Project nº SSP8-006539
EMPAFISH
European Marine Protected Areas as tools for Fisheries management and conservation

Specific Programme "Integrating and strengthening the ERA" (6th Framework Programme), under the activity "Scientific Support to Policies" and the research priority for "Modernisation and sustainability of fisheries, including aquaculture-based production system".

Synthesis of results of meta-analysis of ecological data (WP1)

Deliverable reference number: 17

Due date of deliverable: September 2006
Actual submission date: May 2008

Start date of project: 1st March 2005   ***Duration: 36 months***

Organisation name of lead contractor for this deliverable: CNRS-EPHE, Perpignan (France)

Revision: Final

Dissemination Level		
PU	Public	X
PP	Restricted to other programme participants (including the Commission	
RE	Restricted to a group specified by the consortium (including the	
CO	Confidential, only for members of the consortium (including the Commission Services)	

This publication has been developed in the framework of the project EMPAFISH (SSP8-006539) supported by the Commission of the European Communities within the Sixth Framework Programme. The views expressed in this work do not necessarily reflect those of EC or anticipates the Commission's future policy in the area.

Work Package: 1
Deliverable: D17
Dissemination Level: Public

Published by:

European Marine Protected Areas as tools for Fisheries management and conservation

Citation: Claudet J., Planes S., García-Charton J.A., Sánchez-Meca J., Benedetti-Cecchi L., Domenici P., Badalamenti F., Bayle-Sempere J., Brito A., Bulleri F., Culioli J.M., Dimech M., Falcón J., Guala I., Milazzo M., Somerfield P., Stobart B., Vandeperre F., Valle C. and Pérez-Ruzafa A., 2008. *Synthesis of results of meta-analysis of ecological data*. EMPAFISH Project. 25 pp.

Available from:
http://www.um.es/empafish

Contents

Synthesis of results of meta-analysis of ecological data (WP1)

Introduction

WP1 was devoted to list, explore, and evaluate the ecological effects of MPAs, using data issued from the 20 EMPAFISH selected case studies. These effects were firstly reviewed case by case, confirming the wide occurrence of several expected effects of protection[1]. In general, increasing abundances and changes in size structure of populations of commercial fish species are observed. In addition, spillover is considered to be a general phenomenon, as deduced from the observation of gradients of abundance / biomass across the MPA boundaries, although this process seems to occur at fine spatial scales (hundreds of meters)[2]. Other studies emphasized the effects of protection on benthic communities, on habitats (including the impact of recreational activities), or focused on indirect effects of protection (trophic cascades, changes in assemblages – trophic structure, etc.).

For each case study, we compiled all ecological data under a common format to allow statistical comparisons. The effects of marine reserves are heterogeneous, since they vary both in direction and magnitude. Despite theoretical findings, empirical studies have previously found no effect of size on the effectiveness of marine reserves in protecting commercial fish stocks. We used a meta-analytical approach to compare fully-protected *vs.* unprotected situations against four potential sources of heterogeneity in the response to protection: time since protection, size of the marine reserve (i.e. no-take zone) and of the buffer zone (i.e. partially protected zone), and distance to the nearest MPA. In a first stage, we focused on size-classes of fishes that are of commercial value, and we explored the response to protection of fishes according to different ecological characteristics of the species. Further analyses are to be done in the near future.

Analysis of the commercial fish assemblage[3]

We used a weighted meta-analytical approach to investigate the effects of protection in southern Europe and to explicitly examine heterogeneity among studies. From EMPAFISH WP1 work, a dataset was produced 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 eight years before the establishment of the marine reserves up to 33 years afterwards. We retained studies based on three criteria: 1) the

[1] For further details, see: Planes, S., García-Charton, J.A. & Pérez-Ruzafa, A. (Coord.). 2006. *Ecological effects of Atlanto-Mediterranean Marine Protected Areas in the European Union*. EMPAFISH Project, Booklet nº 1. 158 pp.
[2] See results of EC research project BIOMEX (http://biomex.univ-perp.fr)
[3] This work has been published: Claudet *et al.* (2008) Marine reserves: size and age do matter. *Ecology Letters* 11: 481-489

protected location was a true no-take zone, 2) the control locations were in unprotected areas, and 3) the data set 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 three years before 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. Since 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-structure and assemblage structure 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 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 were assigned by three referees chosen among the researchers who work 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. Because of rarity, true species richness will often be more greatly underestimated in studies with lower sample size. Since 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 for commercially targeted fishes as well as fishes that were not harvested:

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

where $R_{G,i}$ is the log-response ratio for study *i* based on fish in group *G* (i.e. fished, *F*, or unfished, *U*), and $\overline{X}_{G,P,i}$ and $\overline{X}_{G,C,i}$ 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:

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

where D_i is the differential response of species richness for study *i*, and $\overline{S}_{P,i}$ and $\overline{S}_{C,i}$ are the mean species richness for study *i*, in protected and unprotected conditions. We used these two different approaches to model 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 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 controls and reserves sites, we assumed that the most relevant study design was a Control-Impact design. Since protected locations were not replicated for each marine reserve, differences among protected and unprotected conditions at each point in time were compared to 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. For studies with multiple control locations, we obtained the variance associated with a given effect size from asymmetrical analyses of variance as:

$$v_{e,i} = \frac{MS_{C,i}}{n_{C,i}}$$

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

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

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

where *CI* is the confidence interval and $v_{e,i}$ is the variance associated with the effect size e_i for the study *i* and *z* is 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:

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

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:

$$v_b = \frac{Q_E - (k - p)}{tr\mathrm{W} - tr[(\mathrm{WM}(\mathrm{M}^t\mathrm{WM})^{-1}\mathrm{M}^t\mathrm{W}]}$$

where M is the design matrix, W is the diagonal matrix of individual weights w_i, *k* is the number of studies, and *p* is the number of columns of M. Q_E is the residual error heterogeneity which can be computed as:

$$Q_E = (\mathrm{E} - \mathrm{M}\beta)^t \mathrm{W}(\mathrm{E} - \mathrm{M}\beta)$$

where M and W are defined as above, 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:

$$\overline{E} = \left(\frac{\sum_{i=1}^{k} w_i e_i}{\sum_{i=1}^{k} w_i} \right)$$

where $\overline{E}$ 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 $\overline{E}$, $v_{\overline{E}}$, is:

$$v_{\overline{E}} = \frac{1}{\sum_{i=1}^{k} w_i}$$

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 variation in the differences among protected and unprotected conditions in fish densities and species richness. Since 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: 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 neighboring 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 year 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 analyzed or not) were considered. 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.

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 to the adjacent fished areas (log-response ratio of fish densities: $R = 0.90 \pm 0.83$, 95% CI). This effect was, however, heterogeneous ($Q = 2.15$; df = 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 ten-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 ten-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 neighboring reserves on the response of commercial fishes ($P > 0.1$). All interaction terms were nonsignificant (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 were heterogeneous ($Q = 3.85$; df = 29; $P < 0.001$ and $Q = 5.88$; df = 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 ($Q = 4.60$; df = 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 neighboring 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 most compelling result is that the response to protection for densities of commercial species is reserve size-dependent. Increasing the size of the no-take zone increases density of commercial fishes within the reserve compared to outside. In contrast, increasing the size of the buffer zone reduced the effectiveness of the reserve. Although fishery regulations are more restrictive in buffer zones than in unprotected areas, buffer zones are attractive for local artisanal fishers. Consequently, the fishing pressure increase in these areas can be higher than when just "fishing the line" (i.e. fishing along the MPA edges). Since there is no negative correlation between the size of no-take zones and size of buffer zones, increasing the size of one zone was not made at the expense of the other.

These findings provide a new perspective on marine reserves features affecting the heterogeneity of the response to protection of fish species. Theoretical studies have hypothesized that larger marine reserves would be more effective at increasing biodiversity and density of commercial species. 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. Our results provide useful indications for the design and management of marine reserves. For example, the design of marine reserves has often incorporated spatial zoning with different regulatory measures for a feature of integrated coastal zone management. However, buffer zones could have detrimental effects on the protection of fish species. Our results suggest that buffer zones should be allocated to enlarged no-take zone to avoid a decrease of the response of the harvested species.

In addition to the effect of marine reserves size, there also was an effect of the time since protection. The time scale at which a marine reserve becomes effective in restoring biodiversity or densities of commercial species is a key question for coastal resources management. Some reviews and single studies showed fish density and species richness increasing after three years of protection. Others showed that decades could be needed. 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. Moreover, it is important to protect large fish since these have greater reproductive potential and produce larvae with better survival rates than those from younger fishes.

Here we have shown that older European marine reserves are more effective than newly implemented 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. Since recovery of fish communities occurs at a relatively slow rate, a rotating temporal system of spatial closures may therefore be inadequate for conservation purposes. As different reserves were sampled at different times, the effect of years since protection partly accounts for the heterogeneity among reserves.

Distance to the nearest neighbouring marine reserve was another feature included in our analyses. Mathematical models of marine reserve networks advocate for different optimal distances between reserves according to the management goals, the input data considered and the assumptions made. Our study is the first empirical evaluation of the effects of distance among marine reserves. We found no evidence of an optimal distance between reserves. We caution that other factors (in addition to distance) can play also a major role in marine reserve connectivity. In particular, accounting for habitat discontinuities and fragmentation, larval dispersal and species and disturbance dynamics will be relevant for optimised marine reserve networks. Moreover, experimental frameworks using reserve networks could be employed in order to test ecological hypotheses relative to the above-mentioned effects. Such an effort would require the cooperation of scientists and decision-makers.

None of the marine reserve characteristics explained a part of the heterogeneity in the response to protection of non-commercial species. Non-commercial species are not supposed to be directly affected by protection but indirectly by predator intensity and also by habitat characteristics. Therefore, trophic cascades and habitat variables at fine scale should be considered when studying the response to protection of such species.

We anticipate that our study will be the starting point for more sophisticated assays on optimal marine reserves design. Future efforts to manage and protect costal ecosystems should take into account our results on marine reserves size together with unbiased biological data and sound socio-economic local information to best satisfy the management goals when allocating space for no-take and buffer zones.

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	68775	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	78800	3
12. Sinis Mal di Ventre	Italy	1997	529	25144	62

Figure 1 - The location of the 12 European temperate marine reserves involved in the study. 1: La Restinga; 2: La Graciosa; 3: Cabo de Palos; 4: Tabarca; 5: San Antonio; 6: Columbretes Islands; 7: Medes Islands; 8: Cerbere-Banyuls, 9: Cap Couronne; 10: Carry-le-Rouet; 11: Bouches de Bonifacio ; 12 : Sinis Mal di Ventre.

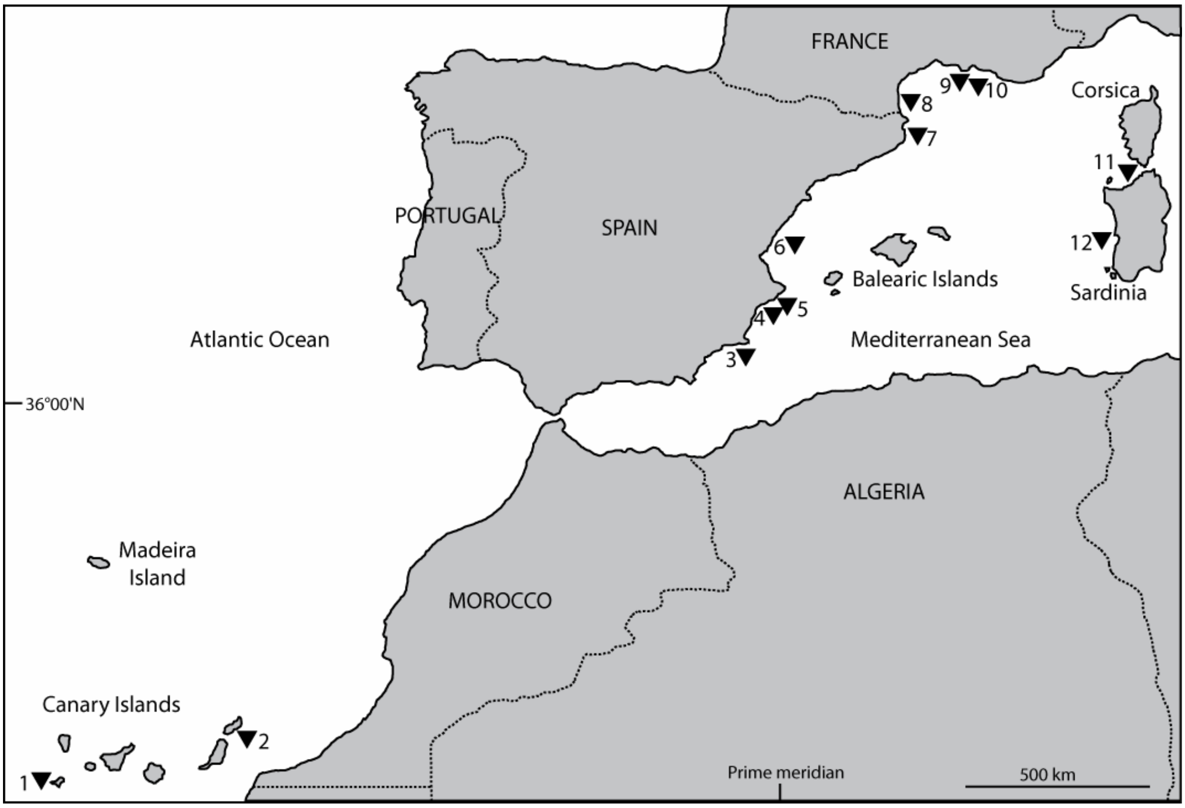
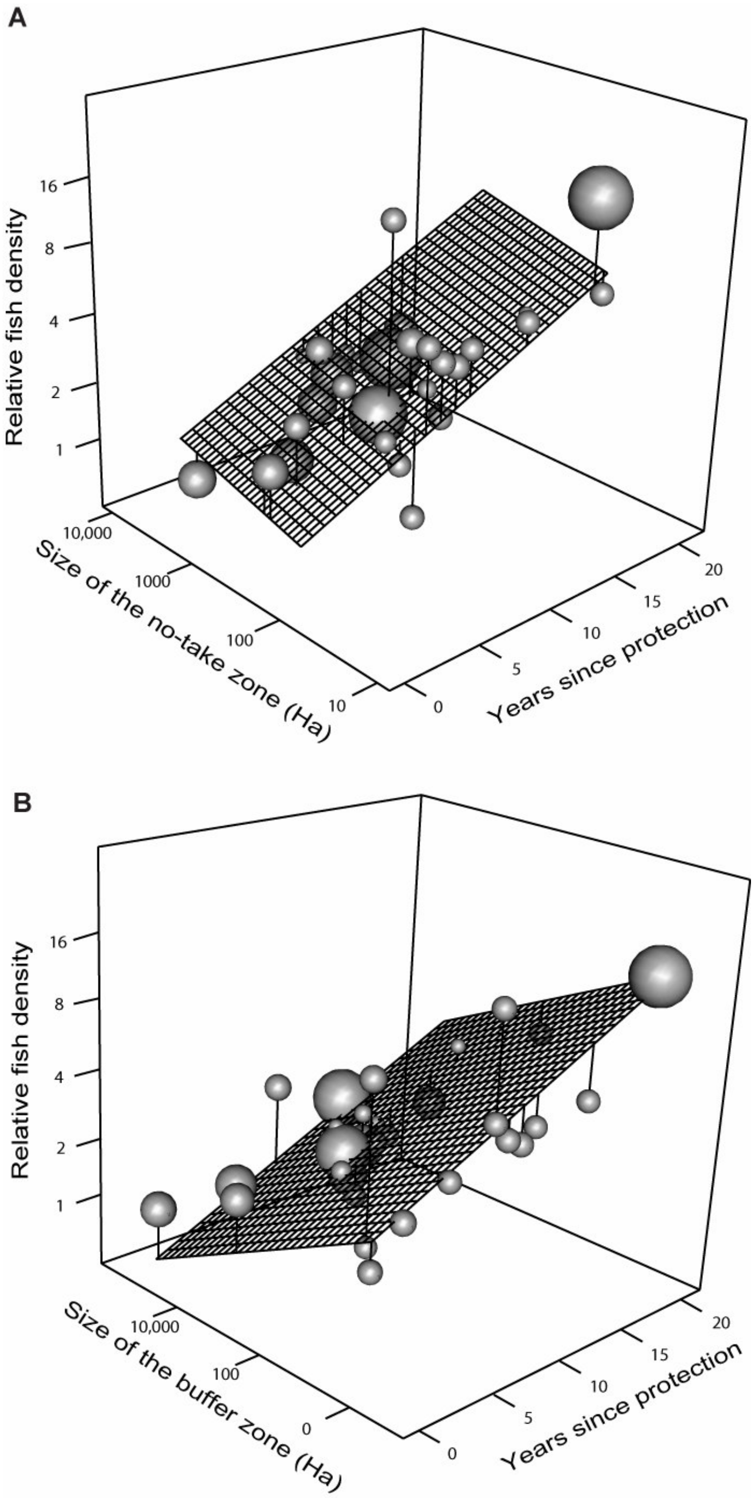


Figure 2 - Effects of marine reserves on commercial fish densities as a function of years since protection and (**A**) the size of the no-take zone and (**B**) the size of the buffer zone. Planes give the fitted effect. The size of the points is proportional to the weight of each study. Stems indicate the distance between the calculated weighted effect size and the fitted effect.



Analysis by fish species groups

In this part of the project we were interested in studying the response to protection of fishes according to different ecological characteristics of the species. These ecological characteristics belonged to three major components: the growth structure (i.e. maximum size of the species); the behaviour (i.e. territoriality, movement ability, home range, yearly displacement, and schooling behaviour); and the habitat (i.e. the general habitat of adults, and the general death range of adults). For each category, the value of each fish species were assigned by three referees chosen among the researchers who work on a marine reserve in which each given species is present. Referees scored each species as commercial or non commercial. Where consensus was not reached, the majority criterion was used. When species were grouped according to their maximum size generally observed, three sub-groups were considered: small (<20 cm), medium ([20;60] cm), and large (> 60 cm). For the territoriality, referees assigned for each species if a species is territorial or not. Three sub-groups were considered for the movement ability: sedentary, vagile, and very vagile. The home range of each species was estimated according to three sub-groups: small (<10 m), medium ([10;100] m), and large (>100 m). Three sub-groups were considered for the fish yearly displacement: small (<100 m), medium ([100;10,000] m), and large (>10 km). The species schooling behaviour were defined by: solitary, facultative schooler, and obligate schooler species. Since the pelagic species were removed from the analyses, the adult general habitats considered were: bentho-pelagic and benthic. Finally, four death ranges were considered: close ([0;10] m), medium (]10;50] m), far (>50 m), and whole range. The appendix presents all fish species categorization. The correlations between each pair of categories were calculated (Table 1). When non available were present for some categories, the correlation between each pair of categories was computed using all complete pairs of observations on those variables.

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 densities per size group. Size groups were defined using 33 and 66 percentiles of the maximum size generally observed in the region. Since the principal consequence of marine reserves is to remove the fishing activities from an area, we studied the differential response of fish according to the above categories on three initial fish groupings: target group, small commercial group, and non commercial species. The group of target fishes is composed of medium and large commercial fishes (i.e. fishable fishes). The small commercial group is composed by the small commercial fishes (i.e. unfishable fish). Finally, the non commercial group is composed by all fishes of non commercial species. The commercial value of each species was assigned by three referees, as stated previously for the ecological categories. Species with a low commercial value were species that were only commercial in a very prescribe area. These species were not included in the target group.

We used effect sizes to model the differences between protected and unprotected conditions. For each initial fish grouping (i.e. target fishes, non target fishes, and non commercial fishes), we calculated log-response ratios:

$$R_{ij} = \ln\left(\frac{\overline{X}_{ijP}}{\overline{X}_{ijC}}\right)$$

where R_{ij} is the log-response ratio for study i based on fish in group j (e.g. territorial, or non territorial, for the fish territoriality category), and $\overline{X}_{ijP}$ and $\overline{X}_{ijC}$ are the mean densities of fishes in group j for study i in protected (P) and unprotected (i.e., control, C) conditions.

Weighted analyses increase the precisions of the combined estimates and increase the power of tests 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. For studies with appropriate control locations, we obtained the variance associated with a given effect size from asymmetrical analyses of variance as:

$$v_{R,i} = \frac{MS_{b/C,i}}{n_{C,i}}$$

where $v_{R,i}$ is the variance associated with the effect size R_i, (i.e., the within-study variance), $MS_{b/C,i}$ is the Mean Square for the between-controls component of variation, and $n_{C,i}$ is the within-controls sample size for the study i. For studies that lacked multiple controls, we estimated v_R by constructing an appropriate $MS_{b/C}$ adding in the analyses of variance an average between-controls variance component from the studies that did have replication.

For each effect size R, confidence intervals were derived from the variances as:

$$CI = R_i \pm z_{\alpha/2} v_{R,i}$$

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

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

$$w_i = \frac{1}{v_{R,i} + v_b}$$

where w_i is the weight for each study, $v_{R,i}$ is defined as above and v_b is the between-study variance.

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

$$\overline{\overline{R}} = \left(\frac{\sum_{i=1}^{k} w_i R_i}{\sum_{i=1}^{k} w_i} \right)$$

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

$$v_{\overline{\overline{R}}} = \frac{1}{\sum_{i=1}^{k} w_i}$$

The total heterogeneity Q_T associated with the sample of studies is defined as:

$$Q_T = \sum_{i=1}^{k} w_i \left(R_i - \overline{\overline{R}}\right)^2$$

Its significance was tested against a χ^2 distribution with k-1 degrees of freedom.

For each groups of a given category, we calculated the group cumulative effect size $\overline{R}_j$ as:

$$\overline{R}_j = \frac{\sum_{i=1}^{m_j} w_{ij} R_{ij}}{\sum_{i=1}^{m_j} w_{ij}}$$

where m_j is the number of studies in the group j, and where w_{ij} and R_{ij} are the weight and effect size for the study I in the group j.

The total heterogeneity Q_T can be partitioned as:

$$Q_T = Q_M + Q_E$$

where Q_M is the explained heterogeneity by the differences between the groups j and Q_E is the residual heterogeneity. Q_M is calculated as

$$Q_M = \sum_{j=1}^{G} \sum_{i=1}^{m_j} w_{ij} \left(\overline{R}_j - \overline{\overline{R}}\right)^2$$

where G is the number of groups, and where m_j, w_{ij}, R_{ij} and $\overline{\overline{R}}$ are defined as above. Its significance was tested against a χ^2 distribution with G -1 degrees of freedom. The residual heterogeneity Q_E is calculated as:

$$Q_E = \sum_{j=1}^{G} \sum_{i=1}^{m_j} w_{ij} \left(R_{ij} - \overline{R}_j\right)^2$$

Its significance was tested against a χ^2 distribution with k -G degrees of freedom.

We saw previously that effects of protection on target fishes varied among the time since protection of the marine reserve, and among the size of no-take and buffer zones. Therefore, when analyses were carried out on the target group of fishes, we analyzed the response of the different ecological categories by studying their interaction with the marine reserve features. We investigated the influence of these interactions using a weighted Generalized Linear Mixed Model (GLMM) to model variation in the differences between protected and unprotected conditions in fish densities; all terms tested (i.e. quantitative variables of marine reserve features and quantitative factor of the fish groups) were simultaneously fitted in the inferential model. 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 before-data to zero. If enforcement did not begin when the reserve was established, we used the first year of enforcement as a reference point. 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. If the entire reserve was fully protected, then this area was 0. Both sizes of no-take and buffer zones were log-transformed. All analyses were conducted with the free statistical software environment R.

Results

[Maximum Size - Target]

When target fishes were grouped according to their species maximum size, there was significant heterogeneity in response among the three size groups (total heterogeneity: Q_T = 2370.66, df = 65, $P < 0.001$). The grouping by species size explained a part of this heterogeneity (model heterogeneity: Q_M =587.46, df = 2, $P < 0.001$). Overall effect sizes were all the greater as a larger species size was considered (Fig. 3a). Densities of target fishes of large species were on average 4.39 times greater within the marine reserves than in the fished areas (log-response ratio of fish densities: $R = 1.48 \pm 0.39$, 95% CI). Densities of target fishes of medium species were in turn 1.52 times greater within the marine reserves than in the fished areas ($R = 0.42 \pm 0.39$, 95% CI). Finally, densities of target fishes of small species were not significantly higher within the marine reserves than in the fished areas ($R = 0.42 \pm 1.05$, 95% CI). However, there was still heterogeneity in the effect sizes (residual heterogeneity: Q_E = 1783.20, df = 63, $P < 0.001$). When a weighted generalized linear mixed effects model (GLMM) was fitted to test for the interactions between the three groups of maximum size (i.e. small, medium and large) and the three marine reserve features (i.e. years since establishment, size of the no-take zone and size of the buffer zone), only the interaction term between the large size group and the size of the no-take zone was found to be significant (coefficient for R: 0.56 ± 0.20, $P = 0.009$) (Table 3).

[Maximum Size - NonTarget]

There was some heterogeneity in the response to protection when the small commercial group fishes were grouped according to the species size (Q_T = 1971.01, df = 54, $P < 0.001$). However, the differences in species size could not explain this heterogeneity (Q_M = 0.115, df = 1, $P = 0.73$) and average effect sizes were not different form zero ($R = -0.26 \pm 0.38$, 95% CI and R = -0.24 ± 0.45, 95% CI, for large and medium species, respectively; no small fishes of small commercial species were found in the studies) (Fig. 3a).

[Maximum Size - NonCommercial]

When all fishes of non commercial species were considered, there was a significant heterogeneity in their response to protection according to the maximum size of the species (Q_T = 5132.04, df = 104, P < 0.001). Part of this heterogeneity was explained by the differences in species size (Q_M = 330.68, df = 2, P < 0.001). There were no significant differences neither for the densities of large non commercial species between the marine reserves and the fished areas (R = 0.19 ± 0.38, 95% CI), nor for the small species (R = -0.20 ± 0.40, 95% CI) (Fig. 3a). Densities in the marine reserves were on average higher for the medium size non commercial species (R = 0.49 ± 0.37, 95% CI) (Fig. 3a). The major part of the heterogeneity was not explained by the different species size (Q_E = 4801.36, df = 102, P < 0.001).

[Territoriality - Target]

Effect sizes calculated according to the territoriality of target fishes are heterogeneous (Q_T = 1027.66, df = 60, P < 0.001). The differentiation of territorial and non territorial species explained a part of this heterogeneity (Q_M = 52.25, df = 1, P < 0.001). Densities of non territorial target fishes were on average 2.98 times greater within the reserves than in fished areas (R = 1.09 ± 0.29, 95% CI), whereas this difference was lower for territorial target fishes (R = 0.73 ± 0.28, 95% CI), their densities being 2.07 times greater in the fully protected areas (Fig. 3b). However, the territoriality of the species did not explained all the heterogeneity (Q_E = 975.41, df = 59, P < 0.001). Results from the weighted GLMM showed that the effect sizes of non territorial species interacted with all the tested marine reserve features. The differences in densities between the reserve and the fished area for these non territorial target fishes increased with the years since protection (coefficient for R: 0.04 ± 0.02, P = 0.02) and with the size of the fully protected area (coefficient for R: 0.49 ± 0.13, P < 0.001) (Table 3). In contrast, these differences decreased with increases of the size of the partially protected area (coefficient for R: -0.33 ± 0.10, P = 0.001) (Table 3). The response of target territorial fishes also increased with the size of the fully protected area (coefficient for R: 0.28 ± 0.14, P = 0.049) (Table 3).

[Territoriality - NonTarget]

Some heterogeneity is also present if the territorially is considered for non target fishes (Q_T = 4349.59, df = 53, P < 0.001). On average, effect sizes of non target and non territorial species were negative (R = -0.56 ± 0.37, 95% CI), showing that their densities were 1.75 higher in the fished areas that in the marine reserves (Fig. 3b). No significant differences between the two areas were found for the territorial non target fishes (R = 0.07 ± 0.56, 95% CI) (Fig. 3b). The difference in the response to protection of these two groups explained a part of the total heterogeneity (Q_M = 241.90, df = 1, P < 0.001), but not all (Q_E = 4107.70, df = 52, P < 0.001).

[Territoriality - NonCommercial]

When considering the territoriality of the non commercial species, effect sizes were heterogeneous (Q_T = 2069.75, df = 70, P < 0.001) and the differences between the territorial and non territorial species explained only a very small fraction of this heterogeneity (Q_M = 17.38, df = 1, P < 0.001), therefore remaining a large amount of residual heterogeneity (Q_E = 2052.37, df = 69, P < 0.001). Moreover, on average, fish densities of territorial and non territorial non commercial species were similar within the marine reserve and outside (R = 0.11 ± 0.32, 95% CI and R = 0.28 ± 0.31, 95% CI, for non territorial and territorial species, respectively) (Fig. 3b).

[Movement - Target]

The response to protection was also heterogeneous when effect sizes were calculated across the movement ability of the target fishes (Q_T = 6121.32, df = 77, P < 0.001). Part of this heterogeneity was explained by the differences between the movement abilities of the species (Q_M = 293.01, df = 2, P < 0.001). Target fishes belonging to very vagile species were the most affected by protection, their densities being on average 4.90 times greater within the marine reserve than in the fished areas (R = 1.59 ± 0.67, 95% CI) (Fig. 3c). These differences were then, on average, higher for sedentary fishes (R = 1.10 ± 0.51, 95% CI) than for vagile fishes (R = 0.83 ± 0.51, 95% CI) (Fig. 3c). However, heterogeneity remained (Q_E = 5828.31, df = 75, P < 0.001) and none of the movement groups interacted significantly with the marine reserve features when a weighted GLMM was fitted on the effect sizes (all P > 0.05).

[Movement - NonTarget]

When the non targeted part of the commercial species was considered, effect sizes based on fish movement abilities were heterogeneous (Q_T = 4518.30, df = 64, P < 0.001). When looking at the differences between the movement groups, a large amount of heterogeneity remained (Q_E = 4457.85, df = 62, P < 0.001) and, on average, densities were similar between the fully protected and the unprotected area for the three groups (R = -0.02 ± 0.44, 95% CI, R = 0.01 ± 0.51, 95% CI and R = 0.30 ± 0.78, 95% CI, for sedentary, vagile and very vagile species, respectively) (Fig. 3c).

[Movement - NonCommercial]

When the differences in the response to protection of non commercial species are considered according to the species movement ability, the overall average response is homogeneous (Q_T = 48.67, df = 68, P = 0.96). On average, fish densities of non commercial species are similar between the marine reserves and the fished areas (R = 0.29 ± 0.39, 95% CI) and do not differ according the different movement abilities of the species (Fig. 3c).

[Home Range – Target]

The response to protection of target fishes was heterogeneous when analysed according to the home range size groups (Q_T = 1863.79, df = 69, P < 0.001). The different home range groups explained a small part of this variation (Q_M = 91.69, df = 2, P < 0.001), with a significant amount of residual heterogeneity (Q_E = 1771.80, df = 67, P < 0.001). Overall effect sizes were on average greater for fishes with smaller home range sizes compared to fishes with high home ranges (Fig. 3d). Densities for fishes with home ranges smaller than 10 m were, on average, 3.89 greater within the marine reserves than in the fished areas (R = 1.36 ± 0.60, 95% CI). The response for fishes with a home range between 10 and 100 m was quite equivalent but with a much smaller confidence interval (R = 1.31 ± 0.33, 95% CI). The overall response of target fishes with the highest small ranges was, on average, lower than for the others home range groups (R = 0.92 ± 0.32, 95% CI). However, the response of these fishes with high home ranges was highly sensible to the marine reserve features. Their response to protection increased with the years since protection (coefficient for R: 0.07 ± 0.02, P < 0.001) and greatly with the size of the marine reserves (coefficient for R: 0.49 ± 0.21, P = 0.02) (Table 3). In contrast, increasing sizes of the partially protected area had a negative effect on the response of target fishes with high home ranges (coefficient for R: -0.40 ± 0.15, P = 0.01) (Table 3). The response of target fishes with medium home ranges increased also with the years since protection (coefficient for R: 0.05 ± 0.02, P = 0.02) (Table 3) but there were no significance for the interactions with the sizes of the fully and partially protected zones. The response of fishes with low home ranges was non sensitive to the marine reserve features.

[Home Range – NonTarget]

When the home ranges of non target fishes were considered, effect sizes were heterogeneous (Q_T = 2578.95, df = 45, P < 0.001). A large amount of heterogeneity residual remained (Q_E = 4457.85, df = 62, P < 0.001) when considering the differential response of the two higher home range groups (Q_M = 24.16, df = 1, P < 0.001; no small fishes of target fishes with the lowest home ranges were found in the studies). On average, densities were similar between the fully protected and the unprotected area for the three groups (R = -0.22 ± 0.54, 95% CI and R = -0.46 ± 0.53, 95% CI, for species with medium and large home ranges, respectively) (Fig. 3d).

[Home Range - NonCommercial]

The response to protection of non commercial species according to their home range groups were heterogeneous (Q_T = 6245.66, df = 56, P < 0.001). Differences in home ranges explained a part of this heterogeneity (Q_M = 539.32, df = 2, P < 0.001; Q_E = 5706.34, df = 54, P <

0.001). The differences between the marine reserves and the fished areas were on average higher for species with small home ranges (*R* = 1.23 ± 0.72, 95% CI) than for species with medium home ranges (*R* = 0.34 ± 0.46, 95% CI) (Fig. 3d). No differences between the protected and unprotected areas were found for species with high home ranges (*R* = 0.38 ± 1.25, 95% CI) (Fig. 3d).

[Yearly Displacement - Target]

A significant amount of heterogeneity was found when effect sizes were calculated according to the species yearly displacement (Q_T = 2675.46, df = 54, *P* < 0.001) but the difference between these groups explained a part of this heterogeneity (Q_M = 950.25, df = 2, *P* < 0.001; Q_E = 1425.22, df = 52, *P* < 0.001). On average, the response to protection was higher for target fishes with yearly displacements lower than a hundred of meters (*R* = 1.76 ± 1.30, 95% CI) than for target fishes with yearly displacements between a hundred and a thousand of meters (*R* = 1.70 ± 0.42, 95% CI), but confidence intervals were larger for the first group considered (Fig. 3e). The densities of target fishes with the highest home ranges were on average similar within the reserves and in the fished areas (*R* = 0.32 ± 0.50, 95% CI) (Fig. 3e). The response of this last group of fishes was the only one to be sensitive to a feature of the marine reserves, showing a negative trend with increasing sizes of partially protected areas (coefficient for *R*: -0.80 ± 0.25, *P* = 0.003) (Table 3).

[Yearly Displacement - NonTarget]

Effect sizes based on yearly displacement groups of non target fishes were heterogeneous (Q_T = 1433.06, df = 35, *P* < 0.001) but differences between the groups only explained a very small amount of this heterogeneity (Q_M = 21.60, df = 1, *P* < 0.001; Q_E = 1411.46, df = 34, *P* < 0.001). In fact, the overall average response to protection were similar for the two groups considered, fish densities being similar within the reserves and the fished areas (*R* = -0.34 ± 0.42, 95% CI and *R* = -0.04 ± 0.69, 95% CI, for species with medium and large yearly displacement, respectively; no small target fishes with low yearly displacement were found) (Fig. 3e).

[Yearly Displacement – NonCommercial]

The case is quite similar for the non commercial species: heterogeneous effect sizes (Q_T = 2299.76, df = 48, *P* < 0.001) but differences between the groups only explained a very small amount of this heterogeneity (Q_M = 56.95, df = 2, *P* < 0.001; Q_E = 2242.81, df = 34, *P* < 0.001). Non commercial species with high yearly displacement were found only in one study and fish densities for the other two groups were on average similar within and outside the reserves (*R* = 0.12 ± 0.69, 95% CI and *R* = 0.31 ± 0.37, 95% CI, for species with small and medium yearly displacement, respectively) (Fig. 3e).

[Schooling behaviour - Target]

When analysing response to protection of all fishes according to their schooling behaviour, obligate schooler species were removed from the analyses since they were found in only two studies. Effect sizes of target species based on schooling behaviour are heterogeneous (Q_T = 1132.47, df = 60, $P < 0.001$) but only a small amount of this heterogeneity is explained by the differences of schooling behaviour (Q_M = 34.53, df = 1, $P < 0.001$; Q_E = 1097.94, df = 59, $P <$ 0.001). Densities of facultative schooler target fishes are on average 2.5 times within the marine reserves than outside ($R = 0.92 \pm 0.29$, 95% CI) (Fig. 3f). This coefficient is lowered to 1.9 when considering the solitary fishes ($R = 0.63 \pm 0.30$, 95% CI) (Fig. 3f). Results of the weighted GLMM showed that the response to protection of target solitary fishes was insensible to the marine reserve feature (all $P > 0.05$) whereas the response to protection of facultative schooler fishes were affected by all the reserve features studies. This response increased with the years since protection (coefficient for R: 0.05 ± 0.02, $P = 0.005$), the size of the fully protected area (coefficient for R: 0.45 ± 0.14, $P = 0.004$), and decreased with the size of the fully protected area (coefficient for R: -0.35 ± 0.10, $P = 0.001$) (Table 3).

[Schooling behaviour - NonTarget]

Effect sizes calculated when non target fishes were grouped by schooling behaviour were heterogeneous (Q_T = 1633.70, df = 54, $P < 0.001$) but differences between the behaviours only explained a very small amount of the heterogeneity (Q_M = 10.93, df = 1, $P < 0.001$; Q_E = 1622.77, df = 53, $P < 0.001$). None of the group response was significantly different from zero ($R = -0.03 \pm 0.38$, 95% CI and $R = -0.19 \pm 0.34$, 95% CI, for facultative schooler and solitary fishes, respectively; no obligate schooler of non target fishes were found) (Fig. 3f).

[Schooling behaviour - NonCommercial]

The response of non commercial species grouped according to their schooling behaviour was heterogeneous (Q_T = 2218.45, df = 71, $P < 0.001$). The differences between the schooling behaviours explained a part of this variability (Q_M = 109.59, df = 1, $P < 0.001$; Q_E = 2108.86, df = 70, $P < 0.001$). On average, densities of non commercial facultative schoolers were higher within the fully protected areas than in the unprotected areas ($R = 0.37 \pm 0.29$, 95% CI) (Fig. 3f). Densities of sedentary non commercial species were similar within the reserves and in the fished areas ($R = 0.00 \pm 0.26$, 95% CI) (Fig. 3f).

[General Habitat - Target]

The overall response of target fishes based on adult fish general habitat is heterogeneous (Q_T = 1373.64, df = 60, $P < 0.001$) but the differences between the two habitats considered did not explain a part of this variability (Q_M = 0.23, df = 1, $P = 0.63$).

[General Habitat - NonTarget]

When considering general adult habitats, the response to protection of non target fishes was heterogeneous (Q_T = 1757.47, df = 52, P < 0.001). Differences between the two habitats explained only a very small amount of this heterogeneity (Q_M = 13.16, df = 1, P < 0.001; Q_E = 1744.31, df = 51, P < 0.001). Average densities of the two groups considered were similar within and outside the marine reserves (R = -0.17 ± 0.37, 95% CI and R = 0.00 ± 0.40, 95% CI, for benthic and bentho-pelagic species, respectively) (Fig. 3g).

[General Habitat - NonCommercial]

For non commercial species, the response to protection was also heterogeneous when the adult habitat was considered (Q_T = 2139.61, df = 71, P < 0.001). Densities of non commercial benthic species were on average similar in the protected and in the unprotected areas (R = -0.11 ± 0.32, 95% CI) (Fig. 3g). Densities of non commercial bentho-pelagic species were on average higher within the reserves than in the fished areas (R = 0.39 ± 0.33, 95% CI) (Fig. 3g). The different response of the two groups explained a part of the total heterogeneity (Q_M = 145.77, df = 1, P < 0.001; Q_E = 1993.84, df = 70, P < 0.001).

[Depth Range Adult - Target]

Target fishes grouped according to the adult depth range showed a heterogeneous response to protection (Q_T = 2905.45, df = 68, P < 0.001). Part of this heterogeneity was due to the average responses the of target fishes living at different death ranges (Q_M = 593.52, df = 2, P < 0.001; Q_E = 2311.93, df = 66, P < 0.001; no target fish belonging to the shallowest depth range was found in the studies). The response was the highest for target fishes able to live in the whole depth ranges considered (R = 0.88 ± 0.43, 95% CI), their densities being on average 2.4 times greater within the reserves than outside (Fig. 3h). Target fishes living between 10 and 50 m from the surface responded also positively on average to protection (R = 0.79 ± 0.42, 95% CI) (Fig. 3h). No differences between the reserve and fished areas were found for target fishes whose adults live preferentially at depths higher than 50 m (R = -0.55 ± 0.82, 95% CI) (Fig. 3h). The response to protection of these was also in part due to the marine reserve features. Results from the weighted GLMM showed that the response of target fishes living between 10 and 50 m increased with the years since protection (coefficient for R: 0.06 ± 0.02, P = 0.01), the size of the fully protected area (coefficient for R: 0.44 ± 0.18, P = 0.02), and decreased with the size of the fully protected area (coefficient for R: -0.36 ± 0.3, P = 0.008) (Table 3). The response of the other groups was not interacting with the reserve features (all P > 0.05).

[Depth Range Adult - NonTarget]

When considering the adult depth range of non target species, there was some heterogeneity in their response to protection (Q_T = 1221.00, df = 52, P < 0.001), but on average, the relative fish densities of all groups considered were similar in the marine reserve and outside (R = -0.07 ± 0.38, 95% CI, R = -0.66 ± 0.72, 95% CI and R = -0.16 ± 0.36, 95% CI, for adult depth range between 10 and 50 m, higher than 50 m and whole depth range, respectively; no none target fishes of adult depth range lower than 10 m were found) (Fig. 3h).

[Depth Range Adult - NonCommercial]

Some heterogeneity were found in effect sizes of non commercial species based on the species adult depth range (Q_T = 6026.06, df = 66, P < 0.001). The average response for each depth range explained a part of this heterogeneity (Q_M = 953.31, df = 2, P < 0.001; Q_E = 5072.75, df = 64, P < 0.001; no non commercial species whose depth range exceeds 50 m were found in the studies). Densities of non commercial species were on average similar for two groups of depth range that do not exceed 50 m (R = 1.56 ± 1.92, 95% CI and R = 0.26 ± 0.48, 95% CI, for adult depth range lower than 10 m and between 10 and 50 m, respectively) (Fig. 3h). On average, densities of non commercial species able to live at all depth ranges were higher in the protected areas than in the fished areas (R = 1.32 ± 0.49, 95% CI) (Fig. 3h).

Discussion

Three main results stand out from the meta-analyses done on the single temperate region marine reserves. First, effects of protection on fishes were, on average, different according to their commercial value, and whatever their behaviour or the size of the species considered. Target fishes reacted positively to protection whereas non commercial species showed very rarely a positive response to protection, their densities being most of the time similar in the protected and in the fished areas. Moreover, densities of non target fishes (i.e. small individual size classes of commercial species) were always equal in the marine reserves and outside. Second, different species size or fish behaviour induced a differentiation in the response to protection of target fishes. Differences in densities between the protected and unprotected areas were higher for large species and for mobile species, but with a pronounced territoriality and small home ranges and yearly displacement, than for other fish groups. Species living in the highest depth range considered did not appear to be affected by protection. Third, even if the design features of the marine reserves have an overall effect on target fishes, not all fish groups are equally sensible to the years since protection or the size of the fully and partially protected areas. Non territorial target fishes, with high home ranges, are more sensible to the number of years since protection. Moreover, the densities of these highly mobile fishes are also positively affected by increasing sizes of the fully protected area and negatively affected by increasing sizes of the partially protected area.

Table 2 - Pairwise correlation between the species ecological categories considered in the meta-analysis.

	ComVal	MaxS	Ter	Mov	HR	YD	Sch	GHabA	DepthA
ComVal	1	-	-	-	-	-	-	-	-
MaxS	0.5	1	-	-	-	-	-	-	-
Ter	0.35	0.42	1	-	-	-	-	-	-
Mov	-0.24	-0.24	-0.55	1	-	-	-	-	-
HR	-0.56	-0.55	-0.61	0.71	1	-	-	-	-
YD	-0.47	-0.42	-0.78	0.76	0.74	1	-	-	-
Sch	0.31	0.23	0.46	-0.58	-0.55	-0.66	1	-	-
GHabA	-0.15	-0.12	-0.26	0.64	0.46	0.46	-0.5	1	-
DepthA	-0.33	-0.31	-0.36	0.24	0.36	0.5	-0.09	0.2	1

ComVal: Commercial value; MaxS: Maximum size; Ter: Territoriality; Mov: Movement ability; HR: Home range; YD: Yearly displacement; Sch: Schooling behaviour; GHabA: Adult general habitat; DepthA: Adult depth range.

Table 3 - Summary of significant interaction terms of the fixed effects of the weighted generalized linear mixed effects models, between the different target fish categories and the marine reserve features.

Ecological category	Interaction term	Value	Standard error	df	*t*-value	*P*-value
Maximum size	FP x L	0.558	0.205	44	2.716	0.0094
Territoriality	Y x NT	0.044	0.018	42	2.45	0.0187
	FP x NT	0.497	0.137	42	3.620	0.0008
	FP x T	0.279	0.138	42	2.022	0.0495
	PP x NT	-0.333	0.099	42	-3.372	0.0016
Home range	Y x M	0.047	0.020	48	2.353	0.0228
	Y x L	0.070	0.019	48	3.556	0.0009
	FP x L	0.490	0.208	48	2.353	0.0227
	PP x L	-0.404	0.151	48	-2.675	0.0102
Yearly displacement	PP x L	-0.790	0.252	34	-3.128	0.0036
Schooling behaviour	Y x FS	0.052	0.017	42	2.978	0.0048
	FP x FS	0.447	0.145	42	3.088	0.0036
	PP x FS	-0.349	0.104	42	-3.352	0.0017
Adult depth range	Y x M	0.056	0.022	47	2.609	0.0121
	FP x M	0.439	0.180	47	2.448	0.0182
	PP x M	-0.364	0.131	47	-2.785	0.0077

Y: Years since protection; FP: Size of the fully protected area; PP: Size of the partially protected area. See Figure 2 for details on the group levels for each category.

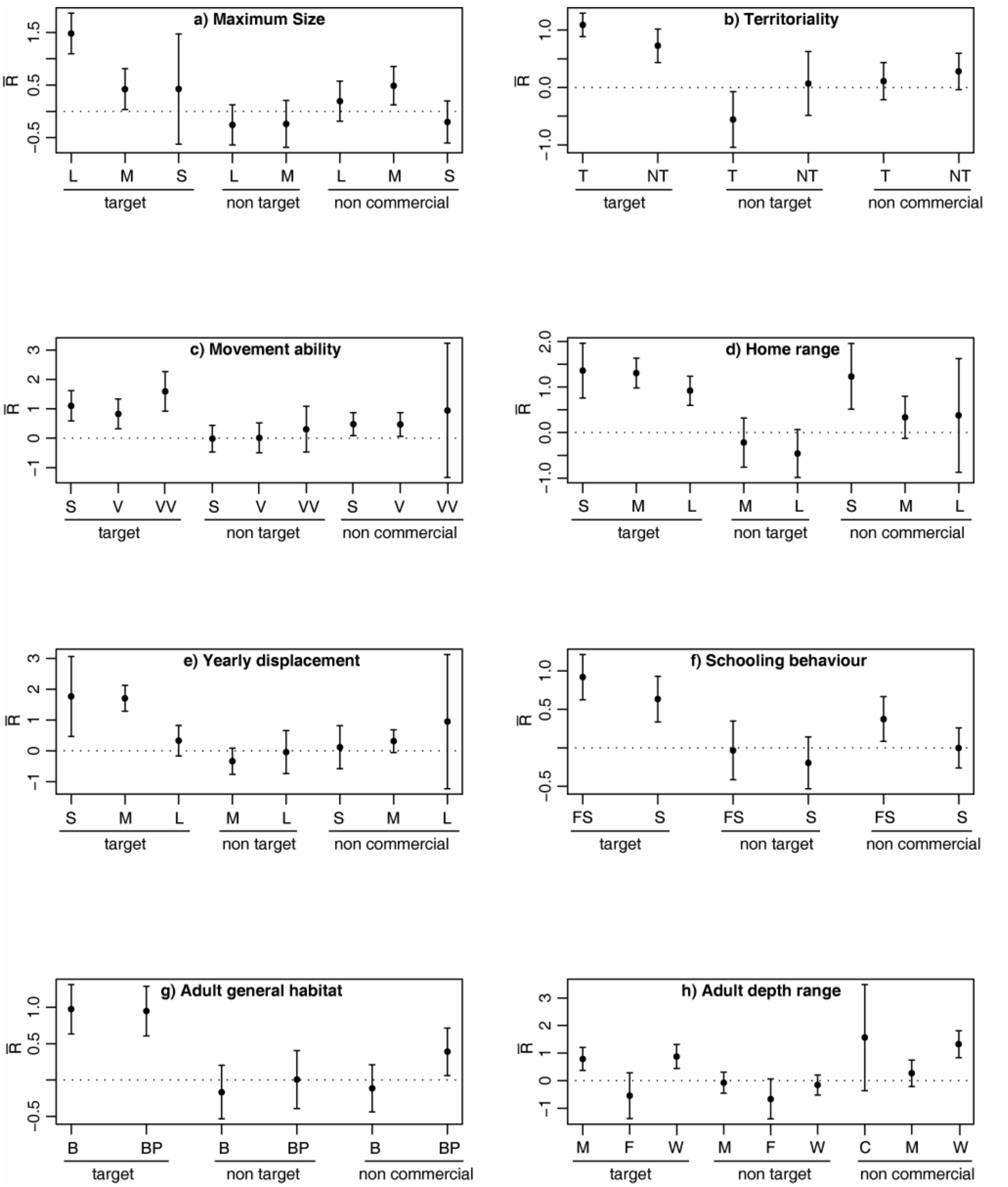


Figure 3 - Average weighted response ratios per fish groups for the different categories considered in the meta-analysis: a) Maximum size, L: large, M: medium, S: small; b) Territoriality, T: territorial, NT: non territorial; c) Movement ability, S: sedentary, V: vagile, VV: very vagile, d) Home range, S: small, M: medium, L: large; e) Yearly displacement, S: small, M: medium, L: large; f) Schooling behaviour, FS: facultative schooler, S: solitary; g) Adult general habitat, B: benthic, BP: bentho-pelagic; h) Adult depth range, C: close, M: medium, F: far, W, whole range. Bar represent 95% confidence intervals.

Appendix - List of the species encountered in the studies and commercial and ecological categories.

Species	ComVal	MaxS	Ter	Mov	HR	YD	Sch	GHabA	DepthA
Abudefduf luridus	NC	M	T	S	S	S	S	BP	M
Aluterus scriptus	NC	L	NT	VV	L	L	FS	BP	W
Anthias anthias	NC	M	NT	S	S	NA	OS	BP	W
Apogon imberbis	NC	L	T	S	NA	NA	FS	BP	M
Aulostomus strigosus	NC	L	NT	V	M	M	FS	BP	M
Balistes capriscus	C	M	NT	VV	L	L	FS	BP	W
Bodianus scrofa	C	L	NT	V	M	M	S	BP	W
Bothus podas	NC	M	NT	S	NA	NA	S	B	M
Callionymus pusillus	NC	M	T	S	NA	NA	S	B	W
Canthidermis sufflamen	C	L	NT	VV	L	L	FS	BP	W
Canthigaster capistratus	NC	S	T	V	S	S	S	BP	W
Caranx latus	C	L	NT	VV	L	L	FS	BP	W
Caranx lugubris	C	L	NT	VV	L	L	FS	BP	W
Centrolabrus trutta	NC	S	T	S	M	S	S	B	M
Chelidonichthys lastoviza	C	M	NA	V	NA	NA	NA	B	W
Chelon labrosus	C	L	NT	V	L	NA	OS	BP	M
Chilomycterus atringa	NC	L	T	V	M	S	S	BP	M
Chromis limbata	NC	S	T	V	M	M	FS	BP	W
Citharus linguatula	C	M	NA	S	NA	NA	S	B	F
Conger conger	C	M	T	S	M	NA	S	B	W
Coris julis	NC	M	T	V	M	M	FS	BP	M
Ctenolabrus rupestris	LC	S	T	S	M	M	S	BP	M
Dasyatis centroura	NC	L	NT	V	L	M	S	B	W
Dasyatis pastinaca	LC	M	NA	S	NA	NA	S	B	W
Dentex dentex	C	L	NT	VV	L	L	FS	BP	W
Diplodus annularis	C	M	NT	V	NA	NA	FS	BP	W
Diplodus cervinus	C	M	NT	V	M	NA	FS	BP	M
Diplodus puntazzo	C	M	NT	V	NA	NA	FS	BP	W
Diplodus sargus	C	M	NT	V	M	M	FS	BP	W
Diplodus vulgaris	C	L	NT	V	L	NA	FS	BP	M
Enchelycore anatina	C	L	NA	V	NA	NA	NA	B	M
Epinephelus aeneus	C	L	NA	V	NA	NA	NA	BP	NA
Epinephelus caninus	C	M	T	S	NA	NA	S	B	M
Epinephelus costae	C	L	T	S	M	NA	S	BP	W
Epinephelus marginatus	C	M	T	S	NA	NA	S	BP	W
Gnatholepis thompsoni	NC	S	T	S	S	S	S	B	M
Gobius auratus	NC	S	T	S	S	S	S	B	W
Gobius bucchichi	NC	S	T	S	NA	NA	S	B	C
Gobius cruentatus	NC	L	T	S	NA	NA	S	B	M
Gobius geniporus	NC	S	NA	S	M	NA	S	B	M
Gobius niger	NC	S	T	S	S	S	S	B	W
Gobius paganellus	NC	S	T	S	S	S	S	B	M
Gobius xanthocephalus	NC	S	T	S	M	S	S	B	M
Gymnothorax miliaris	C	L	T	S	M	S	S	B	M
Gymnothorax unicolor	C	L	T	S	M	S	S	B	W
Helicolenus dactylopterus	C	M	NT	V	M	M	S	B	F
Heteroconger longissimus	NC	M	NT	S	S	M	FS	B	M
Heteropriacanthus cruentatus	C	M	T	S	M	S	FS	BP	M
Kyphosus sectator	C	L	NT	VV	L	M	FS	BP	M
Labrisomus nuchipinnis	NC	M	T	S	S	S	S	B	C
Labrus bergylta	C	L	T	V	M	S	S	BP	M

Species	ComVal	MaxS	Ter	Mov	HR	YD	Sch	GHabA	DepthA
Labrus bimaculatus	NC	M	T	S	M	NA	S	BP	W
Labrus merula	C	M	NT	V	L	M	FS	BP	W
Labrus viridis	LC	M	NT	V	M	NA	S	BP	W
Lepadogaster candollei	NC	S	T	S	S	S	S	B	M
Lepidorhombus boscii	C	M	NA	S	NA	NA	NA	B	F
Lepidotrigla cavillone	NC	M	NA	S	NA	NA	NA	B	F
Lithognathus mormyrus	C	M	NT	V	L	M	FS	BP	M
Liza aurata	C	M	NT	VV	L	NA	OS	BP	M
Lophius budegassa	C	L	NA	S	NA	NA	S	B	F
Lophius piscatorius	C	L	NT	S	M	M	S	B	F
Merluccius merluccius	C	L	NA	V	L	NA	FS	BP	F
Mullus barbatus	C	M	NA	V	L	NA	FS	BP	W
Mullus surmuletus	C	M	NT	V	NA	NA	FS	BP	W
Muraena augusti	C	L	T	S	M	S	S	B	W
Muraena helena	C	L	T	S	NA	NA	S	B	M
Mycteroperca fusca	C	L	T	V	L	M	FS	BP	W
Mycteroperca rubra	C	M	T	S	NA	NA	FS	B	M
Oblada melanura	C	M	NT	V	L	L	FS	BP	M
Pagellus acarne	C	M	NA	V	NA	NA	FS	BP	W
Pagellus bogaraveo	C	L	NA	V	NA	NA	FS	BP	F
Pagellus erythrinus	C	M	NA	V	L	NA	FS	BP	W
Pagrus auriga	C	L	NT	VV	L	NA	S	BP	W
Pagrus pagrus	C	M	NT	V	NA	NA	FS	B	M
Parablennius gattorugine	NC	M	T	S	M	NA	S	B	M
Parablennius pilicornis	NC	S	T	S	S	NA	S	B	NA
Parablennius rouxi	NC	S	T	S	M	NA	S	B	M
Parablennius tentacularis	C	S	T	S	NA	NA	S	B	NA
Paralipophrys trigloides	NC	S	T	S	S	S	S	B	C
Parapristipoma octolineatum	C	M	NA	S	M	NA	FS	BP	M
Peristedion cataphractum	NC	M	NA	V	NA	NA	FS	B	F
Phycis blennoides	C	L	NA	S	NA	NA	NA	B	W
Phycis phycis	C	L	NT	S	M	NA	S	BP	W
Pomadasys incisus	C	L	NT	V	NA	NA	FS	B	M
Pseudocaranx dentex	C	L	NT	VV	L	NA	FS	BP	W
Pteromylaeus bovinus	NC	L	NA	V	NA	NA	S	BP	M
Raja asterias	C	L	NA	S	NA	NA	NA	B	F
Raja clavata	C	L	NA	S	NA	NA	NA	B	W
Raja montagui	C	L	NA	S	NA	NA	NA	B	W
Raja polystigma	C	M	NA	S	NA	NA	NA	B	F
Sarpa salpa	NC	L	NT	V	NA	NA	FS	B	M
Sciaena umbra	C	L	NT	S	NA	NA	FS	B	M
Scorpaena maderensis	C	S	NA	S	NA	NA	S	B	M
Scorpaena notata	C	L	T	S	NA	NA	S	B	W
Scorpaena porcus	C	L	T	S	NA	NA	S	B	M
Scorpaena scrofa	C	L	T	S	S	M	S	B	W
Scyliorhinus canicula	C	L	NA	V	NA	NA	NA	BP	W
Scyliorhinus stellaris	C	L	NA	V	NA	NA	NA	BP	W
Serranus atricauda	C	M	NA	S	M	NA	S	B	W
Serranus cabrilla	C	L	T	S	NA	NA	S	B	M
Serranus scriba	C	M	T	V	NA	NA	S	BP	W
Sparisoma cretense	C	M	NA	V	NA	NA	FS	BP	W
Sparus aurata	C	M	T	V	NA	NA	FS	BP	M
Sphoeroides marmoratus	C	M	NA	V	NA	NA	S	B	W

Species	ComVal	MaxS	Ter	Mov	HR	YD	Sch	GHabA	DepthA
Spicara flexuosa	NC	M	NA	V	NA	NA	OS	BP	W
Spondyliosoma cantharus	C	M	NA	V	L	NA	FS	BP	W
Squalus acanthias	C	L	NA	V	NA	NA	FS	BP	W
Stephanolepis hispidus	C	M	NA	V	NA	NA	NA	BP	W
Symphodus cinereus	NC	S	T	V	NA	NA	FS	B	M
Symphodus doderleini	NC	S	NA	V	M	NA	FS	BP	M
Symphodus mediterraneus	NC	S	NA	V	M	NA	S	BP	M
Symphodus melanocercus	NC	S	T	V	M	NA	NA	BP	M
Symphodus ocellatus	NC	S	T	V	M	NA	S	BP	M
Symphodus roissali	NC	S	T	V	M	NA	S	BP	M
Symphodus rostratus	NC	S	T	V	M	NA	S	BP	M
Symphodus tinca	NC	M	T	V	M	NA	FS	BP	M
Syngnathus typhle	NC	M	NA	S	NA	NA	S	BP	W
Synodus saurus	NC	M	NT	S	M	M	S	B	W
Synodus synodus	C	M	NA	V	NA	NA	NA	BP	F
Taeniura grabata	C	L	NA	S	NA	NA	S	B	W
Thalassoma pavo	NC	M	T	V	M	NA	FS	BP	W
Thorogobius ephippiatus	NC	S	T	S	S	S	S	B	M
Torpedo marmorata	NC	L	NT	S	L	M	S	B	W
Torpedo torpedo	NC	L	NT	V	L	M	S	B	W
Trachinus draco	C	M	NT	S	M	M	S	B	W
Trachinus radiatus	C	M	NA	S	NA	NA	S	B	W
Trachurus mediterraneus	C	M	NT	VV	L	L	OS	BP	W
Trachurus trachurus	C	L	NA	VV	NA	L	OS	BP	W
Trigla lucerna	C	L	NA	V	NA	NA	NA	B	F
Trigloporus lastoviza	C	M	NT	V	L	L	FS	B	W
Tripterygion delaisi	NC	S	T	S	S	S	S	B	M
Tripterygion tripteronotus	NC	S	T	S	S	M	S	B	C
Trisopterus minutus	C	M	NT	V	M	M	OS	BP	F
Umbrina cirrosa	C	L	NT	V	NA	NA	FS	BP	W
Uranoscopus scaber	NC	M	NT	S	M	M	S	B	W
Vanneaugobius canariensis	NC	S	NA	S	NA	NA	S	B	M
Xyrichthys novacula	NC	M	NT	V	M	M	S	BP	W
Zeus faber	C	M	NT	VV	L	L	FS	BP	W

The commercial value (ComVal) has three levels: commercial (C), low commercial (LC), and non commercial (NC). The maximum size (MaxS) category has three levels: small (S), medium (M), and large (L). The territoriality (Ter) category has two levels: territorial (T), and non territorial (NT). The Movement (Mov) category has three levels: sedentary (S), vagile (V), and very vagile (VV). The home range (HR) category has three levels: small (S), medium (M), and large (L). The yearly displacement (YD) category has three levels: small (S), medium (M), and large (L). The schooling behaviour (Sch) has three levels: solitary (S), facultative scholler (FS), and obligate schooler (OS). The general habitat type for adults (GHabA) has two levels: benthic (B), and bentho-pelagic (BP). The depth range of adults (DepthA) has four levels: close (C), medium (M), far (F), and whole range (W). NA: non available values.