



Small-sized and well-enforced Marine Protected Areas provide ecological benefits for piscivorous fish populations worldwide

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ABSTRACT

Many piscivorous fish species are depleted and/or threatened around the world. Marine Protected Areas (MPAs) are tools for conservation and fisheries management, though there is still controversy regarding the best design for increasing their ecological effectiveness. Here, on the basis of a weighted meta-analytical approach, we have assessed the effect of 32 MPAs, distributed worldwide, on the biomass and density of piscivorous fishes. We analysed the MPA features and the biological, commercial and ecological characteristics of fishes that may affect the response of species to protection. We found a positive effect on the biomass and density of piscivores inside MPAs. This effect was stronger for the biomass of medium-sized fishes (in relation to the maximum size reported for the species) and the density of large and gregarious species. The size of the no-take zone had a significant negative impact on both response variables and differed according to the level of enforcement, with smaller no-take zones having higher levels of enforcement. Thus, MPAs help to protect piscivorous fish species, with smaller, but well enforced reserves being more effective for the protection of the local populations of piscivorous fishes throughout the world.

1. Introduction

High trophic level teleost fish (grouper, snapper, emperor, codfish, jewfish, etc.) play a crucial role in the functioning of marine ecosystems (Baum and Worm, 2009; van Denderen et al., 2017), while they are major economic resources for both fisheries and recreational activities (Sala et al., 2016). The presence of piscivorous fish species is indicative of the good status of the whole ecosystem (D'agata et al., 2016; Valdivia et al., 2017; Barrett et al., 2018). However, they have traditionally been targeted by the fishing industry (Pauly et al., 1998; Myers and Worm, 2003), and as a consequence, they are currently depleted in most coastal ecosystems (Jackson, 2008; Sadovy de Mitcheson et al., 2013). Indeed, many piscivorous species are included in one of the IUCN threat categories (IUCN, 2017), such as the endangered *Epinephelus striatus*, *Epinephelus marginatus* or *Petrus rupestris*. Moreover, recent studies have shown that previous estimates on the biomass of highly mobile apex predators were biased, and claim that populations of apex predators are considerably smaller and more precarious than previously thought (Bradley et al., 2017; Oken et al., 2018).

Marine Protected Areas (MPAs) are usually established for both fisheries management and conservation purposes (Pérez-Ruzafa et al., 2017). By banning all kinds of fishing (i.e., no-take zones, hereafter

NTZ) and/or implementing strict fishing regulations (i.e., partially protected or buffer zones) they help to replenish fish populations (Giakoumi et al., 2017; Sala & Giakoumi et al., 2017), improve habitat quality (Rodwell et al., 2003), restore ecosystem functioning (Cheng et al., 2019) and enhance the exportation of biomass to increase fisheries yields in adjacent areas (Harmelin-Vivien et al., 2008). MPAs may consist of only NTZs, known also as marine reserves, or have both NTZs and one or several buffer zones (where certain activities, such as artisanal fishing or recreational diving, are regulated), in which case the most common terminology is MPA (Pérez-Ruzafa et al., 2017).

Many studies and previous meta-analyses have attempted to understand how certain MPA features (size, time since the beginning of protection, enforcement, etc.) can influence the effects of protection on marine populations (Halpern and Warner, 2002; Côté et al., 2001; Micheli et al., 2004; Guidetti and Sala, 2007; Claudet et al., 2008; Edgar et al., 2014; Giakoumi et al., 2017; Gill et al., 2017; Woodcock et al., 2017), as well as the biological, commercial and ecological characteristics (commercial value, maximum size, behaviour, etc.) of fish species that result in greater conservation benefits from protection (Mosquera et al., 2000; Micheli et al., 2004; Claudet et al., 2010). As explained below, however, there is still controversy regarding several of these issues.

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There is a general consensus that highly enforced MPAs are more effective so that enforcement is found to be a critical variable to achieve conservation benefits (Guidetti et al., 2008; McClanahan and Graham, 2015; Giakoumi et al., 2017; Gill et al., 2017). By conservation benefits, we refer to the difference in a conservation outcome (e.g. biomass of fish) when NTZs are compared to unprotected sites; thus, effective MPAs promote ecological restoration inside the MPA by improving conservation outcomes due to the effects of protection. The effectiveness of MPAs appears to increase over time in the long-term (> 20 years) (Claudet et al., 2008; Molloy et al., 2009; Edgar et al., 2014; Friedlander et al., 2017), although it is likely to slow down as populations reach their carrying capacity (García-Rubies et al., 2013). It is noteworthy that large species (Claudet et al., 2010), high trophic level species (Micheli et al., 2004; Guidetti and Sala, 2007) and species with small home range areas (Afonso et al., 2016; Abecasis et al., 2015; Lee et al., 2015) are more likely to benefit from long-term protection. Some studies have even found that biomass and/or abundance can increase in a non-saturating way after more than 20 years (Russ and Alcalá, 2004; McClanahan et al., 2007), highlighting the importance of long-term protection. However, other studies did not find a significant effect of the age of the MPA on the response of fishes to protection (e.g. Côté et al., 2001; Halpern and Warner, 2002; Tetreault and Ambrose, 2007), so no general conclusions can yet be proposed on this issue.

The optimum size of the NTZ has been widely debated. Traditionally, researchers have promoted larger NTZs as being ecologically more beneficial (Claudet et al., 2008, 2010; Edgar et al., 2014; Friedlander et al., 2017), while other analyses found no effect of the size (Côté et al., 2001; Halpern, 2003; Guidetti and Sala, 2007; Lester et al., 2009). Furthermore, some studies have proposed an optimum minimum size, such as closures of at least 5–10 km² to achieve the best conservation potential, in order to avoid the slower recovery trends when sizes are too low (McClanahan and Graham, 2015). However, recent studies have found that in the Mediterranean Sea, smaller but well-enforced NTZs are more effective for some commercial species (Giakoumi et al., 2017). This has important implications for the design and management of MPA networks, but a more global assessment is still needed to generalize this premise.

In general, it is accepted that buffer (or partially protected) zones are less effective than fully protected areas (Lester et al., 2009; Sciberras et al., 2013; Giakoumi et al., 2017), although they can be effective if properly managed (Hackradt et al., 2014). In addition, some studies suggest that latitude may have an effect on protection, with tropical MPAs being more effective than those in temperate zones (Horwood, 2000). In a worldwide study of 87 MPAs, conservation benefits were found to be greatest if at least three out of five key features were included, from no-take, old, large, isolated and well-enforced (Edgar et al., 2014). Among these features, isolated MPAs would show a more evident effect of protection as habitat discontinuity prevents spillover (Edgar et al., 2014).

The potential benefit of MPAs may also depend on the biological, commercial and ecological characteristics of the species (Micheli et al., 2004; Claudet et al., 2010). Large species are expected to respond better to protection as being more susceptible to fishing mortality (Mosquera et al., 2000; Claudet et al., 2010). Moreover, commercially important species have been found to benefit the most from protection measures (Mosquera et al., 2000; Côté et al., 2001; Micheli et al., 2004; Tetreault and Ambrose, 2007; Claudet et al., 2008; Sciberras et al., 2013). Other important characteristics determining species' positive response to protection are related to their habitat and schooling behaviour, so that benthic, solitary or facultative schooling and non-territorial species would show greater benefits (Claudet et al., 2010). Importantly, mobile fish and species with home ranges of any size would profit from protection (Claudet et al., 2010; but see Moffitt et al., 2009; Abecasis et al., 2014). Furthermore, knowledge on how species use space has implications with regard to their potential catchability by fisheries (Jennings and Kaiser, 1998; Little et al., 2009), as different types of gear

are used according to the behaviour of the species, and artisanal and recreational fishery activities decrease with depth (Tyler et al., 2009). Responses also vary according to the trophic level of the species. Some studies have found a positive effect on all major trophic groups (Halpern, 2003; Soler et al. 2015). However, there are a number of studies in which piscivorous fishes show greater responses when compared to other trophic categories. For example, the density and biomass of top predators were 7 and 13 times higher, respectively, inside NTZs when compared to detritivorous fish species in Mediterranean MPAs (Guidetti et al., 2014). In addition, in temperate and tropical MPAs, biomass of piscivores increased 60% and density 12%, while values remained almost constant or decreased for other trophic levels (i.e., detritivores, invertebrate feeders, herbivores, omnivores and planktivores; Micheli et al., 2004).

Most of the previous meta-analyses focused on the whole fish assemblages (Halpern and Warner, 2002; Mosquera et al., 2000; Côté et al., 2001; Halpern, 2003; Claudet et al., 2008, 2010) and/or on a few commercially important species (Edgar et al., 2014; Giakoumi et al., 2017). A few of them, though, addressed the trophic level as a moderator (Micheli et al., 2004; Guidetti and Sala, 2007; Guidetti et al., 2008), indicating that high trophic level species benefitted the most from the protection measures, but without presenting in-depth knowledge on the variables affecting the greater benefits. Those studies did not attempt to identify the MPA features and the biological, commercial and ecological features that affect the responses of the piscivore group to protection, which is of great interest due to the vulnerability of this group to overfishing. Here, by focusing on the piscivore group, we were able to analyse a series of variables regarding the effectiveness of MPAs. Since piscivorous fish species are particularly likely to benefit from the protection offered by MPAs, it is easier to identify the factors affecting the restoration of their populations and to settle controversies regarding which MPA features, among the different available design and management options, provide the greatest ecological benefits. Furthermore, as this trophic group exhibits a wide variety of biological, commercial and ecological characteristics, it is important to ascertain which features make them more prone to benefit from protection, and this is only possible by limiting the analyses to this group alone.

In this study, we explore the effect of MPAs worldwide on piscivorous fish populations using a meta-analytical approach, which is well-suited when trying to identify a general effect among different studies that individually may have low statistical power (Osenberg et al., 1999). The specific aims of the present study were (i) to determine whether and to what extent piscivorous fish benefit from protection worldwide, either in density and/or biomass, (ii) to assess the influence of a series of MPA features on the effectiveness of MPAs in affording better protection of this group of fishes, and (iii) to determine the biological, commercial and ecological characteristics that make piscivorous fish more likely to show a positive response to MPAs. On the basis of the previous literature, we hypothesise that the density and biomass of piscivores will be greater inside NTZs. In addition, we expect older and better-enforced MPAs to afford greater ecological benefits to this group, although larger reserves will not necessarily appear as more effective. Finally, we predict that large species will benefit the most from protection measures. Here, by focusing on the diversity of responses to protection measures within a single trophic group at global scale, we explore patterns that are probably specific to it and that may be different from those previously found for the entire fish community, which is especially important for these commercially valuable populations that are at risk. Our results will help to identify the most important variables influencing the conservation of teleost piscivorous fish species in MPAs worldwide.

2. Methods

2.1. Search for studies and selection criteria

We carried out a bibliographical search on the Web of Science for the period between 1970 and 2016, including the keywords “marine protected area*”, “marine reserve*” or “no-take zone*”, and refined it with the terms “fish”, “biomass” and/or “density*”. The aim of the study was to compare data from NTZs (in which all forms of fishing are prohibited) with unprotected areas that were considered as control. However, selected NTZs could belong to MPAs, i.e., with both NTZs and one or several partially protected areas, or to fully protected areas (i.e., with only NTZs). We generally refer to any type of protected area considered in the study as MPAs because this term includes both types.

We identified 448 studies and included 117 additional research articles identified through Google Scholar, using the same keywords for the search. After duplicates were removed, we screened 503 studies. Those that included a comparison of biomass and/or density in NTZs and unprotected areas for any species, and those in which at least one piscivorous fish species was assessed, whatever the aim of the study was (for instance, telemetry studies that might report data for abundance inside and outside NTZs although the main objective was other), were selected for full-text assessment, giving a total of 135 studies selected. These studies were assessed for eligibility providing that they fulfilled the following criteria: mean fish abundance and/or biomass and its error (measured either as standard deviation, standard error, or variance) were reported for at least one piscivorous species inside the NTZ and in unprotected areas for a single MPA, fish were identified at species level, and control areas were in reality open to fishing.

Our search process finally enabled us to include 29 studies performed on 32 MPAs from different biogeographical areas around the world, and involved data on abundance and/or biomass of 73 piscivorous fish species (see Appendix A for details on the data included in the study). For studies reporting several years of data for the same MPA, only data for the last year were retained in order to avoid temporal autocorrelation. Data on fish abundance/biomass were generally collected by underwater visual census techniques along transects, although other sampling methods were considered too, such as baited underwater video (BUV).

2.2. Data extraction

From each study, we extracted data on mean biomass and/or density, the error reported (standard deviation, standard error, variance) and sample sizes (i.e., number of replicate transects or BUV deployments) in NTZs and unprotected areas from the text, tables and figures (in the latter case, using the GetData Graph Digitizer software, available at <http://getdata-graph-digitizer.com>).

Several characteristics of the MPAs were extracted from the studies in order to examine their potential influence on the effects of protection. MPAs were characterized by the size of the NTZ (measured in hectares); age (i.e., the number of years between the implementation of the reserve and the study date), latitude (in degrees); presence or not of a buffer zone; level of enforcement (according to Guidetti et al., 2008) [low (“common illegal fishing and virtually inexistent surveillance”), medium (“illegal fishing occurring but limited by infrequent surveillance”), high (“poaching very occasional if any, patrolling very active and continuous”]; and level of isolation of the protected area in relation to the unprotected area (following Edgar et al., 2014) [low (reef habitats reaching the limits of the MPA or even running continuous to fished areas; high connectivity of habitats among the MPA and fished areas), medium (reef habitats surrounded by shallow water < 25 m depth, or small patches of sand; medium connectivity of habitats), high (reef habitats inside MPAs surrounded by deep water > 25 m depth, and/or large expanses of sand; low connectivity among reefs] (see Appendix B for details on MPA features). When some of this

information was not available in the study, the corresponding authors were contacted to obtain it.

In addition, for each species, biological (maximum size), commercial (commercial value) and ecological (feeding type, trophic level, habitat, schooling behaviour, territoriality, depth range and mobility) characteristics were compiled from different sources, namely FishBase (Froese and Pauly, 2017), IUCN (IUCN, 2017), original research studies (Carpenter and Allen, 1989; Shpigel and Fishelson, 1991; Heemstra and Randall, 1993; Stewart and Jones, 2001; Eisenhardt, 2003; Floeter et al., 2007; Claudet et al., 2010; Mellin et al., 2016) and expert opinion. Species were categorised according to their maximum size, based on the maximum length reported for the species [small (< 50 cm), medium (51–100 cm), large (> 100 cm)]; commercial value [no value (including species having no or minor commercial value), medium (commercial species with low to medium economic value) and high (commercial species with high to very high economic value)]; feeding type [strict piscivores (those in which more than 90% of their diet is composed of fish), facultative piscivores (those in which fish are part of the diet but there are other components)]; trophic level [predators (reported values of trophic level between 3 and 3.9), high trophic level predators (values higher than 4.0) (Frisch et al., 2014)]; habitat [demersal (including benthic, e.g., grouper), benthopelagic (e.g., barracuda)]; schooling behaviour [gregarious, facultative schooling, solitary]; territoriality [i.e., spatially oriented aggressive behaviour (Börger et al., 2008), territorial, non-territorial]; depth range [shallow (< 10 m), medium (10–50 m), deep (> 50 m), broad (any depth)]; and mobility [sedentary (fish that swim less than 50% of the time, e.g., dusky grouper); vagile (fish that swim more than 50% of the time, e.g., jack) (Claudet et al., 2010)] (see Appendix C for details on the variables for each species).

2.3. Effect size

To quantify the effect of protection on the abundance and biomass of piscivorous fishes, separate meta-analyses were performed for each of the two response variables in order to avoid dependence of data, as in many cases both types of data came from the same study. We used log response ratios as effect sizes (Hedges et al., 1999) to quantify the proportional change in density and biomass between the experimental (NTZ) and control (unprotected area) treatments:

$$L_{RR\ ijkl} = \text{Log}_e(\bar{y}_{NTZ\ ijkl} / \bar{y}_C\ ijkl)$$

For each log response ratio, its sampling variance was calculated as:

$$V(L_{RR\ ijkl}) = \frac{SE_{NTZ\ ijkl}^2}{\bar{y}_{NTZ\ ijkl}^2} + \frac{SE_C\ ijkl^2}{\bar{y}_C\ ijkl^2}$$

with \bar{y}_{NTZ} , SE_{NTZ}^2 , \bar{y}_C and SE_C^2 being the mean and squared standard error of the NTZ and control treatments, respectively, for a response variable, for the combination of i studies and j MPAs, and k moderators and l levels in the moderator, for moderator analyses.

For studies in which fish abundance data were only found in the protected area, we assumed that the zeros in the unprotected area were due to a problem of detectability of rare fish species rather than to the complete absence of these species (Emslie et al., 2018). In traditional strip transects, detection probability is assumed to be one, but sampling units are narrow (between 2 and 6 m) and the area covered by the census is usually small, which sheds doubt on the validity of this assumption. The fact that imperfect detectability can lead to biased estimates for the effective monitoring of marine populations has been pointed out by many authors. MacNeil et al. (2008) found that the observed individual detectability across almost 50 families ranged from 0.05 to 0.54, highlighting the bias associated with UVC, especially for larger species. Moreover, there is a positive relationship between the probability of detection of a species and its abundance (Dorazio and Royle, 2005), so that species exhibiting low abundance and/or patchily

distributed are more likely to be undetected (Goetze et al., 2017). This situation has led to the intensification of efforts to reduce the risk of false absences, such as increasing the number of observers (Bernard et al., 2013), replicates (MacNeil et al., 2008), or using sampling methods such as distance sampling and GPS-tracked roaming transects (Irigoyen et al., 2018). Thus, in cases where no individual was detected outside the MPA, we added one individual of the species to the total number of replicates in the unprotected area and assigned the same standard error as that reported in the treatment NTZ, in order to increase the variance associated with the effect size estimate, and to give less weight to that study in the whole analysis. This transformation constitutes a novel approach that enabled us to include a greater number of studies in the density response variable. Moreover, this modification of the original dataset did not substantially alter the structure of the data: the modified cases represent 23% of the total; and results for mean abundances at the control sites after the transformation were very low compared to the treatment, with meanNTZ/meanControl ranging from 3 to 861.3 (mean 64.4 ± 22 SE). Tables D1, 2, 3, 4, 5 and 6 in Appendix D show the results of response ratios in the absence of this transformation (i.e., excluding the effect size when no fish data were reported in the control area). When this situation occurred for the biomass, the record was deleted.

2.4. Statistical analysis

Weighted random-effect models were applied to statistically integrate the effect size from the studies. This involved weighting each effect size by its inverse variance, the variance defined as the sum of the sampling variance of the individual effect size and the between-studies variance. With this weighting method, better-designed studies (because they have a greater number of replicates and lower sampling variance) receive larger weights in the statistical analyses than those with a lower number of replicates (Gurevitch and Hedges, 1999). To estimate the heterogeneity among studies, we calculated the Q statistic (Hedges and Olkin, 1985) and the I^2 index (Higgins and Thompson, 2002). The two indices are complementary and give a better understanding of the total heterogeneity (Higgins and Thompson, 2002). High heterogeneity (i.e., a Q statistically significant and $I^2 > 50\%$) implies that effect sizes differ among studies more than might be expected on the basis of sampling error alone, thus there may be moderators explaining part (or all) of it.

First, all species and MPAs were considered together in order to find general responses. Because some MPAs were represented by data derived from more than a single study, mean effect sizes and variances were calculated for the combination of study i and MPA j . Positive values for response ratios indicated greater density or biomass inside NTZs. Mean effect sizes and 95% confidence intervals were calculated for each response variable. Results were considered to be significantly different from zero when 95% confidence intervals did not overlap zero. Because negative or non-significant results are less likely to be published (Csada et al., 1996; Koricheva, 2003), Egger's tests (Egger et al., 1997), which allow numerical measurement of funnel plots asymmetry by means of a linear regression, were applied for the total data sets in order to identify evidence of publication bias.

In order to explore the effect of both MPA features and fish species characteristics on the response of fish to protection, mixed-effect models were conducted for each of these moderators. Qualitative moderator variables were analysed by means of weighted ANOVAs, and continuous variables by simple meta-regressions. In both cases, a Q_M statistic was calculated to assess the statistical significance of the moderator, as well as a meta-percentage of variance accounted for by the moderator, R^2 (López-López et al., 2014). In addition, Q_E statistics were also calculated to assess the model misspecification (i.e., the existence of residual heterogeneity among effect sizes; Koricheva et al., 2013; for details on Q_M and Q_E statistics formulas, see Rosenberg, 2013). For each moderator, we calculated mean effect sizes and mean

variances for the combination of study i , MPA j , moderator k and category level l , to avoid dependence of data.

Finally, we performed multiple meta-regression models including both the statistically ($p \leq 0.05$) and marginally ($p \leq 0.1$) significant moderators in order to find a model that best predicts which MPA features do act as predictors of the effectiveness of their benefits, and which characteristics make piscivores more likely to benefit from protection. We performed Spearman correlation tests and t -test comparisons among the variables included in the multiple meta-regressions to find any co-linearity between them.

Size of NTZ was log-transformed, and contrast coding was applied for those moderators with more than two categories (i.e., maximum size, social behaviour, commercial value) to be included in the multiple meta-regressions. All analyses were carried out with the free software R (R Core Team, 2015) and the metafor package (Viechtbauer, 2010).

3. Results

3.1. General description of MPAs and fish studied

The study included 32 MPAs located in the NE Pacific (4), NW Atlantic (2), Caribbean Sea (1), SW Atlantic (1), SE Atlantic (2), Mediterranean Sea (10), SW Indian (1), SE Indian (2), Coral Sea (3), Java Sea (1), Banda Sea (1) and SW Pacific (4) (Appendix B).

The size of NTZs ranged from 6 to 44 200 ha, with almost 70% occupying less than 1000 ha, and only 10% bigger than 10 000 ha. Original studies stated that unprotected areas and NTZs had a comparable habitat structure and were located at distances that allowed independence between them. Fourteen out of 32 MPAs presented buffer zones, in which artisanal fisheries and different kinds of tourism, such as recreational diving or recreational boat trips, were allowed, and generally surround the NTZs. MPA age ranged from one to 37 years. Most MPAs were highly or moderately enforced, with only 2 MPAs categorised as poorly enforced. Regarding the isolation levels, most of the MPAs had low isolation (60%); it should be noted that for 4 MPAs information regarding isolation was not available (see Appendix B).

The 73 fish species included in the study belonged to 15 families (Carangidae, Hexagrammidae, Labridae, Lethrinidae, Lutjanidae, Muraenidae, Ophidiidae, Phycidae, Pinguipedidae, Sciaenidae, Scorpaenidae, Sebastidae, Serranidae, Sparidae, Sphyraenidae). The large-sized category included species such as *Epinephelus marginatus* or *Plectropomus leopardus*; medium species such as *Lutjanus apodus* or *Sciaena umbra*; and small species such as *Cephalopholis fulva* or *Serranus* spp. Regarding mobility, sedentary species included all *Cephalopholis* spp., *Epinephelus* spp., and *Sebastes* spp. (among others), and vagile species included most *Mycteroperca* spp., *Lethrinus* spp., *Lutjanus* spp., *Plectropomus* spp., and *Serranus* spp. Our study did not include species belonging to families such as Carcharhinidae, Merlucciidae or Scombridae, characterized in general by being very vagile and having extensive home ranges (although these characteristics vary depending on the species considered), because data for those families were not reported in any of the studies included in our analyses (see Appendix C).

3.2. Overall effect

There was a positive and statistically significant effect of protection on the biomass and density when all MPAs and species were considered together (biomass: log RR = 1.18, 95% CI: 0.58 to 1.80; density: log RR = 1.52, 95% CI: 0.99 to 2.04). However, for both response variables, high values of total heterogeneity among studies indicated that the effect of protection varies among species and MPAs and there must be moderators accounting for that variability (biomass: $Q(20) = 248.73$, $p < 0.0001$, $I^2 = 91.96\%$; density: $Q(43) = 630.07$, $p < 0.0001$, $I^2 = 93.18\%$; degrees of freedom shown in brackets).

Neither Egger's regression test for biomass ($Z = 0.45$, $p = 0.65$) nor

Table 1
Results of the weighted ANOVAs for MPA features according to (a) biomass and (b) density, taking categorical moderator variables as predictors.

a) Biomass		95% CI			ANOVA results
Moderator	n	log RR	LB	UB	
Isolation					
High	4	1.45	0.06	2.85	$Q_M(2) = 2.91$; $p = 0.23$
Medium	4	0.56	-0.19	1.32	$R^2 = 38.52\%$
Low	11	1.28	0.85	1.72	$Q_E(16) = 34.11$; $p < 0.0001$
Enforcement					
High	9	1.73	0.78	2.69	$Q_M(2) = 3.73$; $p = 0.15$
Medium	10	1.06	0.32	1.78	$R^2 = 0.48\%$
Low	2	-1.06	-2.04	1.57	$Q_E(18) = 166.16$; $p < 0.0001$
Buffer					
Absence	9	0.86	0.14	1.57	$Q_M(1) = 1.10$; $p = 0.19$
Presence	12	1.60	0.74	2.46	$R^2 = 1.82\%$ $Q_E(19) = 232.28$; $p < 0.0001$
b) Density					
Isolation					
High	9	1.34	0.31	2.36	$Q_M(2) = 0.22$; $p = 0.90$
Medium	7	1.39	0.27	2.52	$R^2 = 0\%$
Low	24	1.59	0.97	2.21	$Q_E(37) = 434.67$; $p < 0.0001$
Enforcement					
High	29	1.88	1.32	2.45	$Q_M(2) = 5.27$; $p = 0.07$
Medium	13	0.95	0.17	1.73	$R^2 = 9.30\%$
Low	2	0.18	-1.88	2.26	$Q_E(41) = 612.31$; $p < 0.0001$
Buffer					
Absence	25	1.24	0.65	1.85	$Q_M(1) = 1.76$; $p = 0.18$
Presence	19	1.89	1.16	2.62	$R^2 = 1.39\%$ $Q_E(42) = 616.42$; $p < 0.0001$

n = number of studies. Log RR: effect size 'log response ratio'. LB and UB: lower and upper boundaries of 95% confidence interval around the mean effect size. Q_M : statistic for testing the null hypothesis of no effect of the moderator variable. Q_E : statistic for testing the model misspecification. Degrees of freedom are shown in brackets. R^2 : percentage of variance accounted for by the moderator. Marginally and statistically significant moderators are highlighted in bold.

for density ($Z = 0.90$, $p = 0.37$) was statistically significant, so there is no evidence of publication bias in the response variables according to this test.

3.3. Influence of MPA features

The level of enforcement exerted a marginally significant effect on the density response variable: highly enforced MPAs positively affected the density of fishes, while poorly enforced ones had a non-significant effect. MPAs enforced at intermediate levels responded positively although to a lesser extent than MPAs with high enforcement (Table 1b). This pattern was similar but, unexpectedly, non-significant for the biomass (Table 1a). For isolation and presence or absence of a buffer zone, all categories in the moderators showed positive but non-significant effects in both density and biomass (Table 1). Latitude had a positive effect on the biomass and density response variables, but it was statistically significant only for density (Table 2). Interestingly, the size of the NTZ was statistically significant and affected negatively the biomass and density of fish, so that the bigger the NTZ, the smaller the effect of protection on both response variables (Table 2). Finally, older MPAs showed a positive but non-significant effect on the response variables (Table 2).

Significant and marginally significant moderators (size of NTZ and latitude for biomass and enforcement, size of NTZ and latitude for density) were included in the multiple meta-regression models. Only two MPAs were characterized by having a low level of enforcement, so we excluded them from these analyses in order to increase statistical power (Hempel et al., 2013) and to better discern between the medium and high levels of this moderator.

For biomass, the final model explained 60% of the variance and size

of NTZ was the only statistically significant moderator, with a negative effect on the response variable (Table 3a). Similar results were found for density, the model was statistically significant, with the size of NTZ showing a significant negative response to protection (Table 3b). However, enforcement and size of NTZ appeared not to be independent features, so that smaller MPAs were generally better enforced (t -test = 2.29, $p = 0.03$, geometric mean of NTZ size at high enforcement = 281.84 ha, medium enforcement = 1318.26 ha; Fig. 1A). Moreover, we also found significant differences in enforcement levels at different latitudes, so that enforcement was lower in MPAs situated at lower latitudes (t -test = 4.47, $p < 0.001$, mean latitude at high enforcement = 34.95°, medium enforcement = 21.55°; Fig. 1B). Finally, Spearman correlation test showed a significant correlation between the size of the NTZ and latitude ($r = -0.55$, $p < 0.001$). These findings may explain why neither enforcement nor latitude appeared significant in the final model.

3.4. Biological, commercial and ecological characteristics responses to fishing protection

The biomass of piscivorous fish responded to protection depending on their maximum size, while no significant response was found for the other fish characteristic moderators considered (Table 4a). Biomass of medium-sized species and, to a lesser extent, of larger ones, exhibited a positive, statistically significant response to protection, while the response of small fish was not significant (Table 4a). Depth category was excluded from the analysis because of the low number of effect sizes of most categories (n for depth category broad = 21; deep = 1; medium = 2; shallow = 1).

The response of fish density to protection depended on feeding type, maximum size, commercial value and schooling behaviour of the species (Table 4b). Both facultative and strict piscivorous species showed a positive and significant response to protection, although the effect was greater for the facultative category. Large- and medium-sized species showed similarly greater densities inside NTZs, while for small-sized fishes, the response to protection was non-significant. Commercial species showed higher density inside than outside NTZs, with a greater effect on high-value commercial species compared to those species with a medium value, while the response of species with no commercial value was non-significant. Regarding schooling behaviour, all three categories showed significant differences between inside and outside NTZs, but this effect was much higher for gregarious and facultative schooling species than for solitary ones (Table 4b).

To perform the multiple meta-regression analysis, we included only those moderators which were significant or marginally significant. In the case of biomass, the only significant moderator was maximum size, so no multiple meta-regressions were performed, and this moderator accounted for 13.22% of the explained variance. For the density analysis, the moderators included were feeding type, maximum size (transformed into the contrast variables MaxTL1 and MaxTL2, which represents large and medium sizes, respectively), commercial value (transformed into commercial1, including high commercial value, and commercial2 which includes medium commercial value species) and social behaviour (transformed into social1 - gregarious and social2 - facultative schooling species). The full model was statistically significant (Table 5) and explained a high proportion of the variance in the data (32.79%), with the species categories large (MaxTL1) and gregarious (social1) showing a significant positive response to protection. Because the inclusion of contrast variables did not enable us to understand whether the whole moderator (maximum size and schooling behaviour) were relevant or not in the full model, we performed two additional analyses excluding all variables except the one of interest each time. Thus, once the influence of the other variables was taken into account, both maximum size ($Q_M(2) = 21.09$, $p < 0.0001$; $R^2 = 17.91\%$) and schooling behaviour ($Q_M(2) = 22.03$, $p < 0.0001$, $R^2 = 20.54\%$) were statistically significant in the full model.

Table 2
Results of the simple meta-regressions applied on (a) biomass and (b) density variables for MPA features, taking continuous moderator variables as predictors.

		Model test								
a) Biomass	n	b _j	Q _M	df	p	Q _E	df	p	R ²	
No-take size	21	-1.41	25.10	1	< 0.001	112.80	19	< 0.0001	66.06%	
Age	21	0.06	2.20	1	0.11	223.25	19	< 0.0001	12.03%	
Latitude	21	0.05	2.66	1	0.10	241.87	19	< 0.0001	4.14%	
b) Density										
No-take size	44	-0.89	8.90	1	0.003	422.78	42	< 0.0001	19.87%	
Age	44	0.03	0.79	1	0.37	609.41	42	< 0.0001	0%	
Latitude	44	0.07	8.20	1	0.004	538.96	42	< 0.0001	19.61%	

n = number of studies. b_j: regression coefficient of each predictor. Q_M: statistic for testing the null hypothesis of no effect of the moderator variable. df: degrees of freedom. Q_E: statistic for testing the model misspecification. Degrees of freedom are shown in brackets. R²: percentage of variance accounted for by the moderator. Marginally and statistically significant moderators are highlighted in bold.

Table 3
Multiple meta-regression analysis of MPA features for the biomass (a) and density (b) response variables including the marginally and significant moderators.

a) Biomass				
Variable	b _j	SE	Z	P
Intercept	4.49	1.40	3.21	0.0013
No- take size	-1.28	0.34	-3.76	0.0002
Latitude	0.02	0.03	0.80	0.42
Full model:	Q _M (2) = 19.71; p < 0.0001 R ² = 60.03% Q _E (16) = 112.49; p < 0.0001			
b) Density				
Intercept	2.79	2.04	1.37	0.17
Enforcement	0.44	0.76	0.58	0.57
No-take size	-0.81	0.39	-2.07	0.04
Latitude	0.05	0.03	1.55	0.12
Full model:	Q _M (3) = 12.44; p = 0.006 R ² = 33.35% Q _E (37) = 136.77; p < 0.0001			

b_j: regression coefficient of each predictor. SE: standard error of b_j. Z: statistic for testing the significance of the predictor. p: probability level for the Z statistic. Q_M: statistic for testing the null hypothesis of no effect of the moderator variable. Q_E: statistic for testing the model misspecification. Degrees of freedom are shown in brackets. R²: percentage of variance accounted for by the full model. Statistically significant moderators are highlighted in bold.

4. Discussion

Understanding the MPA features that make piscivorous fishes more likely to benefit from protection is essential for the management of MPAs, because they are a key trophic group in marine ecosystems (Cheng et al., 2019), and the first species to be depleted once the ecosystems are altered (Prato et al., 2013). Our results only partially corroborated our initial hypotheses. Overall, NTZs harbour higher density and biomass of the studied piscivorous fish species compared to adjacent unprotected areas, as already pointed out by other meta-analyses performed on the whole fish assemblages (Mosquera et al., 2000; Côté et al., 2001; Halpern and Warner, 2002; Halpern, 2003; Gill et al., 2017) and on piscivorous fishes (Micheli et al., 2004; Edgar et al., 2014; Giakoumi et al., 2017). However, our study goes further by portraying which MPA features and fish characteristics make these species more likely to benefit from protection measures, thus adding insights regarding which are the best MPA design features to achieve conservation objectives for these species.

An important finding of our research, and contrary to what we might expect, was that small NTZs are more beneficial than larger ones to boost biomass and density within the NTZ compared to neighbouring unprotected sites for the set of 73 species (15 families) of piscivorous fish included in the study. This was previously reported in the Mediterranean Sea for the fish density of the whole assemblage and the density of dusky grouper (*E. marginatus*) (Giakoumi et al., 2017), and now our results support the generalisation of this assertion at global scale for both density and biomass of the teleost piscivorous trophic group. Traditionally, researchers have advocated larger MPAs to

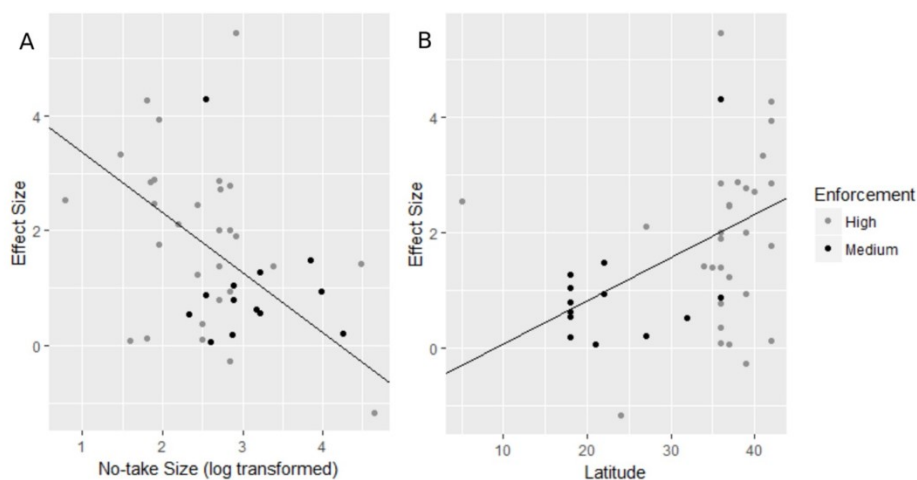


Fig. 1. Effect sizes at different enforcement levels for the size of NTZ (A) and latitude (B) moderators.

Table 4
Results of the weighted ANOVAs applied on log RR for the (a) biomass and (b) density response variables for the biological, commercial and ecological fish characteristics.

a) Biomass					
Variable	n	log RR	95% CI		ANOVA results
			LB	UB	
Feeding type					
Facultative	17	1.14	0.48	1.80	$Q_M(1) = 0.41; p = 0.52;$ $R^2 = 0$ $Q_E(25) = 561.11;$ $p < 0.0001$
Strict	10	0.80	0.02	1.60	
Habitat					
Benthopelagic	4	-0.25	-2.20	1.70	$Q_M(1) = 2.13; p = 0.14$ $R^2 = 4.44%$ $Q_E(22) = 262.00;$ $p < 0.0001$
Demersal	20	1.26	0.65	1.88	
Maximum size					
Large	16	1.19	0.59	1.79	$Q_M(2) = 5.81; p = 0.05$ $R^2 = 13.22%$ $Q_E(29) = 225.78;$ $p < 0.0001$
Medium	8	1.82	0.89	2.76	
Small	8	0.40	-0.32	1.14	
Mobility					
Sedentary	11	1.55	0.60	2.51	$Q_M(1) = 0.01; p = 0.94$ $R^2 = 0$ $Q_E(28) = 284.62;$ $p < 0.0001$
Vagile	19	1.50	0.79	2.22	
Commercial value					
High	20	1.29	0.83	1.75	$Q_M(2) = 2.25; p = 0.32$ $R^2 = 0$ $Q_E(27) = 133.64;$ $p < 0.0001$
Medium	2	0.68	-0.46	1.83	
No value	8	0.77	0.16	1.38	
Schooling behaviour					
Gregarious	5	1.15	-0.06	2.36	$Q_M(2) = 0.05; p = 0.97$ $R^2 = 0$ $Q_E(27) = 278.01;$ $p < 0.0001$
Facultative schooling	5	1.31	-0.05	2.69	
Solitary	20	1.15	0.52	1.77	
Territoriality					
Territorial	19	1.32	0.60	2.05	$Q_M(1) = 2.29; p = 0.13$ $R^2 = 1.56%$ $Q_E(23) = 282.45;$ $p < 0.0001$
Non-territorial	6	0.17	-1.13	1.48	
Trophic level					
Predators	13	1.29	0.59	1.99	$Q_M(1) = 0.06; p = 0.80$ $R^2 = 0$ $Q_E(31) = 279.05;$ $p < 0.0001$
High trophic level predators	20	1.17	0.64	1.71	
b) Density					
Depth					
Broad	44	1.78	1.30	2.26	$Q_M(2) = 2.5; p = 0.28$ $R^2 = 2.92%$ $Q_E(59) = 539.99;$ $p < 0.0001$
Deep	6	1.11	-0.30	2.52	
Medium	12	1.01	0.07	1.94	
Feeding type					
Facultative	41	1.72	1.24	2.19	$Q_M(1) = 4.59; p = 0.03$ $R^2 = 7.68%$ $Q_E(54) = 783.43;$ $p < 0.0001$
Strict	15	0.76	0.02	1.50	
Habitat					
Benthopelagic	8	1.07	-0.26	2.40	$Q_M(1) = 0.46; p = 0.50$ $R^2 = 0$ $Q_E(50) = 653.22;$ $p < 0.0001$
Demersal	44	1.56	1.11	1.99	
Maximum size					
Large	36	1.77	1.32	2.22	$Q_M(2) = 14.23;$ $p = 0.0008$ $R^2 = 17.69%$ $Q_E(73) = 595.69;$ $p < 0.0001$
Medium	21	1.56	0.94	2.20	
Small	19	0.36	-0.25	0.96	

Table 4 (continued)

a) Biomass					
Variable	n	log RR	95% CI		ANOVA results
			LB	UB	
Mobility					
Sedentary	26	1.40	0.79	2.00	$Q_M(1) = 0.61; p = 0.43$ $R^2 = 0$ $Q_E(59) = 667.90;$ $p < 0.0001$
Vagile	35	1.71	1.19	2.24	
Commercial value					
High	42	1.54	1.10	1.99	$Q_M(2) = 5.86;$ $p = 0.053$ $R^2 = 7.14%$ $Q_E(74) = 612.82;$ $p < 0.0001$
Medium	16	1.04	0.19	1.88	
No value	19	0.57	-0.10	1.24	
Schooling behaviour					
Gregarious	21	2.33	1.63	3.02	$Q_M(2) = 7.16;$ $p = 0.028$ $R^2 = 10.75%$ $Q_E(66) = 1239.27;$ $p < 0.0001$
Facultative schooling	16	1.76	0.87	2.64	
Solitary	32	1.12	0.55	1.67	
Territoriality					
Territorial	35	1.42	0.88	1.95	$Q_M(1) = 0.69; p = 0.41$ $R^2 = 0.27%$ $Q_E(55) = 437.05;$ $p < 0.0001$
Non-territorial	22	1.80	1.09	2.50	
Trophic level					
Predators	33	1.57	1.05	2.10	$Q_M(1) = 0.25; p = 0.62$ $R^2 = 0%$ $Q_E(61) = 522.90;$ $p < 0.0001$
High trophic level predators	30	1.39	0.84	1.93	

n = number of studies. Log RR: effect size 'log response ratio'. LB and UB: lower and upper boundaries of 95% confidence interval around the mean effect size. Q_M : statistic for testing the null hypothesis of no effect of the moderator variable. Q_E : statistic for testing the model misspecification. Degrees of freedom are shown in brackets. R^2 : percentage of variance accounted for by the moderator. Marginally and statistically significant moderators are highlighted in bold.

Table 5
Multiple meta-regression analysis of the biological, commercial and ecological fish characteristics for the density response variable including the marginally and statistically significant moderators (i.e., feeding type, maximum size, commercial value and social behaviour).

Density				
Variable	b_j	SE	Z	P
Intercept	1.30	0.19	6.70	< 0.0001
Feeding	0.19	0.18	1.08	0.28
MaxTL1	0.59	0.20	2.92	0.0035
MaxTL2	0.28	0.20	1.39	0.17
Commercial1	-0.09	0.19	-0.49	0.63
Commercial2	-0.08	0.21	-0.37	0.71
Social1	0.76	0.23	3.27	0.0011
Social2	-0.11	0.25	-0.44	0.66
Full model:	$Q_M(7) = 45.14; p < 0.0001$ $R^2 = 32.79%$ $Q_E(113) = 827.52; p < 0.0001$			

b_j : regression coefficient of each predictor. SE: standard error of b_j . Z: statistic for testing the significance of the predictor. P: probability level for the Z statistic. Q_M : statistic for testing the null hypothesis of no effect of the moderator variable. Q_E : statistic for testing the model misspecification. Degrees of freedom are shown in brackets. R^2 : percentage of variance accounted for by the full model. MaxTL1: large fish. MaxTL2: medium fish. Commercial1: high commercial value. Commercial2: medium commercial value. Social1: gregarious. Social2: facultative schooling. Marginally and statistically significant moderators are highlighted in bold.

increase their effectiveness (e.g., Halpern, 2003; Claudet et al., 2008, 2010; Davies et al., 2017), although the implementation of very large MPAs could also entail some disadvantages (Pérez-Ruzafa et al., 2017). In fact, an increase in no-take size relative to buffer areas can result in similar values for density and biomass in the two zones and even a negative effect in the NTZs (Sciberras et al., 2013). Our study included MPAs with NTZs ranging from 6 (Wakatobi Marine National Park) to 44 200 (Exuma Cays Land and Sea Park) ha. There are several advantages in having a small NTZ, such as ease of enforcement, susceptibility of 'spill-in' - i.e., colonization or migration of commercially targeted species from outside to inside MPAs to be detected more easily (McClanahan et al., 2007), or/and protection of species with low mobility, so that the NTZ can embrace their entire home range (Di Franco et al., 2018). In fact, small MPAs are expected to protect species with restricted home ranges (Claudet et al., 2008; Abecasis et al., 2014, 2015), so the minimum size of NTZs will depend on the home range of the species having the highest mobility. In our analysis, we did not include the home range as a moderator (but only mobility) because of a lack of studies for most species and inconsistency in the available estimates in different biogeographical areas. Generally, a positive relationship between body size and home range has been assumed (Kramer and Chapman, 1999; Green et al., 2015), but recently, Di Franco et al. (2018) have found an inverse relationship for a few species in the Mediterranean Sea. For example, our study included large species such as *E. marginatus*, *Plectropomus leopardus*, *Epinephelus costae* or *Pagrus auratus*, with home ranges of around 16.9, 1.9, 2.9 and 13.6 ha, respectively (Zeller, 1997; Parsons et al., 2003; Afonso et al., 2016). These home ranges are smaller than 95% of the NTZs included in the study. So although there is no available information for all species, it is possible that some of the species included in the study do not have large home ranges (as compared to those of most sharks or codfish), which may explain why the studied fish species can benefit from the protection measures offered even by small NTZs.

It has been previously suggested that MPAs would be more effective in tropical zones because the range of fish movements in temperate regions is greater due to wide seasonal variation in water temperatures (Horwood, 2000). Moreover, species tend to have longer planktonic larval duration and gene flow in tropical areas (Laurel and Bradbury, 2006). However, neither Côté et al. (2001) nor Lester et al. (2009) found significant differences in the performance of MPAs in different latitudes, from which they concluded that MPAs would be effective at any latitude. In this respect, our results suggest that there is a weak and marginally significant positive effect of latitude in the effectiveness of NTZs, which actually matches the results of Lester et al. (2009) for the density and biomass response variables. However, we found a positive correlation between latitude and enforcement, with NTZs located in higher latitudes having stronger enforcement, which may explain this pattern.

We had expected that older reserves would be ecologically more beneficial. However, we found a positive but non-significant effect of the age of the MPA. Time since the beginning of protection *per se* would be an important variable modulating the effectiveness of MPAs, especially for the piscivorous fishes that are large, have slow growth, long life and late maturity (Jennings et al., 1999; Reynolds et al., 2005). However, old reserves are more likely to suffer from budgetary restrictions for surveillance at certain times, and thus to trigger periods of poaching (Hogg et al., 2017). In fact, in a study performed in 55 MPAs (Bergseth et al., 2018), surveys showed that 48% of the fishers living close to them had observed poaching events. Thus, long-term protection alone would not be a good indicator of the ecological effectiveness of MPAs.

We have found a marginally significant effect of the level of enforcement on the density of piscivorous fishes, but, surprisingly, not on biomass. This difference could be due to the lower sample size used for biomass than for density. The novel approach used here by considering that at least one individual was present outside when the species was

detected within the MPA (even if zero individuals were censused in the unprotected area) enabled us to include some cases with density data that were not incorporated in the analysis with biomass data. This may have affected the power of the biomass analysis (López-López et al., 2014). Enforcement is an essential variable when assessing MPA effectiveness (Guidetti et al., 2008; Edgar et al., 2014; Giakoumi et al., 2017), and effective biodiversity conservation within MPAs worldwide is strongly dependent on human and financial resources (Gill et al., 2017). Here, we found a significant relationship between NTZ size and enforcement, with smaller NTZs being better enforced and showing greater effects of protection. Recently, Giakoumi et al. (2017) showed that small and well-enforced Mediterranean MPAs are more effective for the whole fish assemblage and for certain commercially important species. Our results suggest that this is not exclusive to the Mediterranean, so that small and well-enforced reserves may be effective for piscivorous fishes worldwide. This is especially important because the establishment of MPAs is a trade-off between ecological, social and economic factors so that if small MPAs are ecologically effective, they involve less economic effort and social conflict (Giakoumi et al., 2017; Pérez-Ruzafa et al., 2017).

The presence or not of a buffer zone does not appear to be a significant factor for the success of protection measures with regard to their effect on the density and biomass of the piscivores included in our study. Buffer zones in the MPAs studied were mostly located immediately surrounding NTZs. These partially protected areas are useful tools as multiple-use zones and are especially important with regard to the achievement of local socio-economic benefits (Di Franco et al., 2016). These zones are assumed to benefit from spillover from NTZs, either by movements of adults or due to larval dispersion. However, some kinds of fishing are carried out, such as small-scale fishery. If the targets of these fisheries are the same species that are being protected by the NTZs, it is to be expected that buffer zones will not benefit the conservation of these species (Sciberras et al., 2013). This result is consistent with the findings that NTZs are generally more effective than partially protected areas in exerting a positive impact on fish assemblages (Lester et al., 2009; Sciberras et al., 2013; Giakoumi et al., 2017; Sala and Giakoumi, 2017). In fact, it has been found that large sized buffer zones may even reduce the effectiveness of MPAs (Claudet et al., 2008; Sciberras et al., 2013), although they can still be very effective if properly designed and managed (Hackradt et al., 2014).

Regarding biological, commercial and ecological fish species characteristics, although commercial value has been widely accepted as the major factor driving the response of fish to protection (Mosquera et al., 2000; Côté et al., 2001; Micheli et al., 2004; Tetreault and Ambrose, 2007; Claudet et al., 2008), examining the studied piscivorous species more closely we found that maximum size and schooling behaviour exert an additional effect. Biomass of medium-sized fish responded best to protection, while large fish, as well as gregarious species, were the groups that responded best in terms of density. Other studies have found a positive significant response of abundance or biomass to protection with increasing individual fish size (Mosquera et al., 2000; Claudet et al., 2010; Edgar et al., 2014), although this pattern did not appear to be consistent throughout the literature (see Micheli et al., 2004), probably because size ranges vary widely across studies. Edgar et al. (2014) classified large fish as > 25 cm on the basis of the size of the fishes recorded in the study. In contrast, Mosquera et al. (2000) classified fish in seven maximum length classes, from < 10 cm to > 60 cm, and Claudet et al. (2010) made three categories, small < 20 cm, medium 20–60 cm and large > 60 cm. Our medium-sized classification is more similar to their large-sized species, so a comparison of these findings is difficult. However, for any classification, which is designed according to the group of species studied in each research project, larger fish tend to benefit more from the effect of protection, either in terms of density (Claudet et al., 2010; Edgar et al., 2014) or biomass (Mosquera et al., 2000; Edgar et al., 2014). Maximum size has been proposed as an indicator of the vulnerability of species to fishing

pressure because it is related to growth, age at maturity and reproductive output (Jennings and Kaiser, 1998; Jennings et al., 1999; Dulvy et al., 2003), as larger and older fish produce more larvae with greater reproductive survival potential. In fact, commercial and recreational fisheries have always targeted medium- and large-sized individuals (Mellin et al., 2016), causing changes in the size structure of the populations.

Schooling fish are well known to be vulnerable to fisheries because schools are easier to target (Dulvy et al., 2003). Since the beginning of commercial fisheries, gear and techniques have undergone extensive development with the aim of increasing the captures (Kennelly and Broadhurst, 2002), and the improvement of electronic devices and instruments that help locate fish aggregations make schooling species even more vulnerable (Valdemarsen, 2001). This may explain why medium- and large-sized species living in schools benefit more from the absence of fishing pressure.

Overall, our results explain part of the total variance in the data, so there may be important moderators that we did not take into account. Moreover, the study has a number of limitations, so results should be taken with caution. Firstly, our study includes only teleost piscivorous fish species, which may rule out generalising our findings to other predatory species, such as sharks or rays. In fact, MPAs are perceived as only moderately effective for the conservation of sharks and rays, although it may be enhanced for spatially restricted populations, such as some reef shark species (MacKeracher et al., 2018).

Moreover, MPAs are typically established in areas where information regarding abundance and/or biomass of fish prior to the establishment of the reserves is lacking (i.e., there is no possibility of performing before-after comparative studies). Thus, the assessment of MPA performance is generally based on a spatial comparison between inside and outside the MPA, and, although individual studies have paid attention to the selection of sampling sites, so that habitats may be comparable, we did not specifically analyse the effect of habitat in our analyses. The effects of protection inside and the influence outside the MPA may depend on (i) the availability of different types of habitats in the two areas, as well as differences in habitat structure (Kramer and Chapman, 1999; García-Charton et al., 2004), and (ii) the occurrence of differences in habitat quality due to the degrading action of fishing activity (Jennings and Kaiser, 1998; Rodwell et al., 2003).

In addition, the fishing pressure outside the MPA is likely to determine how species respond to protection (Hopf et al., 2016; Pérez-Ruzafa et al., 2017), and information regarding fishing intensity and spatial distribution in unprotected areas was lacking. However, in the light of the available data, our research, on the basis of numerous control-impact studies, has enabled us to understand the consistency of the effect of protection under different conditions and offers new general insights on how MPAs enhance teleost piscivorous fish populations worldwide.

In conclusion, our study confirms that both the abundance and biomass of the studied piscivorous fish species benefit from protection measures. MPAs are effective tools to protect piscivores populations even when they are small, but they must be well-enforced to ensure their effectiveness. We thus propose the implementation of networks of small and well-enforced MPAs worldwide in order to provide protection for this key trophic group (Rolim et al., 2019). Moreover, as surveillance costs increase exponentially with MPA size, small and well-connected MPAs offer a promising solution for maximising ecological benefits with limited financial outlay (Pérez-Ruzafa et al., 2017). The characteristics maximum size and social behaviour are good indicators of the vulnerability of species to fishing activities, so that medium- and large-sized piscivorous fishes and those living in shoals benefit more from protection. Recent reports (Di Franco et al., 2016) highlight the importance of stakeholder engagement and compliance as causal determinants of MPA success, so that besides MPA design attributes, a strong emphasis should be put on studies aiming at providing cues to optimizing MPA governance, i.e., considering not only fishes but also

importantly the human component of the management of coastal areas (Hogg et al., 2017).

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2019.06.005>.

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