 1983). The benthic community found in the Tortolì lagoon closely matched to those in the muddy sands of sheltered areas and differs from the other lagoon communities, confirming that differentiation in faunal composition is mainly due to individual rare species (Munari and Mistri, 2008). In this regard, the new entry of the Enteropneusta species (*Glossobalanus minutus*) in the 2021 samples deserves special mention because these invertebrates have been found as a relevant component of the muddy sand fauna of sheltered areas by historical

Table 5
List of the top discriminating taxa with contribution more than 1% by SIMPER analysis between the two investigated periods (2003 vs 2021). Ecological (Ecol.) affinity: O, opportunistic; C, common in coastal sheltered waters; B, brackish; M, properly marine.

2003 vs 2021	Ecol. Affinity	Contrib. %	Cumulative %	Mean 2003	Mean 2021
Polydora ciliata	O	7.70	7.70	31.40	0.00
Abra segmentum	C	6.76	14.45	21.60	27.10
Monocorophium insidiosum	B	6.51	20.96	24.60	0.08
Heteromastus filiformis	O	6.18	27.14	5.75	33.00
Capitella capitata	O	6.05	33.19	21.90	0.04
Apocorophium acutum	M	4.59	37.78	18.40	0.83
Nephtys hombergii	M	4.23	42.01	17.80	1.58
Parvicardium exiguum	M	4.06	46.07	2.75	19.50
Elasmopus rapax	M	3.89	49.96	11.00	5.58
Spiochaetopterus costarum	M	3.18	53.14	18.90	0.00
Myriochele heeri	M	3.01	56.15	17.90	0.00
Cerastoderma glaucum	B	2.70	58.85	9.50	0.00
Paracerceis sculpta	C	2.41	61.27	0.13	9.83
Paradoneis lyra	M	2.36	63.62	0.50	12.50
Cymodoce truncata	M	2.30	65.93	0.00	9.58
Paranemonia cinerea	C	2.15	68.08	1.38	7.58
Amphipholis squamata	M	2.14	70.21	3.25	9.92
Microdeutopus algicola	M	1.93	72.15	9.13	0.00
Polititapes rhomboides	C	1.80	73.95	5.75	10.00
Prionospio cirrifera	O	1.76	75.71	2.75	8.58
Schistomeringos rudolphii	M	1.54	77.24	0.00	7.62
Microdeutopus gryllotalpa	C	1.51	78.75	7.63	0.00
Protodorvillea kefersteini	M	1.48	80.23	2.13	7.54
Styela plicata	C	1.20	81.43	4.00	0.00

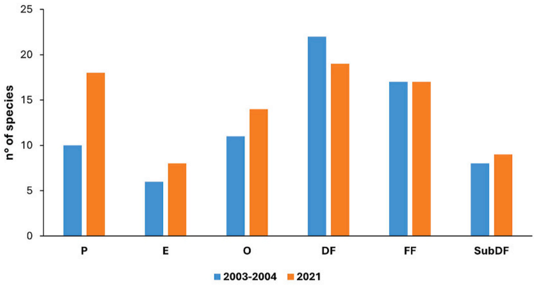

Fig. 8. Comparison in the total number of species for each functional group of macrobenthos between the years 2003–2004 and 2021. P, sessile/motile predators; E, herbivores; O, omnivorous; DF, motile/sessile surface deposit feeders; FF, motile/sessile filter feeders; SubDF, burrower motile/sessile subsurface deposit feeders.

studies (Massé, 1972), but are absent from lists of recent studies in other lagoons, and in Tortolì itself, and are therefore a peculiarity of the Tortolì lagoon in 2021. This proved that the current conditions in this lagoon are still suitable for the settlement of a species which was a common inhabitant of unperturbed environments half a century ago.

Moreover, differences between seasons on the basis of species composition, evidenced by the nMDS result and tested with ANOSIM, were also supported by the variations in indices of species richness, diversity and abundance, which showed significantly higher values at stations T1 and T2 than in stations T3 and T4 only in spring, while no significant changes were recorded in autumn. Such variations observed in Tortolì lagoon are attributable to the increase in number of individuals due to reproductive events and the entry of new species from the sea which were consistent with the seasonal trends in the number of individuals and species commonly recorded in other Mediterranean lagoons (e.g. Gravina et al., 1989; Kevrekidis et al., 2000; Mistri et al., 2000; Specchiulli et al., 2008).

By comparing the zoobenthic communities of 2003 and 2021, cluster analysis highlighted significant changes in the benthic community in the two years under scrutiny, which can be explained in terms of a 50 percent species turnover rate, measured both for the total fauna and for the different individual groups. Past and newly arrived species have shown similar larval development traits: 18 and 12 species of Polychaetes had pelagic larvae in 2003 and 2021, respectively, while the number of species with direct development was quite the same in the two periods (5 and 4 in 2003 and 2021, respectively). Similarly, for Molluscs and Crustaceans, the number of species with pelagic larval development and those with direct/benthic development was quite similar in the two periods. Consistent with the present study, in the Cabras lagoon (western Sardinia), the adult specimens of *A. segmentum* occurred only at the marine site, with similar environmental conditions as the Tortolì lagoon, while its juveniles were found along the whole salinity gradient (Magni et al., 2022). This demonstrates a strong dispersal phase during its juvenile stage and the subsequent establishment of the adult population, as a macrofaunal component, only where the environmental conditions are more appropriate to its auto-ecology requirements (Magni et al., 2022). This result prompts the question of larval dispersal and species recruitments in lagoon ecosystems, which, as basins separated from each other by the sea, can be considered individual "islands" with scarce or no connections (Barnes, 1988). Many studies have addressed this topic and overlooked the direct inference that the longer the larval lifespan, the wider the distribution (Giangrande et al., 2017 and references therein); this has been also highlighted for single groups (e.g. Gambi et al., 1990; Boero and Bouillon, 1993). Concerning the transitional water systems, due to their semi-enclosed state, the connectivity of benthic communities is an intriguing issue because, on the one hand, typical lagoon species do not live in the adjacent marine areas, and on the other hand, strictly marine species do not enter the lagoon (Giangrande and Rubino, 1994). Therefore, alternative modes and means of dispersal should be considered to understand the problems of persistence, variations, colonization of lagoons by benthic species. These may be mainly passive transport by adults attached to algae and drifting objects, human-mediated activities, e.g. bivalve farming, resistance forms of juvenile and adult phases (Bonsdorff, 1992; Giangrande et al., 1994; Bhaud, 2000; Shanks, 2009; Winston, 2012). However, larval transport has a key role in the settlement and adult benthic population dynamics (Giangrande et al., 2017); in this regard, the coastal plankton samples from the Central Tyrrhenian Sea here recorded testified both the supply of populations, which have been maintained for two decades, and the new arrival of some benthic species from adjacent coastal areas. These latter are the cases of the pilidium larvae for the Nemerteans, the veliger of the Gastropod Nassariidae for *Nassarius nitidus* and especially the tornaria of the Enteropneusta *G. minutus*. This latter finding is noteworthy because it can be considered a new record for the transitional waters of an "old species" (Boero, 2011), which has been reported as a characteristic species of the muddy sands of sheltered coastal areas in the 1970s (Massé, 1972). The successive larval stages observed in our samples, from the early stage, to the well-developed tornaria and to the metamorphic stage, demonstrated their presence of neighbouring marine coastal areas which played the role of source and provided the lagoon with the larvae of Enteropneusta, first occurred in Tortolì in November 2021. Furthermore, we assumed the passive transport of adults for most of the peracarid Crustaceans, whose life cycle lack in free living larvae, in agreement with the dispersal mode of adults by algae and drifting objects, that has been showed for some corophid and gammaridean Amphipoda (Bonsdorff, 1992; Myers, 1993). Similarly, the passive dispersal of adults was also suggested for the introduction of alien Isopod species, *P. sculpta* and *Mesanthura* sp., which may be transported in association with the biotic habitat of fouling (Lorenti et al., 2009; Ramalhosa et al., 2017). By contrast, we attribute the non-record of the alien Amphipod *Caprella scaura* to stochastic factors, notwithstanding this species has been found in Santa Gilla lagoon (Southern Sardinia) and in other lagoons along the Central Tyrrhenian coast (Cabiddu et al., 2013). Otherwise, for the Mysidacean *Diamysis bahirensis*, the active dispersal of adults is supported by its benthopelagic behaviour, which leads these benthic invertebrates to move in the water column, especially at night-time (Wittmann, 2001). Indeed, such a dispersal mode has been proved for the colonization of the brackish coastal lake of Ganzirri, in Sicily (Genovese, 1956). Conversely, populations of some species could be maintained in the lagoon, where they reached high density briefly, also thanks to asexual reproduction by fission, alongside the sexual reproduction, such as in the case of the Polychaete *Myriochele heeri* and the Phoronid *P. psammofila* (Gravina et al., 2020a).

In addition to the taxonomic variations between 2003 and 2021 and the high levels of species richness, abundance and diversity which persisted twenty years later, this study also highlighted the persistence in terms of functional groups composition and diversity of the macrobenthic community in the Tortolì lagoon. Based on sediment position, motility pattern and feeding modes, the 19 functional groups identified in the benthic community of Tortolì indicated that invertebrates move on the sediment (epifauna) and inside it (endofauna) in different modes. Some of them were sessile, which either were in tubes or not, and fed mainly from suspended matter of the water column. Some components of the endofauna were semi motile and collected deposit particles from the surface of the sediment; others dug their burrows in the sediment and ate debris below the sediment surface or pumped water into the burrow, so behaving as filter-feeders. This behaviour may have promoted a symbiotic association between species, as in the case of the burrow of *U. pusilla* which provided a suitable microhabitat for possible commensal species, such as the Bivalve *Hemilepton nitidum*, due to the fact that the water current created by the shrimp provides suspension feeding activity for both species (Lavesque et al., 2016). The majority of the epifauna was motile and covered a wide range of feeding modes; many Polychaetes were carnivorous/predators and omnivorous, while the herbivorous/grazers, as well as the scavengers, were Gastropods; most Crustaceans, aside from herbivorous and omnivorous, were surface deposit feeders. Such a high diversity in feeding groups reflects the considerable diversification of trophic levels in the benthic food web and, together with the high level of species richness and taxonomic diversity, is assumed to be indicative of an efficient degree of ecosystem functioning (Mistri et al., 2001a; b; Munari et al., 2003; Alves et al., 2024). This is a relevant result because such healthy condition of the ecosystem in the Tortolì lagoon has ensured the long-term maintenance of aquaculture productivity (Giampaoletti et al., 2023).

The present study-case highlighted the peculiarity of the benthic community of the Tortolì lagoon within the context of the transitional water ecosystems: on the one hand, the richness of the faunal assemblage that supports a well-functioning food web; on the other, the large number of marine species that have continued to successfully inhabit this basin 20 years later. The entrance of new marine species is explainable by the larval supply that is provided by neighbouring coastal areas, according to the supply-side ecology pattern (Underwood and Fairweather, 1989). Many new marine species found suitable conditions for their settlement and have become part of current assemblages. Other species present in the past have been lost, likely according to the well-known processes which drive the maintenance or change of marine benthic communities (Sarà, 1985; Boero, 1994). In any case, the replaced species were taxonomically different, but showed the same functional role, e.g., over the long term, the epi-motile carnivorous Polychaete *Glycera tridactyla* was replaced by the congeneric *Glycera unicornis*; the epi-motile omnivorous Amphipod *Melita palmata* was replaced by *Gammarus aequicauda* and the epi-motile surface deposit feeder Amphipod *Microdeutopus gryllotalpa* was replaced by *Maera grossimana*; the epi-motile filter feeder Cumacean *Iphinoe trispinosa* was replaced by *Diamysis bahirensis*. In the short term of the seasonal fluctuation in 2021, the motile micro-grazer Gastropod *Rissoa membranacea* (found in May) was replaced by *Crisilla semistriata* (found in November). These results demonstrated both the high turnover rate measured and the maintenance of the functional structure of the community.

5. Conclusion

The Tortolì lagoon has emerged as a unicum in the transitional water system due to its high taxonomic diversity and composition of the benthic community, which was found to be ascribable to the biocoenosis of the muddy sand of sheltered coastal areas. These results, together with the remarkable diversity also found in terms of functional groups of the benthic species, are a proxy of an efficient ecosystem. Temporal changes in the benthic community were observed mainly in the species composition but were not such as to alter the structure in terms of functional groups. This latter was found to be persistent after twenty years, thus demonstrating the absence of any particular impact on the community. The comparison of the results of the present study with those of the study twenty years ago supported the sustainability of anthropogenic production activities carried out in the Tortolì lagoon from 20 years ago to the present day. Finally, it is expected that the persistence of the changes will ensure the functioning of the system in the future.

CRediT authorship contribution statement

Jacopo Giampaoletti: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation, Conceptualization. **Simone Galli:** Writing – review & editing, Writing – original draft, Visualization, Validation, Formal analysis, Data curation, Conceptualization. **Maria Flavia Gravina:** Writing – review & editing, Writing – original draft, Supervision. **Paolo Magni:** Writing – review & editing, Writing – original draft, Supervision, Project administration. **Alice Sbrana:** Writing – review & editing, Writing – original draft, Visualization, Validation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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