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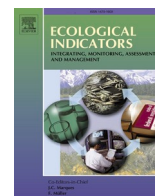
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Inconsistent relationships among protection, benthic assemblage, habitat complexity and fish biomass in Mediterranean temperate rocky reefs

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ABSTRACT

Marine Protected Areas (MPAs) have been proved to effectively protect and restore fish assemblages. There is mixed evidence regarding the effects of MPAs on benthic assemblages, habitat complexity, and how protection might mediate the effects of habitat features (including biotic and abiotic components) on fish assemblages, with very little information concerning temperate areas. Here, our aim is to assess how protection 1) influences benthic assemblages and habitat complexity, and 2) mediates the effects of habitat complexity on fishes.

Using non-destructive methods (photosampling for shallow rocky benthic assemblages, and underwater visual census using strip transects for fish assemblages) to characterize benthic and fish assemblages, we sampled 15 Mediterranean locations, each including protected and unprotected sites. In all, we sampled 90 sites, and analyzed 2,760 photos and 800 replicated transects, gathering information on 44 benthic and 72 fish taxa. Abiotic, biotic and synthetic (i.e. combining the previous two) complexity indices have been computed to synthesize habitat features. Overall, whole benthic assemblages did not significantly differ between protected and unprotected conditions, but higher cover of the ecologically important erect algae belonging to the genus *Cystoseira sensu lato* was recorded within MPAs. Abiotic, biotic and synthetic complexity did not show clear patterns related to protection levels, displaying inconsistent responses between different locations. Our findings highlight that protection has a generally positive effect on fish biomass, this latter variable responding independently of the habitat complexity.

Our study, in conclusion, confirms that MPAs can be effective to protect and restore rocky-reef assemblages, highlighting the need for more in-depth exploration of the mechanisms determining the different responses of benthic taxa to protection and how this can influence the associated fish assemblages.

1. Introduction

Oceans and seas worldwide provide food and other ecosystem services to about 3 billion people (Worm, 2016; Díaz et al., 2018; FAO, 2018). The increasing global demand for seafood is causing considerable over-exploitation of marine resources (Worm, 2016). Over-fishing,

together with other human-driven impacts such as pollution, urbanization and climate change, have induced alterations in species and ecosystems (Jackson et al., 2001; Costello et al., 2016). Human pressures can also cause habitat loss or degradation by simplifying the three-dimensional structure of marine habitats (Munday, 2004; Airoldi et al., 2008; Bianchi et al., 2012; Russ et al., 2015; McClure et al., 2020).

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Habitat structure can be described as the tri-dimensionality of the habitat, usually referred to as ‘habitat complexity’, determined by abiotic (e.g. the physical rugosity) and biotic (e.g. the architecture of the benthic cover) elements (Carvalho and Barros, 2017; Musard et al., 2014). Halvorsen et al. (2020) called ‘ecodiversity’ the variety of units defined by both the abiotic and biotic components. The role of habitat complexity in sustaining rich and diverse assemblages is generally acknowledged (Roberts et al., 2003; Griffin et al., 2009; Munguia et al., 2011) and it involves the provision of a variety of food and refuge resources, (McCoy and Bell, 1991; Friedlander and Parrish, 1998; García-Charton and Ruzafa, 1999; Carminatto et al., 2020).

In the Mediterranean Sea, macroalgal forests (mostly formed by erect macroalgae belonging to the genus *Cystoseira sensu lato* and *Sargassum*) are among the most important benthic assemblages in the infralittoral zone (Thibaut et al., 2014; Mineur et al., 2015). Erect macroalgae play an essential role by providing habitat (e.g. for refuge) and food resources (e.g. as a direct energy resource for herbivores and indirectly by hosting invertebrates that can be preyed upon by other consumers) for several rocky reef fish species thus effectively sustaining fish assemblages (Thiriet et al., 2016; Cheminée et al., 2017). Macroalgal forests in the Mediterranean Sea are significantly declining (Thibaut et al., 2005; Fabbri et al., 2020) due to multiple stressors including pollution (Mangialajo et al., 2008), climate change (Gatti et al., 2017) and overgrazing, the latter being the consequence of: 1) overfishing of sea urchin predators triggering a phase-shift to barren areas (i.e. rocks with encrusting algae, Sala et al., 1998; Guidetti, 2006; Montefalcone et al., 2011; Pinna et al., 2020); 2) grazing pressure by herbivorous fishes, both native (e.g. *Sarpa salpa*; Gianni et al., 2017) and non-indigenous (e.g. *Siganus luridus* and *S. rivulatus*; Stergiou, 1988; Sala et al., 2011; Bianchi et al., 2014). The decline of macroalgal forests is inducing a loss of structural complexity in Mediterranean rocky reefs, potentially impairing the ecological processes determining the patterns of fish distribution and abundance (Bonaca and Lipej, 2005; Thiriet et al., 2016; Cheminée et al., 2017).

To protect marine biodiversity and habitat, >1,000 Marine Protected Areas (MPAs *sensu lato*, including both nationally and internationally designated MPAs) have been established in the Mediterranean basin (PISCO and UNS, 2016). MPAs are widely considered as an effective spatially-explicit tool to manage fish stocks while supporting community- and ecosystem-wide protection and recovery (Fox et al., 2012b; Di Franco et al., 2016; Di Lorenzo et al., 2020). In the Mediterranean region, nationally designated MPAs (that currently outperform internationally designated MPAs in terms of reserve effect; Guidetti et al., 2019) are generally multiple-use MPAs usually including one or more no-take zones. Such no-take zones are often small in size (50% of these areas being <1 km², Di Franco et al., 2018) and do not allow extractive activities. Furthermore, they are surrounded by buffer zones, where some activities (e.g. some forms of fishing, recreational scuba diving) are allowed but which are generally more strictly regulated compared to unprotected zones (i.e. outside MPA borders), thus potentially curbing extractive and non-extractive threats (Dudley, 2013; PISCO and UNS, 2016; Zupan et al., 2018). Overall, 6% of the Mediterranean Sea is covered by protection (including both nationally and internationally designated MPAs), but 95% of this area shows no difference between the regulations imposed inside the MPAs compared with those outside (Claudet et al., 2020).

While it is now widely acknowledged that effectively managed MPAs can support healthy fish assemblages (Fox et al., 2012a; Edgar et al., 2014; Giakoumi et al., 2017), there is contrasting evidence concerning the effect of protection on the composition of benthic assemblages and on biotic habitat complexity (see Russ et al., 2015; Robinson et al., 2019; McClure et al., 2020, 2021). Little information is available about how protection measures can mediate the effect of habitat structure (including biotic and abiotic components) on fish assemblages, with this body of evidence mostly referring to coral reefs (e.g. Russ et al., 2015; Robinson et al., 2019; McClure et al., 2020, 2021) and virtually none

covering temperate regions.

The aims of this study, carried out in 15 Mediterranean MPAs are, therefore, to assess: 1) how protection influences benthic assemblages and habitat complexity (i.e. the tri-dimensionality of the habitat); 2) whether protection can mediate the effect of habitat complexity on fish assemblages. The explicit hypotheses of this study are: 1) habitat complexity is higher in MPAs compared to unprotected areas. This can be the result of the reduction of direct anthropogenic disturbances (e.g. fishing, anchoring) impacting benthic assemblages within MPAs; 2) the relationship between habitat complexity and fish biomass (i.e. the variable widely recognized as the most responsive indicator of the conservation status of fish assemblages, as it inherently integrates both density and size) is significant and positive only inside the MPAs. This can be the result of the significant anthropogenic pressures (e.g. fishing) occurring especially outside the borders of the MPAs, mainly concentrated in areas associated with high complexity, finally altering the natural relationship between fish assemblages and habitat features (Fig. 1).

2. Material and methods

2.1. Study area and sampling design

The study was carried out at 15 locations (each including both protected and unprotected zones) in the Mediterranean Sea (see Supplementary Table S1), listed here from west to east: Cabo de Palos (Spain), Freus d’Eivissa i Formentera (Spain), Cap de Creus (Spain), Medes Islands (Spain), Banyuls (France), Côte Bleue (France), Cap Roux (France), Asinara (Italy), Bonifacio (France), Egadi Islands (Italy), Strunjan (Slovenia), Telascica (Croatia), Torre Guaceto (Italy) and Zakynthos (Greece) (Fig. 2).

At each location, no-take, buffer and unprotected zones were investigated. In each zone, 2 sites were sampled and selected randomly among a subset of available sites characterized by the occurrence of rocky substrate within a depth range of 5–12 m. At each of the two MPAs that do not include a buffer zone (i.e. Côte Bleue and Cap Roux), sampling was done at 2 sites inside the no-take zone and 4 sites in unprotected zones outside the MPA.

2.2. Data collection

2.2.1. Fish assemblages

Fish assemblages were sampled by means of underwater visual census (UVC) using strip transects of 25 m × 5 m (Harmelin-Vivien et al., 1985), thus covering 125 m² each. Along each transect, a trained diver operator using SCUBA swam one way at constant speed (covering each transect in approximately 6–8 min), recording the abundance and size of all fishes encountered. The transect was laid as the fish were counted, to minimize disturbance to the fish (Dickens et al., 2011; Emslie et al., 2018).

Considering that some individuals of crypto-benthic species (e.g. family Blenniidae, Gobiidae, Scorpaenidae), more difficult to spot, could have been missed (Thiriet et al., 2016), after completing the transect, on the way back, the diver focused on counting these species, taking care to check in holes and crevices, and avoiding double counting. At each site, 8 to 12 replicates (transects) were conducted (for a total of 800 UVC performed during this study).

Following the approach of Harmelin-Vivien et al. (1985) and widely adopted in the Mediterranean Sea, fish abundance was estimated by counting individual fishes from one to ten and using the following abundance classes for larger groups: 11–30, 31–50, 51–100, 101–200, 201–500, >500 individuals. Fish density (number of individuals · 125 m⁻²) was estimated by considering the mid-point of each abundance class.

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 the dusky grouper *Epinephelus*

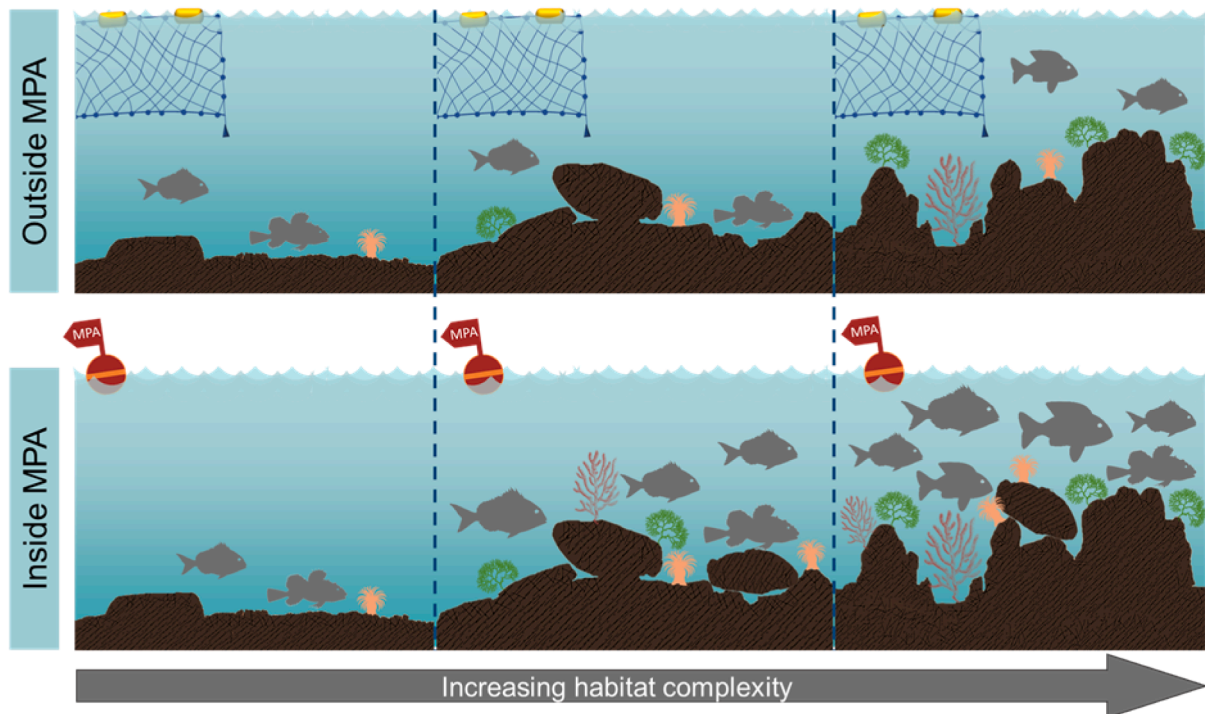


Fig. 1. Schematic representation of the hypothesis regarding how MPAs could mediate the effect of habitat complexity on fish assemblages. This study hypothesizes an increase of biotic and abiotic complexity inside MPAs which in turn would support higher fish biomass inside the MPAs, both in the buffer and no-take zones.



Fig. 2. Locations investigated in the Mediterranean Sea. Each location includes both protected (within MPAs) and unprotected sites.

marginatus.

To maximize consistency in estimations of fish density and size, UVCs were carried out at all sites by the same team of scientific divers (ADF, AC, MDL).

Fish wet weight (hereafter called biomass) was estimated from size data by means of length–weight relationships from the available literature, selecting coefficients referring to Mediterranean samples whenever possible (<http://www.fishbase.org>). Biomass was calculated for each fish in each transect, and then summed to obtain the total biomass of fish per transect (also known as community biomass, Cardinale et al., 2013) that has been used as response variable in the analysis (see below).

2.2.2. Benthic assemblages

To characterize shallow rocky benthic assemblages and estimate

biotic complexity, at each site where UVC were carried out, approximately 50 photos were taken at one-meter vertical distance from the bottom with a GoPro camera mounted on a pole. The photos were randomly interspersed over the site. The GoPro was initially calibrated through a grid of known size to allow quantitative estimation of benthic cover. Pictures (50 × 50 cm, corresponding to 0.25 m² sampling area) were imported on a computer and, after the removal of blurred and uninterpretable photos, a random subset of 30 photos *per* site (for a total of 2760 photos) was selected. Based on assessment of multivariate pseudo-standard error (MultSE) (Anderson and Santana-Garcon, 2015), which is a direct analogue to the univariate standard error and is considered as a useful quantity for assessing sample-size adequacy with multivariate data implemented in dissimilarity-based multivariate analyses, this sample size resulted 2–3 times larger than the minimum required to adequately sample the benthic assemblages for comparative

analysis (between 10 and 15 photos were sufficient to characterize the benthic assemblage at each site i.e. levelling-off MultSE around these sample sizes, see [Supplementary Fig. S1](#)).

Images were analyzed by superimposing a grid of 25 squares, each representing 4% of the total area ([Bianchi et al., 2004](#)). Data consisted of visual estimates of percent cover for conspicuous sessile algae and invertebrates obtained by adding up the 25 estimates by assigning to each square a score from 0 (absence) to 4 (when an identified taxon totally covered a square) ([Giakoumi et al., 2019](#); [Guidetti, 2006](#)). Taxa filling < 1/4 square were given an arbitrary value of 0.5. When it was not possible to identify the organisms to species level, they were attributed to taxa corresponding to a genus (e.g. *Sargassum* spp.), a family (e.g. Stypocaulaceae), phylum (Cyanobacteria) or a growth form (e.g. turf-forming algae) (see [Supplementary Table S2](#)). The use of 'lumped' levels of classification, combining taxa with growth-forms, for epibenthic descriptors is a long-standing tradition in marine ecology, and has been utilized both in rocky and coral reefs (e.g. [Morri et al., 2010](#), and references therein). When the descriptors were species, we adopted the nomenclature of WoRMS, the World Register of Marine Species (www.marinespecies.org).

2.3. Habitat complexity

To describe habitat complexity, three indices have been used: the first index is designed to capture the abiotic complexity, the second to capture the biotic complexity and the third to capture the overall habitat complexity (combining both biotic and abiotic components).

Abiotic complexity is frequently expressed in terms of substrate rugosity, typically measured using quadrats ([Parravicini et al., 2006](#)) or transects ([Morri et al., 2015](#)). As fish are mobile, we preferred a seascape approach such as the one adopted by [Giakoumi et al. \(2019\)](#), with divers estimating abiotic complexity visually after every UVC replicate performed at each sampling site. The *abiotic index* (AI) ranges from 1 (very low: flat bottoms without crevices or holes) to 5 (very high: bottoms with large number of deep crevices and holes > 1 m deep or high presence of rocky boulders > 1 m). The modal value of the scores of the replicates (i.e. the score assigned most frequently at each site) was used to characterize each site. AI therefore describes the abiotic complexity of the habitat at each site: the higher the score the more complex the substrate.

The second index, or *biotic index* (BI), is novel. It is aimed at synthesizing the habitat complexity resulting from the biotic components, i.e. the algal and animal taxa or categories composing the sessile benthic assemblage. Conspicuous macroalgae, seagrass, sponges or corals provide biological habitat and impose a 3-D structure on the benthic seascape, thus acting as physical ecosystem engineers ([Gutiérrez et al., 2011](#)); in contrast, encrusting organisms add little to the abiotic complexity of the underlying substrate. The height of every single organism present in the species-taxon matrix was estimated based on the *Doris* database (<http://doris.ffessm.fr>), and the mean height of the benthic cover was thus calculated for every replicate. In addition to organisms' height, we considered the morphological diversity of the epibenthic community: the more diverse the community, the more heterogeneous the habitat. To do so, from the matrix obtained by the photo analysis, taxa contributing to the benthic cover were classified using 10 growth forms based on the ratio between height (h) and radius (r) of the organisms ([Parravicini et al., 2010a](#)): borers, bushes, domed mounds ($h/r > 1$), hemispherical mounds ($h/r = 1$), flattened mounds ($h/r < 1$), erected plate, determinate sheets, indeterminate sheets, trees and vines (see [Supplementary Table S2](#)). Then, in order to describe the diversity of the growth forms and thus characterize the habitat heterogeneity, the Simpson Dominance index was used. Dominance was preferred to other diversity indices because it is not sensitive to species richness ([Vassallo et al., 2020](#)), which was not suitable here: each growth form usually contained >1 taxonomic unit that in turn included >1 species. In this context, dominance is indicative of how much the

ecological traits represented by the different growth forms are portrayed ([Hillebrand et al., 2008](#)). The dominance index and the mean height of the benthic cover were standardized, averaged between them, and standardized again. Finally, a score was attributed to this standardized mean, ranging from 1 (sites with standardized mean ranging from 0 to 0.20) to 5 (sites ranging from 0.8 to 1). Thus, score 1 corresponds to sites with the lowest biotic complexity and heterogeneity (homogenous and flat biotic cover), whereas score 5 corresponds to sites with the highest biotic complexity and heterogeneity (heterogeneous growth-form composition and tall organisms).

Finally, a third index, called *synthetic index* (SI), was obtained by summing the AI and the BI to obtain a single compound index, ranging from 2 to 10, that accounted for all the components of habitat structure (See [Supplementary Fig. S2](#) for a visual representation of how indices have been computed).

2.4. Data analysis

To compare benthic cover of the whole benthic assemblage between levels of protection, Permutational Analysis of Variance (PERMANOVA), based on Bray Curtis similarity, was performed. The putative responses of the benthic cover to the factors 'Location', 'Protection' and 'Site' have been tested by considering factors as follows: factor 'Location' has 15 levels (corresponding to the 15 MPAs and adjacent unprotected zones) and is random because the locations included in the study represent a subsample of all the potential locations, and replication was considered to account for the variability at this spatial scale without any specific hypothesis about differences between Locations; factor 'Protection' has 3 levels (No-Take, Buffer and Outside), is fixed and orthogonal to Location; factor 'Site' has 2–4 levels, is random (because sites were randomly selected from a pool of potentially suitable sampling sites) and nested in the 'Protection × Location' interaction. Non-metric MultiDimensional Scaling (nMDS) was used to visualize the multivariate patterns in the dataset. Data of the whole benthic assemblage were tested for homogeneity of dispersion using Permutational Analysis of Multivariate Dispersions (PERMDISP) following the approach of [Di Franco et al. \(2014\)](#) as described in [Supplementary Table S3](#) and [Supplementary Text S1](#). PERMDISP did not detect difference in dispersion ($p > 0.05$) for Protection or for Location × Protection. Besides considering the whole benthic assemblage, we also focused on *Cystoseira sensu lato* and barren to assess whether protection could reverse the trend observed in the Mediterranean Sea where macroalgal forests are gradually being replaced by barren grounds. For these analyses, "generalized additive models for location, scale and shape" (GAMLSS, [Rigby and Stasinopoulos, 2005](#)), where 'location', 'scale' and 'shape' represent the parameters of the distribution, were used, implementing the package 'gamlss' in R. This approach was preferred to the classical Generalized Linear Models for the possibility of fitting the beta-inflated (BEINF) distribution. The BEINF is similar to the beta (for fractions between 0 and 1) but allows zeros and ones as values for the response variable. In fact, the response variables in these analyses were fractions of benthic cover (*Cystoseira* or barren) with an excess of zeros and the presence of ones. Model diagnostic was performed by visually inspecting model residuals detecting no departure from normality or from homoscedasticity (see [Supplementary Figs. S3 and S4](#)).

The BIOENV analysis ([Clarke and Ainsworth, 1993](#)) was used to possibly identify a subset of environmental variables that best explain the variability observed in the benthic coverage dataset. Due to the large size of both matrices, we used the variant BVSTEP ([Clarke and Warwick, 1998](#)) of BIOENV that presents a stepwise routine for faster exploration of the subset combinations. The analysis was conducted by self-comparison of the benthic assemblage matrix to establish which taxonomic units best explain the multivariate pattern observed on the benthic assemblage. For the analysis, the number of random restarts was fixed at 10,000 to have a good compromise between computational time and precision of results.

To explore potential correlations between the multivariate fish biomass, the multivariate benthic taxa cover, protection, and complexity indices, we used partial distance-based redundancy analyses (dbRDA; McArdle and Anderson, 2001) using the ‘vegan’ package in R, and implementing the function ‘dbrda’. Random factors, ‘location’ and ‘site’, were included in the conditional matrix (variables to be controlled in the final models) in order to remove their effect from the analysis. The other variables were included as predictors. Based on 999 permutations, the dbRDA was used with stepwise selection to filter the relative importance of explanatory variables of multivariate fish assemblage.

To identify potential predictors of the scores of the 3 indices, ordered logistic regressions (McCullagh, 1980) were performed on each index separately, using the package ‘ordinal’ in R, and implementing the function ‘clmm’ for fitting Cumulative Link Mixed Models with random effects (Christensen, 2018). This analysis was preferred to classical ANOVA because the response variables (scores) were categorical and ordered. The factors included in the analysis were ‘Protection’ (fixed, 3 levels) and ‘Location’ (random, 15 levels, orthogonal to Protection). The factor ‘Site’ was dropped because no replicated values were available at that scale since indices were computed at the scale of site. Significance of factors was assessed through a likelihood ratio test, specified for cumulative link models. In addition to this, we assessed potential predictors of the single components accounting for the BI, by running two mixed linear models on the Height of the canopy and the Dominance of the benthic growth forms and testing the factors ‘Protection’, ‘Location’ and ‘Site’, included in the analysis as mentioned above. Before this, we tested for possible collinearity between BI and the two components considered (height and dominance).

To assess putative effects of MPA features and environmental variables on differences observed among protection levels for the 3 indices (AI, BI and SI), we performed generalized linear models (GLMs) on the Effect Size of each index. MPA features (i.e. MPA age, size of the protected zone, enforcement level) and eco-region were compiled from available literature (Claudet et al., 2008; Giakoumi et al., 2017; Di Lorenzo et al., 2020). Sea surface temperature (SST) data were retrieved from the Copernicus Marine Environment Monitoring Service (CMEMS, <http://marine.copernicus.eu>) by averaging the monthly values of the previous year at each location.

Effect size E was calculated as

$$E = \text{Log} \left(\frac{X_p}{X_e} \right) \quad (1)$$

with X_p the index value inside the protected area (either no-take or buffer) and X_e the index value outside the MPA (in control unprotected sites). We then calculated Variance Inflation Factors (VIF) to check for multicollinearity among the predictors in the GLM. As multicollinearity was never detected ($VIF < 2$) we performed type III ANOVAs on the models to assess significance of terms.

Finally, to test for the effect of protection and complexity indices on total fish biomass, we used generalized linear mixed models (GLMMs) with Gamma distribution. Three separate models, each testing one index, were built because of some correlation between the indices (Supplementary Fig. S5). Model diagnostic was performed, visually inspecting model residuals, detecting no departure from normality or from homoscedasticity (see Supplementary Fig. S6).

As also in ordered logistic regressions in GLMMs with Gamma distribution, the sampling design included only “Location” and “Protection”, and not “Site” since indices were computed at the scale of site. The relationship between habitat complexity and fish biomass was tested at the scale of site according to the evidence regarding the home range of Mediterranean coastal fishes that are generally able to move over areas generally $\leq 1 \text{ km}^2$ (see Di Franco et al., 2018 for a recent review), a surface area comparable to that of the sites we characterized.

Data treatment and analysis were all performed using the R 3.4.3 (R Core Team, 2014) software except for PERMANOVAs that were

conducted using PRIMER 7 with PERMANOVA + add on package (Anderson et al., 2008).

3. Results

3.1. Benthic assemblage

We identified 44 benthic taxa (see Supplementary Tables S4 and S5). The most common taxon was ‘Turf’ (present in 2617 out of the 2760 photos analyzed; i.e. $> 98\%$ of the samples), while ‘*Caulerpa prolifera*’ was the least common (2 photos out of 2760; $< 0.1\%$ of the samples).

The nMDS performed on the similarity matrix of benthic assemblage cover suggested that samples mostly clustered according to ‘Location’ and not to ‘Protection’ levels (Fig. 3). The PERMANOVA performed on the same dataset showed a significant variability between sites (Pseudo-F = 21.152, $p = 0.0001$, see details in Supplementary Table S6) and a significant interaction ‘Location \times Protection’ (Pseudo-F = 1.3277, $p = 0.0001$, see details in Supplementary Table S6). Pairwise post-hoc tests performed on ‘Location \times Protection’ between levels of the fixed factor ‘Protection’ showed a significant effect of protection on whole benthic assemblages at 5 locations: in 4 of them benthic assemblages were significantly different between outside and inside the MPAs (either no-take, buffer or both, see Supplementary Table S7 for significant p -values), while no differences were found between levels of ‘Protection’ at the remaining location.

The BVSTEP analysis identified the best model describing the multivariate distribution of the data concerning the benthic assemblages at the studied locations as the combination of 4 benthic taxa: *Dictyopterus polypodioides*, *Cystoseira sensu lato*, *Cymodocea nodosa* and Barren ($p = 0.51$) (Fig. 3). The most noticeable examples were: i) high cover of the algae of the genus *Cystoseira sensu lato* in the Strait of Bonifacio (Asinara and Bonifacio); ii) high cover of the alga *D. polypodioides* at Cabo de Palos, the westernmost location sampled in this study; iii) the presence of barrens in the Ionian Sea, with Zakynthos being the easternmost sampling location; iv) the presence of the seagrass *C. nodosa* in the Adriatic Sea (found only in Strunjan and displaying very low cover).

The habitat-forming macroalgae belonging to the genus *Cystoseira sensu lato* were recorded at 12 out of the 15 locations studied, and in 8 of them the mean cover was $< 1\%$. The maximum cover recorded was 65% in one of the buffer sites in Egadi. The beta-inflated gamlss showed that, despite having higher probability of occurrence in unprotected areas, *Cystoseira sensu lato* had higher cover in both the buffer and the no-take compared to unprotected sites (Supplementary Fig. S7 and Supplementary Table S8). A significant spatial variability was detected between locations and between sites within locations (Supplementary Table S8).

Barren grounds were found at all locations except Strunjan and their mean cover ranged from 0.1% at Cap Roux to 17% at Zakynthos. The beta-inflated gamlss showed that barrens had higher probability of occurrence in unprotected areas, but the analysis did not detect an effect of protection on coverage. A significant spatial variability was detected between locations and between sites within locations (Supplementary Table S9 and Supplementary Fig. S8).

The general dbRDA model was significant ($p < 0.001$) according to the permutation procedure. Stepwise selection procedure indicated that among the 49 predictive variables (including benthic species, protection levels and complexity indices), 15 were significant ($p < 0.05$) and improved the variance explained by the dbRDA model on multivariate fish biomass (Fig. 4): i.e. protection (no-take and outside), biotic complexity (BI) and cover of barren, encrusting calcifying rhodophytes, massive dark sponges, *Rocellaria dubia*, *Aplysina aerophoba*, *Flabellia petiolata*, *Caulerpa cylindracea*, *Cymodocea nodosa*, *Halopteris spp.*, *D. polypodioides*, *Dasycladus vermicularis*. Among the 80 fish species recorded, the biomass of 8 of those was significantly correlated (p -value < 0.05 and $r^2 > 0.3$) with benthic assemblage structure (i.e. *Dentex dentex*, *Diplodus cervinus*, *Diplodus puntazzo*, *Diplodus sargus*, *Diplodus*

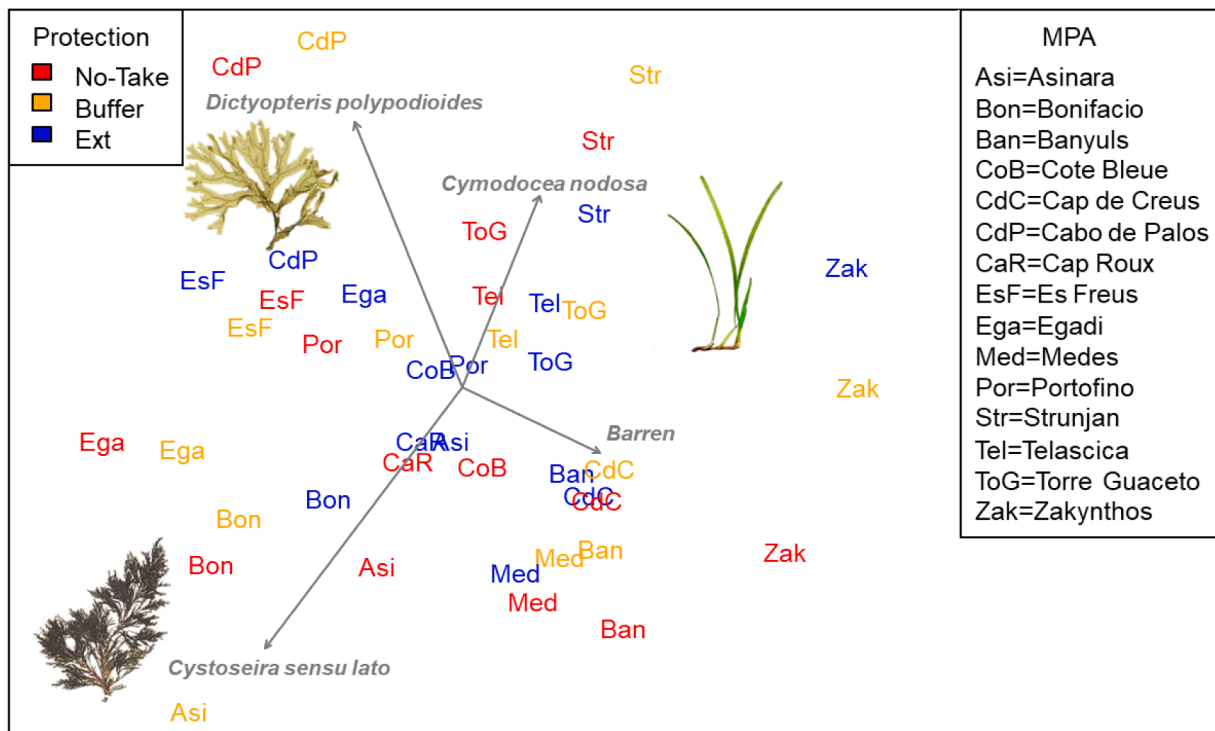


Fig. 3. Non-metric MultiDimensional Scaling of benthic cover on square root transformed data. Only centroids for each protection level (No-take: Inside the No-Take zone of the MPA; Buffer: Inside the buffer zone of the MPA; Ext: unprotected areas outside the MPA) at each location are represented, for a total of 43 points (stress = 0.14). Vectors represent the variables identified by the BVSTEP analysis.

vulgaris, *Epinephelus marginatus*, *Signus luridus* and *Sparisoma cretense*). The biomass of these fish species, as well as the total fish biomass, was higher in no-take zones with high benthic cover of *D. polypodioides*, *C. cylindracea* and encrusting calcifying rhodophytes, while biomass was low in unprotected zones with high cover of barren, *R. dubia*, *C. nodosa* and sponges (massive dark sponges and *A. aerophoba*).

3.2. Habitat complexity index and relationship with fish biomass

Ordered logistic regressions highlighted a significant interaction 'Protection × Location' for all three indices (Fig. 5) (abiotic index AI: $\chi^2 = 212.98$, $p < 2e-16$; biotic index BI: $\chi^2 = 481.47$, $p < 2e-16$; synthetic index SI: $\chi^2 = 237.66$, $p < 2e-16$; see Supplementary Table S10). Focusing on each location, Protection was statistically significant at 3 locations for the abiotic index, 2 locations for the biotic index and 3 locations for the synthetic index (see Supplementary Table S11 for pairwise comparisons between protection levels at each Location), but no clear patterns between protection levels was highlighted in these cases. Focusing on the two components of the *biotic index*, neither canopy height nor dominance were found to be affected by Protection, in line with the result obtained for the index (Supplementary Table S12). Although relatively high, the collinearity between the two components and the BI is considered acceptable for running a separate analysis on each single metric ($\text{cor} < 0.8$ in each case; Supplementary Fig. S5). A significant interaction Protection × Location was highlighted for canopy height indicating an inconsistent effect of protection between locations: in 2 locations out of 15 Protection resulted statistically significant, but no clear pattern was detected in the differences between protection levels (Supplementary Table S13). Height was also found to vary significantly at the level of Site. Significant site variability was also observed for growth form dominance (Supplementary Table S12).

GLMs on the effect size of indices detected significant effects of 1) MPA age on AI in the buffer zone (Supplementary Table S14d) and 2) MPA age and temperature on the SI in the buffer zone (Supplementary Table S14f).

GLMMs showed only a significant relationship between fish biomass and protection level (biomass in No-Take > Buffer > Ext). In each GLMM, the interaction between protection and each index was not significant (Supplementary Table S15), suggesting a consistent pattern, i.e. the absence of relationship between each index and fish biomass across the 3 protection levels. For the three models, a significant variability at the scale of location was highlighted.

4. Discussion

4.1. Benthic assemblages

Our results suggest that Mediterranean benthic assemblages could be affected more by factors acting at different spatial scales than by protection. This is in agreement with Franchetti et al. (2006), who did not find differences in benthic assemblages between protected and unprotected areas in 11 out of 15 Italian MPAs (3 of these MPAs are also present in our study) and Sala et al. (2012), who did not detect any effect of protection on benthic assemblages at 14 Mediterranean MPAs (5 of these are also included in our study). A caveat to consider regarding these the two aforementioned studies, however, is that in the MPAs studied the protection measures were not always well enforced, so the results in terms of protection effects have to be taken with caution. Additional evidence of idiosyncratic effects of protection on benthic assemblages has been reported (Franchetti et al., 2012, 2013). In general, evidence regarding the effect of protection on benthic assemblages is fairly contrasted, with some studies on temperate reefs, kelp forests and coral reefs that highlighted positive effects of protection (Sala et al., 1998; Guidetti and Sala, 2007; Mumby et al., 2007) while others found that protection did not affect benthic assemblages (McClure et al., 2020, 2021). From this perspective, although in our study we did not highlight a clear protection effect on the whole of the benthic assemblages, we report the first evidence of a positive effect of protection on the erect macroalgae of the genus *Cystoseira sensu lato*, representing a key component of Mediterranean rocky algal forests.

Fig. 4. Partial distance-based redundancy analysis (dbRDA) performed on multivariate fish biomass. Panel A): Each circle represents a site (coloured according to the protection level), and its size is proportional to total fish biomass. Locations: Asi = Asinara, Ban = Banyuls, Bon = Bonifacio, CdP = Cabo de Palos, CdC = Cap de Creus, CaR = Cap Roux, CoB = Côte Bleue, Ega = Egadi, EsF = Es Freus, Med = Medes, Por = Portofino, Str = Strunjan, Tel = Telascica, ToG = Torre Guaceto, Zak = Zakynthos. Panel B): Significant environmental variables identified by the analysis. Predictive variables: OUT = unprotected, NT = no-take, Dp = *Dictyopterus polypodioides*, Bar = Barren, Rd = *Rocellaria dubia*, ECR = encrusting calcifying rhodophytes, Aa = *Aplysina aerophoba*, Fp = *Flabellia petiolata*, Cn = *Cymodocea nodosa*, Cc = *Caulerpa cylindracea*, Hal = *Halopteris* spp., BI = Biotic Index, Dv = *Dasycladus vermicularis*, MDS = Massive Dark Sponges. Fish species: Dd = *Dentex dentex*, Dc = *Diplodus cervinus*, Dp = *Diplodus puntazzo*, Ds = *Diplodus sargus*, Dv = *Diplodus vulgaris*, Em = *Epinephelus marginatus*, Sc = *Sparisoma cretense*, Sl = *Siganus luridus*.

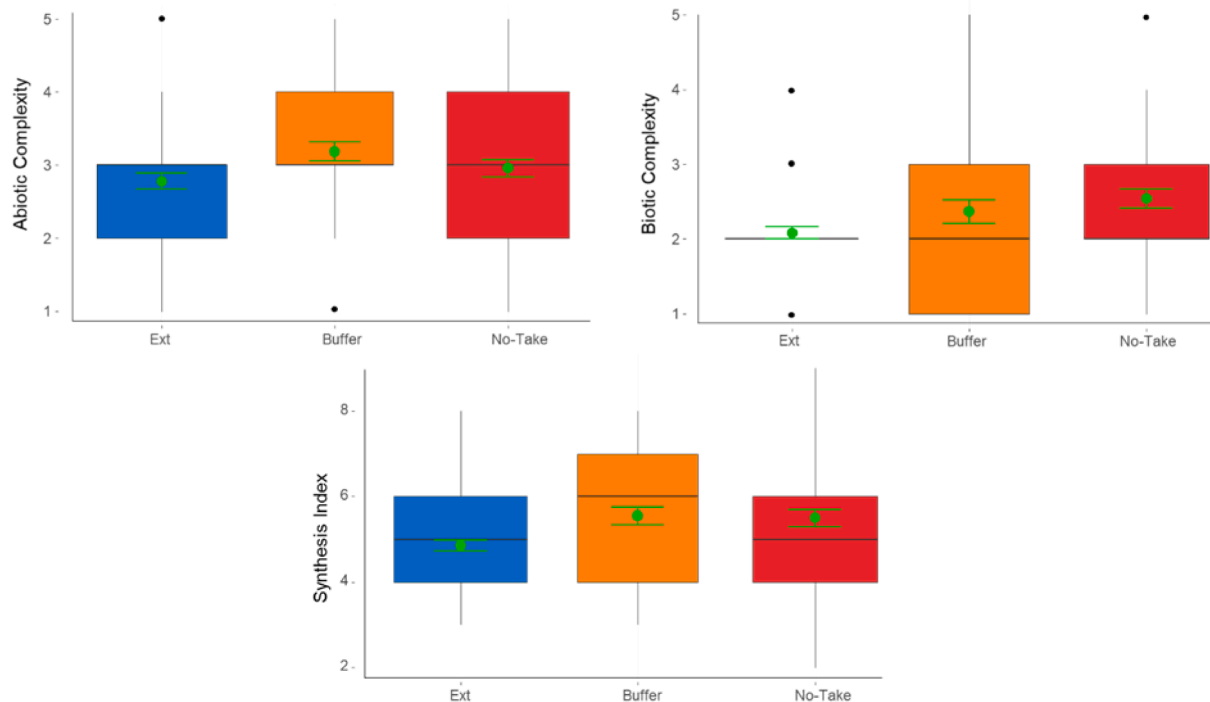


Fig. 5. Boxplots of the 3 indices developed and used in this study, according to the protection levels (Ext = Exterior of the MPA; Buffer = buffer zone within MPA; No-Take = no-take zone within MPA). Minimum ($=Q1-1.5*(Q3-Q1)$), first quartile (Q1), median, mean (in green), confidence intervals (95% CI, in green), third quartile (Q3), maximum ($=Q3 + 1.5*(Q3-Q1)$), and outliers are represented. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Multiple alternative hypotheses could explain the absence of protection effects on benthic assemblages detected in this study. For example, in our large-scale study, some environmental factors acting at regional scale (e.g. temperature gradients) or at local scale (e.g. water turbidity, pollution) could play a major role in shaping benthic assemblages. The locations investigated belong to different biogeographical sectors of the Mediterranean: the high compartmentalization of the Mediterranean Sea implies a wide variety of climatic and hydrologic conditions in the fairly isolated sub-basins, which therefore host different shallow-water biota (Bianchi et al., 2012), possibly responding in a different way to protection.

Furthermore, some specific direct and indirect human impacts cannot be effectively stopped at the MPA borders, which is the case for non-native species, pollution and climate change (Parravicini et al., 2013; Montero-Serra et al., 2019). Some of them could equally impact benthic assemblages inside and outside the MPA (reducing the likelihood of detecting differences between protection levels at each location). Some of these impacts could also be locally strong enough to prevent the recovery of benthic assemblages, as past disturbances may leave long-lasting legacies (Parravicini et al., 2010b). So limiting direct and spatially-explicit human impacts (e.g. fishing) could be sufficient to produce clear positive effects on fish assemblages, depending on the level of enforcement (Guidetti et al., 2014), but may not necessarily cascade down to affect benthic assemblages at large scale (Guidetti and Dulčić, 2007; Sala et al., 2012; McClure et al., 2020).

Many studies found that a phase shift triggered by overfishing can occur between vegetated reefs hosting erect canopy-forming macroalgae and barrens (Guidetti and Sala, 2007, and references therein). Reversing such a phase shift may prove difficult, even under strong protection regimes (Medrano et al., 2019), as is the case for no-take zones, since the legacy of past disturbance may slow down the recovery (Parravicini et al., 2010b) and post-disturbance assemblages may persist in a so-called 'alternative stable state' for a quite long time (Knowlton, 2004). Even if the initial drivers of the shift are halted (such as overfishing inside no-take MPAs), various feedbacks and complex mechanisms (e.g. increase in herbivorous populations and competition for space with turfs) can prevent (at least in the short term) the reversal of the shift or can affect the dynamics of the assemblages (Ceccherelli et al., 2006). All these sources of variability could strongly affect benthic assemblages at large scale, possibly reducing the chance to detect protection effects at local scale.

However, when focusing on a specific group of important and vulnerable erect macroalgae, i.e. *Cystoseira sensu lato*, a positive effect of protection on the cover of this taxon was highlighted. To the best of our knowledge this is the first evidence related to the potential effect of MPAs in protecting and/or supporting the recovery of this taxon, that is declining throughout the Mediterranean (Fabrizzi et al., 2020). This could suggest that the effect of protection on benthic taxa could be idiosyncratic and not easily determined when assessing the entire benthic assemblage.

4.2. Habitat complexity

We assessed the complexity of the benthic habitat by analyzing both abiotic (i.e. substrate topography) and biotic (i.e. heterogeneity and architecture of benthic assemblages) components, and to do so we implemented three indices (AI, BI, SI). The abiotic index AI, which captures the topographic complexity, was associated with a significant interaction 'Location \times Protection'. However, post-hoc analyses showed that the effect of 'Protection' was significant only in 3 out of 15 locations and only in one case did the no-take area have a higher AI score than outside. This is not surprising since human-driven disturbance in coastal areas may mostly affect benthic assemblages but not substrate topography (Watling and Norse, 1998; Guidetti and Boero, 2004; Rovere et al., 2009), with the exception of highly-destructive practices severely damaging the habitat (e.g. date mussel illegal harvesting, see Rovere et al. (2009) and Colletti et al. (2020)). Accordingly, our results highlight no difference in abiotic complexity between protected and unprotected areas, which contradicts the general belief that MPAs are usually established in more naturally complex habitats (García-Charton et al., 2004; García-Charton and Ruzafa, 1999) and do not fully support the "residual MPAs hypothesis", suggesting that MPAs could be established in areas that are remote or unpromising for extractive activities to minimize costs for users of natural resources (Devillers et al., 2015).

The biotic index BI, which captures the complexity of benthic assemblages, was associated with a significant interaction 'Location \times Protection'. However, the effect of 'Protection' was significant only in 2 locations and only one of the two zones considered (no-take or buffer) had a significantly higher BI than outside the MPA.

In order to assess how summing and averaging indices may be leading to information loss, we tested the effect of protection on the two components (heterogeneity and architecture) of the BI separately. This analysis revealed no effect of 'Protection' on either heterogeneity (Simpson dominance) or architecture (height of the benthic components). These outcomes agree with the result of the PERMANOVA that did not highlight any effect of 'Protection' on benthic assemblages.

Finally, the synthetic index SI (the sum of the AI and BI) was also influenced by the interaction 'Location \times Protection'. Pairwise post-hoc comparisons showed a significant effect of protection on this index in 2 of the 15 locations, with one showing higher values inside the MPA, while the other, showed higher values in unprotected areas. This result suggests no effect of 'Protection' on whole habitat complexity but rather a high variability between the different locations. The SI is the one supposed to best characterize whole habitat complexity, embracing both the abiotic and the biotic components (Pittman, 2017). A single, multi-parametric index capable of embedding all the facets of habitat complexity is obviously appealing, and understandably preferred by managers and policy makers dealing with conservation issues (Enrichetti et al., 2019). Due to its construction, the SI is a comprehensive, seascape-approach monitoring tool with the potential to deliver an effective and representative picture of habitat complexity. In the present study, it worked well over a wide spatial scale. However, analyzing separately the two components of the index enabled us to distinguish the respective roles of topography and biotic cover, which proved to be not necessarily linked, as they are differently resistant to, and resilient after, human disturbances (Montefalcone et al., 2011). The preferred option, therefore, should be always to accompany the synthetic index with the two component indices in order to understand which aspect of habitat complexity (e.g., refuge rather than food provision) has more effect on fish biomass.

In the present study, we used an ACI (after control-impact) sampling design which assumes that control sites mimic the conditions of protected sites before the onset of protection. However, control sites may not always fully represent appropriate counterfactual situations (Ferraro and Hanauer, 2015, 2014; Mascia et al., 2017), and therefore our results, besides providing conclusive evidence of a present-day comparison between protected and unprotected conditions at each location, are only

suggestive of differences attributable to the onset of protection in each MPA. Further evidence providing information on what has happened since the implementation of the MPA, or on what occurred at that starting point, should be explored using different approaches, such as BACI (before-after-control-impact; see Guidetti, 2002) or more complex designs that are however very seldom applicable due to the lack of data concerning the phase before the implementation phase of an MPA (Thiault et al., 2017).

4.3. Relationship between habitat complexity and fish biomass

A number of studies have reported protection positively affecting total fish biomass (Claudet et al., 2008; Sala et al., 2012; Edgar et al., 2014; Guidetti et al., 2014, 2019; Giakoumi et al., 2017; Zupan et al., 2018). Our analyses, in addition, highlight some interesting correlative patterns between fish (in terms of biomass) and benthic taxa (in terms of cover). In fact, we found higher total fish biomass in no-take areas with high cover of a set of benthic macroalgae differing among them in terms of growth-form (*Dictyopteria polypodioides*, encrusting calcifying rhodophytes, *Flabellia petiolata*, *Halopectis* spp., and *Caulerpa cilindracea*) that could support fish assemblages, for instance, by providing food resources through hosting invertebrate prey. In contrast, unprotected locations with high cover of barrens and massive sponges are associated with much lower overall fish biomass. Further studies should be devoted to better exploring these relationships and investigating the mechanisms potentially involved. Further work is also needed to investigate the role of top-down and bottom-up processes in structuring benthic assemblages and driving their relationships with fish assemblages in order to identify their relative influence in shaping whole coastal rocky reef assemblages and to better understand ecosystem functioning.

All the benthic assemblages explored here belong to the so-called "biocoenosis of infralittoral algae on rocks" (UNEP/MAP-RAC/SPA, 2015). However, due also to the extensive geographical range of our study, they included distinct associations and facies, as recognized by the European Nature Information System EUNIS (<https://eunis.eea.europa.eu/>), which was designed to provide scientists and policy makers with a standard classification for management actions (Bianchi et al., 2018). To the best of our knowledge, no study has yet attempted to correlate reef fish assemblages with benthic habitats in the Mediterranean Sea, which would be a worth-while endeavor for future research.

5. Conclusion

The present study provided inconsistent evidence regarding the effect of MPAs on Mediterranean benthic assemblages: no clear benefits were detected when considering whole assemblages, whereas consistent positive effects of protection were observed on the habitat-forming algae belonging to the genus *Cystoseira sensu lato*. This latter evidence, along with the higher biomass of fish found inside protected areas, i) confirms that MPAs can be an effective tool to protect and/or restore rocky-reef assemblages in coastal habitats, and ii) suggests the need for further studies aimed at more in-depth exploration of the mechanisms determining the different responses of benthic taxa to protection and how this can influence the associated fish assemblages.

Author contributions

P.G., A.D.F. and A.C. designed the experiments and managed the funding acquisition. A.D.F., A.C. and M.D.L. performed the field work. C. N.B., L.M., S.B. and E.D.F., carried out the benthic species identification. C.N.B. designed the complexity indexes. E.D.F., A.D.F., A.C., and P.G. compiled and analyzed output data and designed and wrote the first version of the manuscript. All authors contributed substantially to the work and participated in manuscript writing.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107850>.

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