Multidecadal monitoring highlighted long-term stability of protected assemblages within a Mediterranean marine reserve

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ABSTRACT

Marine Protected Areas (MPAs) are at the core of management and conservation plans aimed at counteracting the ongoing widespread degradation of marine ecosystems. Although the outcomes of protection in enhancing marine biodiversity and restoring populations of exploited species are widely recognized, the putative effect of MPAs in increasing the resilience of marine communities and ecosystems is still underexplored. In this study, long-term data from a no-take area of a Mediterranean MPA and unprotected locations were used to investigate the effects of full protection on the temporal stability of sessile assemblages on shallow subtidal rocky reefs. Results highlighted that assemblages within the no-take area exhibited a more consistent structure over 20 years of study, whereas a significantly larger temporal variability characterized assemblages at the unprotected locations. Reduced levels of human pressure and stabilizing processes related to the re-establishment of the integrity of trophic networks within the MPA could underlie the observed patterns. Assessing whether MPAs may improve the ability of marine communities to absorb disturbance, from local to large scale sources, is essential to ascertain their contribution to future adaptive conservation strategies in the face of global change. This study provided evidence that MPAs, if well managed, can represent an effective tool to smooth fluctuations in the structure of marine communities, thus potentially reducing their vulnerability to natural and human-driven environmental changes.

1. Introduction

The unprecedented increase of anthropogenic pressures on seas and oceans is determining a profound alteration of marine ecosystems at a global scale (Jones et al., 2018; Halpern et al., 2019). The cumulative effects of long-established sources of human impacts, such as pollution, overfishing, and ocean sprawl, are being exacerbated by the interaction with escalating outcomes of climate change, leading to increasing erosion of the resilience potential of marine ecosystems and proneness towards regime shifts (Harley et al., 2006; Wernberg et al., 2016; Rilov et al., 2019; Gissi et al., 2021). The Mediterranean Sea, where a long history of exploitation of marine resources and uses of marine space combine with a high vulnerability to warming and biological invasions, is exceptionally exposed to such changes (Lejeusne et al., 2010; Coll et al., 2012; Micheli et al., 2013).

Key Mediterranean foundation species (e.g., the seagrass *Posidonia oceanica* (L.) Delile, 1813), habitat-formers (e.g., fucoid algae like *Cystoseira sensu latu*), and bioconstructions, such as coralligenous outcrops and maërl beds, are either declining or being critically threatened, potentially leading to severe losses of marine biodiversity and associated ecosystem functions (Milazzo et al., 2014; Telesca et al., 2015; Ingrosso et al., 2018; Fabbrizzi et al., 2020). The status of shallow subtidal rocky reefs has raised special concerns due to the increasing evidence of degradation of these habitats across the Mediterranean Sea (e.g., Gubbay et al., 2016; Benedetti-Cecchi et al., 2019; Bevilacqua et al., 2020). Main causes underlying this trend include the depletion of populations of top predator fish due to their overexploitation as commercial targets (Sala et al., 1998; Sini et al., 2019), destructive fishing practices (Colletti et al., 2020), coastal artificialization (Bulleri, 2005; Airoldi and Beck, 2007), increase in sedimentation rates (Airoldi, 2003), pollution (Azzurro et al., 2010), biological invasions (Sala et al., 2011; Rilov et al., 2018), and more recently, sea surface temperature increase and

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associated phenomena such as marine heat-waves (Azzurro et al., 2019; Bevilacqua et al., 2019; Garrabou et al., 2021). Direct and indirect impacts from these heterogeneous pressures are probably acting synergistically in causing an oversimplification of subtidal reef community structure and associated ecological processes, driving the transition from species-rich and structurally complex systems, such as for example *Cystoseira s.l.* canopies, towards species-poor and less complex ones, characterized by algal turfs or crusts and bare rocks (Falace et al., 2010; Thibaut et al., 2014; Bevilacqua et al., 2021).

Shallow rocky reefs are among the most productive and diverse coastal environments, where canopy-forming macroalgae and sessile invertebrates often shape a multi-layered and complex architecture of assemblages that provides refuge, nursery and feeding ground for many other species; they are, therefore, critical for the maintenance of biodiversity, the provision of goods and services, and the support of socio-economic systems in the Mediterranean and other temperate coastal areas (Witman and Dayton, 2001). Yet, conservation strategies specifically tailored to protect rocky reefs still lack at European and basin scale, and monitoring programmes are insufficient to provide a consistent base of data in order to assess their conservation status and track future trends (EEA, 2019). For example, rocky reefs are listed in Annex I of the European Habitat Directive (EU Council Directive 92/43/EEC), but are not designated as priority habitats for conservation.

MPAs are recognized as privileged tools for management and conservation of marine biodiversity and ecosystems worldwide (Lester et al., 2009; Giakoumi et al., 2017; Sala et al., 2021; Fraschetti et al., 2022), and more than 1000 MPAs have been established in the Mediterranean Sea (Claudet et al., 2020). Protection has been found to increase community diversity, size of individuals and abundance of populations within the MPAs if compared to unprotected areas, though most studies focused on fish (García-Charton et al., 2004; Claudet et al., 2006; McClure et al., 2020) and primarily on demonstrating the effectiveness of MPAs in preserving marine biodiversity and restoring exploited populations (Halpern, 2003; Micheli et al., 2005; Ferreira et al., 2022). The potential role of MPAs as a tool to sustain also the dynamic properties of marine communities and ecosystems, including their resilience potential, has long been postulated (e.g., Hughes et al., 2005) but rarely explored. In this study, we used data from several sampling campaigns, spanning over 20 years, carried out within and outside the no-take, no access zone of a Mediterranean MPA, to investigate the long-term effects of full protection on sessile assemblages from shallow subtidal rocky reefs. Specifically, we tested the hypothesis that full protection underpins changes in the structure of macrobenthic assemblages and their temporal stability with respect to unprotected locations.

2. Materials and methods

2.1. Study area and sampling design

The MPA of Miramare is located in the northern Adriatic Sea (NE Italy, 45°42′05.4″N, 13°42′50.4″E), a peculiar biogeographic region of the Mediterranean Sea, characterized by low depth, poor water transparency due to strong river run-offs, and wide seasonal and interannual temperature and salinity variations. Also, it is in one of the most anthropized areas of the basin where maritime transport, coastal industries, fishing, and tourism activities densely concentrate (Giani et al., 2012; Furlan et al., 2019). The MPA has a total surface of 120 ha, comprising a no-take, no-access zone (30 ha) enclosed in a buffer zone of partial protection where commercial fishing is forbidden and recreational activities are regulated. Established in 1986 and managed by the World Wildlife Fund – Italy, it received the status of Specially Protected Areas of Mediterranean Importance (SPA/BD, 1995) due to the peculiarity of the resident marine fauna and flora. The main subtidal habitats in the reserve are represented by rocky reefs, both natural bedrocks and artificial reefs, surrounded by soft bottoms of coarse and muddy sand which, in turn, characterize the seabed of the region.

Data on sessile assemblages come from several monitoring campaigns spanning over two decades, from 2001 until 2021. Sampling was carried out during summer (July–September) on five occasions (2001, 2002, 2016, 2019 and 2021) at three locations 2–3 km apart, and namely the no-take zone of the MPA and two unprotected control locations characterized by environmental conditions comparable to those at the protected zone in terms of nature and slope of rocky substrate, exposure to wave actions, currents and dominant winds. In each location, three sites (100–300 m apart) were randomly selected. At each site, sessile assemblages on sub-vertical rocky reefs at 5–7 m depth were sampled with ten randomly-located replicate quadrats of 20 × 20 cm by using a digital underwater camera equipped with strobes. Since the study involved sampling sessile assemblages within a no-take zone, ethical considerations led us to use a non-destructive photographic sampling technique. Despite this could limit taxonomic identification, and therefore a comprehensive quantification of species diversity, the use of photographic sampling is widely recognized as an effective method to assess spatial and temporal patterns of change in sessile assemblages in relation to protection and human impacts (Terlizzi et al., 2005; Parravicini et al., 2008; Bianchi et al., 2022). A total of 450 photographic samples were then analyzed to identify sessile organisms and to estimate their percentage cover. Vagile organisms were not considered in the analysis. A total of 67 taxa were identified (see Appendix 1 in the supplementary material). Most of them (~80%) were identified at the level of species or genus, or at coarser taxonomic levels (~10%). In some cases (~10%) organisms were classified as morphological groups due to the intrinsic difficulties of taxonomic identification from images. However, in such cases, voucher specimens were collected to identify the main species composing morphological groups.

2.2. Statistical analysis

Distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) was used to test for differences in assemblage structure between the protected zone (*P*) and the unprotected control locations (*C1* and *C2*, collectively referred to as *Cs*). The analysis was based on Bray-Curtis dissimilarities on untransformed data, and each term in the analysis was tested with 5000 random permutations. The design for the analysis included three factors: Time [Ti], random, with five levels (the five sampling times); Location [Lo], with three levels, one protected location and two unprotected controls; Site [Si(Lo)], three levels, nested in Lo, with $n = 10$ replicates. The design for the analysis was asymmetrical (Underwood, 1997) as it involved a single protected location to be compared against multiple unprotected locations. The Location term, therefore, was partitioned into two portions: the 1-d.f. fixed contrast of *P* versus *Cs* (*P-vs-Cs*) and the variability between *Cs*. This partitioning was applied to all terms in the analysis that involved the factor Location, i.e. Si(Lo), Ti × Lo, and Ti × Si(Lo). Finally, the residual variation was partitioned in two portions, Res *P* and Res *Cs*, that is the residual variability of observations at *P* and *Cs* respectively. For a full description of variance partitioning and the choice of appropriate denominators for *F*-tests in asymmetrical designs see Terlizzi et al. (2005). Non-metric multidimensional scaling ordination (nMDS) of the Ti × Lo centroids was done to depict temporal patterns in assemblage structure between *P* and *Cs*.

Analysis of variance (ANOVA) on estimates of multivariate variance components associated to factor Time was done to test the hypothesis that protection could enhance the stability of sessile assemblages. Components of variation from hierarchical analyses of variance allow separating sampling error from estimates of the true variability associated to each factor in the analysis (Gaston and McArdle, 1994). A single set of data, however, provides only a single estimate of the variance component for each source of variation in the analysis, whereas formal tests require replicated estimates. To deal with this issue, the dataset was

split into nine subsets corresponding to the nine sites (three for each location). The nine subsets of data were then analyzed running separate PERMANOVAs. The design for the analysis in this case included only the factor Time, with $n = 10$ replicates for each level of the factor. This allowed obtaining three independent estimates of multivariate variance component associated to factor Time for *P* and for the two control locations. Finally, a one-way ANOVA was carried out on variance components to test for differences in temporal variance among locations. The design for the analysis included the single factor Location, considered as fixed, with three levels (*P*, *C1*, and *C2*). Cochran's *C*-test (Underwood, 1997) was used to check the assumption of homogeneity of variances prior to analysis. Post-hoc pairwise *t*-tests were done to compare variance components among the protected location and the two controls.

Since the analysis of variance components detected a higher temporal variability of assemblages at *Cs* with respect to *P* (see Results), the partitioning of the total temporal variance for *C1* and *C2* was used to identify taxa that mostly contributed to such higher temporal variance in the assemblage structure at the unprotected locations. As first, multivariate community data from *C1* and *C2* were averaged at the scale of sites for each time of sampling, obtaining six separate times × taxa data matrices, three for each of the two control locations. The total variance in a given $n \times s$ data matrix (SS_{Tot}), where n are samples and s are the species variables, is a measure of beta-diversity among samples (Legendre et al., 2005) that can be partitioned into 'Species Contributions' (SCBD, i.e. degree of variation of individual species across samples) (Legendre and De Cáceres, 2013). By extending this approach to the times × taxa data matrices, the total variance in the data tables was a measure of temporal beta-diversity of assemblages, which was then partitioned into the contributions of each species (or taxon) to the overall temporal variability of assemblages at each site within the two unprotected locations. Only species or taxa contributing more than 5% to SS_{Tot} at least in one location were considered. For further details on variance partitioning for community data see Legendre and De Cáceres (2013).

We hypothesized that the abundance of taxa mostly contributing to the overall temporal variance at *C1* and *C2* could be, in contrast, more stable over time at *P*. Therefore, three separate one-way ANOVAs, one for each location, were done to test for variations in the percentage cover of each taxon among times of sampling. Coherently with all previous analyses on temporal variance, sites were used as units of observation also in this case. The average percentage cover of taxa at the three sites were used as independent estimates of their abundance at a given location in each time of sampling. The design for the analysis included only factor Time (random, five levels), with $n = 3$ for each level of the factor. Cochran's *C*-test was used to check the assumption of homogeneity of variances prior to analysis, and data were (log) transformed to stabilize variance if required.

Asymmetrical ANOVA on the number of taxa and the total cover was also done to test for differences between *P*-vs-*Cs* in these variables; the design for the analysis was the same as for the asymmetrical PERMANOVA.

Analyses were performed using the Primer v7 software (Clarke and Gorley, 2015), the add-on package PERMANOVA+ (Anderson et al., 2008), and R (R Development Core Team, 2020).

3. Results

PERMANOVA did not detect neither a significant Ti × *P*-vs-*Cs* interaction, nor significant differences in *P*-vs-*Cs* (Table 1), indicating that the structure of assemblages on subtidal rocky reefs did not differ on average between the no-take zone (*P*) and the unprotected control locations (*Cs*), and that this pattern was consistent throughout the investigated period. However, ANOVA on the variance component associated to time detected a significantly lower temporal variability of assemblages at *P* if compared to *Cs*, which instead did not differ between them

Table 1

Results of asymmetrical PERMANOVA testing for differences between assemblages at the protected location (*P*) versus unprotected control locations (*Cs*). The analysis is based on Bray–Curtis dissimilarities (untransformed data) and each test was performed using 5000 random permutations. Significant tests are given in bold.

Source of variation	d.f.	SS	MS	Pseudo-*F*	*p*-perm
Ti	4	233690.0	58422.0		
Lo	2	37558.0	18779.0		
Cs	1	25762.0	25762.0	1.31	0.243
P-vs-*Cs*	1	11796.0	11796.0	0.46	0.845
Si(Lo)	6	22486.0	3747.6	0.89	0.608
Si(*Cs*)	4	13254.0	3313.5	0.88	0.624
Si(*P*)	2	9232.0	4616.0	0.92	0.488
Ti × Lo	8	107070.0	13384.0	3.19	**0.000**
Ti × *Cs*	4	76694.0	19174.0	5.07	**0.000**
Ti × *P*-vs-*Cs*	4	30376.0	7594.0	0.40	0.991
Ti × Si(Lo)	24	100570.0	4190.5	2.90	**0.000**
Ti × Si(*Cs*)	16	60566.0	3785.4	3.05	**0.000**
Ti × Si(*P*)	8	40004.0	5000.5	2.70	**0.000**
Res	405	585700.0	1446.2		
Res *Cs*	270	335570.0	1242.9		
Res *P*	135	250130.0	1852.8		

Table 2

Results of ANOVA testing for differences among locations in multivariate variance components associated to factor Time. Pairwise comparisons among locations are also reported. *P* = protected location; *C1*, *C2* = unprotected control locations. Significant tests are given in bold.

Source of variation	d.f.	SS	MS	F	p
Lo	2	700600.0	350300.0	18.80	**0.003**
Res	6	111820.0	18636.6		

Pairwise tests		
	t	p
P vs. *C1*	7.242	**0.002**
P vs. *C2*	4.986	**0.005**
C1 vs. *C2*	0.463	0.677

(Table 2, Fig. 1a). These patterns were clearly depicted in the nMDS plot of Ti × Lo centroids (Fig. 1b) showing that, while the clouds of centroids of *P* and *Cs* substantially overlapped, temporal trajectories were more scattered in the unprotected controls than in the no-take zone.

ANOVAs on the number and total abundance of taxa did not detect significant differences in the diversity of assemblages and in their total percentage cover between *P* and *Cs* (Table 3). As for PERMANOVA (Table 2), significant Ti × Si(*P*) and Ti × Si(*Cs*) interactions were detected also for these variables (Table 3), indicating high spatial and temporal variations of diversity, total abundance, and overall structure at the scale of sites for both protected and unprotected assemblages.

The total temporal variance in the data matrix was higher for *C1* and *C2* (SS_{Tot} equal to 1.14 and 1.09 respectively) than for *P* ($SS_{Tot} = 0.77$). Variance partitioning indicated that six taxa of macroalgae were responsible for ≥60% of the increased temporal variability observed in sessile assemblages at the two unprotected locations (Table 4). ANOVA on the abundance of these taxa at the three locations detected a significant temporal variability in almost all cases for unprotected locations, and only for two taxa in the no-take zone (Table 5). Specifically, the abundance of Turf algae and *Peyssonnelia squamaria* (S.G. Gmelin) Decaisne ex J. Agardh, 1842 strongly varied during the twenty years of monitoring at *Cs*, ranging from less than 10% to 30–60%, but did not showed significant variations at *P* (Table 5, Fig. 2a and b). *Ellisolandia elongata* (J. Ellis & Solander) K.R. Hind & G.W. Saunders, 2013 and Encrusting Rhodophytes also remained constant at *P*, showing significant interannual variations either at *C1* or at *C2* (Table 5, Fig. c,f). A significant temporal variability, instead, characterized the abundance of *Jania rubens* J.V. Lamouroux, 1816 and *Dictyota* spp. irrespective of
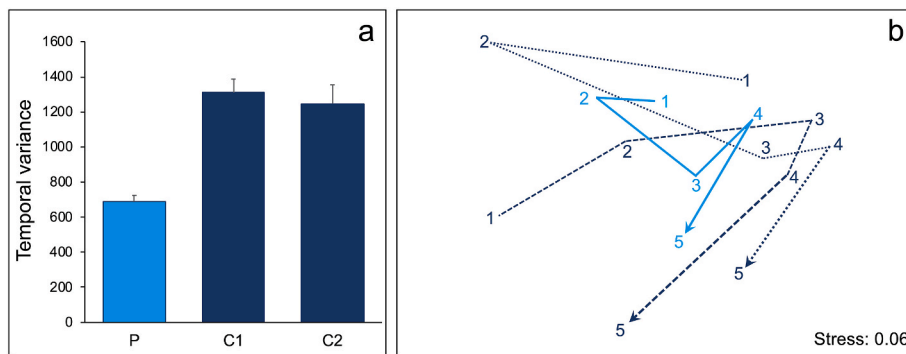
Fig. 1. (a) Non-metric multidimensional scaling ordination (nMDS) based on Bray–Curtis dissimilarities of Ti × Lo centroids, with temporal trajectories. P = light blue solid line; C1 = dark blue dotted line; C2 = dark blue dashed line. Numbers indicate years of sampling. (b) Mean value ± SE (n = 3) of multivariate variance component associated to factor Time (see text for details) for the three locations. T1 = 2001, T2 = 2002, T3 = 2016, T4 = 2019, T5 = 2021. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3
Summary of asymmetrical ANOVAs testing for differences in the number of taxa and total cover of assemblages at the protected location (P) versus unprotected control locations (Cs). * = $p < 0.05$; *** = $p < 0.001$.

Source of variation	d.f.	No. of taxa		Total cover	
		MS	F	MS	F
Ti	4	54.2	2.76	2288.2	2.38
Lo	2	0.6	0.03	1377.6	1.48
Cs	1	1.0	0.63	462.9	0.48
P-vs-Cs	1	0.2	0.01	2292.0	2.39
Si(Lo)	6	7.8	0.60	322.6	0.62
Si(Cs)	4	8.4	0.63	128.8	0.34
Si(P)	2	6.8	0.79	710.1	0.89
Ti × Lo	8	19.6	1.50	960.5	1.85
Ti × Cs	4	17.5	1.14	1613.5	**4.23***
Ti × P-vs-Cs	4	21.7	1.66	307.4	0.19
Ti × Si(Lo)	24	13.1	**3.10***	519.5	**3.34***
Ti × Si(Cs)	16	15.3	**3.73***	381.5	**2.91***
Ti × Si(P)	8	8.6	1.96	795.5	**3.89***
Res	405	4.2	155.5		
Res Cs	270	4.1	131.1		
Res P	135	4.4	204.5		

Table 4
Relative contribution of taxa to the overall temporal variance of assemblages at C1 and C2. Only taxa whose contribution was ≥5% at least for one of the two unprotected locations were considered.

Taxon	C1	C2
Turf algae	16%	20%
Peyssonnelia squamaria	20%	9%
Ellisolandia elongata	2%	14%
Jania rubens	9%	10%
Dictyota spp.	10%	5%
Encrusting Rhodophytes	7%	2%
Cumulative contribution	64%	60%

protection (Table 5, Fig. 2d and e).

4. Discussion

Full protection within the no-take zone did not cause noticeable changes in the average structure of sessile assemblages. They were comparable between P and Cs and were dominated by sciaphilic turf and small erect algae, with the presence of several invertebrate taxa that are typical of dim light conditions or tolerant to high sediment load (e.g., *Tethya aurantium* (Pallas, 1766), *Aplysina aerophoba* (Nardo, 1833)), reflecting the overall environmental situation of high turbidity and high sedimentation rates that characterized the region. Nevertheless, full protection seemed to exert a significant effect in reducing the magnitude of temporal variations of protected assemblages with respect to what occurred in the unprotected areas. A few taxa of macroalgae mostly contributed to such differences in temporal stability between P and Cs, explaining about 2/3 of the overall temporal variance of unprotected assemblages. The disproportionate influence of these taxa on temporal variance, which could have masked the contribution of other organisms, could be due to the fact that they encompassed several species which have been collapsed due to the intrinsic difficulty of identification from photographic samples. On the other hand, it is not surprising that this small group of taxa was the main driver of temporal variations as they were the dominant components of sessile assemblages on shallow subtidal reefs in the area, accounting for >60% of the total cover in all sampling locations. The lack of data from 2003 until 2015 might have also limited the quantification of temporal trajectories during the first decade of the study, and could have led to overestimate the temporal variations of unprotected assemblages (or the opposite for protected assemblages). However, it is worth noting that large temporal variations occurred even between subsequent times of sampling (e.g., between 2001 and 2002 for C1, or between 2019 and 2021 for C2, Fig. 1), indicating that the magnitude of fluctuations could not necessarily be related to the time elapsed among sampling occasions.

Above all, the results of this study support the assumption that protection may also affect the emergent properties of protected marine communities, including their ability to absorb disturbance (Babcock et al., 2010; Aller et al., 2017; Roberts et al., 2017), irrespective of
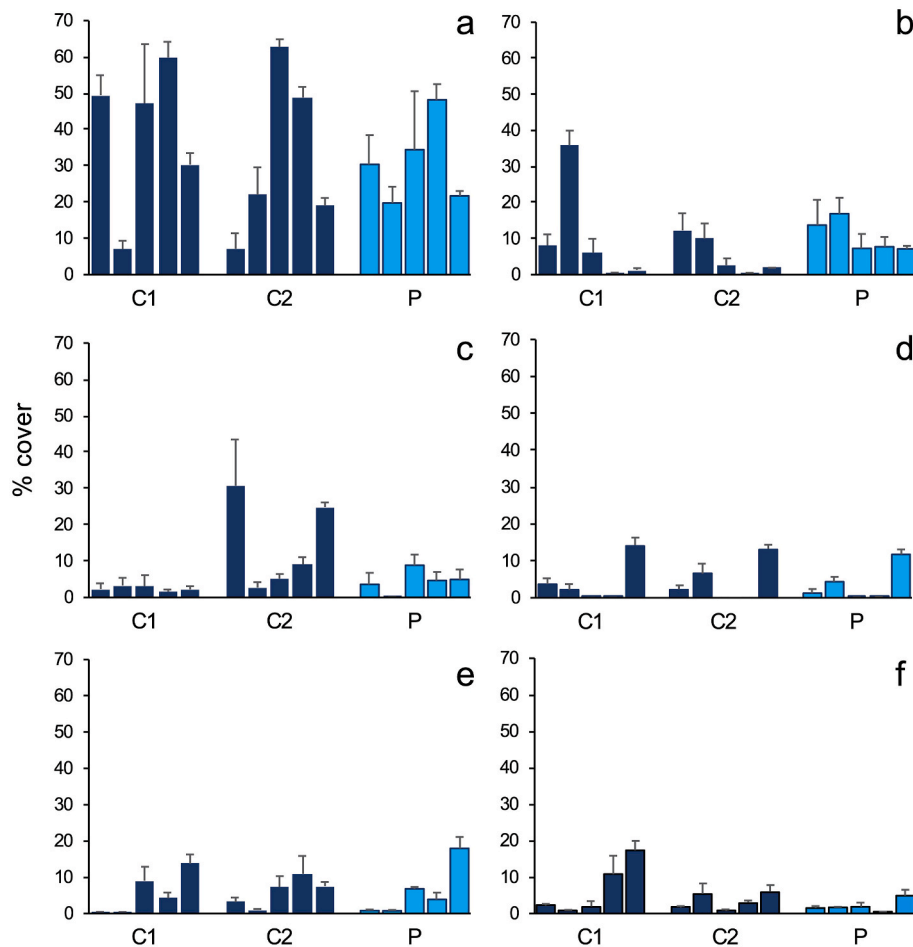
Table 5
Summary of ANOVAs testing for temporal variations in the percentage cover of taxa that mostly contributed to variance components associated to factor Time at unprotected locations (C1 and C2), and for the same taxa at the protected location (P). Significant results are given in bold. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

	P		C1		C2	
	MS	F	MS	F	MS	F
Turf algae	78.77	1.39	616.38	**8.97***	2.62	**9.60***
Peyssonnelia squamaria	60.71	1.09	645.33	**26.67***	2.27	**5.04***
Ellisolandia elongata	1.55	0.25	1.44	0.14	470.24	**4.58***
Jania rubens	72.81	**24.94***	104.87	**19.95***	4.10	**29.32***
Dictyota spp.	3.10	**20.47***	3.61	**11.62***	1.34	**4.19***
Encrusting Rhodophytes	8.44	3.28	155.90	**7.48***	15.91	2.26

Fig. 2. Mean percentage cover ±SE ($n = 3$) of taxa mostly contributing to temporal variance at unprotected locations *C1* and *C2*. Values for the protected location *P* were also showed for comparison. Histogram bars for each location referred to the five years of sampling from the oldest (2001) to the latest (2021). (a) Turf algae, (b) *Peyssonnelia squamaria*, (c) *Ellisolandia elongata*, (d) *Jania rubens*, (e) *Dictyota* spp., (f) Encrusting Rhodophytes.

changes on their structure. This potential outcome of protection has been poorly studied, especially in the benthic realm, where most research has focused on the effect of MPAs in increasing the size or abundance of target macroinvertebrates like scallops, lobsters, and sea urchins (Halpern, 2003; Sciberras et al., 2013). At community level, common short-term analyses of macrobenthos intrinsically limit the chance to detect the effects of protection on temporal variability, and it may take a relatively long time for community-wide indirect effects of protection to become apparent (Babcock et al., 2010).

Studies in the Mediterranean Sea and elsewhere that have benefited of long-term monitoring data, as in our case, have provided a better understanding of the effects of protection on the resilience of macrobenthic communities. Full protection in the no-take zone of Mediterranean MPAs has been found to increase the stability of macrobenthic assemblages from different habitats, including the midlittoral *Cystoseira s.l.* fringe, shallow subtidal reefs, and seagrass beds, suggesting that MPAs can play a role in strengthening the resistance of marine communities to environmental instability and mitigating human pressures acting in the region (e.g., Fraschetti et al., 2013). Manipulative experiments, testing for the response to physical disturbance of sessile assemblages from Mediterranean shallow rocky reefs within and outside a no-take zone, demonstrated that protected assemblages recovered more than six times faster with respect to those in unprotected reefs (Bevilacqua et al., 2006). Evidence from coral reefs emphasized the effect of MPAs in improving community resilience acting both on the resistance and recovery components, showing that reef community structure was more stable, the magnitude of impacts was lower, and subsequent

recovery was faster in protected than in unprotected areas (Mellin et al., 2016).

Different processes, directly or indirectly related to protection, could determine the enhanced response of protected communities against human impacts and environmental variations. MPAs can often lead to an increase in species diversity of protected assemblages (Blowes et al., 2020; Ferreira et al., 2022), which in turn could support temporal stability through increased interspecific facilitation (Cardinale et al., 2002), or due to the 'sampling effect' (Hooper et al., 2005), as highly-diverse assemblages could have more chance to include species able to tolerate environmental variations or persist under different regimes of disturbance. However, these mechanisms imply substantial changes in community composition and diversity induced by protection, which were not detected in the present study. The number of taxa of sessile assemblages in protected and unprotected areas were comparable over twenty years of monitoring, at least at the taxonomic resolution allowed by the photographic sampling, suggesting that factors other than diversity-stability relationships could underlie the observed differences in patterns of temporal variability between *P* and *Cs*.

The lack of significant effects of MPAs in modifying species composition and relative abundances of assemblages does not exclude stabilizing effects of protection against disturbance, whether natural or anthropogenic. For example, increased temporal stability of communities within no-take areas may arise as most direct sources of anthropogenic pressure (e.g., fishing, boating, diving, anchoring) are excluded, so that the higher level of cumulative human disturbance outside their boundaries could make unprotected communities more vulnerable to

environmental or to pulse episodes of environmental stress (Aller et al., 2017). The exclusion of fishing practices in no-take areas, and more generally their regulation within MPAs, may lead to increased resilience of marine communities by preserving the functioning of trophic networks (Shears and Babcock, 2002; Guidetti, 2006; Sala et al., 2012). In the Mediterranean Sea, seabreams of the genus *Diplodus*, such as *Diplodus sargus* (Linnaeus, 1758) and *Diplodus vulgaris* (Geoffroy Saint-Hilaire, 1817), might regulate population dynamics of main herbivores in shallow rocky reefs, namely the sea urchins *Paracentrotus lividus* (Lamarck, 1816) and *Arbacia lixula* (Linnaeus, 1758), by actively feeding on them, thus preventing the overgrazing of macroalgal stands (Sala et al., 1998). The depletion of these predator fish of high commercial value could disrupt, especially in overfished areas, the control exerted on sea urchin populations that, once released from predation, could experience an exceptional increase and overgraze macroalgal stands (Guidetti and Sala, 2007). These cascading effects can largely contribute to increasing the instability of macrobenthic assemblages outside MPAs generating spatial and temporal heterogeneity in their structure due to intermittent/reduced top-down control processes (Guidetti, 2006; Fraschetti et al., 2013).

The Northern Adriatic Sea has been traditionally exposed to intense fishing pressure, which has led to overexploiting fishery resources, and particularly demersal fish stocks (Giani et al., 2012; Bastardie et al., 2017). The MPA of Miramare is the unique marine reserve in the region and, despite its limited spatial extension, represents one of the best performing Italian MPAs in terms of enforcement and positive effects on fish assemblages (Guidetti et al., 2008). Reiterate assessments in the no-take zone of the MPA and in adjacent unprotected areas confirmed higher abundance and biomass of several fish species of commercial interest, and especially of sparids like *D. sargus*, *D. vulgaris*, *Sparus aurata* Linnaeus, 1758, and other top-predator fishes such as *Dicentrarchus labrax* (Linnaeus, 1758) (Guidetti et al., 2005a, 2008). The descriptive nature of the present study prevented inferences about cause–effect relationships behind the observed patterns, but the integrity of high trophic levels and associated top-down control on sea urchin grazing could have played a role in determining the temporal consistency of assemblages observed in the no-take zone in contrast to the large temporal variability that characterized assemblages at the unprotected locations. The alternate proliferation of turf algae and other, grazing-resistant, coralline algae, which was most responsible for these differences in temporal stability between *P* and *Cs*, provided further clues in this direction. In the last three years, sea urchins almost disappeared from the protected and unprotected reefs with populations showing signs of recovery only in 2021 (authors' personal observation). Previous assessments in the same sampling locations of the present study (from 2002 until 2003) did not detect significantly higher densities of sea urchins (*P. lividus*) in unprotected reefs if compared to those in the no-take zone (with sea urchins ranging between 2 and 12 individuals/m^2), although a high temporal variability in sea urchin densities characterized the unprotected controls (Guidetti et al., 2005b). More recent surveys detected significant differences in age classes of sea urchin populations at *P* with respect to adjacent areas, with the former being dominated by small-sized juveniles and the latter by older and larger individuals (Favoretto and Tempesta, 2014), indicating a reduced survival until the adult stage in the protected reefs possibly due to higher predation rates. Wide temporal fluctuations of sea urchin populations in the whole region, therefore, were probably leveled within the MPA due to fish predation, reflecting into a reduced temporal variability of macroalgal stands at *P*. Differences in abundance of herbivorous fish between protected and unprotected areas could have also contributed to this pattern. The native salema *Sarpa salpa* (Linnaeus, 1758), for example, may exert intense grazing pressure representing a serious threat to Mediterranean macroalgal canopies (Gianni et al., 2017). However, available data did not provide strong evidence of changes in densities of *S. sarpa* between *P* and *Cs* during the period of study (Guidetti et al., 2005a; Savonitto et al., 2020), supporting the hypothesis that the grazing pressure of these

herbivores was consistent over the whole study area, irrespective of protection.

The cumulative effects of climate change and other human pressures are causing drastic changes in the structural components and disrupting regulative processes of marine ecosystems (Gissi et al., 2021), with delayed recovery and increased temporal variance being often the symptoms of the ensuing increased ecosystem fragility (Scheffer et al., 2012). Therefore, management tools able to reverse this trend are of paramount importance to reduce the risk of critical ecological transitions. Our long-term assessment highlighted the interannual persistence of a consistent structure of sessile assemblages within the no-take zone over twenty years. In contrast, unprotected areas experienced a major effect of environmental variations determining alternate dominance of different taxa, and larger fluctuations of assemblage structure in the whole period of monitoring. Such findings reinforce the idea that MPAs could substantially contribute to adaptive conservation strategies in the face of global change. Though MPAs alone cannot represent the one-fit-all solution to pressing environmental issues which are increasingly concerning Mediterranean marine ecosystems (Coll et al., 2012), we are still far from fully exploiting their potential within a systematic and integrated framework tailored to satisfy conservation needs from local to basin scale (Fraschetti et al., 2018). As first, marine space under full protection is still too limited and not representative of all biogeographic regions (Claudet et al., 2020), and the current purposes to extend the cover of protected areas should contemplate this unbalanced distribution (Kay and Butenschön, 2018), habitats deserving urgent interventions such as rocky reefs (Bevilacqua et al., 2021), and advancing the effectiveness of existing reserve networks (Katsanevakis et al., 2020), before setting future conservation priorities (Campbell and Gray, 2019). Secondly, since reserve boundaries cannot prevent all human-driven environmental alterations, understanding the role of protection in improving the resilience of marine ecosystems will be essential to ascertain whether, beyond mitigating the effects of small-scale direct human activities, MPAs might also provide an insurance against indirect and/or extensive human impacts which often escape the reach of local management actions.

CRediT authorship contribution statement

Stanislao Bevilacqua: Writing – original draft, Writing – Review & Edit, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Verdiana Vellani:** Investigation, Writing – original draft. **Paolo Fabbrizio:** Investigation. **Annalisa Falace:** Investigation, Writing – Review & Edit. **Saul Ciriaco:** Investigation, Writing – Review & Edit. **Marco Segarich:** Investigation. **Maurizio Spoto:** Investigation, Writing – Review & Edit.

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.

Data availability

Data will be made available on request.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2022.107946.

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