

Marine reserves: Fish life history and ecological traits matter

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Abstract. Marine reserves are assumed to protect a wide range of species from deleterious effects stemming from exploitation. However, some species, due to their ecological characteristics, may not respond positively to protection. Very little is known about the effects of life history and ecological traits (e.g., mobility, growth, and habitat) on responses of fish species to marine reserves. Using 40 data sets from 12 European marine reserves, we show that there is significant variation in the response of different species of fish to protection and that this heterogeneity can be explained, in part, by differences in their traits. Densities of targeted size-classes of commercial species were greater in protected than unprotected areas. This effect of protection increased as the maximum body size of the targeted species increased, and it was greater for species that were not obligate schoolers. However, contrary to previous theoretical findings, even mobile species with wide home ranges benefited from protection: the effect of protection was at least as strong for mobile species as it was for sedentary ones. Noncommercial bycatch and unexploited species rarely responded to protection, and when they did (in the case of unexploited benthic-pelagic species), they exhibited the opposite response: their densities were lower inside reserves. The use of marine reserves for marine conservation and fisheries management implies that they should ensure protection for a wide range of species with different life-history and ecological traits. Our results suggest this is not the case, and instead that effects vary with economic value, body size, habitat, depth range, and schooling behavior.

Key words: body size; bycatch; habitat; home range; life history traits; marine protected area; marine reserve age; marine reserve design; schooling behavior; species mobility; territoriality; weighted meta-analysis.

INTRODUCTION

Anthropogenic activities have strongly affected the world's coastal areas (Jackson et al. 2001, Lotze et al. 2006). As a result, conservation of marine biodiversity and sustainability of fisheries are now major environ-

mental and economic challenges (Lauck et al. 1998, Balmford et al. 2005). Marine reserves (defined here as no-take zones, potentially surrounded by buffer zones) are often heralded as an effective tool to manage fishery activities (Hastings and Botsford 1999, Roberts et al. 2001, Pauly et al. 2002, Goñi et al. 2008, Harmelin-Vivien et al. 2008), enhance over-harvested marine resources (Schrope 2001, Claudet et al. 2006a, 2008) and restore biodiversity (Halpern 2003, Micheli et al. 2004, Rodrigues et al. 2004, Claudet et al. 2008).

Manuscript received 18 November 2008; revised 28 April 2009; accepted 22 July 2009. Corresponding Editor: P. K. Dayton.

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However, some studies have failed to detect significant differences in ecological response variables between no-take and reference areas, or have criticized the design of existing studies, fuelling the view that the importance of marine reserves as a managerial tool may have been overstated (Hilborn et al. 2004, Murawski et al. 2005, Osenberg et al. 2006).

In contrast to traditional fisheries management, which focuses on particular species, marine reserves provide a refuge in space to all species and are not generally designed for a specific species (Claudet et al. 2006b). Thus, to be effective in an ecosystem context, reserves must protect species with different life histories and ecological characteristics (Palumbi 2004). However, effects of marine reserves vary both in direction and magnitude (Halpern and Warner 2002, Claudet et al. 2008). This heterogeneity in response to protection may stem from differences in design or age among reserves, differences in the life histories of focal taxa, or a combination of these effects. While the effects of reserve design, regulation and enforcement on the efficacy of protection have been investigated intensively (Côté et al. 2001, Halpern and Warner 2002, Halpern 2003, Micheli et al. 2004, Guidetti and Sala 2007, Claudet et al. 2008, Guidetti et al. 2008), much less empirical attention has been devoted to the role of species life history and ecological traits.

For example, spatially explicit demographic models have hypothesized that highly mobile fish will not be affected by protection (e.g., DeMartini 1993, Walters et al. 1999). The few empirical studies to date have offered limited or no support for this prediction (Micheli et al. 2004, Blyth-Skyrme et al. 2006, Goñi et al. 2008). Besides mobility, a species' response to protection may also depend on its body size (Tupper 2007) and habitat requirements (García-Charton and Pérez-Ruzafa 1999, Ashworth and Ormond 2005). Because some fishing activities are highly size selective (e.g., spear-fishing; Frisch et al. 2008), fish species having larger body size may respond more strongly to protection (Mosquera et al. 2000). Association with benthic habitats also can affect a species' response to protection, possibly because benthic fishes are more readily caught with certain types of fishing gear than are pelagic fishes (Hickford and Schiel 2008). In addition to target species, fishing activities may also affect noncommercial species caught as bycatch. Thus, an additional potential source of heterogeneity in the species' response to marine reserves could be the traits that make a noncommercial species vulnerable to bycatch.

The results of a previous meta-analysis (using the same set of marine reserves we use in this study) showed that the response of fishes to protection depended on reserve characteristics (such as reserve size and age). However, responses of individual fish species remained heterogeneous even after accounting for reserve characteristics (Claudet et al. 2008), and this residual heterogeneity was not explored. Here, we examine how different fish life history and ecological traits (i.e.,

species size, habitat type, depth range, schooling behavior, yearly displacement, home range, territoriality, and mobility) affect species' density in responses to protection. We also assessed the response of species according to their exploitation status, including bycatch species. Moreover, we analyzed how the traits of species may interact with age and size of marine reserve, which also affect responses to protection (Claudet et al. 2008). We used a meta-analytical framework based on data from reserves within a single temperate region, the central Mediterranean and north-eastern Atlantic Ocean to avoid the aggregation of data across different biogeographic regions. We obtained these data on fish assemblages from the owners of the data sets to avoid publication biases.

MATERIAL AND METHODS

Our analysis is based on a database containing the raw data of 58 case studies that examined the effects of 19 marine reserves in Southern Europe (Appendix A; Claudet et al. 2008). Our approach is a notable departure from other meta-analyses in two respects. First, we focus on a single region of the world, thus eliminating sources of variation (e.g., due to biogeography or climate) that can limit detection of the role of ecological traits. Second, by having access to raw data, we were not limited to the data summaries provided in published reports and papers, as is the case in classic meta-analyses. Instead, we could estimate the effect sizes of most interest to our study, avoid any reporting bias (e.g., due to response or taxonomy), and use a more flexible statistical approach than is available with standard meta-analysis software (e.g., Rosenberg et al. 2000). While avoiding many of the problems of other meta-analyses, our approach, like all meta-analytical procedures, compares the outcomes of studies with different underlying designs. Thus, it is important that these design differences be dealt with directly to avoid possible confounding with the factors of interest (Osenberg et al. 1999).

Starting with the 58 available studies, we retained studies based on three criteria: (1) the protected location was a true no-take zone (i.e., no harvesting was allowed); (2) control locations were in fully accessible, unprotected areas; and (3) the data set reported all fish species that could be identified and counted in the marine reserve and the control locations according to the sampling technique used (i.e., there was no taxonomic bias in reporting). The final data set consisted of data from 40 studies from 12 marine reserves, spanning a period of 33 years (Appendix A). Only one study used experimental fishing (trammel net) to estimate fish abundances; the others used underwater visual censuses. Because visual census techniques are not well suited for estimating the abundance of pelagic species (Harmelin-Vivien et al. 1985) and because these species were only rarely observed in the studies used, we excluded pelagic fish from the analyses.

We hypothesized that three key ecological traits could affect species' responses to protection: (1) maximum body size, as a surrogate of different life history traits such as age at maturity, growth, and reproductive output (Jennings 2001); (2) habitat (i.e., depth range and habitat type of adults); and (3) behavior (i.e., schooling behavior, yearly displacement, daily home range, territoriality, and mobility). To characterize the natural history of fish species for the region of investigation, we used an expert opinion approach in which three independent referees, with specific knowledge of the life history of target fish for the region of interest, assigned traits to species (see Appendices C, D, and E). When there was not unanimous agreement among the three referees (6% of cases), the majority view was taken (Balmford et al. 1993, Domenici 2003). We did not use available global databases such as FishBase (Froese and Pauly 2008), because those data are not site specific and this may introduce a bias in the analysis of fish traits that are known to vary geographically.

Referees classified traits as follows: (1) maximum size of fish species observed was small (<20 cm), medium (20–60 cm), or large (>60 cm); (2) depth range was shallow (<10 m), medium (10–50 m), deep (>50 m), or broad (species that can be found in all depth categories); (3) habitat was benthic-pelagic (e.g., jacks) or benthic, which includes truly benthic (e.g., gobies) as well as demersal species (e.g., groupers); (4) schooling behavior was classified as non-schooling (fish that are nearly always solitary), facultative schooler (fish that can be seen in school aggregations), or obligate schooler (fish that are always in schools); (5) yearly displacement (the distance that a fish typically migrated over a year due to ontogenic or seasonal movements) was small (<100 m), medium (100–10 000 m), or large (>10 000 m); (6) daily home range (Börger et al. 2008) was classified as small (<10 m), medium (10–100 m), or large (>100 m); (7) territoriality (Börger et al. 2008) was territorial or non-territorial; and (8) mobility was sedentary (fish that swim less than 50% of the time), vagile (fish that swim more than 50% of the time), and very vagile (fish that swim almost all of the time).

Referees also assigned a commercial value and catchability (i.e., vulnerability to capture) to each species because fishing is typically size selective and noncommercial species may be subjected to bycatch (i.e., subjected to fishing-related mortality). Regarding commercial value, species were classified as commercial (species targeted in most of the study locales) or noncommercial (species not targeted in any locale). Three species were targeted in only one of the study locales and, due to the low samples size and ambiguous status, were excluded from the analyses. Species were further classified based upon their catchability. Because fish sizes were estimated in 31 of the 40 studies, we used individual fish body size to further resolve these classifications as follows: (1) commercial fishes were considered to be exploited (individuals with body size

≥33% of the maximum size of that species for that study locale) or unexploited (individuals with body size <33% of the maximum size of that species in the study locale); and (2) noncommercial species were considered to be exploited (individuals of bycatch species with body size ≥33% of the maximum size of that species) or unexploited (all individuals of non-bycatch species and individuals of bycatch species with body size <33% of the maximum size observed). Thus, fishes were divided in four commercial groups: commercial exploited, commercial unexploited, noncommercial exploited, and noncommercial unexploited.

We used log-response ratios (Hedges et al. 1999) to quantify the response of fish to protection:

$$R_{ijk} = \ln \left(\frac{\bar{X}_{ijkP}}{\bar{X}_{ijkU}} \right)$$

where R_{ijk} is the log-response ratio for study i based on fish trait group j (e.g., territorial, or non-territorial, for the territoriality category) in commercial group k (i.e., commercial exploited, commercial unexploited, non-commercial exploited, or noncommercial unexploited), and \bar{X}_{ijkP} and \bar{X}_{ijkU} are the mean summed densities in fish trait group j of commercial group k for study i , under protected (P) and unprotected (U) conditions.

Weighted analyses increase the precision of the combined estimates and the power of tests (Gurevitch and Hedges 1999, Osenberg et al. 1999) by giving more weight to studies that have the most powerful experimental designs (i.e., those with greater and more appropriate replication). We used a weighted mixed model meta-analytical approach that reflected differences in sampling design, sampling intensity and spatial scales addressed in the studies (Appendix B). Weights were based on asymmetrical analyses of variance (see Claudet et al. 2008 for more details on the weighting scheme).

For each commercial group, we subdivided fishes into categories based on their traits and calculated the weighted average effect size for the j th trait group within commercial group k as

$$\bar{R}_{jk} = \frac{\sum_{i=1}^{m_{jk}} w_{ijk} R_{ijk}}{\sum_{i=1}^{m_{jk}} w_{ijk}}$$

where m_{jk} is the number of studies for the fish trait group j of the commercial group k , w_{ijk} is the weight for each study i and for each combination of fish trait group j and commercial group k , and where R_{ijk} is defined as above.

The variance of \bar{R}_{jk} , $v_{\bar{R},jk}$, is

$$v_{\bar{R},jk} = \frac{1}{\sum_{i=1}^{m_{jk}} w_{ijk}}$$

To assess whether a set of effect sizes are heterogeneous, we calculated the total heterogeneity Q_{T_k} as

follows (Hedges and Olkin 1985):

$$Q_{T_k} = \sum_{i=1}^{m_k} w_{ijk} (R_{ijk} - \bar{R}_k)^2$$

where

$$\bar{R}_k = \frac{\sum_{i=1}^{m_k} w_{ijk} R_{ijk}}{\sum_{i=1}^{m_k} w_{ijk}}$$

and represents the weighted average effect size for a commercial group k , across all trait groups. The total heterogeneity can be partitioned as

$$Q_{T_k} = Q_{M_k} + Q_{E_k}$$

with

$$Q_{M_k} = \sum_{j=1}^{G_k} \sum_{i=1}^{m_{jk}} w_{ijk} (\bar{R}_{jk} - \bar{R}_k)^2$$

$$Q_{E_k} = \sum_{j=1}^{G_k} \sum_{i=1}^{m_{jk}} w_{ijk} (R_{ijk} - \bar{R}_{jk})^2$$

where Q_{M_k} is the heterogeneity explained by the fish trait groups within a given commercial group k , Q_{E_k} is the residual heterogeneity, G_k is the number of fish trait groups within a given commercial group k , and where m_{jk} , w_{ijk} , R_{ijk} , and \bar{R}_k are defined as above. The significance of Q_{T_k} , Q_{M_k} , and Q_{E_k} were tested against χ^2 distributions with $m_k - 1$, $G_k - 1$, and $m_k - G_k$ degrees of freedom, respectively.

Previous results showed that commercial exploited fishes were sensitive to the time since protection of the marine reserve, and to the size of no-take and buffer zones (Claudet et al. 2008). Therefore, we analyzed the response to protection of the different fish trait categories by assessing their interaction with the marine reserve features: i.e., if the traits were important, then fishes with different traits should respond faster or slower to time since protection (and reserve size). We used a weighted generalized linear mixed model (GLMM) to model variation in fish density differences between protected and unprotected conditions. All terms tested (i.e., quantitative variables of marine reserve features and qualitative categories of fish groups) were simultaneously fitted (Chatfield 1995). We set the number of years since protection for all “before data” to zero. The size of the no-take and buffer zones was measured in hectares and log-transformed in the analyses. The buffer zone was defined as any area adjacent to the no-take zone that had an intermediate level of protection (see Claudet et al. 2008). All analyses were conducted with the free statistical software environment R (R Development Core Team 2006).

RESULTS

Maximum size

Response of commercial exploited fishes to protection depended on the species maximum size (Fig. 1a), with large species showing an approximately 15-fold increase in density inside the reserve, medium species showing a three-fold increase, and small species exhibiting a small (15%), and non-significant, increase. These three size classes explained 54.9% of the total heterogeneity in the response of commercial exploited fishes to marine reserves (Table 1). In addition, within this category, the response of large species increased with time of protection (Table 2). No significant response to protection was found among size categories for the unexploited commercial or noncommercial groups (Fig. 1a).

Habitat

When commercial exploited fishes were grouped according to their depth range affinities, only species with broad depth range responded positively to protection (Fig. 1b). Differences among depth range groups accounted for 28.9% of the total heterogeneity (Table 1). Similarly, for noncommercial unexploited fishes, a positive response was found only for those living at more than one depth range (Fig. 1b). The pattern was different for noncommercial exploited fishes, with a positive response to protection being displayed only by species that live in the medium depth range (Fig. 1b).

Commercial exploited fishes that were categorized as benthic responded positively to protection, with an average 2.9-fold increase inside the reserve (Fig. 1c). This response to protection increased with size of the no-take zones (Table 2). Benthopelagic fishes did not show a demonstrable response to protection. Variation in response to protection among habitat of commercial exploited fishes accounted for 15.6% of the total heterogeneity (Table 1). For noncommercial unexploited fishes, densities were significantly higher inside than outside protected areas for benthic species, whereas densities were significantly higher outside for benthopelagic species (Fig. 1c). These differences in effect sizes among habitat groups accounted for 25.2% of the total heterogeneity (Table 1).

Behavior, movement, territoriality

Commercial exploited fishes that were categorized as solitary or facultative schoolers exhibited a significant positive response to protection (Fig. 1d); the average response being higher for facultative schoolers than for solitary fishes (3.2- and 2.2-fold increase inside the reserve, respectively). Facultative schoolers were sensitive to the time of protection and sizes of the buffer and no-take zones (Table 2). Obligate schoolers did not show a significant response to protection. The observed differences among schooling behaviors explained 11.4% of the total heterogeneity (Table 1). All other groups did not respond significantly to protection, except obligate

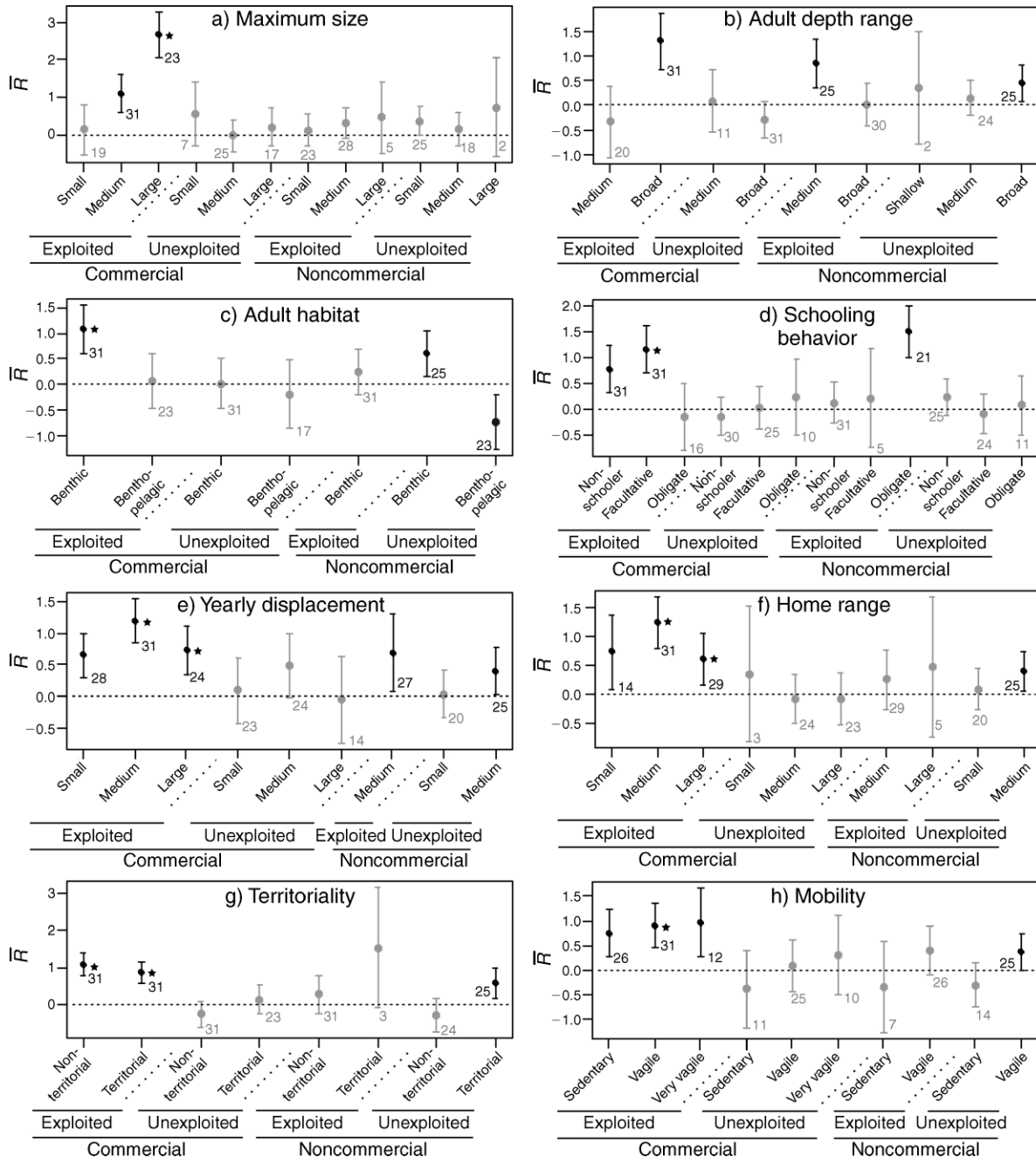


FIG. 1. Effect of protection (mean $\ln[\text{response ratios}]$, \bar{R} , \pm 95% confidence intervals) for fishes in different ecological and commercial categories. Stars indicate that effects depend on marine reserve design features (see Table 2). Significant weighted average effect sizes are shown by black symbols. The number of studies is indicated for each category. Where ecological groups for a given category are missing, it implies that this species subset was recorded from only one study.

schoolers of noncommercial exploited fishes, which showed significantly higher densities inside reserves (Fig. 1d). This response to protection accounted for 18.7% of the total heterogeneity in effect sizes (Table 1).

Commercial exploited fishes with medium yearly displacement exhibited a higher average response to protection (3.3-fold increase inside the reserve) than fishes with large or small yearly displacement (2.1- and

1.9-fold increase, respectively) (Fig. 1e). However, these differences explained only 6% of the total heterogeneity (Table 1). The response of commercial exploited fishes having medium yearly displacement was positively affected by the time of protection and size of the no-take zones (Table 2). The response of those with large yearly displacement were positively affected by the size of the no-take zone and negatively affected by the size of

TABLE 1. Heterogeneity statistics (Q) for effect sizes categorized by life history, ecological traits, and commercial status.

Species traits and commercial category	Total heterogeneity			Model heterogeneity			Residual heterogeneity		
	Q_T	df	P	Q_M	df	P	Q_E	df	P
Maximum size									
Commercial exploited	5062.17	72	<0.001	2777.3	2	<0.001	2278.25	57	<0.001
Commercial unexploited	1894.73	48	<0.001	56.85	2	<0.001	1837.77	43	<0.001
Noncommercial exploited	4012.43	55	<0.001	53.91	2	<0.001	3958.9	49	<0.001
Noncommercial unexploited	832.48	44	<0.001	26.13	2	<0.001	805.6	48	<0.001
Depth range									
Commercial exploited	3745.99	51	<0.001	1082.4	2	<0.001	2665.4	66	<0.001
Commercial unexploited	1235.03	41	<0.001	29.75	1	<0.001	1205	50	<0.001
Noncommercial exploited	4669.22	54	<0.001	458.76	1	<0.001	4210.89	34	<0.001
Noncommercial unexploited	875.21	50	<0.001	24.15	2	<0.001	850.19	39	<0.001
Habitat									
Commercial exploited	2471.54	53	<0.001	384.43	1	<0.001	2087.21	59	<0.001
Commercial unexploited	2811.41	47	<0.001	14.51	1	<0.001	2795.93	51	<0.001
Noncommercial exploited	2235.66	31	<0.001	44.5	1	<0.001	2191.01	50	<0.001
Noncommercial unexploited	1112.4	47	<0.001	280.24	1	<0.001	832.53	45	<0.001
Schooling behavior									
Commercial exploited	3853.08	77	<0.001	439.73	2	<0.001	3414.46	60	<0.001
Commercial unexploited	2372.25	64	<0.001	32.33	2	<0.001	2338.92	53	<0.001
Noncommercial exploited	4186.65	56	<0.001	781.16	2	<0.001	3398.14	50	<0.001
Noncommercial unexploited	1342.68	59	<0.001	28.29	2	<0.001	1315.01	47	<0.001
Yearly displacement									
Commercial exploited	2398.66	82	<0.001	142.86	2	<0.001	2255.52	52	<0.001
Commercial unexploited	4354.13	60	<0.001	130.62	2	<0.001	4225.83	34	<0.001
Noncommercial exploited	2461.47	27	<0.001	6.12	1	0.01	2455.14	6	<0.001
Noncommercial unexploited	669.3	44	<0.001	30.09	1	<0.001	639.6	32	<0.001
Home range									
Commercial exploited	4037.84	73	<0.001	175.95	2	<0.001	3861.03	67	<0.001
Commercial unexploited	2262.06	49	<0.001	36.6	2	<0.001	2226.1	44	<0.001
Noncommercial exploited	3135.61	33	<0.001	14.37	1	<0.001	3121.67	31	<0.001
Noncommercial unexploited	680.86	44	<0.001	25	1	<0.001	655.42	33	<0.001
Territoriality									
Commercial exploited	1290.01	61	<0.001	18.53	1	<0.001	1272.51	59	<0.001
Commercial unexploited	2103.33	53	<0.001	89.03	1	<0.001	2015.04	52	<0.001
Noncommercial exploited	3431.51	33	<0.001	399.03	1	<0.001	3034.35	47	<0.001
Noncommercial unexploited	814.71	48	<0.001	135.83	1	<0.001	679.09	36	<0.001
Mobility									
Commercial exploited	3605.96	68	<0.001	22.66	2	<0.001	3582.67	73	<0.001
Commercial unexploited	3260.76	45	<0.001	141.73	2	<0.001	3119.34	62	<0.001
Noncommercial exploited	2438.69	32	<0.001	209.52	1	<0.001	2230.58	32	<0.001
Noncommercial unexploited	1133.14	38	<0.001	146.99	1	<0.001	982.15	44	<0.001

the partially protected areas. Both noncommercial groups with medium yearly displacement responded positively to protection (Fig. 1e).

All home range groups of commercial exploited fishes responded positively to protection (Fig. 1f). The average response to protection was larger for fishes with medium home ranges (3.45-fold increase inside the reserve) than for fishes of small or large home ranges (2- and 1.8-fold increase, respectively). These differences among home-range groups explained only 4.4% of the total heterogeneity (Table 1). The response to protection of commercial exploited fishes having large home ranges increased with the size of the no-take zones and decreased with the size of the partially protected areas, while those with medium home ranges were only sensitive to the size of no-take zones (Table 2). In the other commercial groups, only noncommercial unex-

ploited species with medium home ranges exhibited a significant positive response to protection (Fig. 1f).

Whether territorial or not, commercial exploited fishes responded positively to protection. The average effect of protection was significantly greater for non-territorial species than for territorial ones (Fig. 1g), although territoriality explained only 1.4% of the total heterogeneity (Table 1). Non-territorial fishes were sensitive to all considered marine reserve features (Table 2). Their response to protection increased with time since protection and with the size of the no-take zone. In contrast, their response was inversely related to the size of the buffer zone. The response of territorial fishes increased with time, but did not vary with respect to other reserve attributes (Table 2). For the three remaining commercial groups, only the response of territorial noncommercial unexploited fishes was signif-

TABLE 2. Summary of significant interaction terms of the fixed effects of the weighted generalized linear mixed-effects models, between the different ecological groups of target fishes and the marine reserve features.

Traits and interaction terms	Value	SE	df	<i>t</i>	<i>P</i>
Maximum size					
Year \times large	0.429	0.206	51	2.078	0.0428
Adult habitat					
No-take size \times benthic	0.426	0.205	35	2.077	0.0452
Schooling behavior					
Year \times facultative schooler	0.063	0.020	43	3.158	0.0029
No-take size \times facultative schooler	0.416	0.168	43	2.472	0.0175
Buffer size \times facultative schooler	-0.320	0.123	43	-2.608	0.0125
Yearly displacement					
Year \times medium	0.056	0.023	61	0.372	0.0208
No-take size \times medium	0.461	0.201	61	2.295	0.0252
No-take size \times large	1.316	0.318	61	4.133	<0.001
Buffer size \times large	-0.773	0.203	61	-3.815	<0.001
Home range					
No-take size \times medium	0.421	0.173	52	2.428	0.0187
No-take size \times large	0.588	0.194	52	3.024	0.0039
Buffer size \times large	-0.361	0.126	52	-2.860	0.0061
Territoriality					
Year \times non-territorial	0.049	0.018	43	2.71	0.0096
Year \times territorial	0.052	0.017	43	2.90	0.0058
No-take \times non-territorial	0.579	0.179	43	3.238	0.0023
Buffer size \times non-territorial	-0.390	0.130	43	-2.988	0.0046
Mobility					
Year \times vagile	0.055	0.027	47	2.010	0.0501
Buffer size \times vagile	-0.335	0.135	47	-2.477	0.0169

icantly greater within protected than unprotected areas (Fig. 1g). This pattern accounted for 16.7% of the total heterogeneity (Table 1).

The average response to protection increased with the mobility of commercial exploited fishes: sedentary species showed an approximately 2-fold increase inside the reserve, vagile species a 2.46-fold increase, and very vagile species a 2.64-fold increase (Fig. 1h). The response to protection of vagile fishes increased with time and decreased with the size of the partially protected area (Table 2). No significant response to protection was found for the other commercial groups (Fig. 1h), except for vagile noncommercial unexploited fishes which were more abundant inside reserves (Fig. 1h).

DISCUSSION

Two main findings stand out from our meta-analysis. First, effects of protection on fishes depended on their commercial value and, to a lesser extent, whether they were affected as bycatch. Because species of no commercial interest unintentionally caught are subjected to fishing mortality outside of reserves, we expected their response to be as large as those of commercial exploited species. It was not, suggesting that unintended exploitation of noncommercial species has a smaller deleterious effect than targeted exploitation of the commercial species. Second, fishes differed in their response to protection depending on their maximum size, habitat

preferences (i.e., habitat type and depth range), or schooling behavior. Moreover, while the design features of marine reserves had an overall notable effect on commercial exploited fishes (Claudet et al. 2008), not all the trait characteristics of the fish species were equally sensitive to the time of protection or size of the no-take and buffer zones.

In marine reserves, trophic cascades have been documented for predator fishes preying on invertebrates (Micheli et al. 2005, Guidetti 2006). There is, however, no clear evidence for trophic cascades (or predator release) involving prey fishes. Nevertheless, our finding of lower abundances of noncommercial unexploited benthic-pelagic species inside reserves could reflect potential predator-prey interactions, with the increased number of commercial exploited fishes (some of which are piscivorous), preying upon non-exploited species. Conversely, benthic species which are not directly affected by fishing mortality had greater densities within reserves, suggesting that they indirectly benefited from protection (an effect that was not negated by increased densities of their potential predators inside the reserves). These unexploited benthic species potentially became relatively more abundant inside marine reserves as a consequence of habitat degradation in fished areas or improved habitat quality inside reserves.

Commercial unexploited fishes did not show a positive response to protection (no matter how the species were more finely categorized). Because these fishes are too

small to be fished, increased densities would be expected if reserves were effective at retaining the larvae of the protected adult stocks or if reserves facilitated settlement (e.g., via conspecific attraction). Although conspecific attraction (Schmitt and Holbrook 1996, Lecchini et al. 2007a) and local retention of larvae (Swearer et al. 1999, Almany et al. 2007) has been demonstrated for a few fishes, a better understanding of larval transport and settlement, and the spatial scales over which they operate, is required to appropriately evaluate these hypotheses (Sale and Kritzer 2003, Cowen and Sponaugle 2009).

There were insufficient numbers of shallow-water specialists to draw a clear picture of the effect of adult depth distribution; however, commercial exploited species with broad depth ranges (that included <10 m) showed strong responses to protection while mid-range species (inhabiting 10–50 m) did not (Fig. 1h). This pattern might result from a higher fishing pressure exerted at shallower depths by local artisanal and recreational fishers (Ashworth and Ormond 2005, Tyler et al. 2009).

Our most compelling finding is that protection benefited very vagile benthic and benthopelagic commercial exploited species, whatever their home range size and yearly displacement, and irrespective of the size of the marine reserves. Previous modeling studies showed that marine reserves should not be effective at enhancing densities of mobile species (for review, see Palumbi 2004). A possible explanation for our contrasting results is that protection also increases habitat quality inside, compared to outside protected areas, thereby reducing the propensity of fish to move out of the reserves (Rodwell et al. 2003). Modeling studies that do not consider habitat quality may therefore fail to match empirical patterns for mobile species. Increased densities of noncommercial unexploited benthic fishes inside marine reserves could also act as a source of potential prey for the mobile species, and therefore either attract mobile fishes or help retain them within reserves (Stewart and Jones 2001, Beukers-Stewart and Jones 2004). Moreover, factors other than resources could induce complex behavioral patterns (Roshier et al. 2008) and fishing pressure outside could attract species inside reserves (Eggleston and Parsons 2008). It has been shown that fish species can modify their daily home range and seasonal displacement based on the local social dynamics and their social status (Afonso et al. 2008). Moreover, sensory cue stimuli from conspecifics, as seen for recruitment of coral fish larvae (Lecchini et al. 2007a, b), may increase the probability that certain very vagile fish species remain within the marine reserves rather than moving to the fished areas, where competition may be lower but mortality rates are higher as a result of fishing activities.

Strictly pelagic species that are highly vagile were only rarely recorded in the case studies used and were excluded from the analyses. Such species would provide

an interesting test of the effect of mobility. However, reliable data on pelagic fishes is hard to obtain due to high spatiotemporal variability in their distribution and abundance, and ability to avoid survey equipment (Freon and Misund 1999). Different field methods (rather than underwater visual census or experimental fishing) would be needed to conduct rigorous assessments of pelagic fish populations, including novel techniques such as mid-water baited remote underwater video (Heagney et al. 2007).

The results of our analysis also suggest that the design of marine reserves and time of protection affected species with different life history and ecological traits in different ways. Time of protection strongly affected large species (but not small or medium species), possibly because larger species require greater time for growth and reproduction. Effects of time of protection may also involve increased survival through improved habitat quality, which should exhibit a time lag after establishment of a reserve (Rodwell et al. 2003). The size of the no-take zone also had strong positive effects on some species, especially those that are non-territorial or have large home ranges. These fish are more likely to remain in a large reserve, relative to a small reserve. Increased sizes of buffer zones have negative effects on species with the highest level of displacements, i.e., non-territorial species with large home ranges. Increased fishing pressure in buffer zones may be the cause for such negative effects (see Claudet et al. 2008 for a discussion on the role of buffer zones).

Our study examined the response of fish density to the cessation of fishing in marine reserves according to a set of life history and ecological traits of the adult populations and reserve size and age. Further work is needed to enable a better understanding of how different fish life history and ecological traits may induce different patterns of larval dispersal from (and back into) marine reserves. The extent to which the larvae of protected species can replenish adjacent fished areas or self-recruit within the reserves is fundamental for conservation purposes and for fisheries management (Almany et al. 2007), yet these regional effects have not been addressed in most marine reserve studies (including those we reviewed; see Osenberg et al. 2006).

ACKNOWLEDGMENTS

We thank two anonymous reviewers for helpful comments that substantially improved the manuscript. This work was conducted as part of the European Marine Protected Areas as Tools for Fisheries Management and Conservation project (EMPAFISH, funded by European Union, Contract No. SSP-2003-006539). It does not necessarily reflect the European Union's views, nor does it anticipate the Commission's future policy in this area. We appreciate the efforts of the investigators and staff responsible for the raw data included in this meta-analysis.

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APPENDIX A

Location, design, and other characteristics of the European marine reserves included in the meta-analysis (*Ecological Archives* A020-027-A1).

APPENDIX B

Description of the field methods of the 40 studies used in the meta-analysis (*Ecological Archives* A020-027-A2).

APPENDIX C

List of the species recorded from the studies and their commercial and ecological categories (*Ecological Archives* A020-027-A3).

APPENDIX D

Pairwise Pearson correlation coefficients between the commercial and ecological traits considered in the meta-analysis (*Ecological Archives* A020-027-A4).

APPENDIX E

Number of species in each combination of commercial category and ecological trait (*Ecological Archives* A020-027-A5).