LETTER

Marine reserves: size and age do matter

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Abstract

Marine reserves are widely used throughout the world to prevent overfishing and conserve biodiversity, but uncertainties remain about their optimal design. The effects of marine reserves are heterogeneous. Despite theoretical findings, empirical studies have previously found no effect of size on the effectiveness of marine reserves in protecting commercial fish stocks. Using 58 datasets from 19 European marine reserves, we show that reserve size and age do matter: Increasing the size of the no-take zone increases the density of commercial fishes within the reserve compared with outside; whereas the size of the buffer zone has the opposite effect. Moreover, positive effects of marine reserve on commercial fish species and species richness are linked to the time elapsed since the establishment of the protection scheme. The reserve size-dependency of the response to protection has strong implications for the spatial management of coastal areas because marine reserves are used for spatial zoning.

Keywords

Asymmetrical analysis of variance, coastal marine ecosystems, commercial species, fish assemblages, heterogeneity, marine protected area, marine reserve age, marine reserve design, marine reserve network, marine reserve size, weighted meta-analysis.

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INTRODUCTION

Human-induced environmental disturbance, through tourism, pollution and fishery activities can have strong negative impacts on the world's coastal areas (Jackson *et al.* 2001; Lotze *et al.* 2006). Concerns are rising over observed declines in the abundance of particular species (EEA 2006) as well as reductions in functional diversity (Micheli & Halpern 2005). As a result, the restoration and conservation of marine biodiversity is a major challenge (Balmford *et al.* 2005). Marine reserves, where all extractive uses are forbidden (i.e. no-take zones), have been recom-

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mended as tools for an ecosystem approach to fisheries management (Hastings & Botsford 1999; Roberts *et al.* 2001; Pauly *et al.* 2002; Claudet *et al.* 2006b) and for biodiversity conservation (Schrope 2001; Rodrigues *et al.* 2004).

Effectiveness of marine reserves regarding fisheries and ecosystem restoration goals has been widely studied (Sale *et al.* 2005), but very few attempts have been made to generalize their ecological effects (Côté *et al.* 2001; Halpern 2003; Micheli *et al.* 2004; Guidetti & Sala 2007). Previous analyses have emphasized that the density of harvested fish species inside marine reserves increases compared with unprotected areas; there are many documented examples where fished species have benefited from reserve establishment, in particular through increases in mean size and abundance (for reviews, see Roberts & Polunin 1991; Dugan & Davis 1993; Rowley 1994; Bohnsack 1998; Russ 2002; Halpern 2003; Pelletier *et al.* 2005). Despite these tantalizing results, the effects of marine reserves vary both in direction and magnitude (Halpern & Warner 2002), and the basis for this heterogeneity is still unknown. Insights into these patterns of heterogeneity are fundamental for the development of a more general theory of marine reserve effectiveness and design. Linking possible heterogeneity in the effects of marine reserves with the age and design of the reserves (Botsford *et al.* 2003) and with their inclusion in reserve networks is also necessary for conservation purposes.

Previous studies have explored some sources of heterogeneity in the effectiveness of marine reserves. For example, theoretical studies suggest that large reserves should be more effective for conservation purposes than small reserves (Botsford *et al.* 2001, 2003; Hastings & Botsford 2003; Roberts *et al.* 2003). However, empirical studies have not supported this hypothesis (Côté *et al.* 2001; Halpern 2003; Guidetti & Sala 2007). This discrepancy could represent a failure of the theory or the synthesis of data across both temperate and tropical ecosystems that could obscure the size effects (but see Guidetti & Sala 2007), or to analytic schemes that weighted poorly designed studies as much as well-designed ones (Gurevitch & Hedges 1999). Other empirical studies (including meta-analyses) have reached conflicting results about time since protection (Halpern & Warner 2002; Micheli *et al.* 2004; Russ & Alcala 2004). No previous empirical quantitative synthesis has analysed the effects of connectivity between marine reserves.

Here, we examine how duration of protection, size and spacing of marine reserves may affect populations of commercial fishes and levels of biodiversity in a single temperate region in Europe. We obtained data on entire fish assemblages from the original investigators. We thus avoided many problems arising from species selection, publication bias and the aggregation of data across different biogeographic regions that have plagued other meta-analyses. We show that positive effects of marine reserves on commercial fish species and species richness are linked to the time elapsed since the establishment of protection. Moreover, we show that the response to protection is reserve size-dependent, contrary to previous empirical studies that found no effect of size (Côté *et al.* 2001; Halpern 2003; Guidetti & Sala 2007). Increasing the size of the no-take zone and decreasing the size of the buffer zone (where some extractions activities are regulated) has positive effects on the abundance of commercial fishes. Finally, our results suggest that the efficacy of a marine reserve is not affected by the distance to its nearest neighbouring reserve.

METHODS

We used a weighted meta-analytical approach to investigate the effects of protection in southern Europe and to explicitly examine heterogeneity among studies (Osenberg *et al.* 1999). We developed a programme (EMPAFISH) involving 14 European research teams to synthesize most of the available data from marine reserves in this single region. This resulted in a dataset of 58 case studies from 19 marine reserves distributed over 3000 km from the central Mediterranean Sea to the north-eastern Atlantic Ocean. The data spanned a period of 42 years, from 8 years before the establishment of the marine reserves up to 33 years afterwards. We retained studies based on three criteria: (1) the protected location was a true no-take zone, (2) the control locations were in unprotected areas and (3) the dataset reported all fish species that could be identified and counted based on the sampling technique used. This led to a final database consisting of data from 40 studies from 12 marine reserves distributed over 2500 km from north-western Mediterranean to central-eastern Atlantic (Fig. 1) and ranging from 3 years before the establishment of marine reserves to 30 years after.

For 39 of the selected studies, fish were identified and counted by underwater visual census along transects or visual point counts. One study used experimental fishing to estimate catch per unit of effort. As visual censuses are not well designed to estimate pelagic species densities and as it is expected that most of these highly mobile species are not protected by a marine reserve, we excluded pelagic species from the analyses. The main goal stated by the managers of the marine reserves studied is the restoration of size and assemblage structures of fish species that have been over-harvested by commercial fisheries. Thus, we focused our analyses on the size classes of fishes that are of commercial value. In 31 studies, fish sizes were estimated according to three size groups (small, medium and large) for each species; the total fish density of a species being the sum of the

Figure 1 The location of the 12 European temperate marine reserves involved in the study.

densities per size group. Size groups were defined using 33 and 66 percentiles of the maximum size generally observed in the region. The commercial value of each fish species (see Appendix S1 in Supplementary Material) was assigned by three referees chosen among the researchers who worked on a marine reserve in which each given species was present. Referees scored each species as commercial, non-commercial or as species with low commercial value. Where consensus was not reached, the majority criterion was used. We defined the total density of commercial fishes by summing the density of all medium and large size classes of commercial species. For the analysis of density of commercial fish, we excluded the nine studies where sizes were not recorded. Species with low commercial value were excluded from the analyses. After this, 82 commercial species and 55 non-commercial species were retained.

In addition, we examined the response to protection of the species richness of the entire fish assemblage. All studies and all species were included in this analysis. In total, 139 fish species were considered over the 40 studies (see Appendix S1). Because of rarity, true species richness will often be more greatly underestimated in studies with lower sample size. Because in the studies involved in our meta-analysis sample sizes outside the marine reserve were either equal to or higher than inside the reserve, possible bias in examining species richness should make the analysis more conservative.

We used effect sizes to model the differences between protected and unprotected conditions. We calculated log-response ratios (Hedges *et al.* 1999) for commercially targeted fishes as well as fishes that were not harvested:

$$R_{\mathrm{G},i} = \ln\left(\frac{\bar{X}_{\mathrm{G,P},i}}{\bar{X}_{\mathrm{G,C},i}}\right),$$

where $R_{\mathrm{G},i}$ is the log-response ratio for study i based on fish in group G (i.e. fished, F, or unfished, U), and $\bar{X}_{\mathrm{G,P},i}$ and $\bar{X}_{\mathrm{G,C},i}$ are the mean densities of fishes in group G for study i in protected (P) and unprotected (i.e. control, C) conditions, respectively. For species richness, we focused on the differences in species richness of the whole assemblage between protected and unprotected conditions:

$$D_i = \bar{S}_{\mathrm{P},i} - \bar{S}_{\mathrm{C},i},$$

where D_i is the differential response of species richness for study i, and $\bar{S}_{\mathrm{P},i}$ and $\bar{S}_{\mathrm{C},i}$ are the mean species richness for study i, in protected and unprotected conditions, respectively. We used these two different approaches to model the effect sizes based on fish densities and on fish species richness because we assumed managers were most interested in percent increases in density (i.e. a change from 10 to 11 fish m^{-2} was equivalent to a change from 100 to 110 and greater than a change from 100 to 101) but absolute changes in species richness (i.e. an increase from 1 to 2 species was treated the same as an increase from 10 to 11).

In addition to obtaining effect sizes for each study, we also estimated the variances associated with these estimates, which were then used to derive weights in the meta-analysis. Weighted analyses increase the precisions of the combined estimates and increase the power of tests (Gurevitch &

Hedges 1999) by giving more weight to the studies with the most powerful experimental designs (i.e. those with greater and more appropriate replication). The various case studies included in the meta-analysis differed with respect to the underlying sampling design, sampling intensity and spatial or temporal scales addressed. We therefore used an approach that reflected these differences. Because no study had a full time series of data both before and after establishment of the marine reserve at multiple control and reserve sites, we assumed that the most relevant study design was a Control-Impact design (Osenberg *et al.* 2006). As protected locations were not replicated for each marine reserve, differences among protected and unprotected conditions at each point in time were compared with the spatial variation estimated from multiple control locations. The relevant error term for testing an effect of protection at any particular time would be the variance associated with among-location variation. A measure of the variance associated with the estimated means of the protected and unprotected locations is provided by the ratio between the mean square for the control locations and the sample size used to estimate these means (Neter *et al.* 1996). For studies with multiple control locations, we obtained the variance associated with a given effect size from asymmetrical analyses of variance (Glasby 1997) as:

$$v_{e,i} = \frac{\mathrm{MS}_{\mathrm{C},i}}{n_{\mathrm{C},i}},$$

where $v_{e,i}$ is the variance associated with the effect size e_i, (i.e. the within-study variance), $\mathrm{MS}_{\mathrm{C},i}$ the mean square for the among-controls component of variation and $n_{\mathrm{C},i}$ the number of control sites for the study i. For studies that lacked multiple controls, we estimated v_e adding the average MS_{C} from the studies with replication and setting $n_{\mathrm{C},i} = 1$.

For each effect size e (i.e. either R or D), confidence intervals were derived from the variances as:

$$\mathrm{CI} = e_i \pm z_{\alpha/2} v_{e,i},$$

where CI is the confidence interval, $v_{e,i}$ the variance associated with the effect size e_i for the study i and z the two-tailed critical value found from the standard normal distribution at the critical level α.

We then used a mixed effects meta-analysis to incorporate these variances into a weighting scheme:

$$w_i = \frac{1}{v_{e,i} + v_{\mathrm{a}}},$$

where w_i is the weight, $v_{e,i}$ is defined as above and v_{a} is the among-study variance. For mixed effects models, we can obtain v_{a} from the generalized equation (Hedges & Pigott 2004):

$$v_b = \frac{Q_{\mathrm{E}} - (k - p)}{\mathrm{tr}\mathbf{W} - \mathrm{tr}[(\mathbf{WM}(\mathbf{M}'\mathbf{WM})^{-1}\mathbf{M}'\mathbf{W}]},$$

where $\mathbf{M}$ is the design matrix, $\mathbf{W}$ the diagonal matrix of individual weights w_i, k the number of studies and p the number of columns of $\mathbf{M}$. Q_{E} is the residual error heterogeneity that can be computed as:

$$Q_{\mathrm{E}} = (\mathbf{E} - \mathbf{M}\beta)^{\mathrm{t}} \mathbf{W}(\mathbf{E} - \mathbf{M}\beta),$$

where $\mathbf{M}$ and $\mathbf{W}$ are defined as above, $\mathbf{E}$ is the vector of effect sizes e_i and β is the matrix of model coefficients.

The weighted average effect size for a sample of studies can be obtained as:

$$\bar{E} = \left(\frac{\sum\limits_{i=1}^{k} w_i e_i}{\sum\limits_{i=1}^{k} w_i} \right),$$

where $\bar{E}$ is the average effect size, e_i and w_i are the effect size and weights associated with the study i, respectively, and k is the number of studies. The variance of $\bar{E}$, $v_{\bar{E}}$, is:

$$v_{\bar{E}} = \frac{1}{\sum\limits_{i=1}^{k} w_i}.$$

We investigated the influence of different features of marine reserves (i.e. differences in design and years since implementation) using a weighted generalized linear mixed model (GLMM) to model the variation in the differences among protected and unprotected conditions in fish densities and species richness. As multiple studies could come from the same reserve, we applied a random intercept with studies nested in marine reserves. We examined the performance of marine reserves in relation to four predictor variables (Table 1), which were fitted simultaneously in the inferential model (Chatfield 1995): (1) number of years since their establishment, (2) size of the no-take zone, (3) size of the buffer zone and (4) distance to the nearest neighbouring reserve. We used the number of years since the establishment of marine reserves to examine the temporal effect and potential trend of response to protection; we set the number of years since protection for all before data to zero. If enforcement did not begin when the reserve was established, we used the first year of enforcement as the first year of protection. The size of the no-take and buffer zones was measured in hectares. The buffer zone was defined as any area adjacent to the no-take zone that had an intermediate level of protection, and thus permitted some forms of extraction. If the entire reserve was fully protected, then this area was 0. Sizes of no-take and buffer zones were log-transformed. For the distance to the closest marine reserve, all existing reserves (whether they were among the 19 reserves analysed or not) were considered.

Table 1 Design and age characteristics of the 12 European marine reserves included in the meta-analysis

Marine reserve	Country	Year of establishment	Size of the no-take zone (ha)	Size of the buffer zone (ha)	Distance to the nearest marine reserve (km)
(1) La Restinga	Spain	1996	180	813	100
(2) La Graciosa	Spain	1995	1225	68 775	450
(3) Cabo de Palos	Spain	1995	270	1628	55
(4) Tabarca	Spain	1986	120	1280	40
(5) San Antonio	Spain	1993	110	390	60
(6) Columbretes	Spain	1990	1883	2517	180
(7) Medes Islands	Spain	1983	93	418	15
(8) Cerbere-Banyuls	France	1974	65	585	40
(9) Cap Couronne	France	1996	210	0	20
(10) Carry-le-Rouet	France	1982	85	0	20
(11) Bouches de Bonifacio	France	1999	1200	78 800	3
(12) Sinis Mal di Ventre	Italy	1997	529	25 144	62

All interactions between the marine reserve features were tested in the model, and non-significant interaction terms were removed from the final model. All analyses were conducted with the free software environment R (R Development Core Team 2006).

RESULTS

There was an overall positive effect of marine reserves on the density of commercial fishes. Mean densities were 2.46 times larger inside the marine reserves compared with the adjacent fished areas (log-response ratio of fish densities: $R = 0.90 \pm 0.83$, 95% CI). This effect was, however, heterogeneous ($Q = 2.15$; d.f. $= 29$; $P < 0.001$), suggesting that the effects of protection on commercial fishes varied among reserves. Time since reserve establishment and the size of no-take and buffer zones collectively explained a part of this variability (Fig. 2). For each year since protection, the mean relative density of commercial fishes increased by 8.3% (i.e. slope of regression of R on years since protection: 0.08; SE $= 0.017$; $P < 0.001$). For every 10-fold increase in the size of a no-take zone, there was a 35% increase in the density of commercial fishes (slope: 0.30; SE $= 0.12$; $P = 0.038$) (Fig. 2a). The size of the buffer zone had a similar size of effect on commercial fishes, although it was in the opposite direction (Fig. 2b): for every 10-fold increase in the size of the buffer, there was a 31% decrease in density (slope $= -0.27$; SE $= 0.09$; $P = 0.014$). There was no effect of distance to neighbouring reserves on the response of commercial fishes ($P > 0.1$). All interaction terms were non-significant (all $P > 0.1$).

There was no overall significant effect of protection on the density of small fishes of commercial species or on non-commercial species ($R = -0.34 \pm 0.75$ and $R = 0.13 \pm 0.53$, 95% CI, respectively). The effect of protection on small fishes of commercial species and on non-commercial species was heterogeneous ($Q = 3.85$; d.f. $= 29$; $P < 0.001$ and $Q = 5.88$; d.f. $= 37$; $P < 0.001$) but none of the marine reserve characteristics examined explained this heterogeneity (all $P > 0.1$).

The average effect of protection on species richness was not significantly different from 0 (difference in species richness: $D = 0.8 \pm 3.14$, 95% CI); however, this effect was significantly heterogeneous ($Q = 4.60$; d.f. $= 38$; $P < 0.001$). The duration of protection explained a portion of this heterogeneity, with the mean number of species increasing within the marine reserve by 0.20 (SE $= 0.07$; $P < 0.012$) for each year since enforcement. The size of the marine reserve, the size of the buffer zone and the distance to the nearest neighbouring marine reserve did not play any significant role in explaining the variation in the response of species richness to protection (all $P > 0.1$).

DISCUSSION

Our findings provide novel insights into the features of marine reserves that most affect the response of fishes to protection, and therefore reconcile conflicting outcomes of theoretical and empirical studies. Theoretical studies have hypothesized that larger marine reserves would be more effective at increasing biodiversity (Botsford *et al.* 2003; Roberts *et al.* 2003) and density of commercial species (Botsford *et al.* 2001; Hastings & Botsford 2003). However, all previous meta-analytical approaches failed to support this hypothesis and concluded that the effects of marine reserves were independent of the reserve size (Côté *et al.* 2001; Halpern 2003; Guidetti & Sala 2007). Some meta-analyses (Halpern 2003) have taken an unweighted approach and could not therefore partition the within-study variance compared with the between-study variance. As a result, they could not evaluate the heterogeneity in response among reserves. Others (Côté *et al.* 2001; Guidetti & Sala 2007),
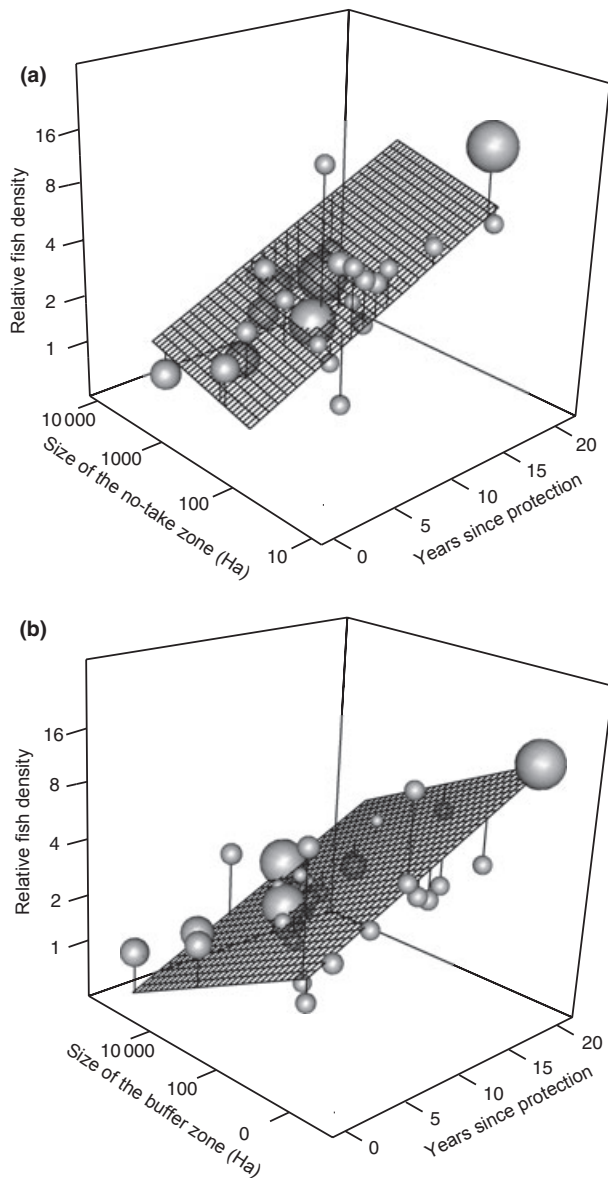
Figure 2 Effects of marine reserves on commercial fish densities as a function of years since protection and (a) the size of the no-take zone and (b) the size of the buffer zone. Planes give the fitted effect. The size of the points is proportional to the weight of each study. Stems indicate the distance between the calculated weighted effect size and the fitted effect.

without having full access to original datasets, were unable to build weights incorporating the full intrinsic variability of the different studies and used a weighting scheme based on the total area censused in each study. In addition, apart from the work of Guidetti & Sala (2007), previous meta-analyses have synthesized data across vastly different ecosystems, possibly obscuring the effects of reserve design within regions (Côté *et al.* 2001; Halpern 2003; but see Tetreault & Ambrose 2007 for a recent exception).

Our most compelling result is that the response of commercial species to protection is reserve size-dependent. Increasing the size of the no-take zone resulted in increased density of commercial fishes within the reserve compared with outside. A biological mechanism explaining this result is that large no-take zones may allow a greater fraction of mobile fishes with wide home ranges to remain protected within the marine reserve, compared with smaller ones (Chapman & Kramer 2000; Jennings 2001; Apostolaki *et al.* 2002). Large reserves may also increase self-recruitment (Botsford *et al.* 2003). Unfortunately, fish mobility and dispersal are rarely reported in studies of marine reserves or even known for most fish species (but see Polunin 2002), precluding a formal investigation of the relevance of these processes in the current meta-analysis. Although we show that effectiveness increases with marine reserve size, this does not imply that small marine reserves are ineffective. Our results suggest that any sized marine reserve increases fish density and diversity (although larger ones would be even more effective).

In contrast to the effect of increasing the size of the protected area, increasing the size of the buffer zone reduced the effectiveness of the reserve. The size of no-take zones and the size of buffer zones were not correlated (Spearman's rank test for negative association, $P > 0.9$), suggesting that increasing the size of one zone was not made at the expense of the other. Although fishery regulations may be more restrictive in buffer zones than in unprotected areas, buffer zones are attractive for local artisanal fishers (Stelzenmüller *et al.* 2007). Consequently, the fishing pressure can increase in these areas (e.g. Stelzenmüller *et al.* 2007) and can be higher than when just fishing the line (i.e. fishing along the reserve edges, Kellner *et al.* 2007).

Our findings provide useful information for the design and management of marine reserves. The design of marine reserves has often incorporated spatial zoning, each with different regulatory measures as part of an integrated coastal zone management plan (Cicin-Sain & Belfiore 2005; Claudet *et al.* 2006b). Our analysis would suggest that buffer zones could have detrimental effects on the protection of fish species. However, our limited understanding of the underlying mechanisms cautions against this conclusion and further research is needed towards the understanding of the distribution of fishing effort in the buffer zones and adjacent areas. Moreover, buffer zones are multiple use areas, and the choice of size is a complex problem involving ecology as well as economics and politics. In the case in which the establishment of a buffer zone is required for coastal management purposes, our results suggest that increasing the size of the no-take zone could be a solution to prevail against their potential effects.

In addition to the effect of marine reserve size, there also was an effect of the time since protection.

The time required for a marine reserve to become effective in restoring the biodiversity and density of commercial fish species is a key question for coastal resources management (Lotze *et al.* 2006). Some reviews and single studies showed fish density and species richness increasing after 3 years of protection (Halpern & Warner 2002; Russ *et al.* 2005; Claudet *et al.* 2006a). Others showed that decades could be needed (Micheli *et al.* 2004). Also, by removing the fishing activity, which targets specific fish species and sizes, the magnitude of the response to a reserve establishment across time is expected to be related to fish commercial value and size, as shown on single marine reserve studies (Claudet *et al.* 2006a). Moreover, it is important to protect large fish, as these have greater reproductive potential and produce larvae with better survival rates than those from younger fishes (Birkeland & Dayton 2005). Here, we have shown that older European marine reserves are more effective than newly established reserves in increasing catchable sizes of commercial fishes and in conserving fish species richness. This could be explained in part by the life span of some commercially targeted large species (e.g. Serranidae) that can live as long as 40 years. As recovery of fish communities occurs at a relatively slow rate, a rotating temporal system of spatial closures may therefore be inadequate for conservation purposes (let alone the unknown effects of increasing temporal variance of fishing pressure on mean population densities, Benedetti-Cecchi *et al.* 2003). As different reserves were sampled at different times, the effect of years since protection partly accounts for the heterogeneity among reserves. There was no correlation between the time since protection and the size of the no-take zones ($P = 0.80$), or with the size of the buffer zones ($P = 0.34$), suggesting that these effects were not confounded in our analyses.

The age of a reserve was less important than its size and the size of its buffer in determining commercial fish density in our dataset. This too has implications for management. A strong cumulative effect of time since enforcement of protection can be expected for marine reserves, suggesting that the evaluation of their efficacy for re-stocking exploited populations or preserving biodiversity should be framed in a temporal context. As all the studied marine reserves were established to last indefinitely, the time over which these are likely to become effective does not directly influence their planning, although strong enforcement is required. In contrast, the site and design selection prior the establishment of a marine reserve, and alternative options of modifying the reserve designs once they are established, are important management-related actions.

Distance to the nearest neighbouring marine reserve can be selected by managers during the planning phase. Indeed, mathematical models of marine reserve networks demonstrate the importance of proximity, although the optimal distance between reserves depends on management goals, the input data considered and the assumptions made (Sala *et al.* 2002; Hastings & Botsford 2003). Our study is the first empirical evaluation of the effects of distance among marine reserves. We found no evidence of an effect of distance between reserves, suggesting that this aspect is not crucial when planning the establishment of new marine reserves within a regional context. We, however, caution that other factors (in addition to distance) such as habitat discontinuities and fragmentation (Banks & Skilleter 2007; Moilanen & Wintle 2007), larval dispersal (Cowen *et al.* 2006; Steneck 2006), and species and disturbance dynamics (Cottenie 2005; Leroux *et al.* 2007) can play a major role in marine reserve connectivity and thus marine reserve networks. Moreover, if exportation of biomass from marine reserves takes place at small spatial scales (Murawski *et al.* 2004; Goñi *et al.* 2006), Mediterranean reserves may be too far apart to act as a network at a regional scale. Experimental frameworks using reserve networks could be used to test ecological hypotheses about factors that potentially influence connectivity. Such an effort would require the cooperation of scientists and decision-makers.

None of the marine reserve characteristics examined explained heterogeneity in the response to protection of non-commercial species. Non-commercial species are often assumed to be little affected by protection (unless they are killed via by-catch). Thus, any response of non-commercial fishes must arise through indirect effects, such as changes in the food web (Micheli *et al.* 2005) or habitat availability (Willis & Anderson 2003). We did not, however, observe responses of the non-commercial fishes in response to recovery of the fished species (mirroring the results from five marine reserves in southern California, Tetreault & Ambrose 2007). This may be because positive effects of changes in habitat compensated for negative effects of trophic cascades, because the non-fished species varied in their vulnerabilities to fished species and our aggregation masked the effect on a subset of the species, or because the trophic cascades in these systems are actually weak. Monitoring habitat variables and incorporating greater detail about food-web structure could improve the evaluation of these hypotheses.

We anticipate that our study will be the starting point for more thorough analyses on optimal marine reserves design. Future efforts to manage and protect coastal ecosystems should take into account our results on marine reserve size together with unbiased biological data (Grand *et al.* 2007) and sound socio-economic local information to best satisfy the management goals (Claudet & Pelletier 2004) when allocating space for no-take and buffer zones.

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