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Evaluating effects of total and partial restrictions to fishing on Mediterranean rocky-reef fish assemblages

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ABSTRACT: Fish assemblages were assessed by visual census in sublittoral rocky reefs at the Tavolara-Punta Coda Cavallo Marine Protected Area (TMPA; Mediterranean Sea) and compared among locations characterised by different protection levels: no-take/no-access zones, 2 types of partial protected areas (PPAs, where professional and recreational fishing are regulated in different ways) and locations outside the TMPA. Fish assemblage structures evaluated on abundance data did not differ among different protection levels, while no-take/no-access zones clearly differed from the rest when data were expressed as biomass. Biomass of many target species was higher in no-take/no-access zones mostly due to greater fish size rather than density. For some fish (e.g. the dusky grouper *Epinephelus marginatus*), however, both greater density and larger size contributed to the greater biomass in no-take/no-access zones. No differences were found between the 2 types of PPAs, and between PPAs and the locations outside the TMPA, in terms of assemblage structures, and in density, size and biomass of target species. These results suggest the need to (1) improve management in PPAs or re-think their role, and (2) quantitatively assess pressure of both professional and recreational fishing operating within and adjacent to MPAs. This will allow MPAs to set up proper regulations (e.g. limiting professional or recreational fishermen, number and type of gears), and achieve the best balance between ecological targets and reduction of conflicts among different categories of marine resource users.

KEY WORDS: Marine protected areas · Fishing regulation · Fish assemblages · Partially protected areas · Visual census · Mediterranean Sea

INTRODUCTION

Many studies have reported on the ecological effects of marine protected areas (hereinafter MPAs) in terms of population or community recovery from overfishing (Sala et al. 1998, Halpern & Warner 2002, Claudet et al. 2006, Guidetti & Sala 2007), and benefits for fisheries (Westera et al. 2003, Harmelin-Vivien et al. 2008, White et al. 2008). Effective MPAs usually harbour more diverse fish assemblages, and more abundant and larger fishes than fished areas (Halpern 2003, Claudet et al. 2006). Species targeted by fishing generally respond to protection in a positive way compared to non-target species (Micheli et al. 2005, Claudet et al. 2006, Floeter et al. 2006, Guidetti & Sala 2007). In addition, protection from fishing can indirectly influence whole community structures and ecosystem functioning via trophic interactions (Sala et al. 1998, Micheli et al. 2005). Ecological responses to protection can be associated with economic and socio-cultural benefits of MPAs to local human communities (Costa-Neto 2000). Such successful achievements depend on enforcement, design and management of MPAs (Claudet et al. 2008, Guidetti et al. 2008).

In the Mediterranean basin approximately 100 MPAs have been established so far (Abdulla et al. 2008). Their ecological effectiveness is typically assessed by contrasting no-take reserves to areas open to fishing (Guidetti & Sala 2007), similar to most empirical assessments conducted in other regions of the world

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(Halpern 2003, Micheli et al. 2004). 'No-take reserves' are usually areas where any extractive activity is forbidden, while the term 'MPA' defines sectors of the coastline and/or sea where human activities, particularly fishing, are regulated but not necessarily totally banned. From this perspective, MPAs in Italy and in other Mediterranean countries are usually divided into subareas regulated by different protection regimes, i.e. sectors integrally protected (no-access/no-take zones) and sectors (often called 'buffer zones') where fishing and other human activities are allowed but restricted/regulated compared with areas outside the MPAs (Francour et al. 2001). The need for buffer zones around no-access/no-take reserves is attributable to the fact that the Mediterranean basin is one of the most crowded areas of the world, where human populations and related activities are concentrated in coastal areas (Airoldi & Beck 2007), and where some categories of users and stakeholders would consider no-take/no-access reserves as a contentious management option (Lester & Halpern 2008). Partially protected areas (PPAs), therefore, can be a compromise between conservation needs and human uses (Denny & Babcock 2004, Shears et al. 2006, Lester & Halpern 2008) in coastal regions where activities from different categories of users are to be harmonised. Little information, however, is available about the ecological effects of PPAs (Denny & Babcock 2004, Shears et al. 2006, Lester & Halpern 2008 and references therein). Recent studies provided increasing evidence that PPAs may attract and concentrate both professional and recreational fishermen (Stelzenmuller et al. 2007, Lloret et al. 2008) with consequent non-negligible impacts on local fish stocks (Westera et al. 2003, Cooke & Cowx 2006, Lewin et al. 2006, Lloret et al. 2008). Due to such potential increase of fishing pressure in buffer zones (Westera et al. 2003, Denny & Babcock 2004), there is a need to better assess the role of PPAs as conservation tool.

The aim of this study, therefore, is to assess the effects of different levels of protection from fishing on fish assemblages in a Mediterranean MPA, comparing potential descriptors of ecological effects among 4 zones with different fishing regulations.

MATERIALS AND METHODS

Study area. This study was carried out at the Tavolara-Punta Coda Cavallo MPA (hereafter TMPA; 40° 35′ N, 09° 49′ E) located in north-east Sardinia (Italy). The MPA was established in 1997 but enforcement became effective around 2003-04. The TMPA includes 76 km of coastline, covers 15 357 ha, and is divided into various subareas characterised by different levels of protection. Such subareas are designated (according to Italian law) Zone A (integral reserves = no-take/no-access zone: 529 ha), Zone B (partial reserves: 3113 ha) and Zone C (general reserve: 11 715 ha) (Fig. 1). Access to Zone A is restricted to scientists, reserve personnel and police authorities (e.g. coast guard). In Zone B only local professional fishermen (i.e. those that are formally resident in coastal villages within the MPA) are allowed to fish (at the TMPA most of them use trammel/gillnets and longlines; Bianchi & Morri 2006) and only professional fishermen are permitted to sell their catches (or products thereof). In Zone C, both professional and regulated recreational fishing are allowed, with the exception of spearfishing. Outside the MPA, fishing regulations are less restrictive compared to regulations within the MPA (e.g. spearfishing is allowed).

Sampling design and data collection. Sampling was done in Zones A, B, and C of the TMPA and in external zones (EXT: outside the TMPA; Fig. 1). For each zone, 2 locations (separated by 5 to 10 km) were chosen: Tavolara (A1) and Molarotto (A2) (Zone A); Capo Ceraso (B1) and Molara (B2) (Zone B); Monte Pedrosu (C1) and Capo Coda Cavallo (C2) (Zone C); Capo Figari (EXT1) and Capo Ceraso (EXT2) (Zone EXT). In each location 2 sites (separated by ~100 m) were randomly selected where 4 replicates (i.e. visual census transects) were performed at 2 different depth intervals (5–10 m and 12–18 m). Sampling was repeated in 4 periods (September–October 2005, June 2006, July–August 2007 and November–December 2007), for a total of 512 visual census transects.

Fish assemblages were sampled by means of underwater visual census using strip transects of 25 × 5 m (Harmelin-Vivien et al. 1985). In each transect abundance and size of fish encountered were recorded. The spatial distribution of major habitat types has been mapped (Bianchi & Morri 2006), and we used this information to ensure that our sampling unit locations fell only within rocky areas. Visual census were therefore haphazardly performed on 'pure' rocky substrates where other substrate types such as sand or seagrasses represented less than 5% in cover (both within and around transects).

The assessment of protection effects on fish assemblages can be influenced by habitat complexity (García-Charton et al. 2004). A previous study in the area, however, reports that habitat features (e.g. rugosity or mineralogy) were similar or properly interspersed between protected and unprotected zones (Guidetti et al. 2004). The only feature that we could not control is the fact that the 2 PPAs (i.e. Zones B and C) were both exclusively granitic; neither included carbonate rocky substrates. However, the majority of species which respond to substrate mineralogy are not important for fishing (e.g. some small labrid fish belonging to genus *Symphodus*), and relevant target species (e.g. *Diplo-*

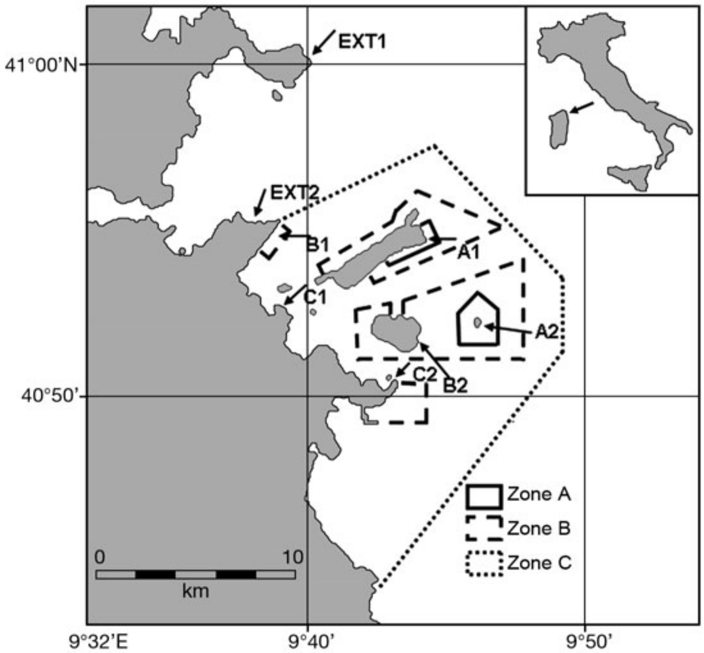

Fig. 1. Location and zoning of the Tavolara-Punta Coda Cavallo Marine Protected Area (TMPA) in Sardinia, Italy. Abbreviations represent sampling locations. Zone A: fully-protected, all fishing prohibited; Zone B: local professional fishers only; Zone C: local professional and recreational fishing, no spearfishing; EXT: external to TMPA, all fishing types permitted under Italian legislation

dus sargus) do not appear to be affected by substrate mineralogy (Guidetti et al. 2004).

Only 23 fish taxa locally targeted by professional and/or recreational fishermen were considered in the present study (Bianchi & Morri 2006) (Table 1), thus our use of the phrase 'fish assemblages' henceforth includes only this subset of species. Planktivorous species living in the water column (i.e. *Spicara maena*, *Spicara smaris, Oblada melanura* and *Boops boops*) were excluded in order to avoid high spatio-temporal variability masking protection effects (Harmelin-Vivien et al. 2008). Actual number of fish encountered was recorded up to 10 ind., whereas larger groups were recorded using categories of abundance (i.e. 11–30, 31–50, 51–200, 201–500, >500 ind.; see Harmelin-Vivien et al. 1985). Fish size (total length, TL) was recorded within 2 cm size classes for most of the species, and within 5 cm size classes for large-sized species (maximum size >50 cm) such as *Epinephelus marginatus* and *Sciaena umbra*. Finally, fish wet-weight was estimated from size data by means of length–weight relationships from the available literature, selecting coefficients referring to Mediterranean samples whenever possible (Bayle-Sempere et al. 2002, www.fishbase.org).

Data analyses. The effects of different protection regimes on whole fish assemblage structures (using 'species × sample' matrices; n = 23 species, n = 512 samples) were analyzed, as abundance and biomass data, using 5-way permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001). 'Time' (Ti) was treated as a random factor (4 levels), 'Zone' (Zo) as a fixed factor (4 levels), 'Location' (Lo) as a random factor (2 levels) nested in Zo, 'Site' (Si) as a random factor (2 levels) nested in Lo, and 'Depth' (De) as a fixed and orthogonal factor (2 levels).

To visualize multivariate patterns, non-metric multidimensional scaling (nMDS) ordinations were obtained from Bray-Curtis dissimilarity matrices calculated from square root transformed data. Due to the high number of total observations (n = 512), only the 32 centroids for the combined factor Time × Zone × Depth were visualised. Stress values were shown for each MDS plot to indicate the goodness of representation. Species relevant for contributing to the significant differences among zones were identified using similarity percentage (SIMPER) (Clarke & Warwick 2001).

Table 1. Species targeted by commercial and recreational fisheries at Tavolara-Punta Coda Cavallo MPA

Species	Common name	Family
Dentex dentex	Common dentex	Sparidae
Dicentrarchus labrax	European seabass	Moronidae
Diplodus annularis	Annular seabream	Sparidae
Diplodus puntazzo	Sharpsnout seabream	Sparidae
Diplodus sargus	White seabream	Sparidae
Diplodus vulgaris	Common two-banded seabream	Sparidae
Epinephelus costae	Goldblotch grouper	Serranidae
Epinephelus marginatus	Dusky grouper	Serranidae
Labrus merula	Brown wrasse	Labridae
Labrus viridis	Green wrasse	Labridae
Mullus surmuletus	Striped red mullet	Mullidae
Muraena helena	Mediterranean moray	Muraenidae
Sarpa salpa	Salema	Sparidae
Sciaena umbra	Brown meagre	Sciaenidae
Scorpaena porcus	Black scorpionfish	Scorpaenidae
Scorpaena scrofa	Largescaled scorpionfish	Scorpaenidae
Seriola dumerilii	Greater amberjack	Carangidae
Serranus cabrilla	Comber	Serranidae
Serranus scriba	Painted comber	Serranidae
Sparus aurata	Gilthead seabream	Sparidae
Sphyraena viridensis	Yellomouth barracuda	Sphyraenidae
Spondyliosoma cantharus	Black seabream	Sparidae
Symphodus tinca	East Atlantic peacock wrasse	Labridae

Species richness, total abundance and biomass of fish (all species pooled), and biomass and density of relevant species (identified by SIMPER and because they are commercially important species targeted by fishing; Bianchi & Morri 2006) were analysed using permutational ANOVA (PERANOVA) (Anderson 2001) based on Euclidean distance measure (Terlizzi et al. 2007), in order to avoid any assumption about the distribution of the variables (Anderson 2001, Anderson & ter Braak 2002). In this analysis the *F*-statistics are calculated but the p-values are obtained by permutation.

For the sake of synthesis, we mostly discussed the effect of the factor 'zone' in the analyses concerning single species, although we report the complete results in Appendices 1 to 3.

To test for potential differences in size of the relevant target species among the different zones and to avoid any assumption about the distribution of the variable (Anderson 2001), we used 1-way PERANOVA. Individual fish size data of each target species were pooled for each zone type, plotted as size–frequency distributions and analysed by comparing average size among the 4 zone types.

The PRIMER 6 and PERMANOVA + B20 package (Plymouth Marine Laboratory) was used to perform the analyses.

RESULTS

Species richness (S) and total abundance of fish (N) did not differ among zones (Table 2). This pattern was consistent across the 4 sampling times (Fig. 2a,b). Total biomass in Zone A was significantly higher (supporting 3-fold more fish biomass than all other zones) than in the other zones, with no statistical differences among Zones B, C and EXT. In addition, a significant variability was detected among sampling times (Table 2, Fig. 2c).

Multivariate analyses on the abundance data matrix did not provide any evidence of differences in fish assemblage structures attributable to the factor 'zone', a pattern that was consistent across the 4 sampling times (Ti × Zo, not significant; Table 3, Fig. 3a). Fish assemblages were highly variable in time, which was not consistent between the 2 different depth intervals considered here (see the significant interaction Ti × De; Table 3). A significant variability was also detected at the scales of locations and sites, with spatial differences that changed at the scale of locations among times, and at the scale of sites between the 2 depth levels (Table 3). When data of fish assemblages were expressed as biomass, the factor 'Zone' was found to be highly significant (Table 3, Fig. 3b). Pairwise tests revealed that Zone A differed from all other zones (i.e. A ≠ B = C = EXT), a pattern that appeared to be coherent at all the spatial scales considered, between depth levels and in time. A significant variability was also detected in time (in a different way between the 2 depths: Ti × De significant) and in space, at both location and site scales (Table 3).

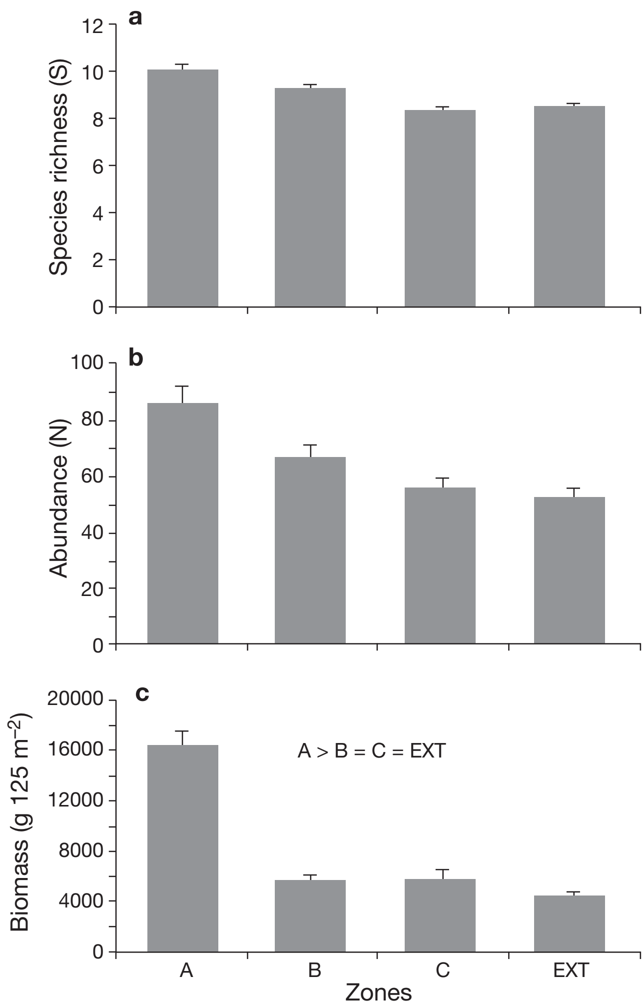

Fig. 2. Mean values (± SE) of (a) species richness, (b) total fish abundance and (c) total biomass assessed at the 4 different zone types (see Fig. 1) at the TMPA. Results of the pairwise tests (when appropriate) are also shown

In order to highlight the species that mainly contributed to the differences in fish assemblages between Zone A vs. the other zones, fish assemblages recorded in Zones B, C and EXT were pooled into a single group (called Group O). The species mostly responsible for the difference observed (up to 56 % of the total dissimilarity between Zone A vs. other zones) were dusky grouper *Epinephelus marginatus* (contributing 12.52 % to the total dissimilarity between the Zone A and Group O), salema *Sarpa salpa* (12.25 %), common two-banded seabream *Diplodus vulgaris* (9.18 %), white

Table 2. PERANOVA on square root transformed data. Species richness (S), total fish abundance (N) and biomass (B). ns: not significant; *p < 0.05; **p < 0.01; ***p < 0.001. Ti: Time; Zo: Zone; De: Depth; Lo: Location; Si: Site (see 'Materials and methods' for more details)

Source		S		N		B	
	df	MS	Pseudo-*F*	MS	Pseudo-*F*	MS	Pseudo-*F*
Ti	3	0.66	2.55^{ns}	18.23	0.64^{ns}	12001	5.43^{**}
Zo	3	2.49	1.85^{ns}	80.80	1.08^{ns}	92426	7.37^{***}
De	1	1.93	12.67^{***}	1.76	0.39^{ns}	22064	3.44^{ns}
Lo(Zo)	4	0.87	1.88^{ns}	89.64	2.91^{**}	8711.2	3.14^{**}
Ti × Zo	9	0.61	2.37^{ns}	11.20	0.39^{ns}	4121.9	1.86^{ns}
Ti × De	3	0.13	3.43^{ns}	6.26	3.50^{ns}	3619.5	7.63^{***}
Zo × De	3	0.01	0.54^{ns}	3.06	0.61^{ns}	1059.2	0.36^{ns}
Si(Lo(Zo))	8	0.22	5.80^{***}	4.37	0.79^{ns}	887.4	0.85^{ns}
Ti × Lo(Zo)	12	0.25	6.72^{***}	28.29	5.17^{***}	2209.2	2.12^{ns}
Lo(Zo) × De	4	0.01	1.13^{ns}	2.75	1.23^{ns}	2927.9	2.31^{*}
Ti × Zo × De	9	0.08	1.99^{ns}	5.10	2.85^{*}	1238.7	2.61^{ns}
Ti × Si(Lo(Zo))	24	0.03	0.45^{ns}	5.46	1.03^{ns}	1038.5	0.87^{ns}
Si(Lo(Zo)) × De	8	0.02	0.43^{ns}	3.81	0.92^{ns}	1269.3	1.14^{ns}
Ti × Lo(Zo) × De	12	0.04	0.69^{ns}	1.78	0.43^{ns}	474.07	0.42^{ns}
Ti × Si(Lo(Zo)) × De	24	0.05	0.68^{ns}	4.13	0.78^{ns}	1106.9	0.93^{ns}
Residual	384	0.08		5.30		1189.8	
Total	511						

Table 3. PERMANOVA (multivariate analysis) on square root transformed data. Fish density (N) and biomass (B). ns: not significant; *p < 0.05; **p < 0.01; ***p < 0.001. Ti: Time; Zo: Zone; De: Depth; Lo: Location; Si: Site (see 'Materials and methods' for more details)

Source		N		B	
	df	MS	Pseudo-*F*	MS	Pseudo-*F*
Ti	3	7537.4	4.18^{***}	9958.4	4.2^{***}
Zo	3	8974.4	1.31^{ns}	27811	3.44^{***}
De	1	5010.7	2.34^{*}	9963.8	3.16^{***}
Lo(Zo)	4	5922.1	2.18^{***}	5443.3	1.53^{*}
Ti × Zo	9	2268.8	1.25^{ns}	3319.7	1.40^{ns}
Ti × De	3	1482.9	2.13^{**}	2007.4	1.84^{*}
Zo × De	3	1680.8	1.47^{ns}	2400.9	1.35^{ns}
Si(Lo(Zo))	8	1147.9	2.14^{***}	1713.4	2.12^{***}
Ti × Lo(Zo)	12	1803	3.37^{***}	2357.6	2.93^{***}
Lo(Zo) × De	4	952.45	0.97^{ns}	1484.5	0.88^{ns}
Ti × Zo × De	9	652.77	0.94^{ns}	1090.1	1^{ns}
Ti × Si(Lo(Zo))	24	534.72	0.72^{ns}	804.57	0.74^{ns}
Si(Lo(Zo)) × De	8	860.36	1.54^{*}	1523.8	1.84^{***}
Ti × Lo(Zo) × De	12	693.93	1.24^{ns}	1087.1	1.31^{ns}
Ti × Si(Lo(Zo)) × De	24	555.51	0.75^{ns}	824.53	0.76^{ns}
Res	384	735.62		1083.5	
Total	511				

seabream *Diplodus sargus* (9%), brown meagre *Sciaena umbra* (6.72%) and sharpsnout seabream *Diplodus puntazzo* (6.03%). We thus evaluated distribution patterns of these species, considering that SIMPER takes into account global dissimilarity between groups.

Epinephelus marginatus and *Sciaena umbra* showed significantly higher biomass and density in the Zone A compared to the rest (Fig. 4, Appendices 1 & 2). Biomass values for *E. marginatus* and *S. umbra* were 12× and 9× higher, respectively, in the Zone A than in the other zones (no differences were detected among Zones B, C and EXT). Size distribution showed significant differences among zones for both species, with bigger fish sizes observed in Zone A, and no differences recorded among Zones B, C and EXT for both species (Fig. 5). These data suggest that higher biomasses of *E. marginatus* and *S. umbra* in Zone A are the result of both higher densities and bigger sizes (Figs. 4 & 5, Appendix 3).

Diplodus puntazzo, *D. sargus* and *D. vulgaris* showed significantly higher biomasses in Zone A compared to the other zones, whereas no differences among zones were found in terms of density of individuals (Fig. 6, Appendices 1 & 2). The fact that the 3 seabream species showed similar densities among zones, but higher biomass in Zone A indicates that differences were mostly due to larger fish size there (Fig. 7, Appendix 3).

In spite of its relevant contribution in the SIMPER analysis, no significant differences among zones in terms of density or biomass were recorded for *Sarpa salpa* (Appendices 1 & 2).

DISCUSSION

The clearest outcomes of this study comparing fish assemblages from no-take/no-access areas, 2 types of PPAs and locations outside the TMPA, are that (1) only no-take/no-access zones clearly differed from the rest (with different assemblage structures, and bigger size and higher biomass of target fishes in the no-take/no-access zones), and (2) the 2 types of PPAs did not differ from each other, nor from locations outside the TMPA.

With regard to no-take areas, protection was found to affect biomass and size rather than abundance for many fish species, although some fish (i.e. *Epinephelus marginatus* and *Sciaena umbra*) responded in terms of density, size and biomass. This is in agreement with the outcomes of previous studies (Denny & Babcock 2004, Pelletier et al. 2005, Floeter et al. 2006, Harmelin-Vivien et al. 2008, but see Lester & Halpern 2008), and can be explained considering that total abundance can be affected by processes partially independent of protection (e.g. a successful annual recruitment). In contrast, fish biomass is a function of both size and density. Fish size is

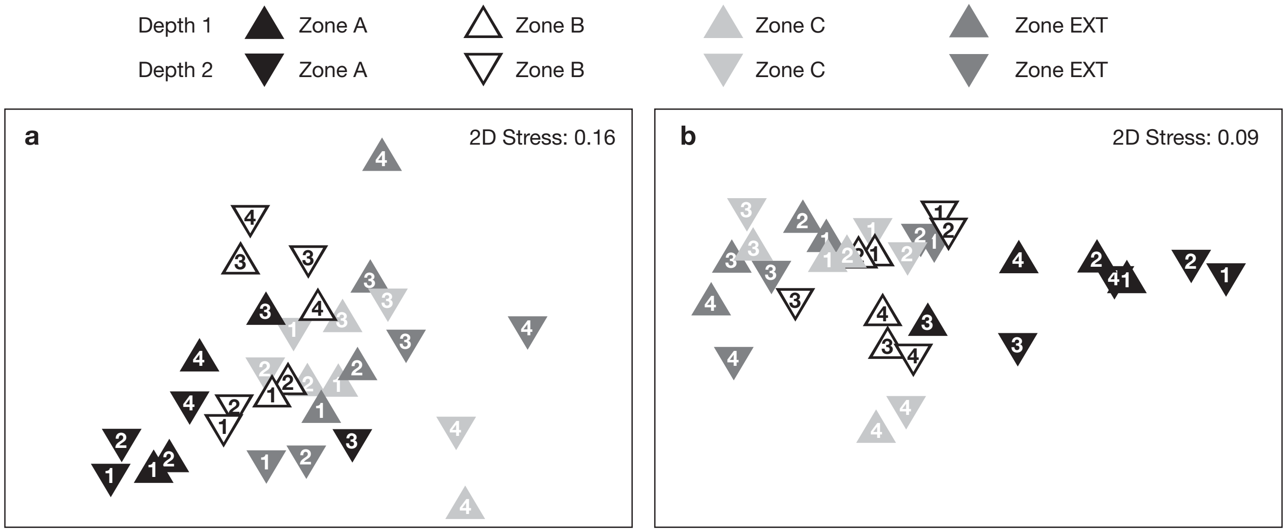

Fig. 3. Fish assemblage structures assessed on (a) density and (b) biomass data. Two-dimensional nMDS ordinations of centroids for the combined factor Time × Zone × Depth are shown. Sampling times are numbered chronologically from 1 to 4 within the symbols

increasingly indicated as one of the best indicators of the effects of protection from fishing (Pelletier et al. 2005), especially taking into account that fishing selectively targets large individuals (Erzini et al. 2006). Patterns of species richness, however, were not related to protection from fishing, as observed also by Francour (1991, 1994) and Vacchi et al. (1998).

Enforcement at the TMPA had been effective for a relatively short time (approx. 2 yr) before we started our sampling (see 'Materials and methods'). If one considers the life-history traits of some target species there is an apparent mismatch between e.g. growth rates and the presence of large individuals after a couple of years of protection. For instance, *Epinephelus margi-*

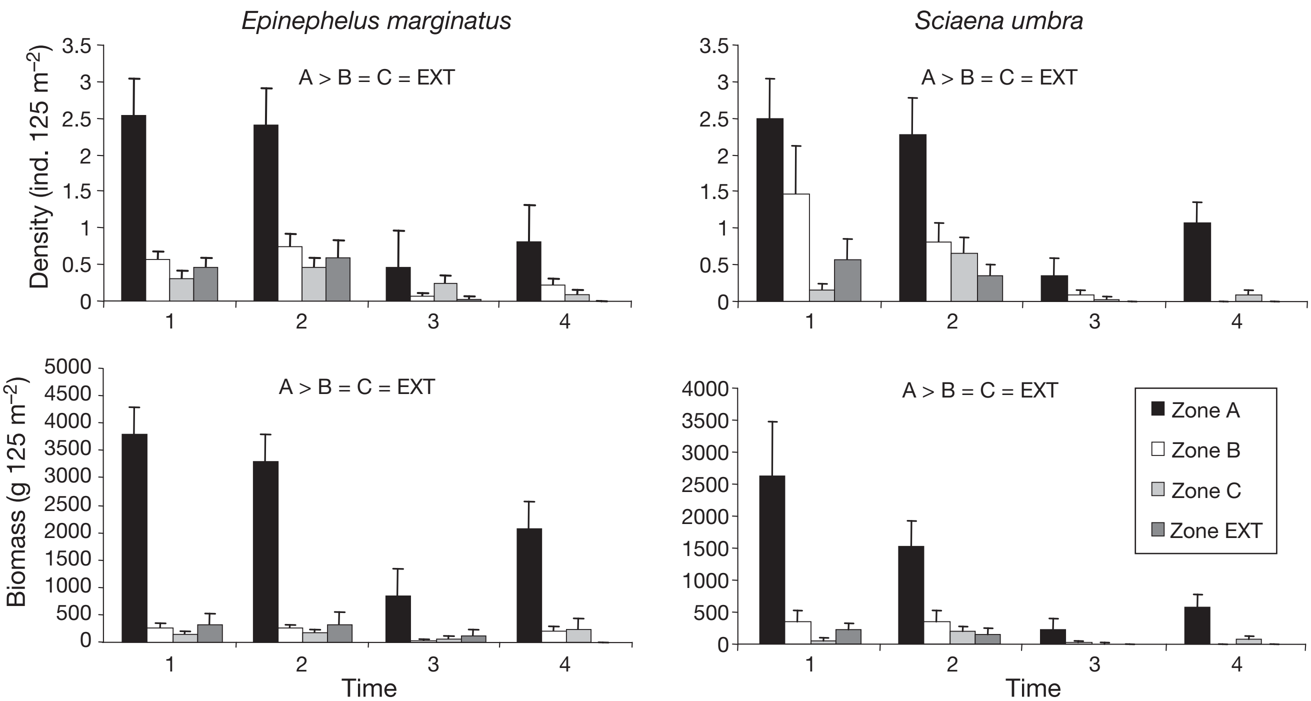

Fig. 4. *Epinephelus marginatus* and *Sciaena umbra*. Mean values (± SE) of density and biomass assessed at the 4 different zone types (see Fig. 1) at the TMPA and during the 4 sampling times. Results of *a posteriori* tests among zones are also shown

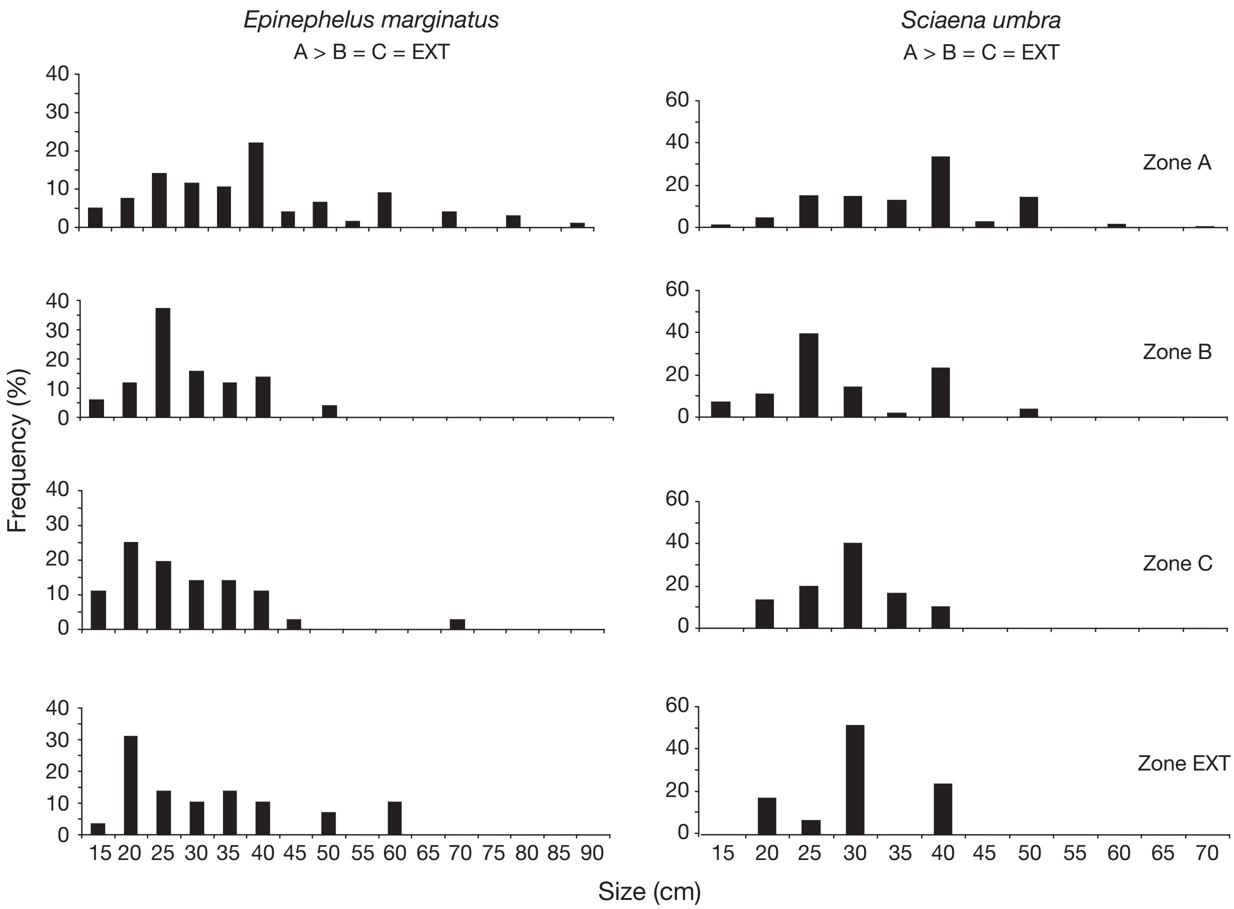

Fig. 5. *Epinephelus marginatus* and *Sciaena umbra.* Size–frequency distributions. Results of *a posteriori* tests among zones are also shown

natus is a slow-growing fish that may achieve a large maximum size (1.5 m TL) and may live to 50 yr (www.fishbase.org). The fact we clearly observed higher densities and larger individuals in the no-take zones compared to relatively recent previous observations (Murenu et al. 2004, P. Guidetti unpubl. data) can only be explained by considering mechanisms of recovery related to behavioural changes (as opposed to typical recruitment, individual growth and reduced fishing mortality), e.g. in terms of increased confidence around divers, but also of re-appropriation of shallow rocky reefs. In fact, deeper reefs could act as refugia where large fish can find shelter against fishing (e.g. spearfishing). From this perspective, behavioural aspects and local habitat distribution in depth should be considered (along with species traits such as growth rates and intrinsic rates of population increase; Mosquera et al. 2000) to explain the non-negligible variability observed, on a large scale, in the fish response to protection related to the age of MPAs (Halpern & Warner 2002, Micheli et al. 2004, Guidetti & Sala 2007).

The various target species considered in this study did not show the same response to protection from fishing. Explaining why the responses to protection vary from one to another target fish is not an easy task, but it is a common pattern also reported by other studies (e.g. Mosquera et al. 2000). The actual pressure of fishing methods or gears locally used, however, has been reported to potentially impact the various target species differently from one place to another (Guidetti et al. 2008).

The 2 types of PPAs (i.e. Zone B where only professional fishing is authorised, and Zone C where both professional and regulated recreational fishing are allowed) did not differ significantly from the locations outside the MPA. Increased biomass compared to external zones was evident, in fact, only for fully protected areas (i.e. Zone A). This outcome is similar to the patterns observed in other MPAs in the Mediterranean (Francour 1991, 1994, Vacchi et al. 1998) and elsewhere (Denny & Babcock 2004, Shears et al. 2006), and may suggest that even moderate fishing pressure (i.e. due to local artisanal and/or recreational fishing) can

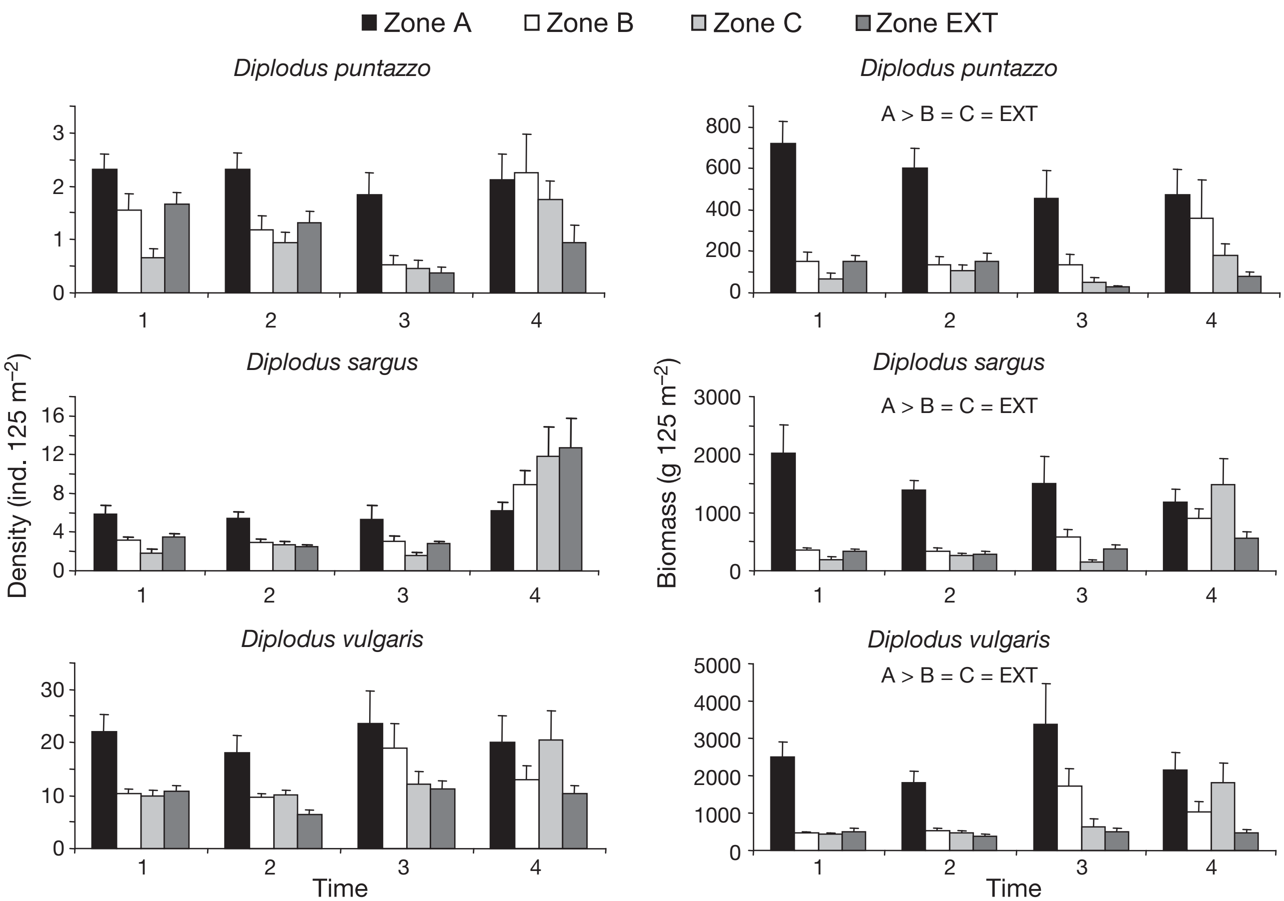

Fig. 6. *Diplodus puntazzo, Diplodus vulgaris* and *Diplodus sargus*. Mean values (± SE) of density and biomass assessed at the 4 different zone types (see Fig. 1) at the TMPA and during the 4 sampling times. Results of *a posteriori* tests among zones are also shown

remove a significant proportion of large-sized specimens of target species. From this perspective, recreational fishing was found to be an important source of impact on target fish (Francour 1994, Francour et al. 2001, Cooke & Cowx 2006, Lester & Halpern 2008). The few studies focused on the role of PPAs reported contrasting results. Some concluded that PPAs are similar to open access areas (Francour 1991, Denny & Babcock 2004, Shears et al. 2006, Lester & Halpern 2008) and do not produce clear benefits compared to totally protected areas (Vacchi et al. 1998, Shears et al. 2006, Lester & Halpern 2008), whereas for instance Floeter et al. (2006) observed some positive ecological responses for commercial species in PPAs if compared to areas open to fishing. A recent meta-analysis by Lester & Halpern (2008) showed that PPAs can produce some ecological benefits compared with openly fished areas, but responses calculated on several variables (i.e. biomass, density, size and species richness) are not statistically significant.

It is worth noting the absence of any difference in fish assemblage structures and variables related to single target species between the 2 types of PPAs (i.e. Zones B and C of the TMPA). The permission of recreational fishing in addition to professional fishing in Zone C does not appear to cause any additional impact on fish, and nor does spearfishing in areas outside the TMPA, but there is still insufficient data to make this conclusion definitive. To properly assess the relative impact of the various types of fishing, quantitative data about the local fishing effort in each zone (e.g. number of boats, of fishermen and of gears used by both professional and recreational fishermen) are necessary. Concentrations of professional fishermen in Zone B, and of recreational fishermen in Zone C (attracted by the expectation of catching more fish within the MPA than outside; Stelzenmuller et al. 2007) could have affected the fish response to protection in the various zones of the TMPA. Therefore, it is still important not only to regulate the type of fishing in the subzones of an MPA, but also the number of fishermen, gears or boats in order to properly regulate the fishing impact on fish assemblages within PPAs, whose proper management can reinforce their role as buffers between the no-take

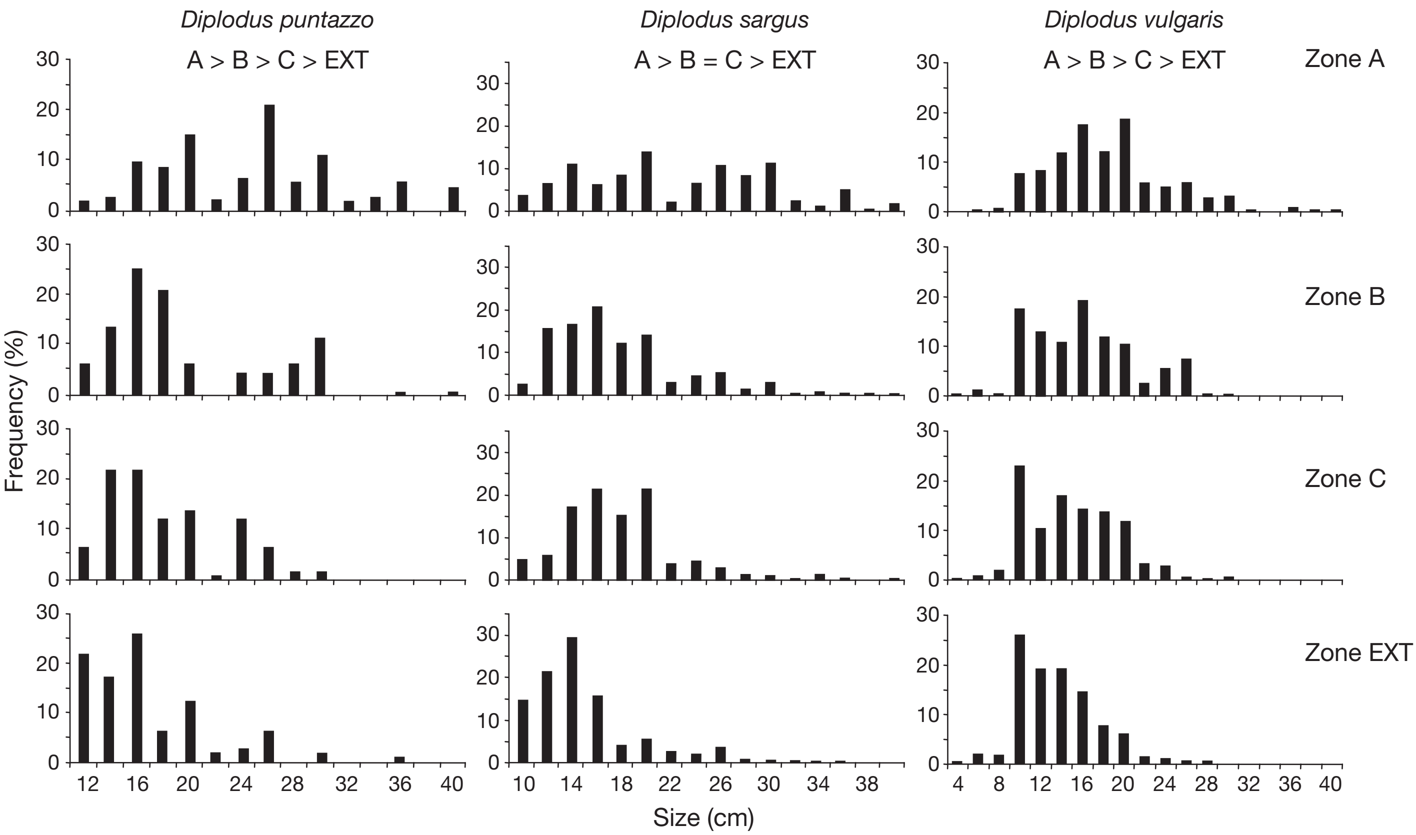

Fig. 7. *Diplodus puntazzo, Diplodus sargus* and *Diplodus vulgaris.* Size–frequency distribution. Results of *a posteriori* tests among zones are also shown

reserves and the areas outside the MPAs (see also Goni et al. 2008). In the specific case of the MPAs that include different types of PPAs, this outcome thus suggest the need for improving their management or for possibly re-thinking about their role and actual utility in the MPA's design and regulation.

Fish assemblages are well known to be influenced by the 3-dimensional habitat complexity provided by both biological (e.g. erect macroalgae) and physical structures (Turner et al. 1999, García-Charton & Pèrez-Ruzafa 2001), and by mineralogical characteristics of rocks (Guidetti et al. 2004), that might mask or experimentally confound (sensu Underwood 1997) protection effects on fish (García-Charton et al. 2004, Harmelin-Vivien et al. 2008). The differences we have detected and attributed to protection levels, however, are not likely to be confounded by habitat features for the following reasons: (1) physical habitat features (e.g. slope, rugosity, presence of boulders) in the study area were quantitatively assessed in a previous investigation, and they were similar or properly interspersed among zones characterised by different levels of protection, or do not affect species considered in this study (e.g. for mineralogical features) (Guidetti et al. 2004); (2) habitat microstructure (e.g. holes of rock-boring date mussels or other smaller cavities) only affect distribution patterns of small benthic fishes (Patzner 1999), which are not targeted by fishing and consequently, they were not taken into account in this study; (3) some years ago, when the enforcement was not yet effective at the TMPA, differences among zones in benthic subtidal assemblages were detected (Ceccherelli et al. 2006), but these differences were not reflected in the abundance and biomass of commercial fish at the time (Murenu et al. 2004). The differences among zones characterised by different levels of protection we have detected in this study, therefore, are likely to be explained in terms of changes in fish assemblages as a consequence of the enforcement of protection from fishing that took place around 2003–04.

This study, in conclusion, emphasises the need for further data about the effectiveness of PPAs that usually surround no-take reserves. This is especially important for MPAs created in regions such as the Mediterranean basin, where human populations are highly concentrated along the coasts and where tourism (which also includes seasonal recreational fishing) is one of the most important sources of economic income (Abdulla et al. 2008). Having data on professional and recreational fishing fleets (which stably or seasonally exploit fishing resources), the gears used, the number of people and boats involved, and so on, would allow (1) quantification of the fishing effort and the relative impacts of the various kinds of fishing in order to properly regulate professional and recreational fishing in MPAs' subzones, and (2) design of MPAs in order to properly balance conservation, ecological and socio-economic needs (e.g. in terms of number and size of MPAs, and PPAs types; Claudet et al. 2008), especially considering that no-take zones and surrounding PPAs are likely to reciprocally influence each other.

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Appendix 1. PERANOVA summaries of square root transformed data. Density of relevant species (see 'Materials and methods: Data analyses'). ns: not significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. Ti: Time; Zo: Zone; De: Depth; Lo: Location; Si: Site (see 'Materials and methods' for more details). *E.m.*: *Epinephelus marginatus*, *S.u.*: *Sciaena umbra*, *D.p.*: *Diplodus puntazzo*, *D.s.*: *Diplodus sargus*, *D.v.*: *Diplodus vulgaris*, *S.s.*: *Sarpa salpa*

Source	*E.m.*	*S.u.*	*D.p.*	*D.s.*	*D.v.*	*S.s.*
Ti	***	***	**	ns	ns	ns
Zo	***	*	ns	ns	ns	ns
De	ns	*	ns	ns	ns	ns
Lo(Zo)	ns	ns	ns	ns	***	ns
Ti × Zo	***	ns	ns	ns	ns	ns
Ti × De	ns	ns	ns	ns	ns	*
Zo × De	ns	ns	ns	***	ns	ns
Si(Lo(Zo))	ns	***	***	ns	ns	ns
Ti × Lo(Zo)	ns	ns	***	***	ns	**
Lo(Zo) × De	ns	ns	*	ns	ns	ns
Ti × Zo × De	ns	ns	ns	ns	ns	**
Ti × Si(Lo(Zo))	ns	ns	ns	ns	ns	ns
Si(Lo(Zo)) × De	***	ns	ns	ns	**	ns
Ti × Lo(Zo) × De	ns	ns	ns	ns	*	ns
Ti × Si(Lo(Zo)) × De	ns	*	ns	ns	ns	*

Appendix 2. PERANOVA summaries on square root transformed data. Biomass of relevant species (see 'Materials and methods: Data analyses'). ns: not significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. Ti: Time; Zo: Zone; De: Depth; Lo: Location; Si: Site (see 'Materials and methods' for more details). *E.m.*: *Epinephelus marginatus*, *S.u.*: *Sciaena umbra*, *D.p.*: *Diplodus puntazzo*, *D.s.*: *Diplodus sargus*, *D.v.*: *Diplodus vulgaris*, *S.s.*: *Sarpa salpa*

Source	*E.m.*	*S.u.*	*D.p.*	*D.s.*	*D.v.*	*S.s.*
Ti	***	***	*	ns	ns	ns
Zo	***	***	***	***	***	ns
De	*	*	ns	ns	ns	ns
Lo(Zo)	ns	ns	ns	ns	ns	ns
Ti × Zo	***	***	ns	ns	ns	ns
Ti × De	*	ns	ns	ns	*	ns
Zo × De	***	ns	ns	***	ns	ns
Si(Lo(Zo))	ns	***	*	ns	ns	ns
Ti × Lo(Zo)	ns	ns	*	***	ns	ns
Lo(Zo) × De	ns	ns	*	ns	ns	*
Ti × Zo × De	ns	ns	ns	ns	ns	ns
Ti × Si(Lo(Zo))	ns	ns	ns	ns	ns	ns
Si(Lo(Zo)) × De	***	ns	ns	ns	***	ns
Ti × Lo(Zo) × De	ns	ns	ns	ns	*	ns
Ti × Si(Lo(Zo)) × De	ns	*	ns	ns	ns	***

Appendix 3. PERANOVA summaries comparing fish size among different zones (see Fig. 1). ***$p < 0.001$

Species	MS	Pseudo-*F*
Epinephelus marginatus	2453.2	11.739***
Sciaena umbra	7194.8	15.377***
Diplodus sargus	3551.7	111.02***
Diplodus vulgaris	962.4	38.905***
Diplodus puntazzo	2410.8	70.19***

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