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RESEARCH ARTICLE

Does full protection count for the maintenance of β-diversity patterns in marine communities? Evidence from Mediterranean fish assemblages

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Abstract

1. Although it is widely recognized that protection may enhance size, abundance, and diversity of fish, its effect on spatial heterogeneity of fish assemblages and species turnover is still poorly understood.
2. Here the effect of full protection within a Mediterranean marine protected area on β-diversity patterns of fish assemblages along a depth gradient comparing a no-take zone with multiple unprotected areas is explored. The no-take zone showed significantly higher synecological parameters, higher β-diversity among depths, and lower small-scale heterogeneity of fish assemblages relative to unprotected areas.
3. Such patterns might likely depend on the high level of fishing pressure outside the no-take zone, as also abundance-biomass curves seemed to indicate. Results suggested that full protection could play a role in maintaining high β-diversity, thus reducing the fragility of marine communities and ecosystems, and spatial heterogeneity may represent a reliable predictor of how management actions could provide insurance against undesirable phase shifts.

KEYWORDS

coastal, conservation evaluation, ecological status, fish, fishing, marine protected area

1 | INTRODUCTION

Over recent decades, marine protected areas (MPAs) have been recognized as useful tools in mitigating human-driven changes to marine ecosystems (Bevilacqua, Terlizzi, Fraschetti, Russo, & Boero, 2006; Edgar et al., 2014; Halpern, 2003; Micheli & Halpern, 2005). They play an important role in contrasting biodiversity loss (Allison, Lubchenco & Carr, 1998), preventing the overexploitation of natural resources (Roberts, Bohnsack, Gell, Hawkins, & Goodridge, 2001; Rogers-Bennett, Haaker, Karpov, & Kushner, 2002) and enhancing fishery yields within and outside their boundaries (Alcala, Russ, Maypa, & Calumpong, 2005; Di Franco et al., 2012; Goñi et al., 2008).

Most evidence on the effectiveness of MPAs stems from quantitative assessments on fish populations (Claudet et al., 2008; Guidetti et al., 2014; McClanahan, Graham, Calnan, & MacNeil, 2007), owing to their rapid and direct response to protection, especially in no-take areas, leading to a general increase in size and abundance of fish (Claudet, Garcia-Charton, & Lenfant, 2011; Dugan & Davis, 1993; Guidetti, 2006; Halpern & Warner, 2002). The commercial or ecological relevance of many fish species, moreover, prioritizes the re-establishment of natural stocks as a conservation target, which, in turn, makes fish privileged descriptors of the effectiveness of MPAs (Guidetti, 2006).

The effects of protection on fish assemblages have often been assessed taking into account single response variables, such as density, biomass, or diversity (Claudet & Fraschetti, 2010; Claudet et al., 2008; Guidetti et al., 2008; Lester et al., 2009). Yet, community-wide assessments may provide a more comprehensive picture of the ecological outcomes of MPAs, as changes in the multivariate structure of communities reflect the integrated response of species to human disturbance and protection regimes (Guidetti & Sala, 2007; McClanahan, Davies, & Maina, 2005; Micheli, Halpern, Botsford, & Warner, 2004). Several studies on different ecological compartments, from benthos to fish, demonstrated significant differences in assemblage structure when comparing protected versus unprotected areas (Ceccherelli, Casu, Pala,

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Pinna, & Sechi, 2006; Fraschetti, Bevilacqua, Guarnieri, & Terlizzi, 2012; Micheli et al., 2005). Human impacts, in addition, are more likely to alter the spatial heterogeneity of assemblages, increasing or decreasing their spatial variability, rather than modifying exclusively their average structure (Fraschetti et al., 2001; Sandulli et al., 2004; Terlizzi et al., 2005; Warwick & Clarke, 1993). Therefore, it could be expected that protection could also play a role in maintaining natural patterns of spatial heterogeneity of assemblages by reducing the effects of anthropogenic disturbance on their spatial distribution.

The heterogeneity in the distribution of species composing assemblages within a given spatial extent reflects the β-component of species diversity (Anderson et al., 2011; Vellend, 2001). β-diversity was originally defined as the extent of change of community composition (Whittaker, 1960, 1972). Recently, it was also described as either species turnover or as non-directional variations in species composition (Anderson et al., 2011; Baeten et al., 2012). The first notion relates to directional changes in community composition from one position to another along any spatial, temporal or environmental gradient. The second notion, instead, considers variations occurring in community composition among a set of sample units within a given spatial, temporal, or environmental extent, without referring to any particular direction. Therefore, while β-diversity as turnover measures the extent of changes in species composition *between* two communities, β-diversity as variation measures the heterogeneity in species composition *within* communities (Bevilacqua, Plicanti, Sandulli, & Terlizzi, 2012).

β-diversity has a central role in tracking the relationships between local and regional diversity (Thrush et al., 2009; Witman, Etter, & Smith, 2004). It identifies biological and environmental factors structuring biogeographical gradients (Ellingsen, 2002) and, more generally, it highlights ecological processes that drive meta-community assembly (Baiser, Olden, Record, Lockwood, & McKinney, 2012; Thrush, Hewitt, Cummings, Norkko, & Chiantore, 2010). Measuring the spatial heterogeneity of assemblage structure may also provide useful insights into subtle mechanisms underlying ecological hetero−/homogenization related to anthropogenic activities (Balata, Piazzi, & Benedetti-Cecchi, 2007; Bevilacqua et al., 2012). Human impacts, in fact, could cause spatial homogeneity of assemblages and smooth natural environmental gradients by selecting a few dominant species that tolerate perturbed environmental conditions (Balata et al., 2007; Claudet & Fraschetti, 2010; Magurran, Dornelas, Moyes, Gotelli, & McGill, 2015), or could increase assemblage heterogeneity by creating a mosaic of disturbed patches (Fraschetti et al., 2001; Guarnieri, Terlizzi, Bevilacqua, & Fraschetti, 2012).

Quantifying patterns of spatial heterogeneity in assemblage structure is indispensable for guiding the siting and spacing of marine reserves (Margules & Pressey, 2000) in order to ensure an effective networking through adequate levels of complementarity among protected communities (Hewitt, Thrush, Halliday, & Duffy, 2005; Winberg, Lynch, Murray, Jones, & Davis, 2007).

Communities characterized by high β-diversity should be more resistant to disturbance, whether natural or anthropogenic, than others, acting as refuges from which neighbouring patches can be sustained (Soininen, 2010). In this respect, β-diversity has been proposed as a measure of ecological connectivity (de Juan, Thrush, & Hewitt, 2013; Thrush et al., 2009), thus providing an indication of the potential resilience of assemblages (Thrush et al., 2010). At the local scale, strong connectivity among patches could promote recovery after disturbance through supplementary inputs from the whole system (Scheffer et al., 2012). Several studies have documented the role of protection in enhancing the recovery trajectories of disturbed assemblages (Bellwood, Hughes, Folke, & Nyström, 2004; Bevilacqua et al., 2006; Micheli et al., 2004; Mumby et al., 2006), or in increasing their temporal stability (Fraschetti et al., 2012). However, despite the recognized importance of evaluating direct and indirect effects of protection in modifying patterns of spatial heterogeneity of marine assemblages (Benedetti-Cecchi et al., 2003; Charton & Ruzafa, 1999), very few attempts have been made in this direction (Fraschetti, Guarnieri, Bevilacqua, Terlizzi, & Boero, 2013; Guarnieri et al., 2012).

Here, the effects of full protection on the structure and spatial heterogeneity of fish assemblages within a Mediterranean MPA are assessed. Specifically, the response of fish assemblages associated with rocky reefs at different depths are investigated in order to test if: (i) full protection had an effect on the overall assemblage structure, total abundance and biomass, and species richness; (ii) patterns of change in assemblages along the investigated depth gradient were comparable between protected and unprotected areas; (iii) protected and unprotected assemblages exhibited different levels of spatial heterogeneity and if such patterns were consistent among depths.

2 | MATERIALS AND METHODS

2.1 | Study area

The MPA of Punta Campanella extends over 1300 ha, from the coastline to 55–60 m depth, around the distal part of the Sorrento peninsula between the Bay of Naples and the Bay of Salerno (Tyrrhenian Sea) (Figure 1). The MPA is embedded within a human-dominated environmental context with high levels of anthropogenic pressure on the whole coastal ecosystem (Bavestrello, Bo, Canese, Sandulli, & Cattaneo-Vietti, 2014; Cianelli et al., 2011).

The no-take zone considered in the present study, covering 21 ha, is located at about 0.7 nm from the coast around the emerging part of a carbonate pinnacle. A partial protected area (hereafter referred to as 'unprotected area'), where most human activities are allowed (fishing and diving included), surrounds the no-take zone (hereafter referred to as 'protected area'). Geo-morphological features of the rocky coast in the protected area are comparable with those characterizing the unprotected area. Both areas comprise submerged cliffs covered with pre-coralligenous assemblages alternating with rocky terraces dominated by macro-algal stands.

2.2 | Sampling design

Sampling was carried out between June and October 2008 on rocky cliffs within the only protected zone (P) in the Bay of Naples and within an unprotected zone (F) relatively close to the no-take zone (Figure 1). The no-take zone (island of Vervece) is a very small-emerged rock where it was not possible to define more than a single visual census sampling site. However, the unprotected zone is located along the more extended coastline of the Sorrento peninsula where six sampling sites

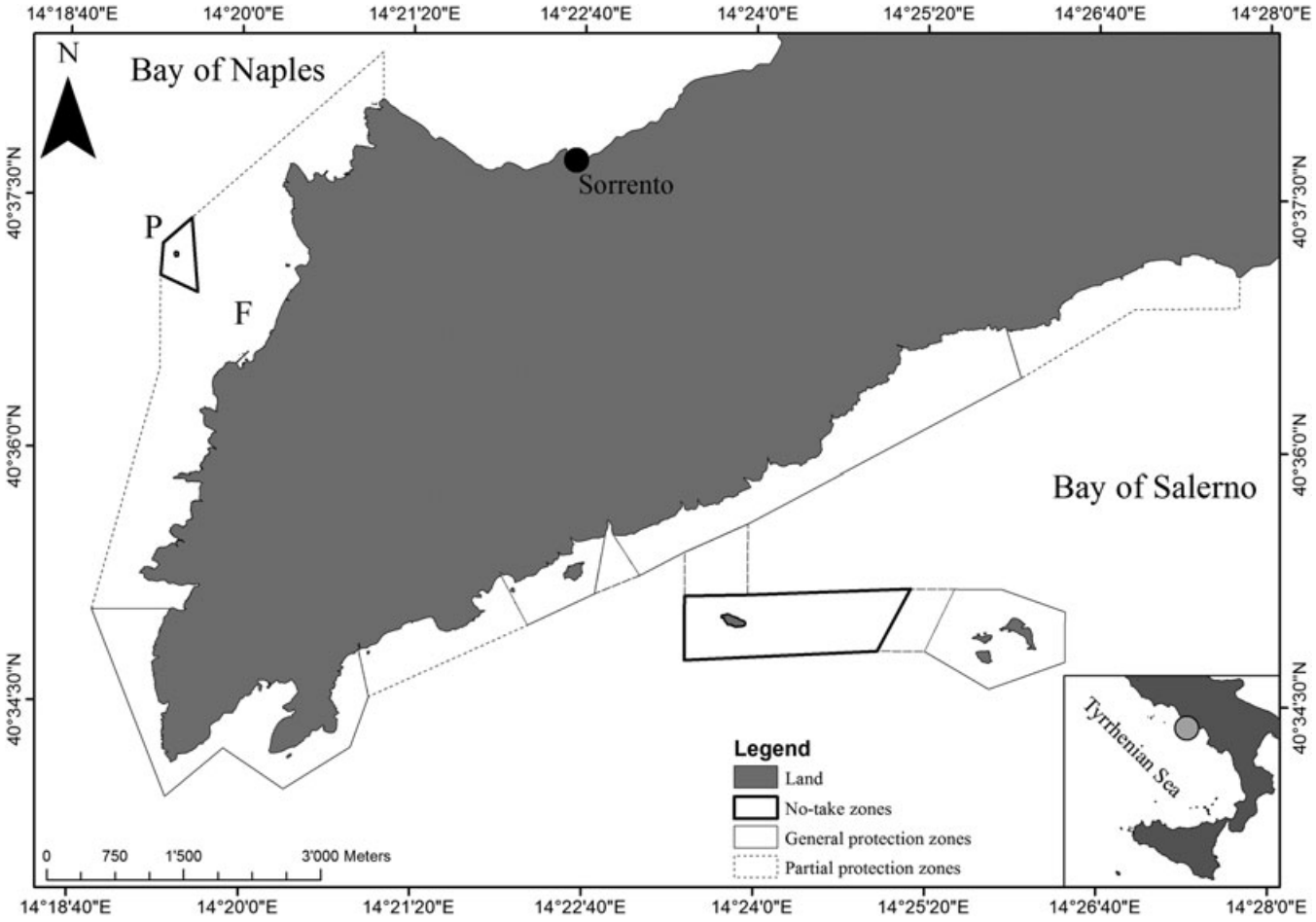

FIGURE 1 Punta Campanella MPA and location of study area with protected (P) and unprotected (F) sites

(F1, F2, F3, F4, F5, F6) were selected to detect possible differences in the fish assemblages of the rocky reefs of the unprotected zone.

At each site, fish assemblages were sampled at three depths (5 m, 10 m, 20 m). For each site and each depth, abundance of fish species and size of individuals were assessed along three strip transects, for a total of 63 sampling units. Fish species were assigned to seven ranks of abundance (1; 2–5; 6–10; 11–30; 31–50; 51–100; >101) according to La Mesa and Vacchi (1999), and three size categories (i.e. small, medium, large) based on the maximum total length attained by each species were used. Biomass of fishes was estimated using the population size-structure and length–weight relationship (Froese & Pauly, 2012).

Visual counts along strip transects (L = 25 m; W = 5 m; H = 5 m) according to standardized procedures (Harmelin-Vivien et al., 1985) were performed when the horizontal visibility was at least 2.5 m.

2.3 | Data analysis

A distance-based permutation multivariate analysis of variance (PERMANOVA; Anderson, 2001a) was carried out on density and biomass, in order to test for differences in assemblage structure imputable to protection. As sites in the unprotected area were spatially segregated, with three sites north and three sites south of the protected area, a preliminary analysis was carried out considering only unprotected sites in order to exclude confounding effects due to the different geographic position. The design for the analysis involved the factor Depth (De, fixed, three levels), Position (Po, two levels, fixed), and Site (Si(Po), random, three levels, nested in Po) with $n = 3$. No significant differences were detected for factor Position either analysing abundance or biomass of fish assemblages or all the investigated single response variables (see Results). This allowed testing for differences in fish assemblages related to protection by contrasting the single site within the protected area against all six sites from the unprotected area. In this case, the design for the analysis comprised three factors: Depth (De, fixed, three levels), Protection (Pr, fixed, two levels), and Site (Si(Pr), random, nested in Pr). As there was only one site within the protected area the design was asymmetrical (Glasby, 1997; Terlizzi et al., 2005).

Prior to analyses, fish density and biomass data were square root transformed (Guidetti et al., 2014) to reduce the weight of very abundant species. All multivariate analyses were based on Bray–Curtis similarity, and each term in the analysis was tested by 4999 random permutations (Anderson, 2001b; Anderson & Braak, 2003). Post hoc pair-wise comparisons using the PERMANOVA *t*-statistic and 4999 permutations were conducted if necessary. Multivariate patterns were visualized through nMDS ordination of De × Pr centroids. Permutation tests of multivariate dispersion (PERMDISP; Anderson, Ellingsen, & McArdle, 2006) based on Bray–Curtis similarity matrices were carried out for the interaction term De × Pr to investigate possible effects of protection on small-scale (among replicates) spatial heterogeneity of fish assemblages. Multivariate dispersion values were employed as a

measure of variation in β-diversity (Anderson et al., 2006) between protected and unprotected areas.

PERMANOVA based on Euclidean distance (Terlizzi, Anderson, Fraschetti, & Benedetti-Cecchi, 2007) was conducted on species richness, total abundance and total biomass of the whole assemblage, and abundance and biomass of target species (classified into two categories, namely commercial species and species with low commercial value), and non-target species. Species were assigned to different categories according to Froese and Pauly (2012). The design for analyses was the same as for multivariate analyses.

Finally, ABC curves (Warwick & Clarke, 1994) were employed to compare abundance-biomass relationships between protected and unprotected areas.

3 | RESULTS

Thirty-five fish taxa from 14 families were identified. Some taxa were recorded only in the protected area (i.e. *Sphyraena viridensis*, *Diplodus puntazzo*, *Muraena helena*).

PERMANOVA on data (abundance and biomass) from the unprotected area showed no significant effect of geographic position of sites. Also, no significant differences due to position were detected analysing all the investigated single response variables (Table 1). This allows us to test for differences in the contrast between the protected site versus all the unprotected sites.

PERMANOVA on fish abundance and biomass based on the full dataset detected a significant De × Pr interaction, indicating that differences in assemblage structure among depths varied between protected versus unprotected areas (Table 2).

Post hoc pair-wise comparisons from abundance data showed that, in the unprotected area, fish assemblages did not differ among depths. In contrast, in the protected area, the depth gradient was clear with assemblages differing at each depth. Patterns of difference in biomass among depths were consistent with those for abundance data for the protected area, whereas in the unprotected area, assemblages at 20 m differed from those characterizing the shallower depths (Table 2).

Such patterns were clearly depicted in the nMDS ordination plots of De × Pr centroids that also showed a clear separation of fish assemblages between protected and unprotected areas (Figure 2).

TABLE 2 PERMANOVA results for difference in abundance and biomass of fish assemblages between protected and unprotected areas. Pair-wise comparisons for differences in fish assemblages among depths in protected (Pr) and unprotected (F) areas are also reported. Significant tests relevant to the hypothesis are given in bold

Abundance					
Source	**df**	**SS**	**MS**	**Pseudo-*F***	***P*(perm)**
De	2	5812.5	2906.3	41.559	
Pr	1	10571.0	10571.0	20.877	
Si(Pr)	5	25317.0	5063.5	12.616	
De × Pr	2	2676.0	1338.0	19.133	**0.023**
De × Si(Pr)	10	6993.1	699.3	17.424	0.003
Res	42	16857.0	401.3		
Total	62	69761.0			
	Within F		**Within Pr**		
Groups	***t***	***P***	***t***	***P***	
5 m - 10 m	1.436	0.099	2.135	**0.048**	
5 m - 20 m	26.921	0.108	36.511	**0.005**	
10 m - 20 m	19.547	0.252	29.298	**0.011**	
Biomass					
Source	**df**	**SS**	**MS**	**Pseudo-*F***	***P*(perm)**
De	2	10933.0	5466.4	41.889	
Pr	1	21824.0	21824.0	27.247	
Si(Pr)	5	40047.0	8009.5	10.176	
De × Pr	2	7165.0	3582.5	27.452	**0.004**
De × Si(Pr)	10	13050.0	1305.0	1.658	0.001
Res	42	33057.0	787.1		
Total	62	128000.0			
	Within F		**Within Pr**		
Groups	***t***	***P***	***T***	***P***	
5 m – 10 m	15.401	0.067	27.482	**0.015**	
5 m – 20 m	25.466	**0.011**	26.376	**0.015**	
10 m – 20 m	19.346	0.054	27.294	**0.011**	

Results of PERMDISP showed a greater small-scale heterogeneity of fish assemblages in unprotected areas with respect to the protected area at each of the investigated depths (Figure 3; Table 3), whereas multivariate dispersion did not differ significantly along the depth gradient in both areas.

TABLE 1 Summary of results of PERMANOVA tests for differences related to geographic position in fish assemblages and single response variables. Only tests relevant to the hypothesis were reported; De × Po = interaction between Depth (De) and Position (Po) (see Method section for further details)

	De × Po		**Po**	
	Pseudo-*F*	***P***	**Pseudo-*F***	***P***
Fish assemblages (abundance data)	0.6	0.791	1.1	0.402
Fish assemblages (biomass data)	0.7	0.716	1.1	0.379
Species richness	4.2	0.060	1.3	0.317
Total abundance	4.3	0.060	4.1	0.111
Total biomass	0.8	0.549	3.2	0.135
Total abundance target species	1.9	0.220	1.3	0.305
Total biomass target species	0.4	0.677	0.8	0.407
Total abundance non-target species	1.2	0.346	0.1	0.819
Total biomass non-target species	0.8	0.509	2.0	0.221

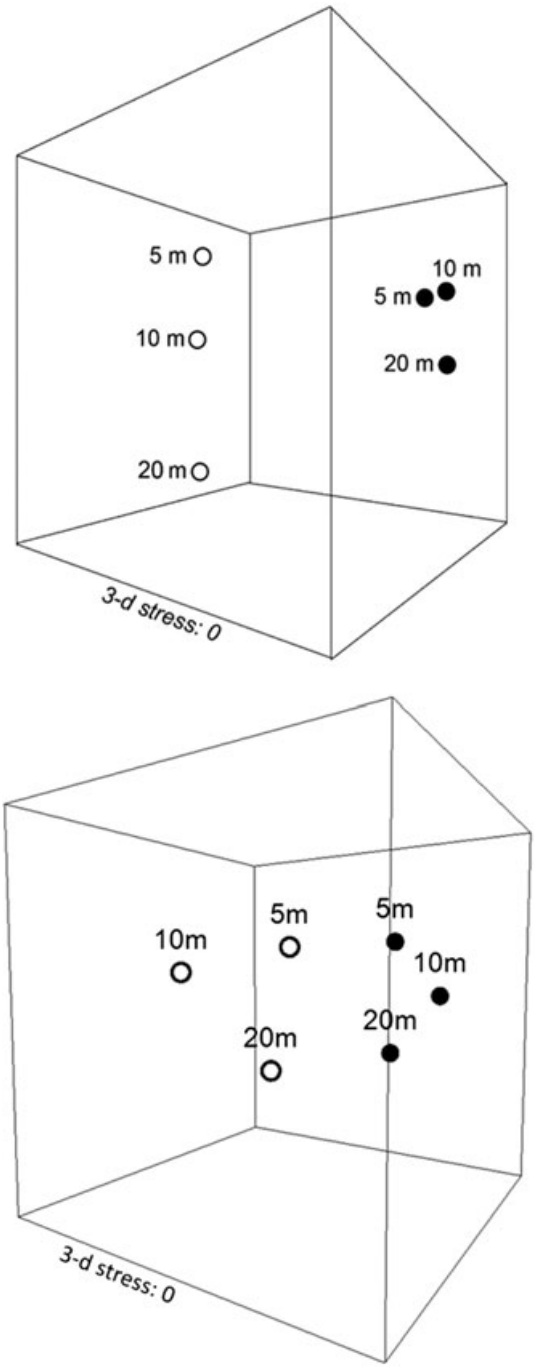

FIGURE 2 3-d nMDS plot of DexPr centroids for abundance (a) and biomass (b). White circles = protected area, black circles = unprotected areas. Depths are also indicated (5 m, 10 m, 20 m)

PERMANOVA on species richness, total abundance and total biomass detected a significant De × Pr interaction for all the investigated variables (Table 4). However, pair-wise tests showed higher species richness, total abundance, and total biomass comparing protected versus unprotected areas at each depth (Figure 4).

PERMANOVA on total abundance of target species detected a significant De × Pr interaction (Table 4) and subsequent pair-wise comparisons showed a significantly higher abundance of target species in the protected area with respect to unprotected areas at 5 m and 10 m but not at 20 m (Figure 5). Similar results were obtained when analysing total biomass of target species, although significantly higher

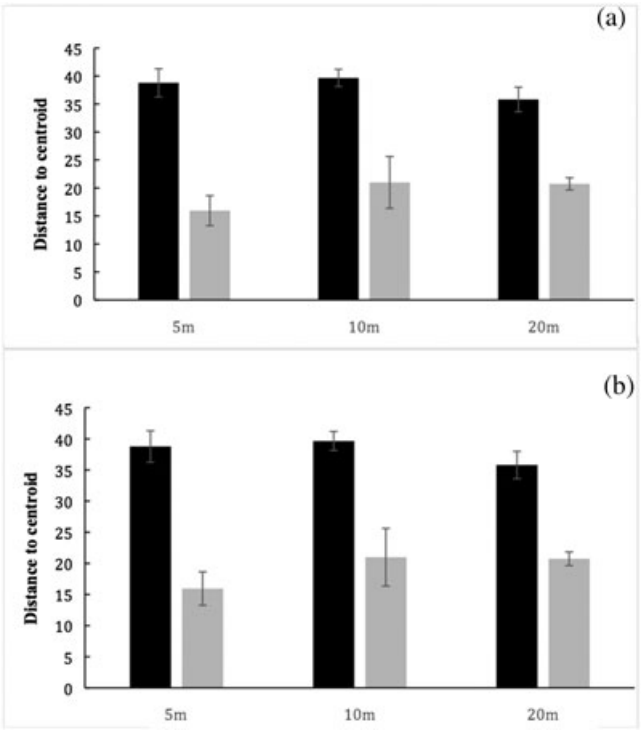

FIGURE 3 Mean (±SE, *n* = 3) multivariate dispersion of replicates around De × Pr centroids calculated on abundance (a) and biomass (b) data for unprotected (black bars) and protected (grey bars) areas

TABLE 3 Results of test for differences in multivariate dispersion (PERMDISP) between protected (Pr) and unprotected (F) areas for abundance and biomass data at different depths

Abundance			Biomass		
F	*P*		*F*	*P*	
9.5718	0.0002		7.7374	0.0004	
Pair-wise comparisons					
	t	*P*		*t*	*P*
5 m Pr – 5 m F	41.724	0.001	5 m Pr – 5 m F	35.775	0.002
10 m Pr – 10 m F	45.705	0.002	10 m Pr – 10 m F	44.725	0.010
20 m Pr – 20 m F	29.414	0.019	20 m Pr – 20 m F	27.317	0.020

biomass of target species characterized the protected area at each of the depths considered (Figure 5). No significant differences between protected versus unprotected areas were recorded for both total abundance and biomass of non-target species (Table 4).

The ABC curves showed that the abundance curve was above the biomass curve (W = −0.067) in fished areas, whereas the opposite occurred in the protected area (W = 0.318), indicating a typical pattern of stressed condition of fish assemblages in the unprotected area (Figure 6).

4 | DISCUSSION

The structure of fish assemblages differed significantly in abundance or biomass for protected and unprotected areas. These results demonstrate the potential of full protection to significantly increase diversity, number and size of individuals of fish species as shown in several other

TABLE 4 Summary of results of PERMANOVA tests (see text for details) for species richness, total abundance and total biomass of fish assemblages, and for total abundance and biomass of target and non-target species. Significant tests relevant to the hypothesis are given in bold

	De × Pr		Pr	
	Pseudo-*F*	*P*	Pseudo-*F*	*P*
Species richness	4.7	**0.040**		
Total abundance	8.6	**0.015**		
Total biomass	5702.8	**0.000**		
Total abundance target species	56.4	**0.001**		
Total biomass target species	83400.0	**0.000**		
Total abundance non-target species	2.1	0.170	1.5	0.150
Total biomass non-target species	0.2	0.747	0.1	0.283

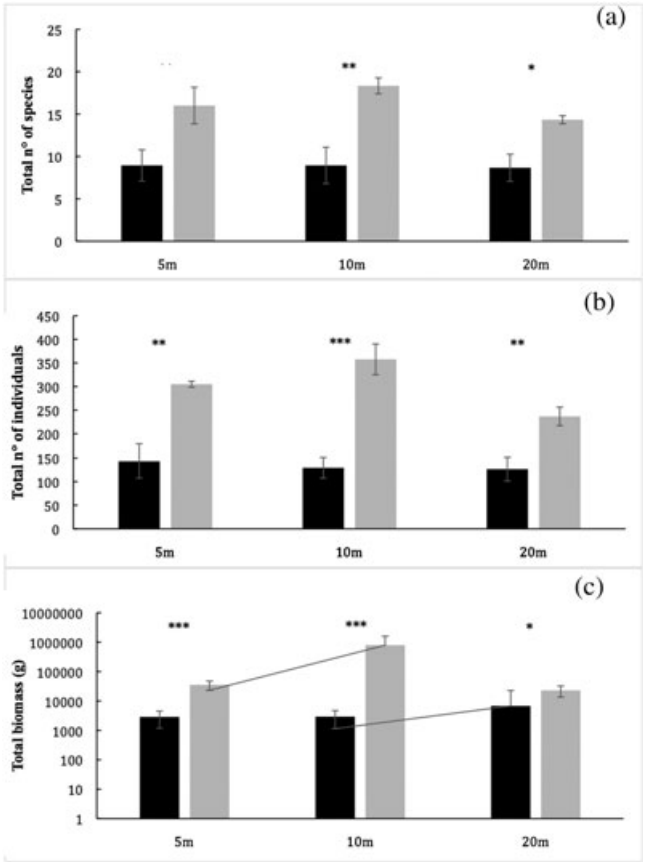

FIGURE 4 Mean (±SE, *n* = 6) values of (a) species richness, (b) total abundance (no. of individuals), and (c) total biomass (log scale) of fish assemblages for each depth in protected (grey bars) and unprotected areas (black bars). Results of pair-wise tests are also reported.
* = *P* < 0.05; ** = *P* < 0.01; *** = *P* < 0.001

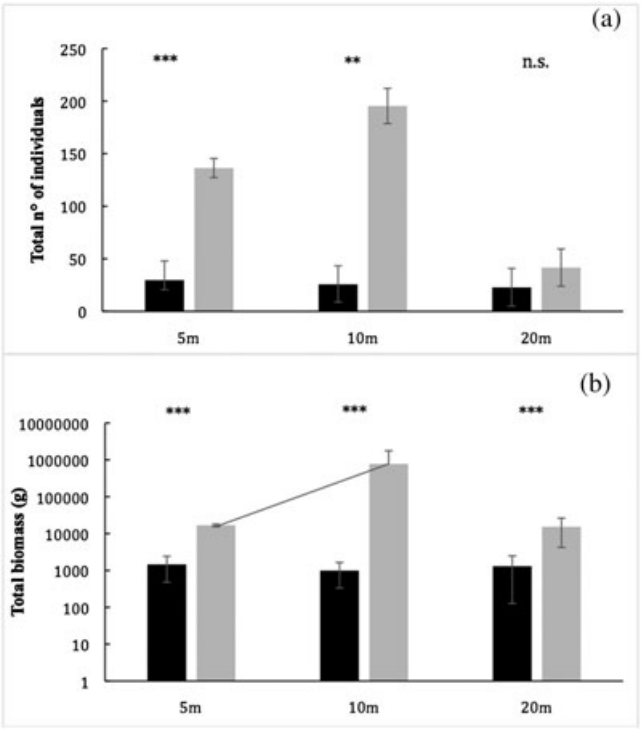

FIGURE 5 Mean (±SE, *n* = 6) values of (a) total abundance (no. of individuals) and (b) total biomass (log scale) of target species for each depth in protected (grey bars) and fished areas (black bars). Results of pair-wise tests were also reported. n.s. = not significant; ** = *P* < 0.01; *** = *P* < 0.001

studies (Denny & Babcock, 2004; Di Franco, Bussotti, Navone, Panzalis, & Guidetti, 2009; Floeter, Halpern, & Ferreira, 2006; García-Charton et al., 2004; Halpern, 2003; Harmelin-Vivien et al., 2008; Lester et al., 2009; Seytre et al., 2013). It could be argued that the observed differences between the protected and unprotected areas might depend on the insular nature of the protected site with respect to the unprotected sites on the mainland, since isolated spots of hard substrates could serve as attractors for fish (Cresson, Ruitton, & Harmelin-Vivien, 2014; Scott, Smith, Lowry, Taylor, & Suthers, 2015). However, the abundance-biomass curves highlighted highly stressed conditions in unprotected assemblages (Yemane, Field, & Leslie, 2005), suggesting that the observed differences between protected and unprotected areas are human-driven (Matić-Skoko et al., 2011; Penczak & Kruk, 1999). Moreover, differences between protected and unprotected areas were mostly driven by changes in abundance and biomass of commercial species, such as large predators (e.g. *Diplodus puntazzo*, *Epinephelus marginatus*, *Sphyraena viridensis*), whereas non-target fish were almost unaffected by protection. The removal of large individuals from target populations is a typical outcome of intense fishing activities (Erzini et al., 2006; Pelletier et al., 2005), indicating that the high fishing pressure outside the no-take area (Bavestrello et al., 2014; Sbrescia, Di Stefano, Russo, & Russo, 2008, 2010) is likely responsible for the observed patterns, over and beyond site-specific natural variations (e.g. isolation, geomorphology) between protected and unprotected areas.

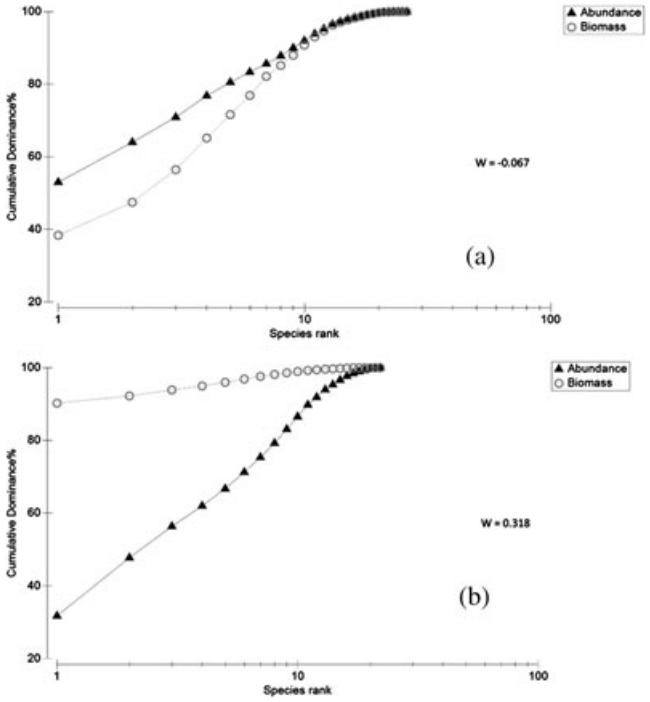

FIGURE 6 Abundance-biomass curves for unprotected (a) and protected (b) areas

In the MPA of Punta Campanella, fishing activity is allowed within 6 nautical miles from the coast only to local fishermen, and by means of <10 GT boats. The most widely used gears are long-lines and gill nets that allow the capture of pelagic and demersal species (Sbrescia et al., 2008, 2010), most of which are large top predators (Lloret, Zaragoza, Caballero, & Riera, 2008; Pauly et al., 2002; Planque et al., 2010). These species are frequently the most susceptible to fishing (Babcock et al., 2010; Pauly et al., 2002; Perry et al., 2010), and consequently respond positively to protection (Babcock et al., 2010; Bianchi & Morri, 2000; Halpern, 2003; Harmelin, Bachet, & Garcia, 1995). Although long-lines and gill nets are generally considered as highly selective gears (Stobart et al., 2009 and references therein), they also catch numerous by-catch species. Therefore, the high intensity of fishing in the area (Sbrescia et al., 2008, 2010) could have also had more subtle direct and indirect effects on spatial patterns of the whole fish assemblage (Farina et al., 2008; Griffin, Pearce, & Handy, 2012; Marriott, Latchford, & McCarthy, 2010; Sala & Lucchetti, 2010), including changes in small-scale heterogeneity.

In the absence of strong sources of human disturbance, habitat type and related environmental features are among the main factors structuring fish assemblages (Brokovich, Baranes, & Goren, 2006; Lara & González, 1998; McGehee, 1994; Wantiez & Chauvet, 2003), determining their species composition and trophic structure (Carpenter, Miclat, Albaladejo, & Corpuz, 1981; Friedlander & Parrish, 1998; Meekan, Steven, & Fortin, 1995; Nanami & Nishihira, 2002). In such context, spatial distribution of fish assemblages largely reflects local environmental gradients (Hewitt et al., 2005), and well-structured associated patterns of distribution of fish species can be considered as a feature of good ecological conditions (Becker, Levin, Fodrie, & McMillan, 2007; Caley et al., 1996; Levin & Talley, 2002; Lundquist et al., 2006). In the no-take zone, fish assemblages were distinct at each depth, although assemblages at 10 m depth seemed to have an intermediate structure. At this depth the highest number of species was recorded, composed of a combination of those species found at 5 m and 20 m; it represents a mid-point for the increase of Labridae and Serranidae, and for the decrease of Sparidae and Pomacentridae abundances and, thus, is a transition zone between shallow and deeper assemblages due to the mid-domain effect (Colwell & Lees, 2000, Connolly, Bellwood, & Hughes, 2003; Zapata, Gaston, & Chown, 2003, 2005). In contrast, assemblages in unprotected areas showed comparable structure among depths, indicating disruption of the natural depth gradient as a likely result of fishing pressure.

Results also showed the potential of fishing pressure to significantly increase small-scale heterogeneity (patchiness) of assemblages. Several studies have outlined increased heterogeneity of assemblages as a result of human disturbance (Balata et al., 2007; Bevilacqua et al., 2012; Claudet & Fraschetti, 2010; Warwick & Clarke, 1993). This phenomenon could be seen as a symptom of reduced ecological connectivity in the system (Scheffer et al., 2012; Thrush et al., 2010), which in turn might increase the fragility of the whole system (Fernandes et al., 2005; Steneck et al., 2009; Terlizzi et al., 2005; Thrush et al., 2009), leading to reduced resilience potential (Mellin, Bradshaw, Fordham, & Caley, 2013) and increased probability of phase shifts (Andersen, Carstensen, Hernandez-Garcia, & Duarte, 2009; Anderson & Thompson, 2004; Bevilacqua et al., 2012; Underwood, 1991). Moreover, reduced species richness in unprotected areas might further increase the vulnerability of fish assemblages to environmental changes due to reduced functional redundancy (Guillemot, Kulbicki, Chabanet, & Vigliola, 2011; Micheli & Halpern, 2005).

Resilience capacity is always the result of interactions between species (dominance, inhibition or facilitation), extrinsic factors (e.g. colonist supply and environmental setting) (Dayton, 1989; Thrush et al., 2009) and history of environmental exploitation (Jackson et al., 2001; Lotze & Milewski, 2004; Thrush, Halliday, Hewitt, & Lohrer, 2008). Full protection, through the exclusion of all direct forms of human disturbance, particularly fishing, may have important consequences for the dynamic properties of fish assemblages, such as their ability to persist and absorb fluctuations, by increasing their diversity and homogeneity in space (Holyoak, Leibold, Mouquet, Holt, & Hoopes, 2005). In unprotected areas, the exclusion of large predators and spawners, instead, may profoundly erode the resilience potential of the whole system (Hughes, Bellwood, Folke, McCook, & Pandolfi, 2007; Nyström, Folke, & Moberg, 2000), as a consequence of reduced diversity and disrupted top-down control (Guidetti, 2006; Levine, 1976; Mumby et al., 2006; Sala et al., 2012; Vandermeer, 1980).

Several studies highlighted the role of MPAs in enhancing the temporal stability and recovery trajectories of protected assemblages (Bevilacqua et al., 2006; Fraschetti et al., 2013; Hughes et al., 2007), and understanding how protection may affect such properties of marine communities represents a critical focus of future research in these systems (Mumby & Harborne, 2010). These results suggest that underlying mechanisms could include the potential for protection to mitigate the effects of human disturbance on species turnover along natural environmental gradients and on spatial heterogeneity of assemblages. In this respect, β-diversity may play an important role as a good predictor of how management actions could translate into

an increased ability of communities and ecosystems to escape regime shifts and reverse undesirable trends.

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