

'Reserve effect' within a temperate marine protected area in the north-eastern Atlantic (Arrábida Marine Park, Portugal)

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ABSTRACT: Benefits of marine protected areas depend on local ecological and socio-cultural aspects which are critical to the success of the protection measures. In particular, before–after comparisons are indispensable to disentangle the effects of protection from those of different physical and ecological characteristics among areas. Using underwater visual surveys, we assessed whether biomass and abundance of temperate reef fish assemblages and target invertebrates increased inside a no-take area in the Arrábida Marine Park (Portugal) 3 to 4 yr after its establishment. Data were compared to a previous study, conducted 10 yr before protection was effective. Control–effect comparisons after reserve establishment showed a positive response of legal-size demersal fish and below legal-size target invertebrates. The first evidence of protection was found in biomass but not in numbers. Non-target groups and below legal-size demersal fish had a significant interaction among reserve and habitat complexity indices for either density or biomass, suggesting a lack of a reserve effect. Before–after comparisons revealed non-significant patterns of increase in numbers of target species compared to non-target ones. The most important commercial species showed the largest increase in density after protection was established. Significantly higher abundances and proportionally heavier individuals of these species were also found inside the reserve in the control–effect comparisons. These findings are reinforced by an increasing trend in landings which are consistent with the early detection of a reserve effect.

KEY WORDS: Marine protected area · Before–after data · Temperate reef fishes · Target species · Habitat · Artisanal fisheries

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INTRODUCTION

A major goal of conservation and fisheries science is to restore exploited marine resources, habitats, ecosystems and biodiversity that have suffered human-induced declines in abundance, genetic and functional diversity and altered food web structure (Claudet et al. 2011a). Marine protected areas (MPAs) have been increasingly promoted as tools for ecosystem-based management of marine systems (Frascchetti et al. 2011) since they restrict or exclude

human uses in some areas, and are often aimed at protecting whole communities and ecosystems. When an MPA or a particular zone within an MPA excludes extractive uses (becoming a no-take zone), it is called a marine reserve (Lubchenco et al. 2003). Although some studies failed to show effects in marine reserves due to a range of different causes (Claudet et al. 2011a), the majority of reserves have shown the so-called 'reserve effect' with increasing levels of biomass, density and sizes of individuals inside the reserve (Lester et al. 2009). Effects are

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expected to be greater when fishing pressure is high before protection (Micheli et al. 2004, Tetreault & Ambrose 2007, Lester et al. 2009), and the magnitude of those effects has been related to species composition, size, trophic level, mobility, habitat dependence and commercial value (Pelletier et al. 2008, Claudet et al. 2010, 2011a,b). The efficacy of a marine reserve also depends on effective enforcement and compliance by local users (Claudet & Guidetti 2010), time since protection started (Micheli et al. 2004, Di Franco et al. 2009, Claudet et al. 2010), size of no-take and adjacent buffer areas (Claudet et al. 2008, 2010, Claudet & Guidetti 2010), species–habitat interactions (García-Charton et al. 2004, Pérez-Matus & Shima 2010, Claudet et al. 2011b) and connectivity with adjacent zones (Vega Fernández et al. 2008).

The primary direct effect predicted by closures is the elimination of fisheries-related mortality allowing target individuals to live longer and produce more young. Moreover, when fishing gears affect habitat and are unselective, marine reserves safeguard habitat integrity and increase fish density and size, also leading to an increase in fecundity and spawning biomass (Lester et al. 2009). These effects might increase commercial stocks, and benefits may be exported to adjacent areas through the migration of adults (Kramer & Chapman 1999, Goñi et al. 2008, 2010) or spillover of larvae (Pelc et al. 2010). Indirectly, restoring a particular assemblage within a reserve may also affect predator–prey interactions and the dynamics of food webs, as larger target predators that had historically been caught will increase in abundance and size (Halpern 2003, Claudet et al. 2011a). However, the build-up of top predators is usually a slow process (Russ & Alcala 2004, 2010, Hamilton et al. 2010).

Marine reserves can, in the long term, become control areas for the evaluation of population and ecosystem effects of fishing and other influences on the marine environment. Coupling historical data from before the establishment of a reserve with data collected after its implementation, in which variables related to ecological changes in the assemblages (such as density, diversity, size, biomass) are monitored, may help to understand the sources of ecological variability at different scales, as well as the response of different systems to conservation and fisheries measures (Pelletier et al. 2008).

To assess the effectiveness of MPAs, multiple designs can be used, but all rely on the comparison of a control site or time to an affected situation (Osenberg et al. 2011). In fact, misleading estimates of the

effect of protection may arise when control–effect designs do not consider intrinsic habitat or other environmental features which may vary among nearby sites. In many situations, MPAs are likely established in places with a high ecological value, and when assessing protection benefits, this should not be disregarded (García-Charton & Pérez-Ruzafa 1999, Côté et al. 2001).

We performed our study at the Arrábida Marine Park in Portugal, which was designated in 1998. The management plan, approved in 2005, created different protection zones based on the natural values present (Gonçalves et al. 2003), and included a transition phase for fisheries measures with the successive implementation of areas with different protection status until 2009. This marine park is among the few where data were collected before and after its implementation and can be compared. We aimed to evaluate the reserve effect in this temperate MPA using before–after and control–effect comparisons of rocky reef fish assemblages, including commercially important invertebrate species. For that, we examined abundance and biomass responses to protection, comparing species that are targeted and not targeted by fishing before and after the implementation of the park and inside and outside the no-take areas. We also explored species–habitat interactions and fishing effort trends in order to account for such sources of variability.

MATERIALS AND METHODS

Study area

The Arrábida Marine Park is a 38 km stretch of coastline (53 km²) on the west coast of Portugal, adjacent to a terrestrial nature reserve created in 1976, the Arrábida Nature Park. The marine park includes the rocky shore and adjacent mixed sandy substrata between Cape Espichel (38° 27' N, 9° 12' W) and Portinho da Arrábida (38° 29' N, 8° 57' W; Fig. 1). This area is utilized year-round for commercial and recreational activities, as it faces south and is protected from the prevailing north–northwest winds and waves. Nearby are the cities of Lisboa and Setúbal, the latter being an important fishing port located to the east of the park in the estuary of the Sado River. In the middle of the park, the small touristic town of Sesimbra has a long fishing tradition. This area is a biogeographic and oceanographic transition zone between warm and cold temperate waters and is also near the northern limit of the main north-east

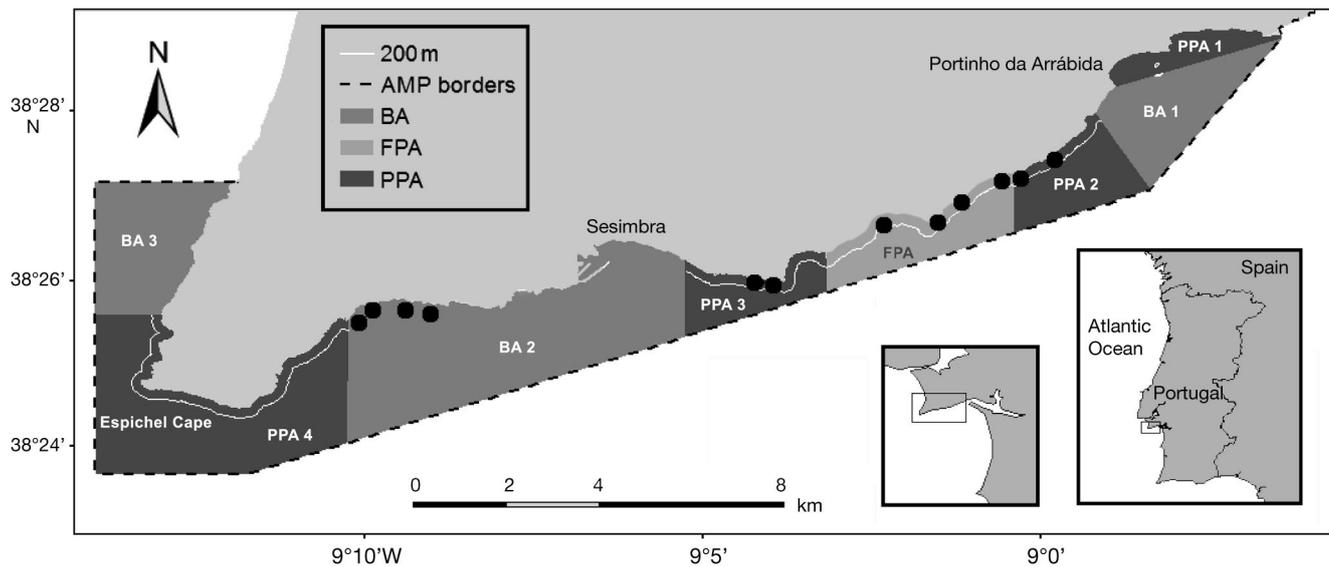


Fig. 1. Arrábida Marine Park zoning. FPA: fully protected area; PPA 1 to 4: partially protected areas; BA 1 to 3: buffer areas. ●: survey sites (outside of the reserve: 4 sites in BA2; inside the reserve: 4 sites in PPA2 and 3, and 4 sites in FPA)

Atlantic upwelling events (Wooster et al. 1976), which are stronger in the summer and increase the productivity of coastal waters. The intertidal zone is steep, and subtidal rocky reefs are dominated by boulders originated from the erosion of the cliffs and by bedrock with fissures and crevices, creating a complex diversity of macro- and microhabitats which supports a high diversity of algae, invertebrates and fish. These features make this area an important hotspot of diversity for this biogeographic region (Henriques et al. 1999, Gonçalves et al. 2003). North and south of the park, extensive sandy shores prevail, making this marine park a 'continental island' for coastal species living on rocky reefs.

The management plan of the park was approved in 2005, and different areas with different levels of protection have been designated (Fig. 1): a fully-protected area (FPA, 4 km²); 4 partially-protected areas (PPAs, totalling 21 km²); and 2 buffer areas (BAs, totalling 28 km²). The FPA is a no-take, no-go area (with the exception of research, monitoring and education purposes). The PPAs allow local commercial fishing with traps and lines, but only beyond 200 m from shore, and no extractive recreational activities (e.g. angling, spearfishing) are permitted. In the BAs, fishing vessels <7 m in length and recreational fishing are allowed. In the whole park, commercial diving for bivalves or other marine organisms, spearfishing, trawling and purse seine netting are forbidden. Commercial fishing licences for the park were allocated only to fishers from Sesimbra.

The park's management plan was implemented with a transitional period for fisheries in which the different zones were gradually implemented during the first 4 yr. In 2006, management measures were enforced in the BAs, the east half of the current FPA began as a PPA, and the Portinho PPA (PPA1) was implemented. In 2007, the remaining PPAs were implemented, and the west half of the FPA started as a PPA. In 2008, the east half of the (current) FPA changed from PPA to FPA. The west half of the FPA was enforced in the summer of 2009, which ended the transition period.

Since fishing is prohibited from the shoreline out to 200 m in the PPAs and the full extent of rocky reefs is encompassed within this range in most of the park (only at the west tip of the park the reefs extend beyond this range), we considered both the FPA and PPAs surrounding it as (no-take) reserves (PPA2 + PPA3 = 6.78 km² and FPA = 4.32 km², total = 11.1 km², Fig. 1) and compared them to fishing areas (BA2 = 16.13 km²). Thus, the outside-reserve data were collected in the BA whereas the inside-reserve aggregates data from the FPA and PPAs. Since no similar habitats are found adjacent to the park, the 'control' area is the BA.

Community survey methodology

During 2009 and 2010, 3 trained divers performed 65 m strip transect surveys perpendicular to the

coastline using underwater visual census at 12 fixed stations (Fig. 1), containing a continuous rocky reef habitat. We arranged 4 replicate transects at each station in spring and autumn each year, totalling 192 replicates (48 per season). Due to a known seasonal variability in these coastal fish assemblages (Beldade et al. 2006, Claudet et al. 2011b), we opted to survey the sampling sites twice a year. These surveys were done after the final stage of the management plan implementation and so this is considered the 'after' period in the analyses. The 'before' data were collected by E.J.G. and colleagues (Gonçalves et al. 2003, Henriques et al. 2007, see data analysis below).

Each diver collected the following information for demersal and cryptobenthic fish and commercially important invertebrates: species, number and estimated total length (or mean lengths for fish in schools). Demersal species were recorded in the first pass, and at the end of the transect the diver turned back, moved 2 m to the side and did another pass to record cryptobenthic fish and invertebrates. Several dive tests were conducted at the different stations before sampling was initiated, and the estimated modal length of rocky reefs was ~65 m among sites. Thus, we used a 65 × 4 m strip transect (2 m on each side of the diver) for demersal fish species and a 65 × 1 m (0.5 m on each side of the diver) for cryptobenthic fish and invertebrate species. Data for both groups (demersal and cryptobenthic) were pooled together, and no species were counted on both passes. Initial and ending depths and duration of each census were recorded. Visibility at each site was also recorded with a minimum of 5 m visibility established for the visual surveys. Densities refer to abundance in no. m⁻². Lengths (L) were transformed to weights (W) using an L–W relationship for each species from published literature (using whenever possible primary references from the closest region or information from Froese & Pauly 2011); if this was not available for a particular species, the closest congener was used as a proxy. Biomass was then calculated by multiplying abundance in number and individual weight.

Small juveniles (<3 cm) were not included to overcome inflated estimates of recent recruits, as is widely adopted in visual census studies (Bellwood & Alcalá 1988). The Mediterranean rainbow wrasse *Coris julis* was also not counted in surveys due to the very high abundance of this species. Unpublished data from the previous study showed that *C. julis* was ubiquitous and very abundant throughout the marine park, representing almost 1/3 of all encounters with abundances ~3 times higher than the second most abundant species. The accuracy of the visual census

technique was incompatible with including this species, and a similar procedure may be found in Colton & Alevizon (1981). Pelagic species (e.g. mackerel, sardines, bogue) were counted but not included in the analysis due to their high mobility and weak association with the rocky reefs. On the other hand, large commercial benthic fish with cryptic habits (e.g. Mediterranean moray eel, forkbeard, scorpionfish, Lusitanian toadfish) were very hard to detect and clearly underestimated due to their dependence on large refuges during daytime; therefore, these species were also excluded from the analysis.

Habitat data were gathered in 2009 (spring and autumn) and 2010 (spring) at all survey sites. Three transects were conducted with 1 × 1 m quadrats (n = 6) in each transect, with 1 quadrat laid each 10 m from the deeper to the shallower zones of the transect. Each quadrat was divided in four 0.5 × 0.5 m areas. Divers recorded detailed physical habitat categories that, for the purpose of this paper, were pooled together as shown in Table 1. Percent cover was calculated for each category at each site. Biotic habitat included algae and benthic invertebrates which were identified to species whenever possible.

Table 1. Physical habitat categories of the surveyed sites in Arrábida Marine Park, Portugal

Habitat	Description
Sand	Grains <0.2 cm
Gravel	Grains between 0.2 and 5.0 cm
Cobbles/ pebbles	Small round rocks between 5.0 and 25.0 cm
Boulders	Small (<30.0 cm), medium (30.0 cm to 1.0 m) and large rocks (>1.0 m), usually originated from the erosion of the high coastal cliffs
Bedrock	Rock adjacent and continuous to the coastal rock
Vertical rock	Vertical wall in an intertidal bedrock or a very large boulder
Holes	Small (opening <30.0 cm), medium (opening 30.0 cm to 1 m), large (opening >1.0 m)
Caves	Large and deep vertical holes (>1 m)
Overhangs	Oblique spaces below rocks, generally boulders: small (opening <30 cm), medium (opening 30 cm to 1 m)
Crevice	Narrow and thin spaces between rocks: small (length <30 cm), medium (length 30 cm to 1 m)
Fissures	Passages or corridors generally in the bedrock: medium (width <30 cm), large (width >30 cm)

Table 2. Biotic habitat (algae and invertebrates): algae functional groups and corresponding algae groups (species, genus or type); invertebrate groups (aggregated by phylum) surveyed in Arrábida Marine Park, Portugal

ALGAE	
Functional group	Algae group
Corticated macrophytes	<i>Asparagopsis</i> sp., <i>Codium</i> sp. (erect or encrusting), <i>Cystoseira</i> sp., <i>Halopteris</i> sp., <i>Plocamium</i> sp., <i>Rhodymenia pseudopalmata</i> , <i>Sargassum</i> sp., <i>Sphaerococcus</i> sp.
Articulate calcareous algae	Erected coralline
Crustose algae	Encrusting coralline
Corticated foliose algae	<i>Dictyopteris polypodioides</i> , <i>Dictyota dichotoma</i> , <i>Padina pavonica</i>
Filamentous algae	<i>Falkenbergia rufolanosa</i>
Foliose algae	<i>Ulva</i> sp.
Leathery macrophytes	Unidentified <i>Laminaria</i> (Phaeophyceae)
INVERTEBRATES	
Annelida	
Arthropoda (<i>Balanus</i> sp.)	
Bryozoa	
Chordata (unidentified ascidean)	
Cnidaria	
Echinodermata (sea stars, sea urchins, sea cucumbers, brittle stars)	
Echiura (<i>Bonellia viridis</i>)	
Mollusca	
Porifera	

But, due to the high diversity of species in the area and difficulties with *in situ* identification, algae were aggregated by functional groups (Steneck & Dethier 1994) identifying whenever possible the most common genus or species (algae groups), and invertebrates were grouped by phylum (Table 2). The intervals of percent biotic cover (the midpoint class was used for the analysis) were A = <5; B = 5–15; C = 15–25; D = 25–50; E = 50–75; F = 75–100%.

Data analysis

'Control-effect' comparison

The response of fish and target invertebrates to protection was compared based on the average response variables biomass (g m^{-2}) and density (no. m^{-2}) of all sites inside the reserve (In) to the average response of all sites outside (Out), in the after period. In:Out ratios and their standard errors (SE) were calculated for the following groups of species which might respond differently to fisheries effects: non-target cryptobenthic fish, non-target demersal fish, target demersal fish and target invertebrates. For commercial fish, individuals larger than legal size (for those with size limits) were analysed separately from those below legal size.

Species without legal size limits were included in the legal-size target group. Ratios >1 indicate higher density or biomass inside the reserve relative to outside, and the opposite is the case for ratios <1.

To understand the role of protection while accounting for possible habitat differences, 2 non-collinear variables, viz. roughness and boulder size diversity indices, were used as proxies for structural complexity. Shannon-Wiener's diversity index was calculated for the percent cover of the different sized boulders and cobbles/pebbles (Claudet et al. 2011b). Roughness was estimated as the ratio between the length measured with a leaded cable contouring the bottom profile of the whole extension of the reef and the linear distance measured as the reef length perpendicular to the coast obtained by a geographic information system (GIS) shape file of rocky reefs provided by the marine park authority.

Statistical comparisons were performed using generalized linear models (GLMs; McCullagh & Nelder 1989, Dobson 1990), testing the fixed effect 'reserve' and its interaction with habitat covariates (reserve \times roughness + reserve \times boulder diversity) for the response variables biomass and density of each group of species. Data from both seasons were pooled together to encompass intra-annual variability and to increase replication and statistical power. Choosing gamma as the exponential family and using a fourth-root transformation, the residuals showed good approximation to normality. Linear models were run to assess the reserve effect on roughness and boulder diversity indices (square root transformed). After each model, analyses of variance (ANOVAs) were applied. These analyses were conducted using the open-source statistical software R (version 2.12.2, R Development Core Team 2012).

Responses of assemblages' biomass to the percent cover of different habitat features were assessed using the BEST (BIO-ENV) routine in PRIMER 6.0 (Clarke & Warwick 1994). This procedure searches for all possible combinations of environmental variables and selects the subset that best explains the multivariate pattern of fish assemblages. Moreover, it calculates a global BEST match permutation test (using 999 permutations) to evaluate significant asso-

ciations between species groups' assemblages and the environmental variables.

Since habitat transects within each site could not be assigned to each species' observations, comparisons were done at the site level using both percent cover and average biomass. Abiotic data (Table 1) were previously normalized and the resemblance matrix calculated using the Euclidean distance (procedure for environmental data). For algae and invertebrate groupings (Table 2), percent cover data was fourth-root transformed and the resemblance matrix was calculated using the Bray-Curtis similarity index. To account for the protection level, a dummy variable of '1' was assigned to sites inside the reserve and '0' for those outside (Forcada et al. 2008). PERMANOVA with 999 permutations was also used to test for the effect of protection (fixed effect) on each habitat cover type (PRIMER 6.0).

In:Out response ratios and correspondent SEs for biomass and density were also calculated for the most frequently observed species from each group. To test the significance of the obtained species ratios, the original ratio was compared with 9999 random In:Out ratios (bootstrap procedure) using the same number of In and Out observations but randomly permuting the response vector (biomass or density) at each 9999 replicates. Then, from the bootstrap results, a confidence interval (CI) was calculated and compared to the original species In:Out ratio, which was considered significantly different from random if it fell above or below the correspondent CI (R Development Core Team 2012).

'Before–after' comparison

Underwater surveys of rocky reef assemblages were conducted by 2 divers in the autumn of 1998 and spring of 1999 using the same methodology described above at 3 sites common to both time periods. This period is referred hereafter as 'before'. Data from the same stations were used with 2 of the 3 sites being currently placed in the FPA and the third in an adjacent PPA. Transects in both periods were run perpendicular to the coast, and the same groups of species were recorded in each direction (except target invertebrates which were not documented before). Although earlier surveys were based on timed counts and not on fixed transect length, dive tests with researchers from both periods ensured that survey procedures were identical. In the 'after' period, transects noting time and distance were performed by the team members, and speeds were kept con-

stant and comparable with the before data set. In addition, in the after period, the initial and ending time of each survey was always registered. Thus, in order to accurately compare both periods, analyses were based on time instead of area since this was the common metric to both data sets, and density was calculated as fish min^{-1} (hereafter designated density min^{-1}). Finally, the before surveys recorded fish length in categories (small, medium, large), so no comparisons of size structure or biomass were attempted.

Although data are available from before and after as well as in the reserve and fished areas, a before–after–control–impact (BACI) design could not be used to assess changes in these stations in relation to protection since all before data came from stations which were categorised as inside the reserve. Therefore, separate before–after and control–effect (for after data) analyses were performed. The response of fish to protection was assessed by comparing the average density min^{-1} at each site in the before and after periods (with seasons and years within each period pooled together). After:Before ratios and SEs were calculated for the groups of species referred to above (except for target invertebrates, which were not surveyed before). For these comparisons, all sizes were used since before data did not provide enough detail to evaluate legal size limits. A GLM analysis was conducted to test the 'period' (i.e. before–after) fixed effect using the same procedures as described above for the GLMs from the 'after' data. Additionally, After:Before ratios and SEs were also obtained to the most frequently observed species followed by a bootstrap and CI analysis, as explained above.

Landings data

To detect possible inter-annual trends for some target species, complementing the observations from visual census, we analysed landings data at the Sesimbra port using the available information for the years 1995 through 2009 since licences to fish within this marine park were all assigned to fishers from Sesimbra. To ensure that fishing effort was comparable among years, we followed landings only from vessels with active licences for 2010 ($n = 73$ vessels). Moreover, these local and small vessels (<7 m) maintained their gear licences and vessel capacity through time, fishing mainly close to port and within the marine park. Annual total landings (kg) were averaged by year for each target species

to allow inter-annual comparisons. Price per kg (in euros) by species or groups of species was also obtained. Data were provided by the General Directorate of Fisheries and Aquaculture (DGPA). Revenues (in euros) were calculated through landings and price per kg.

RESULTS

Control-effect comparison

In the shallow rocky reefs of the Arrábida Marine Park, the groups analysed were composed of 17 species (from 6 families) of non-target cryptobenthic species (NTCF), 14 species (from 5 families) of non-target demersal fish (NTDF), 24 species (from 13 families) of target demersal fish (TDF) and 7 species (from 7 families) of target invertebrates (TI; Appendix 1).

Ratios of abundance and biomass revealed higher values inside than outside for most species groups (Fig. 2, Appendix 1). However, differences were larger for target species, especially for the response variable biomass in legal size (LS) specimens, suggesting that commercial fish and invertebrates are larger inside the reserve. Although LS TI did not show significantly higher values of biomass inside the reserve due to the large variability observed, TDF showed a highly significant positive effect (Table 3). Both groups also showed a significant association between bottom roughness and biomass and between boulder diversity and density.

On the other hand, the 2 non-target groups did not show positive responses to protection since significant interactions were found between reserve and habitat complexity indices. NTDF density varied with

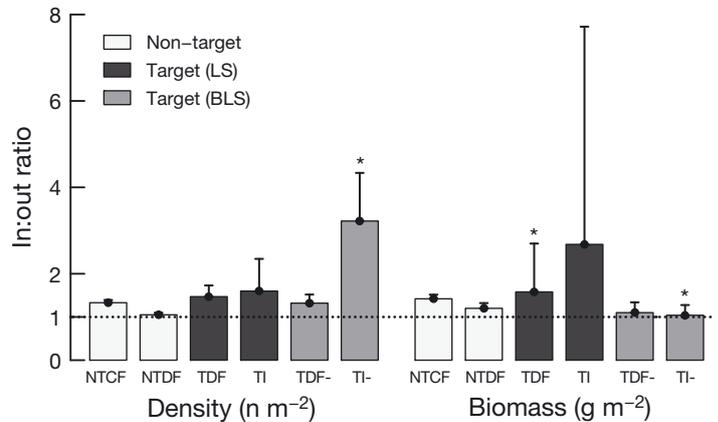


Fig. 2. Response ratio In:Out reserve + SE for density and biomass of non-target (light bars), legal size (dark bars) and below legal size (grey bars; indicated with -) target groups; NTCF: non-target cryptobenthic fish; NTDF: non-target demersal fish; TDF: target demersal fish; TI: target invertebrates. LS: legal size; BLS: below legal size. Ratios >1 (dotted line) indicate that response variables are higher inside the reserve. *: significant ratios (GLM results)

the interaction between reserve and both roughness and boulder diversity, whereas NTCF biomass and density showed a significant interaction between reserve and boulder diversity.

In contrast to the LS target groups, below legal-size (BLS) individuals for both demersal fish and invertebrates showed a larger response in density when compared to biomass (Fig. 2). The density of BLS TDF tended to be higher inside the reserve. However, both density and biomass showed a significant interaction between reserve and boulder diversity (Table 3). On the other hand, the density of BLS TI showed the largest In:Out ratio (Fig. 2) and a positive significant effect of reserve. Biomass was also affected by reserve and roughness without an inter-

Table 3. Generalized linear model results of reserve and habitat complexity indices effects (roughness and boulder diversity) on biomass (g m^{-2}) and density (no. m^{-2}) of the 4 species groups (NTCF: non-target cryptobenthic fish; NTDF: non-target demersal fish; TDF: target demersal fish; TI: target invertebrates) (LS: legal size; BLS: below legal size). Significant post hoc comparisons of factor reserve are indicated (highest values): (+) significant reserve effects; significant p-values in **bold**

Control-effect comparison	Reserve		Roughness		Boulder diversity		Reserve × Roughness		Reserve × Boulders diversity	
	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density
NTCF	<0.001	<0.001	0.002	0.32	0.81	0.45	0.27	0.27	0.003	0.001
NTDF	0.16	0.12	0.36	0.60	0.38	0.003	0.66	0.02	0.57	<0.001
TDF (LS)	<0.001 (+)	0.30	0.006	0.43	0.28	<0.001	0.38	0.60	0.96	0.96
TI (LS)	0.21	0.08	0.012	0.72	0.11	0.007	0.24	0.98	0.08	0.84
TDF (BLS)	0.28	0.004	<0.001	0.002	0.036	0.005	0.65	0.37	0.006	<0.001
TI (BLS)	0.016 (+)	<0.001 (+)	0.004	0.09	0.13	0.61	0.40	0.31	0.58	0.57

Table 4. BEST (Bio-Env) results of correlation between habitat features (multivariate data) with a dummy-coded variable for protection and the biomass of the 4 species groups (NTCF: non-target cryptobenthic fish; NTDF: non-target demersal fish; TDF: target demersal fish; TI: target invertebrates) (LS: legal size; BLS: below legal size). For physical and biotic habitats, see Tables 1 & 2, respectively. Spearman correlation coefficient (Rho) is included; significant p-values in **bold**

Control-effect comparison	Algae groups		Algae functional groups		Invertebrate phylum		Physical habitat	
	p	Rho	p	Rho	p	Rho	p	Rho
NTCF	0.01	0.48	0.01	0.32	0.07	0.28	0.34	0.24
NTDF	0.63	0.20	0.73	0.10	0.43	0.19	0.81	0.17
TDF (LS)	0.01	0.39	0.02	0.38	0.09	0.29	0.41	0.24
TI (LS)	0.11	0.31	0.054	0.27	0.016	0.38	0.08	0.41
TDF (BLS)	0.07	0.28	0.18	0.20	0.13	0.24	0.60	0.18
TI (BLS)	0.34	0.28	0.44	0.2	0.75	0.17	0.51	0.27

action of these factors (Table 3). Additionally, the relation between protection and habitat complexity indices revealed similar values for roughness ($p = 0.77$) but higher diversity of boulders inside the reserve ($p = 0.027$).

The relationship between habitat features and the different species groups was analysed for the variable biomass using protection level as a dummy variable (Table 4). NTCF and LS TDF revealed a significant correlation with algae cover, whereas NTDF did not associate with any habitat type. On the other hand, TI (LS) showed a dependence on invertebrate

cover and a marginally non-significant relation with algae functional groups. For BLS groups, no correlations with habitat features were detected. Interestingly, none of the groups showed a significant correlation with physical habitat, although this was the only habitat variable with significant differences between reserve and fished locations ($p = 0.007$).

Comparing the In:Out ratios for the most common species detected in the visual surveys, the following patterns in density (Fig. 3a) and biomass (Fig. 3b) emerged: (1) in general, target species showed a higher variability, especially in biomass; (2) LS *Octopus vulgaris* tended to be more abundant and were significantly larger inside the reserve, and BLS individuals also showed significantly higher biomass and density values inside the reserve; (3) white seabreams *Diplodus sargus* of all sizes were significantly more abundant and larger inside the reserve, as was the target velvet crab *Necora puber*; (4) the salema *Sarpa salpa* was more abundant and larger inside the reserve but showed a large variability and therefore In:Out ratios were not significant; (5) the small cryptobenthic triplefin blenny *Tripterygion delaisi* was the nontarget species with the largest sig-

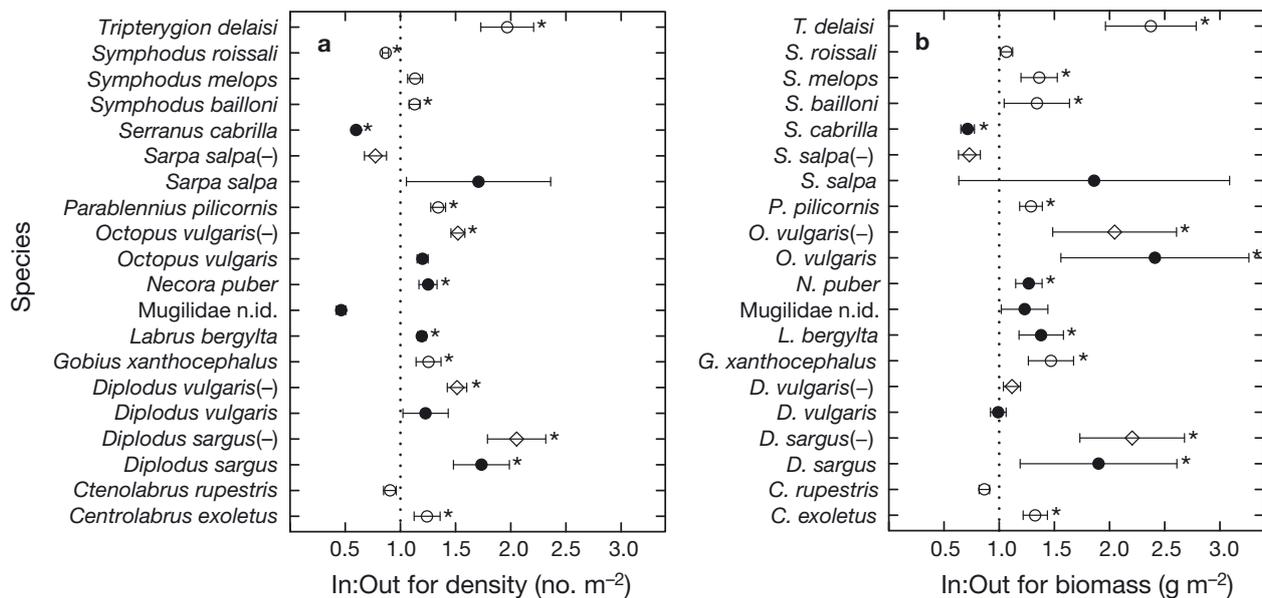


Fig. 3. Response ratio In:Out reserve \pm SE for (a) density and (b) biomass of the most frequently observed non-target species (O), legal size (●) and below legal size (◊; species indicated with '-') target species in the Arrábida Marine Park. Ratios > 1 (dotted line) indicate that response variables are higher inside the reserve. *: significant ratio

nificant reserve effect on both variables; (6) for the LS common 2-banded seabream *D. vulgaris*, biomass and density were similar outside and inside, but small specimens were significantly more abundant inside; (7) Mugilidae did not show significant ratios, but nevertheless presented higher abundances outside but larger biomass inside; (8) the comber *Serranus cabrilla*, which has no LS limit, was the only species having a significant ratio <1 (indicating higher values outside) both in density and biomass; (9) the non-target wrasse *Symphodus roissali* was significantly more abundant outside, but biomass values were similar between protected and fished areas.

Before–after comparison

The data collected in this study were compared to previous work performed in the same area before the establishment of the marine park (see Materials and Methods). Target species were more abundant in the after period, but no significant differences were found for any group (Fig. 4).

After:Before density ratios for the most frequently observed species (Fig. 5) show that the only significant variation was for *Serranus cabrilla*, which was more abundant in the before period. In addition, all other ratios <1 (albeit non-significant) were from non-target species. The sparids *Diplodus vulgaris*, *D. sargus* and *Sarpa salpa* showed the largest variability but also the largest increase among periods.

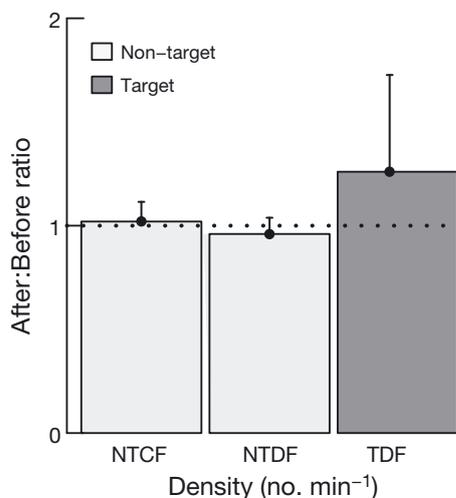


Fig. 4. Response ratio After:Before the implementation of the management plan + SE for density of non-target (light bars) and target (dark bar) groups; NTCF: non-target cryptobenthic fish; NTDF: non-target demersal fish; TDF: target demersal fish. Ratios >1 (dotted line) indicate that response variables are higher inside the reserve

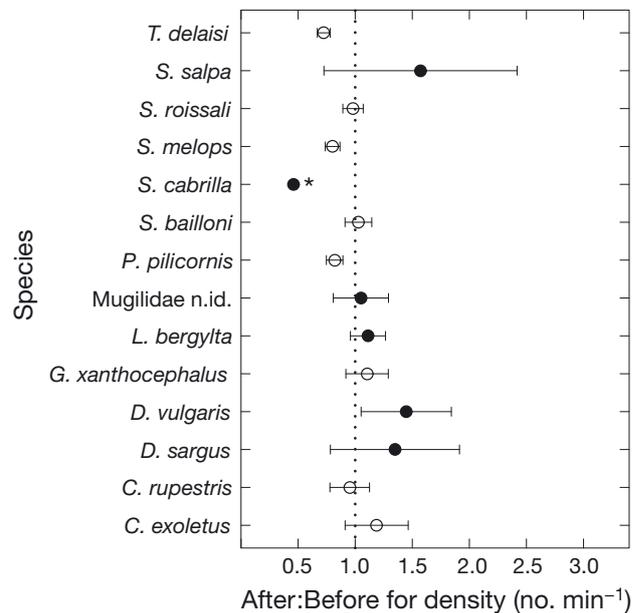


Fig. 5. Response ratio After:Before the implementation of the management plan ± SE for density of the most frequently observed non-target (O) and target (●) species in the Arrábida Marine Park. Ratios >1 (dotted line) indicate that response variables are higher in the after period. *: significant ratio. For full species names see Fig. 3a

Landings data

Octopus vulgaris was by far the most captured species from the local fishing fleet in the marine park (Table 5). The sparid *Diplodus sargus* was the most valuable species in price per kg. *Sarpa salpa*, mullets (Mugilidae) and wrasses (Labridae) are bycatch species with low market value. *Serranus cabrilla*, also a bycatch species with low market value, was shown to be a valuable species due to data aggregation in the official records with other more valuable subtropical serranids caught elsewhere (West African coast).

Landing patterns of park-licensed vessels (Fig. 6) showed a steady increase and great dependence of the local fisheries on octopus, with a significant increase in landings immediately before the park was established (2004–2005) followed by a decrease (2006–2007) compensated with another increase in the most recent years (2008–2009). A decrease in captures of seabreams from 2003 to 2006 is also apparent, followed by an increase in landings until the last year with official statistics (before 2006, *Diplodus sargus* was mixed with other seabreams, though not with *D. vulgaris*, in the category *Diplodus* spp., of which it represents the largest element; this explains the sharp decline of this group from 2007 on).

Table 5. Mean annual landings and price kg^{-1} of the most important commercial species from vessels with a licence to operate in the marine park in 2010. Means were calculated from 1995 to 2009. *Diplodus sargus* price was obtained from *Diplodus* spp. and *Sarpa salpa* price was obtained from the unidentified Sparidae category. No price information was available for unidentified Mugilidae or Labridae (source: General Directorate of Fisheries and Aquaculture, DGPA). For full species names see Fig. 3a

Species	Landings (kg)	Price kg^{-1} (euros)	Revenue (euros)
<i>Octopus vulgaris</i>	105679	4.2	443852
<i>D. sargus</i>	976	6.2	6052
<i>D. vulgaris</i>	575	4	2303
Unidentified Mugilidae	306	–	–
<i>S. salpa</i>	188	0.9	169
Unidentified Labridae	28	–	–
Unidentified Serranidae	5	4.9	23

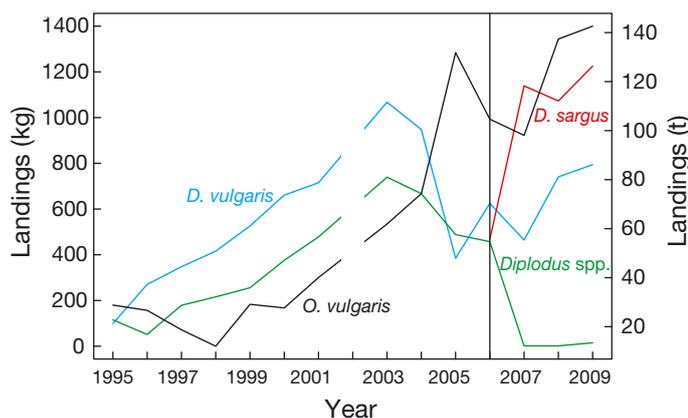


Fig. 6. Fisheries landings of *Diplodus vulgaris*, *D. sargus* and *Diplodus* spp. Landings of *Octopus vulgaris* are in metric tons (right y-axis). Data are from vessels with a licence to fish in the park. No data are available for 2002 (source: General Directorate of Fisheries and Aquaculture, DGPA). Vertical black line in 2006: implementation of the management plan approved in August 2005. For full species names see Fig. 3a

DISCUSSION

MPAs have been widely studied, and several reviews have confirmed their global potential to recover marine resources and ecosystems (Halpern 2003, Micheli et al. 2004, Lester et al. 2009, Hamilton et al. 2010). However, a major challenge is disentangling the effects of protection from those of unique habitat characteristics (García-Charton & Pérez-Ruzafa 1999). In fact, there is a general lack of before data, which is particularly evident in temperate systems (but see Claudet et al. 2006, Shears et al.

2006). This is a potential confounding effect in the assessment of MPA effectiveness and the interpretation of positive responses, since some differences between reserve and fished areas in, for example, habitat quality, could pre-date MPA implementation. In fact, it has been hypothesised that the location of several marine reserves is associated with particularly diverse habitats or assemblages and therefore the observed differences between fished and reserve sites could be due to the fact that reserves are in better areas than fished zones (García-Charton & Pérez-Ruzafa 1999, Côté et al. 2001). Nevertheless, the observed reserve effect in many MPAs does not seem to be an artifact of reserves being situated in better locations (Lester et al. 2009). The existence of data collected before the establishment of marine reserves is therefore central to disentangle habitat influences in the assemblages' composition from responses to management effects.

Our study addressed some of these shortcomings through a control-effect (inside-outside) and a before-after (inside only) comparison. Although outside data were not available in the before period, the evaluation of the reserve effect in the after period was complemented by a habitat assessment inside and outside the reserve and the analysis of landings trends of the artisanal fishing feet operating in the marine park. The small size of the studied reserve, the phasing-in of the management plan during the first 4 yr of its implementation and the multiple activities affecting this marine region over time, led us to expect small differences, if any, between the reserve and fished areas of the Arrábida Marine Park.

Most species groups showed higher density and biomass ratios inside the reserve. This raises the hypotheses that (1) the reserve is starting to produce effects which are widespread for all groups of species; (2) the reserve could be a zone with more favourable habitat features for local species; (3) there is an interaction between these 2 effects (more diverse habitats inside and a reserve effect) that could explain the observed trends. The largest effects were detected in the target species groups, with significantly higher biomass of demersal fish and small invertebrates (BLS) inside the reserve. These differences were not influenced by habitat complexity.

In fact, all groups showed a significant effect of either roughness or boulder diversity in relation to biomass, density or both. However, only small species such as those from the NTCF or BLS demersal groups revealed a strong interaction between the reserve and boulder diversity in biomass or density,

indicating a lack of reserve effect. When the response to the reserve was tested for complexity indices, only boulder diversity showed significantly higher values inside the reserve. This predictor did not influence the biomass of target groups. The greater variability of boulder sizes potentially increases the abundance of small refuges, which may affect cryptobenthic species such as gobies and blennies, which are by definition strongly dependent on habitat (Willis & Anderson 2003). Additionally, despite the differences in the physical features of the habitat between reserve and fished sites, no correlation was found between any species groups' assemblages and these characteristics. Moreover, there were significant correlations with different biotic habitats for all species groups, but these did not vary with the reserve.

Contrary to what could be expected, TI did not reveal a significant response to protection, in spite of being the second group with the highest In:Out ratio for density and by far the highest ratio for biomass. The lack of a significant reserve effect in this group is probably related to the high variability associated with this ratio which suggests large differences between samples.

The analyses of the most frequently observed species support our hypothesis that the positive response to protection of target species is a first sign of the reserve effect since both the valuable seabreams (especially *Diplodus sargus*) and *Octopus vulgaris* (the most landed target species) showed proportionally the largest increase in biomass, suggesting larger individuals inside the reserve. It is particularly striking that *D. sargus* showed such a strong response to protection since it is potentially a vagile species with a wide home range (Abecasis et al. 2009, Lino et al. 2009) and low habitat connectivity requirements, allowing it to cross large sandy areas (Vega Fernández et al. 2008). This species is therefore potentially vulnerable to fishing when it moves out from the reserve. Further studies on the behaviour of this species throughout ontogeny as well as patterns of movement of individuals within the reserve habitats are needed to fully explain these results. Claudet et al. (2010) found that the effect of protection was as strong for mobile as for sedentary species and that this effect was enhanced for larger species that were not found in obligate schools (which is the case for seabreams). Di Franco et al. (2009) also found high densities of large fishes inside reserves which were attributed to a change in behaviour since fish seemed to avoid the reefs when they were intensively fished. Daily and seasonal move-

ments can also be influenced by local social dynamics and fish social status (Afonso et al. 2008) which together with attraction from conspecifics may increase the probability that certain vagile species will remain within the reserve, increasing competition but benefiting from a decrease of mortality from fishing (Claudet et al. 2010).

Prior to the implementation of the marine reserve, the nearshore rocky reefs were intensively exploited by spearfishing and recreational angling due to the prevailing year-round calm seas in the park, its shallow rocky reefs and high habitat complexity (Gonçalves et al. 2003). Recreational fishing has been shown to have large effects on higher trophic levels and in particular on nearshore shallow ecosystems (Cooke & Cowx 2004), since even at moderate levels, continuous fishing effort can remove a significant proportion of larger fishes (Di Franco et al. 2009). This recreational fishery is mainly directed to large sparids and octopus (Rocklin et al. 2011), which are also targeted by commercial fishing with hooks and lines, traps and jigs (Erzini et al. 2008). The exclusion of these fishing pressures from the reserve may explain why these formerly intensively exploited species on the shallow rocky reefs showed the largest responses in biomass among different protection zones.

Comparisons between before and after periods in species patterns suggest that almost all non-target species reduced or maintained their abundance, whereas target species showed the opposite trend towards an increase in density after the establishment of the marine park. However, due to the high variability in species responses, these differences were non-significant. Additionally, no sites were sampled in the current fished zones in the before period. For these reasons, these trends should be interpreted with caution. Several studies have demonstrated that time since protection is essential to detect reserve effects (Micheli et al. 2004, Claudet et al. 2008), especially for large and long-lived species since they require time to grow and reproduce.

In the non-target groups, a few species, especially *Tripterygion delaisi* and some wrasses, were more abundant inside than outside but showed a decreasing pattern in the reserve from before to after protection was established. Possible differences in habitat quality (with higher boulder diversity inside) could be an important factor leading to a higher abundance of *T. delaisi* inside and also supporting a higher rate of post-settlement survivorship in wrasses (Pérez-Matus & Shima 2010). In fact, adult wrasses require a

high level of connectivity among similar habitats to be able to migrate between different coastal zones since, unlike sparids, these species do not easily cross extensive areas of sand (Vega Fernández et al. 2008). Another interesting result was that the only target species having a significantly higher density and biomass outside the reserve (*Serranus cabrilla*) also showed a significant decrease in density between periods. The lack of a reserve effect for this species was also found in other studies (García-Rubies & Zabala 1990). Nevertheless, further work is needed to explain its decrease in density.

Despite the recent implementation of the marine park management plan, comparing areas inside and outside the reserve and the before and after periods showed that target species are responding positively to protection, whereas non-target ones are not, and these responses are occurring in biomass but not yet in numbers. The positive response to protection of individuals' size and biomass have been described as early indicators of the reserve effect (Pelletier et al. 2008, Di Franco et al. 2009, Lester et al. 2009), even after only a few years of closure, especially when fishing targets large individuals (Erzini et al. 2006). Indeed, in other studies, effects were found a short time (2 to 4 yr) after the establishment of the reserve (García-Charton et al. 2004, Micheli et al. 2005, Claudet et al. 2008, Di Franco et al. 2009). The increase in number takes a longer time to become detectable as it depends on inter-annual biological and environmental conditions such as variability in recruitment patterns, changes in pre- and post-settlement mortality, larval dynamics and oceanographic features (García-Charton et al. 2004). Additionally, although reserve size and age affects the magnitude of the response (Tetreault & Ambrose 2007), effects in small reserves (similar in size to the present case) have shown large increases in average individual size (Claudet et al. 2008, 2010, Lester et al. 2009), particularly for intensively fished species (Micheli et al. 2004).

While commonly lacking in MPA studies, information on spatial and temporal patterns of fishing effort relative to reserve placement and timing may be one of the most critical factors for interpreting patterns of change (Claudet et al. 2008, Di Franco et al. 2009). In fact, it has been shown that positive responses to protection may be influenced by an increase in fishing effort in adjacent fished areas due to displacement (Tetreault & Ambrose 2007, Claudet & Guidetti 2010). We followed the same licensed vessels operating with a stable fishing capacity throughout time, and interestingly, there was a steep increase in land-

ings immediately before the implementation of management measures, especially for the most captured species (*Octopus vulgaris*), suggesting that fishers were concerned about the effects of the impending reserve implementation and the loss of fishing grounds. There are 2 potential and non-mutually exclusive explanations for this increase. (1) Fishermen fished harder in the time leading up to reserve implementation to bolster revenues before a perceived loss. (2) Reporting of catches increased in order to guarantee a renewal of the park fishing licence, which required a minimum of 100 sales yr⁻¹. We know of no published cases where fishing pressure increased specifically in response to future reserve implementation, but the ramifications to fisheries-independent studies of reserves are potentially large. Fisheries data also revealed an increase in landings for commercial species targeted by the local artisanal fishing fleet after the marine park implementation, supporting the positive trend in response to protection, and reinforcing the evidence of a recovery in size and possibly in numbers for these species. Both larger octopus and seabreams could perform movements possibly related to some degree of spillover which may explain this increase.

The inclusion of previous baseline data and landings information together with habitat influence and control-effect comparisons, discriminating commercial LS individuals from juveniles and small fish, provided a stronger case for the detection of reserve effects even after only 3 to 4 yr since the establishment of protection.

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LITERATURE CITED

Abecasis D, Bentes L, Erzini K (2009) Home range, residency and movements of *Diplodus sargus* and *Diplodus vulgaris* in a coastal lagoon: connectivity between nursery and adult habitats. *Estuar Coast Shelf Sci* 85:525–529

- Afonso P, Fontes J, Holland KN, Santos RS (2008) Social status determines behaviour and habitat usage in a temperate parrotfish: implications for marine reserve design. *Mar Ecol Prog Ser* 359:215–227
- Beldade R, Erzini K, Gonçalves EJ (2006) Composition and temporal dynamics of a temperate rocky cryptobenthic fish assemblage. *J Mar Biol Assoc UK* 86:1221–1228
- Bellwood DR, Alcalá AC (1988) The effect of a minimum length specification on visual estimates of density and biomass of coral reef fishes. *Coral Reefs* 7:23–27
- Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth
- Claudet J, Guidetti P (2010) Improving assessments of marine protected areas. *Aquatic Conserv* 20:239–242
- Claudet J, Pelletier D, Jouvenel JY, Bachet F, Galzin R (2006) Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: identifying community-based indicators. *Biol Conserv* 130:349–369
- Claudet J, Osenberg CW, Benedetti-Cecchi L, Domenici P and others (2008) Marine reserves: Size and age do matter. *Ecol Lett* 11:481–489
- Claudet J, Osenberg CW, Domenici P, Badalamenti F and others (2010) Marine reserves: Fish life history and ecological traits matter. *Ecol Appl* 20:830–839
- Claudet J, Guidetti P, Mouillot D, Shears NT, Micheli F (2011a) Ecological effects of marine protected areas: conservation, restoration, and functioning. In: Claudet J (ed) *Marine protected areas—a multidisciplinary approach*. Cambridge University Press, Cambridge, p 37–71
- Claudet J, García-Charton J, Lenfant P (2011b) Combined effects of levels of protection and environmental variables at different spatial resolutions on fish assemblages in a marine protected area. *Conserv Biol* 25:105–114
- Colton DE, Alevizon WS (1981) Diurnal variability in a fish assemblage of a Bahamian coral reef. *Environ Biol Fishes* 6:341–345
- Cooke SJ, Cowx I (2004) The role of recreational fishing in global fish crises. *Bioscience* 54:857–859
- Côté IM, Mosqueira I, Reynolds JD (2001) Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *J Fish Biol* 59:178–189
- Di Franco A, Bussotti S, Navone A, Panzalis P, Guidetti P (2009) Evaluating effects of total and partial restrictions to fishing on Mediterranean rocky-reef fish assemblages. *Mar Ecol Prog Ser* 387:275–285
- Dobson A (1990) An introduction to generalized linear models. Chapman and Hall, London
- Erzini K, Gonçalves JMS, Bentes L, Moutopoulos DK and others (2006) Size selectivity of trammel nets in southern European small-scale fisheries. *Fish Res* 79:183–201
- Erzini K, Bentes L, Coelho R, Lino PG, Monteiro P, Ribeiro J, Gonçalves JMS (2008) Catches in ghost-fishing octopus and fish traps in the northeastern Atlantic Ocean. *Fish Bull* 327:321–327
- Forcada A, Bayle-Sempere JT, Valle C, Sanchez-Jerez P (2008) Habitat continuity effects on gradients of fish biomass across marine protected area boundaries. *Mar Environ Res* 66:536–547
- Fraschetti S, Claudet J, Grorud-Colvert K (2011) Transitioning from single-sector management to ecosystem-based management: What can marine protected areas offer? In: Claudet J (ed) *Marine protected areas—a multidisciplinary approach*. Cambridge University Press, Cambridge, p 11–34
- Froese R, Pauly D (eds) (2011) *FishBase*. www.fishbase.org
- García-Charton JA, Pérez-Ruzafa A (1999) Ecological heterogeneity and the evaluation of the effects of marine reserves. *Fish Res* 42:1–20
- García-Charton JA, Pérez-Ruzafa A, Sánchez-Jerez P, Bayle-Sempere JT, Reñones O, Moreno D (2004) Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. *Mar Biol* 144:161–182
- García-Rubies A, Zabala M (1990) Effects of total fishing prohibition on the rocky fish assemblages of Medes Islands marine reserve (NW Mediterranean). *Sci Mar* 54:317–328
- Gonçalves EJ, Henriques M, Almada VC (2003) Use of a temperate reef-fish community to identify priorities in the establishment of a marine protected area. In: Beumer JP, Grant A, Smith DC (eds) *Aquatic protected areas: What works best and how do we know? Proceedings of the World Congress on Aquatic Protected Areas*. Australian Society for Fish Biology, North Beach, p 261–272
- Goñi R, Adlerstein S, Alvarez-Berastegui D, Forcada A and others (2008) Spillover from six western Mediterranean marine protected areas: evidence from artisanal fisheries. *Mar Ecol Prog Ser* 366:159–174
- Goñi R, Hilborn R, Díaz D, Mallol S, Adlerstein S (2010) Net contribution of spillover from a marine reserve to fishery catches. *Mar Ecol Prog Ser* 400:233–243
- Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? *Ecol Appl* 13:117–137
- Hamilton SL, Caselle JE, Malone DP, Carr MH (2010) Incorporating biogeography into evaluations of the Channel Islands marine reserve network. *Proc Natl Acad Sci USA* 107:18272–18277
- Henriques M, Gonçalves E, Almada V (1999) The conservation of littoral fish communities: a case study at Arrábida coast (Portugal). In: Almada V, Oliveira R, Gonçalves E (eds) *Behaviour and conservation of littoral fishes*. ISPA, Lisbon, p 473–513
- Henriques M, Gonçalves EJ, Almada VC (2007) Rapid shifts in a marine fish assemblage follow fluctuations in winter sea conditions. *Mar Ecol Prog Ser* 340:259–270
- Kramer D, Chapman M (1999) Implications of fish home range size and relocation for marine reserve function. *Environ Biol Fishes* 55:65–79
- Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J and others (2009) Biological effects within no-take marine reserves: a global synthesis. *Mar Ecol Prog Ser* 384:33–46
- Lino PG, Abecasis D, Neves M, Erzini K (2009) Comparative behavior of wild and hatchery reared white sea bream (*Diplodus sargus*) released on artificial reefs off the Algarve (Southern Portugal). In: Nielsen JL, Arrizabalaga H, Fragoso N, Hobday A, Lutcavage M, Sibert J (eds) *Tagging and tracking of marine animals with electronic devices*. Springer, Dordrecht, p 23–34
- Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: the emerging science of marine reserves. *Ecol Appl* 13:3–7
- McCullagh P, Nelder JA (1989) *Generalized linear models*. Chapman and Hall, London
- Micheli F, Halpern BS, Botsford LW, Warner RR (2004) Trajectories and correlates of community change in no-take marine reserves. *Ecol Appl* 14:1709–1723

- Micheli F, Benedetti-Cecchi L, Gambaccini S, Bertocci I, Borsini C, Osio GC, Romano F (2005) Cascading human impacts, marine protected areas, and the structure of Mediterranean reef fish assemblages. *Ecol Monogr* 75: 81–102
- Osenberg CW, Shima JS, Miller SL, Stier AC (2011) Assessing the effects of marine protected areas: confounding in space and possible solutions. In: Claudet J (ed) *Marine protected areas—a multidisciplinary approach*. Cambridge University Press, Cambridge, p 143–167
- Pelc RA, Warner RR, Gaines SD, Paris CB (2010) Detecting larval export from marine reserves. *Proc Natl Acad Sci USA* 107:18266–18271
- Pelletier D, Claudet J, Ferraris J, Benedetti-Cecchi L, García-Charton JA (2008) Models and indicators for assessing conservation and fisheries-related effects of marine protected areas. *Can J Fish Aquat Sci* 65:765–779
- Pérez-Matus A, Shima JS (2010) Disentangling the effects of macroalgae on the abundance of temperate reef fishes. *J Exp Mar Biol Ecol* 388:1–10
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at www.R-project.org
- Rocklin D, Tomasini JA, Culioli JM, Pelletier D, Mouillot D (2011) Spearfishing regulation benefits artisanal fisheries: the ReGS indicator and its application to a multiple-use Mediterranean marine protected area. *PLoS ONE* 6:e23820
- Russ GR, Alcalá AC (2004) Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* 138:622–627
- Russ GR, Alcalá AC (2010) Decadal-scale rebuilding of predator biomass in Philippine marine reserves. *Oecologia* 163:1103–1106
- Shears NT, Grace RV, Usmar NR, Kerr V, Babcock RC (2006) Long-term trends in lobster populations in a partially protected vs. no-take marine park. *Biol Conserv* 132: 222–231
- Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* 69:476–498
- Tetreault I, Ambrose R (2007) Temperate marine reserves enhance targeted but non-targeted fishes in multiple no-take MPAs. *Ecol Appl* 17:2251–2267
- Vega Fernández T, D'Anna G, Badalamenti F, Pérez-Ruzafa AP (2008) Habitat connectivity as a factor affecting fish assemblages in temperate reefs. *Aquat Biol* 1:239–248
- Willis TJ, Anderson MJ (2003) Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Mar Ecol Prog Ser* 257:209–221
- Wooster WS, Bakun A, McLain DR (1976) The seasonal upwelling cycle along the eastern boundary of the North Atlantic. *J Mar Res* 34:131–141

Appendix 1. Biomass and density (mean \pm SE; minimum and maximum values in parentheses), frequency of occurrence, number of species and families between inside vs. outside the reserve for each species group analysed: NTCF: non-target cryptobenthic fish; NTDF: non-target demersal fish; TDF: target demersal fish; TI: target invertebrates; LS: legal size; BLS: below legal size

Group	Biomass		Density		Frequency		No. species	No. families
	Inside	Outside	Inside	Outside	Inside	Outside		
NTCF	0.48 \pm 0.01 (0.005–4.72)	0.34 \pm 0.01 (0.006–3.83)	0.094 \pm 0.002 (0.015–0.711)	0.071 \pm 0.002 (0.015–0.785)	3399	1169	17	6
NTDF	0.3 \pm 0.01 (0.001–6.87)	0.25 \pm 0.01 (0.002–4.29)	0.018 \pm 0.0004 (0.004–0.308)	0.017 \pm 0.001 (0.004–0.25)	3198	1334	14	5
TDF (LS)	4.3 \pm 0.24 (0.001–166.9)	2.73 \pm 0.4 (0.009–181.8)	0.035 \pm 0.002 (0.004–0.833)	0.024 \pm 0.001 (0.004–0.25)	2145	811	24	13
TI (LS)	10.48 \pm 1.59 (0.011–328)	3.9 \pm 0.842 (0.023–45.7)	0.039 \pm 0.0045 (0.004–1.231)	0.024 \pm 0.0017 (0.004–0.077)	498	132	7	7
TDF (BLS)	3.01 \pm 0.16 (0–66.24)	2.73 \pm 0.28 (0.01–55.88)	0.063 \pm 0.004 (0.004–1.386)	0.077 \pm 0.006 (0.004–1.154)	1224	405	20	12
TI (BLS)	4.35 \pm 0.48 (0–34.42)	4.16 \pm 0.54 (0.01–10.59)	0.063 \pm 0.005 (0.005–0.308)	0.019 \pm 0.002 (0.015–0.077)	225	60	5	5

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