Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis

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Meta-analyses of published data for 19 marine reserves reveal that marine protected areas enhance species richness consistently, but their effect on fish abundance is more variable. Overall, there was a slight (11%) but significant increase in fish species number inside marine reserves, with all reserves sharing a common effect. There was a substantial but non-significant increase in overall fish abundance inside marine reserves compared to adjacent, non-reserve areas. When only species that are the target of fisheries were considered, fish abundance was significantly higher (by 28%) within reserve boundaries. Marine reserves vary significantly in the extent and direction of their response. This variability in relative abundance was not attributable to differences in survey methodology among studies, nor correlated with reserve characteristics such as reserve area, years since protection, latitude nor species diversity. The effectiveness of marine reserves in enhancing fish abundance may be largely related to the intensity of exploitation outside reserve boundaries and to the composition of the fish community within boundaries. It is recommended that studies of marine reserve effectiveness should routinely report fishing intensity, effectiveness of enforcement and habitat characteristics.

INTRODUCTION

There is growing interest in the use of marine protected areas (MPAs) as a method for protecting fish populations from excessive exploitation, particularly in developing countries (Polunin, 2002). Indeed, in areas in which a lack of scientific information precludes conventional population-based management, the establishment of MPAs simplifies management and reduces enforcement costs (Bohnsack, 1998; Johannes, 1998). Many MPAs appear to be successful, at least in terms of increasing fish numbers within reserve boundaries (Roberts & Polunin, 1991; Dugan & Davis, 1993; Rowley, 1994; Bohnsack, 1998). Although responses to protection are highly variable among fish taxa, those species that are the target of exploitation respond significantly better than non-target species (Mosqueira et al., 2000). Higher fish abundances within MPAs have the potential to enhance fisheries in adjacent areas. This may occur through increased larval export from MPAs owing to increased spawning stock biomass within MPAs (Bohnsack, 1996; Sladek Nowlis & Roberts, 1997) and/or spillover of exploitable fish into neighbouring non-reserve areas (Roberts & Polunin, 1991; DeMartini, 1993; Russ & Alcala, 1996; McClanahan & Mangi, 2000).

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Another goal of MPAs is to protect sensitive habitats and non-target species, which may otherwise be damaged or depleted through recreational or exploitative uses (Roberts & Polunin, 1991). How well marine reserves fulfill this goal is less clear than their success at protecting exploited fish populations. McClanahan (1994), for example, found that protected areas had higher structural complexity and coral cover than non-protected areas, and the number of fish species was correlated with substratum rugosity. However, it is not clear whether the apparent increase in habitat quality resulted from protection from destructive practices, or whether protected areas were initially located in better-quality sites (Russ, 1985). Several other studies failed to find any differences in substratum complexity or live coral cover between reserve and non-reserve areas (Polunin & Roberts, 1993; Rakitin & Kramer, 1996; McClanahan et al., 1999). This suggests that a priori siting of reserves in good areas may be relatively uncommon. Non-target species appear either not to respond to protection (Jennings et al., 1995; Rakitin & Kramer, 1996) or to respond negatively by showing reduced abundances, perhaps in response to greater predator pressure within reserves (Letourneur, 1996; McClanahan et al., 1999). Nevertheless, given the potential benefits of MPAs for both fisheries and conservation, it is crucial to understand the characteristics of such reserves that promote the fulfillment of these dual goals.

There has been much theoretical interest in predicting the most appropriate design and location of MPAs in relation to the biology of fishes (Man et al., 1995; Mangel, 2000). For example, species typically exhibiting small home ranges may be well protected by small harvest refugia (Holland et al., 1993). Protection of specific habitat types and depth may be necessary for many species that show distinct associations with particular substrata or depths (Bell, 1983). Thus, variability in habitat types and depth, both within and among reserves in a network, should promote species richness. Additional reserve characteristics that may be important involve biogeographical location. For example, it has often been argued that reserves will be less effective in temperate regions than on tropical reefs, due to larger movements of fishes and a greater capacity of fishers to divert their effort to areas outside of protected zones that are managed by quotas (Horwood, 2000). Thus, while it is understood that both the size and siting of marine reserves often depends on socio-economic and political factors, it is also useful to integrate these concerns with information about the biology of the fishes and physical characteristics of the reserves in order to optimize reserve design.

In this study, meta-analysis was used to provide quantitative measures of success, in terms of enhanced fish abundance and species diversity, for a number of marine reserves around the world. Meta-analysis is a set of quantitative methods designed to synthesize the results of disparate studies which may have used different designs, sample sizes or taxa to test a similar question (Hedges & Olkin, 1985). The main advantage of meta-analysis over traditional qualitative reviews is that it allows the calculation of both the magnitude and significance of an overall effect shared among studies. This overall ‘effect size’ is based on the calculation of effect sizes for each contributing study, and these study-effect sizes do not depend on sample size (Fernández-Duque, 1997). Therefore, small-scale studies, which may produce non-significant results because of their small sample
size and which would normally be excluded from traditional reviews, contribute to the overall effect calculated. However, the meta-analysis approach also acknowledges that studies with large sample sizes may be more reliable, and the contribution of each study to the overall effect size is weighted by its sample size or some measure of reliability (Cooper & Hedges, 1994; Arnquist & Wooster, 1995).

In an earlier meta-analysis (Mosqueira et al., 2000), the responses of individual fish species and genera to marine reserve protection were investigated and the effects of body size and fishing status on the magnitude of these responses were examined. In the present study the overall response to protection in terms of fish species diversity and abundance was studied at the reserve level and related to specific reserve characteristics such as area, time since protection and latitude, in an attempt to identify general rules that may guide the design of marine reserves.

MATERIALS AND METHODS

DATA SELECTION AND MANIPULATION

Fish abundance and species richness were obtained from a literature search using the Scientific Citation Index (SCI), Aquatic Science and Fisheries Abstracts (ASFA) and GeoBase (SilverPlatter Inc.), from 1981, 1988 and 1990, respectively. In addition, a number of authors were contacted in search of grey literature, internal reports and unpublished data.

Studies were included if they fulfilled the following criteria: (1) mean fish abundances, measured as number of fish per unit area, and or species diversity, measured as total number of species or number of species per unit area, were reported for sites inside and outside a single marine reserve; studies presenting data aggregated for several reserves were not included, unless data for individual reserves were also presented or made available by the authors (Edgar & Barrett, 1999); (2) a sizeable proportion of the fish fauna had been surveyed, so that those studies reporting abundances of <10 species were omitted; (3) the reserve was a true no-take zone, with enforcement described as being reasonably successful; and (4) the study reported the most recent assessment of the effects of protection in a specific reserve. Two exceptions were made: the Barbados Marine Reserve, where the more recent census (Chapman & Kramer, 1999) was restricted to a smaller number of species than an earlier census (Rakitin & Kramer, 1996), and Sumilon Island reserve in the Philippines, where the survey used (Russ & Alcala, 1989) occurred just prior to the breakdown and later reinstatement of protection. Studies that presented before-after comparisons were not used since there were too few of them. When abundance data were presented separately for fish species, genera, or families, they were aggregated into a single mean abundance estimate. Similarly, when data were provided for a number of sites within and outside each reserve (García-Rubies & Zabala, 1990), they were converted to single weighted mean abundance (X) for the reserve and control areas:

$$\bar{X} = \left( \frac{\sum_{i=1}^{h} \bar{x}_i \cdot n_i}{\sum_{i=1}^{h} n_i} \right)^{-1}$$

where \(\bar{x}_i\) and \(n_i\) are the mean abundance of fish and sample size of abundance estimate (i.e. number of transects or point counts) in the \(i^{th}\) site, respectively, and \(h\) is the number of sites to be aggregated.

In addition to abundance and species diversity, several reserve characteristics were recorded which could affect the relative abundance of fish within reserve boundaries. Reserve area, latitude, time between implementation of protection and census, and total fish diversity recorded in the census were noted. Methodological information was also
recorded such as census area (relative to total reserve area), census method (linear transects or point counts), and whether the study reported abundances for all or only some species within the reserve. Finally, whenever possible, fishery status of each species surveyed was noted, to examine the abundances of a subset of species restricted to those targeted by fisheries.

META-ANALYSIS

The most commonly used effect size metric in meta-analysis is Hedge’s $d$, which requires variances, as well as means, to be known. Variance, however, is not always reported in ecological studies (Adams et al., 1997). The response ratio, $RR$, was therefore used, which can be calculated without knowledge of sample variances (Rosenberg et al., 1997). $RR$ is defined as the ratio of the means measured in experimental and control areas (i.e. in the present study, abundance or richness inside and outside each marine reserve) and is better suited than other metrics for a study of changes brought by protection because it is designed to measure relative differences (Goldberg et al., 1999; Osenberg et al., 1999). The statistical properties of $RR$ have been examined thoroughly (Hedges et al., 1999), and the natural logarithm of the response ratio is usually recommended since it behaves better statistically (Rosenberg et al., 1997). The metric we used is thus defined as: $\ln RR = \ln (\bar{X}_I) \div (\bar{X}_O)$ where $\bar{X}_I$ and $\bar{X}_O$ are the means of the abundance or richness estimates in the experimental (inside reserve) and control (outside reserve) areas.

Estimation of means can be affected by sampling effort. To account for variation among studies in sample size, effect sizes are usually weighted individually, often by the inverse of the sample variance when this is reported (Shadish & Haddock, 1994). In this study, variability in sampling effort (number of transects or point counts) was very high, ranging from five to 200 per study, and applying a weighting scheme using variances generated extreme weights that did not reflect adequately the quality of abundance estimates. A more biologically meaningful weighting scheme was therefore designed based on the total area censused in each study. Each abundance and richness estimate was weighted by $w_j$, which is defined as the natural logarithm of the total area covered by the census from which the estimate was obtained.

Separate meta-analyses were first carried out using all abundance and species richness estimates (one each per marine reserve) to quantify the overall effect of marine protection in terms of each of these correlates of reserve effectiveness. All mean effect sizes are presented back-transformed, so that they can be interpreted easily, for example, as the ratio of densities inside and outside the reserves. Effect sizes are considered to be significantly different from zero when the confidence interval does not include zero (or 1 after back-transformation) (Shadish & Haddock, 1994). Confidence intervals were generated by bootstrapping (Rosenberg et al., 1997), corrected for bias in unequal distribution of samples on both sides of the mean (Efron & Tibshirani, 1993). Analyses were conducted using the software package MetaWin (v. 1.0; Rosenberg et al., 1997).

To test whether all reserves showed homogeneous responses to protection, the homogeneity statistic $Q_{w_i}$ was used (Hedges & Olkin, 1985):

$$Q_{w_i} = \sum_{j=1}^{k} w_j \ln RR_j^2 - \left( \sum_{j=1}^{k} w_j \ln RR_j \right)^2 \left( \sum_{j=1}^{k} w_j \right)^{-1}$$

where $k$ is the number of marine reserves in the analysis, and $\ln RR_j$ is the response ratio of the $j$th estimate. The significance of $Q_{w_i}$ was tested against a $\chi^2$ distribution with $k - 1$ degrees of freedom. If $Q_{w_i}$ is significant, then all reserves do not share a common effect size and the data set is considered to be heterogeneous.

To explain heterogeneity among reserves in their response to protection, the data set was divided into a number of biologically meaningful classes and response ratios, confidence intervals and $Q_{w_i}$ for each class were recalculated. Thus two further meta-analyses were performed to eliminate potential methodological effects. Comparisons were made of (1) the responses to protection of reserves censused using
different survey methods (two classes: transects v. point counts), and (2) the response ratios in reserves in which all or only a portion of the fish fauna was surveyed (two classes: all v. some). Differences in response to protection between classes were estimated using the statistic \( Q_b \) (Hedges & Olkin, 1985):

\[
Q_b = \sum_{i=1}^{m} \sum_{j=1}^{k} w_j (\ln RR_{+i} - \ln RR_{++})^2
\]

where \( \ln RR_{+i} \) is the response ratio for the \( i \)th class, and \( \ln RR_{++} \) is the overall response ratio. The terms \( k \) and \( m \) represent the number of abundance or richness estimates in each class and the number of classes, respectively. The significance of \( Q_b \) was then tested against a distribution generated from 10 000 iterations of a randomization test (Manly, 1991; Rosenberg et al., 1997).

In addition, correlations were performed between reserve effect sizes and continuous variables which characterized either the census methodology (i.e. proportion of reserve area surveyed) or each reserve, i.e. latitude, reserve area and time between implementation of protection and census, and total fish diversity surveyed. Finally, all analyses were repeated using abundance estimates for target species only. Meta-analysis of target species richness was not carried out because target species formed only a sub-set of the total fish assemblages surveyed.

**RESULTS**

**METHODOLOGICAL EFFECTS**

The literature search yielded 15 studies that provided information fulfilling our selection criteria for 19 marine reserves (Table I). Studies using transects and point counts showed similar effect sizes in abundance (transects: \( RR=1.29 \) (0.84–2.29), point counts: \( RR=1.03 \) (0.89–1.30); \( Q_b=1.10, \text{d.f.}=1, P=0.10 \) and species richness (transects: \( RR=1.14 \) (1.07–1.23), point counts: \( RR=0.98 \) (0.92–1.04); \( Q_b=0.49, \text{d.f.}=1, P=0.10 \)). Similarly, studies in which all or only some of the fish species were surveyed did not differ in relative abundance (all: \( RR=1.36 \) (0.83–2.54), some: \( RR=0.96 \) (0.75–1.35); \( Q_b=3.60, \text{d.f.}=1, P=0.55 \) or relative species richness (all: \( RR=1.11 \) (1.03–1.22), some: \( RR=1.10 \) (0.98–1.23); \( Q_b=0.006, \text{d.f.}=1, P=0.87 \)). Finally, effect sizes for abundance and species richness were not related to the area surveyed (abundance: \( r^2=0.04, F_{1,17}=0.78, P=0.39 \); species richness: \( r^2=0.007, F_{1,17}=0.12, P=0.74 \) or to the proportion of the reserve area surveyed (abundance: \( r^2=0.004, F_{1,17}=0.07, P=0.80 \); species richness: \( r^2=0.11, F_{1,17}=2.12, P=0.16 \)). Therefore, differences in survey methodology among studies do not appear to explain differences in responses of reserves to protection.

When only target species were considered, the present sample was restricted to 16 reserves. As was found for all species combined, methodology had no effect on the response of reserves on fish abundance (statistics not shown). All reserves were therefore pooled, regardless of survey methodology.

**FISH ABUNDANCE AND SPECIES RICHNESS**

Overall fish abundance (including both target and non-target species) was higher inside than outside reserves. The response ratio [\( RR=1.25, \text{confidence interval (CI)}=0.86–2.00 \)] indicates that fish abundance was, on average, 25% greater within reserve boundaries; however, the confidence interval, which overlaps 1, shows that this difference is not statistically significant. There was
### Table I. Summary of marine reserves included in the analysis

<table>
<thead>
<tr>
<th>Reserve</th>
<th>Latitude</th>
<th>Year of protection (years to survey)</th>
<th>Reserve area (ha)</th>
<th>Reserve area surveyed (m²)</th>
<th>Survey method</th>
<th>Fish species surveyed</th>
<th>Abundance</th>
<th>Diversity</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Goat Isl., New Zealand</td>
<td>35° S</td>
<td>1975 (13)</td>
<td>54</td>
<td>1875</td>
<td>Transects</td>
<td>Some</td>
<td>12.6</td>
<td>20.3</td>
<td>Cole et al. (1990)</td>
</tr>
<tr>
<td>Banyuls/mer, France</td>
<td>42° N</td>
<td>1974 (18)</td>
<td>20</td>
<td>1200</td>
<td>Transects</td>
<td>All</td>
<td>335.5</td>
<td>351.5</td>
<td>Dufour et al. (1995)</td>
</tr>
<tr>
<td>Maria Isl., Tasmania</td>
<td>42° S</td>
<td>1991 (6)</td>
<td>550</td>
<td>12000</td>
<td>Transects</td>
<td>All</td>
<td>200</td>
<td>225</td>
<td>Edgar &amp; Barrett (1999)</td>
</tr>
<tr>
<td>Governor Isl., Tasmania</td>
<td>42° S</td>
<td>1991 (6)</td>
<td>60</td>
<td>4000</td>
<td>Transects</td>
<td>All</td>
<td>400</td>
<td>500</td>
<td>Edgar &amp; Barrett (1999)</td>
</tr>
<tr>
<td>Tinderbox, Tasmania</td>
<td>43° S</td>
<td>1991 (6)</td>
<td>72.5</td>
<td>4000</td>
<td>Transects</td>
<td>All</td>
<td>700</td>
<td>1000</td>
<td>Edgar &amp; Barrett (1999)</td>
</tr>
<tr>
<td>Ninepin Pt, Tasmania</td>
<td>43° S</td>
<td>1991 (6)</td>
<td>59</td>
<td>2000</td>
<td>Transects</td>
<td>All</td>
<td>554.5</td>
<td>1327.5</td>
<td>Francour (1991)</td>
</tr>
<tr>
<td>Scandola, Corsica</td>
<td>42° N</td>
<td>1975 (13)</td>
<td>1000</td>
<td>400</td>
<td>Transects</td>
<td>Some</td>
<td>3.1</td>
<td>3.4</td>
<td>Garcia-Rubies &amp; Zabala (1990)</td>
</tr>
<tr>
<td>Isl. Medes, Spain</td>
<td>42° N</td>
<td>1983 (5)</td>
<td>2</td>
<td>3750</td>
<td>Transects</td>
<td>All</td>
<td>55.4</td>
<td>1327.5</td>
<td>Harms et al. (1995)</td>
</tr>
<tr>
<td>Carry-le-Rouet, France</td>
<td>43° N</td>
<td>1982 (11)</td>
<td>8</td>
<td>500</td>
<td>Transects</td>
<td>All</td>
<td>2133</td>
<td>1199</td>
<td>Letourneur (1996)</td>
</tr>
<tr>
<td>Cousin Isl., Seychelles</td>
<td>4° S</td>
<td>1968 (26)</td>
<td>4</td>
<td>6160</td>
<td>Points</td>
<td>All</td>
<td>821.2</td>
<td>632.4</td>
<td>McClanahan et al. (1999)</td>
</tr>
<tr>
<td>Mayote Isl., Indian Ocean</td>
<td>12° S</td>
<td>1992 (3)</td>
<td>46.5</td>
<td>600</td>
<td>Transects</td>
<td>All</td>
<td>751</td>
<td>905</td>
<td>McClanahan et al. (1999)</td>
</tr>
<tr>
<td>Chumbe, Tanzania</td>
<td>6° S</td>
<td>1992 (4)</td>
<td>0.3</td>
<td>2000</td>
<td>Transects</td>
<td>All</td>
<td>462.7</td>
<td>489.9</td>
<td>McClanahan et al. (1999)</td>
</tr>
<tr>
<td>Kisite, Kenya</td>
<td>4° S</td>
<td>1978 (11)</td>
<td>110</td>
<td>3000</td>
<td>Transects</td>
<td>All</td>
<td>350.7</td>
<td>639.0</td>
<td>McClanahan et al. (1999)</td>
</tr>
<tr>
<td>Barbados, West Indies</td>
<td>13° N</td>
<td>1981 (11)</td>
<td>2.5</td>
<td>3120</td>
<td>Points</td>
<td>All</td>
<td>142.7</td>
<td>72.7</td>
<td>McClanahan et al. (1999)</td>
</tr>
<tr>
<td>Ras Mohamed, Egypt</td>
<td>27° N</td>
<td>1983 (7)</td>
<td>615</td>
<td>2112</td>
<td>Points</td>
<td>All</td>
<td>23.2</td>
<td>27.2</td>
<td>Roberts (1995)</td>
</tr>
<tr>
<td>Saba, West Indies</td>
<td>17° N</td>
<td>1987 (6)</td>
<td>10</td>
<td>3140</td>
<td>Points</td>
<td>All</td>
<td>21.9</td>
<td>22.6</td>
<td>Roberts &amp; Polunin (1992)</td>
</tr>
<tr>
<td>Sumilon, Philippines</td>
<td>9° N</td>
<td>1974 (9)</td>
<td>50</td>
<td>5250</td>
<td>Transects</td>
<td>Some</td>
<td>15 000</td>
<td>9000</td>
<td>Russ &amp; Alcala (1989)</td>
</tr>
<tr>
<td>Apo, Philippines</td>
<td>9N</td>
<td>1982 (11)</td>
<td>1.7</td>
<td>6000</td>
<td>Transects</td>
<td>All</td>
<td>12 000</td>
<td>6000</td>
<td>Russ &amp; Alcala (1998)</td>
</tr>
<tr>
<td>Watamu, Kenya</td>
<td>3° S</td>
<td>1968 (20)</td>
<td>100</td>
<td>5000</td>
<td>Transects</td>
<td>All</td>
<td>1150</td>
<td>1600</td>
<td>Samoilys (1988)</td>
</tr>
</tbody>
</table>
significant heterogeneity among reserves \((Q_w = 142.8, \text{ d.f.} = 18, P < 0.001)\), indicating that all reserves do not respond to protection with the same magnitude or in the same direction. When the analysis was restricted to target species, fish abundance was significantly greater inside marine reserves \((RR = 1.28, \text{ CI} = 1.01–1.65)\), although marine reserves were again heterogeneous in their response to protection \((Q_w = 33.92, \text{ d.f.} = 15, P = 0.004)\).

By contrast, species richness was significantly higher in marine reserves than beyond reserve boundaries \((RR = 1.11, \text{ CI} = 1.03–1.21)\). Marine reserves were homogeneous in showing an enhancement of fish species number in response to protection \((Q_w = 5.15, \text{ d.f.} = 18, P = 0.99)\). Consequently, no attempt was made to explain inter-reserve variability in relative species richness.

**RESERVE CHARACTERISTICS AND RELATIVE FISH ABUNDANCE**

With target and non-target species combined, none of the reserve characteristics examined explained a significant amount of variation in abundance effect sizes among reserves. Response ratios of abundance were not related to latitude \(r^2 = 0.03, F_{1,17} = 0.47, P = 0.50; \text{ Fig. 1(a)}\), reserve area \(r^2 = 0.01, F_{1,17} = 0.001, P = 0.98; \text{ Fig. 1(b)}\), time between implementation of protection and census \(r^2 = 0.02, F_{1,17} = 0.39, P = 0.54; \text{ Fig. 1(c)}\), or fish diversity \(r^2 = 0.01, F_{1,17} = 0.24, P = 0.63)\).

Similarly, the analyses were restricted to the abundance of species that were targeted by fisheries, reserve response ratios did not vary with latitude \(r^2 = 0.10, F_{1,14} = 1.49, P = 0.24)\), or reserve area \(r^2 = 0.01, F_{1,14} = 0.09, P = 0.77)\), or years of protection: \(r^2 = 0.01, F_{1,14} = 0.18, P = 0.67)\).

**DISCUSSION**

Marine protected areas enhance species richness consistently, but their effects on overall fish abundance are more variable. There was a 25% increase in fish numbers inside marine reserves compared to adjacent, non-reserve areas. However, this difference is not statistically significant and marine reserves vary significantly in the extent and direction of their response. This result appears at odds with the conclusions of other qualitative and quantitative reviews of the effect of marine reserves on fish abundances \(\text{Roberts & Polunin, 1991; Dugan & Davis, 1993; Rowley, 1994; Mosqueira et al., 2000)}\). For example, Mosqueira et al. (2000), also using meta-analyses, found a 3.7-fold increase in abundance of fish inside marine reserves. However, in that study, the unit of analysis was individual fish species, rather than reserves, as in this study. Furthermore, the reported increase was apparent only for species that were the target of exploitation and for large-bodied non-target species, which may experience heavy by-catch mortality. The present reserve-level analysis first combined target and non-target fish species so that a more limited increase in overall abundance is not surprising. Indeed, when only target species were considered, a significant increase in abundance within reserve boundaries was found.

A slight (11%) but significant increase in species richness was noted within reserve boundaries, which was consistent across all reserves. Increased species richness may be associated with better-quality or more variable habitats within MPAs. This may result from the prevention of habitat disturbance by
destructive fishing gear (Jones, 1992), but McClanahan (1994) found that given equal habitat quality, marine reserves in Kenya hosted significantly greater numbers of fish species than non-reserve areas. This suggests that species richness in some marine reserves may be enhanced owing to direct effects on fish populations rather than indirectly via habitat improvement. It is not clear whether this is a general effect because for most reserves in this study (i.e. 12 of

Fig. 1. Relationship between response ratio of abundance (target and non-target species combined) and (a) latitude, (b) reserve area (ha), and (c) years since implementation of protection.
19 reserves) habitat variables were not measured. This should be done more often to disentangle the relative roles of fishing and habitat.

Another measure of success for MPAs, which was not considered in the present study, is an increase in fish body size, particularly for target species. This has been a widespread finding (Garcia-Rubies & Zabala, 1995; Harmelin et al., 1995; Letourneur, 1996; Rakitin & Kramer, 1996; Edgar & Barrett, 1999). For example, while Roberts & Polunin (1992) also found no increase in abundance they reported a significant increase in body size of key target species. Unfortunately, body effects were not reported in enough studies in the present sample to permit meta-analysis.

The studies published to date do not indicate clear general rules to guide the design of marine protected areas. The high variability among reserves in abundance response to protection was not correlated to any of the reserve characteristics examined, i.e. latitude, reserve area, time since implementation of protection, and fish species diversity. These results held whether all fish species or only target species were considered. This is surprising given theoretical predictions that large reserves should contain more species and larger population sizes (Shafer, 1990; Carr & Reed, 1992). Several empirical studies have also shown a build-up of fish biomass occurring within reserves over time for individual reserves (Roberts, 1995), hence a correlation between relative abundance and time elapsed since protection should perhaps have been expected.

Three factors may have prevented the detection of reserve characteristics with universal impacts. First, in a cross-reserve comparison such as the present study, an important determinant of the difference in fish abundance between reserve and non-reserve areas may be the relative intensity of exploitation in the two areas. Jennings et al. (1995) found strong negative relationships between fishing intensity and the biomass of several species targeted by fishermen in the Seychelles, suggesting that if fishing intensity is very high outside reserves, the potential for finding enhanced abundances within reserves is greater. Indeed, Roberts & Polunin (1992) suggested that the low fishing intensity found outside the Red Sea reserve they studied explains the similarity in fish abundance in and out of the reserve. Data on fishing intensity were not available for most reserves in the present study. These should always be reported whenever possible. Second, a reserve-level analysis invariably includes assemblages of fish species that have a wide variety of life histories, behaviours and population dynamics, both within and among reserves. Reserve characteristics suitable for the protection of some species may not be adequate for others. Furthermore, while within latitudes or habitat types, larger reserves may be more beneficial (Edgar & Barrett, 1999), the wide variation in habitats, fish diversity and forms of exploitation that occur around the world will obscure any general trends. Finally, although the analyses were restricted to reserves where protection was described as reasonably well enforced, there may still be variation in enforcement which could confound the analyses. For example, if enforcement were less effective on larger reserves, the greater success expected for large reserves would not be realized.

In conclusion, this study confirms the expectation that marine protected areas should enhance fish diversity, and the abundance of target fish species. It also
reveals a trend toward increased abundance of all species combined (i.e. target and non-target species). Although there is significant variation among reserves in the responses of fish populations to protection, it is not possible to find any correlations with any of the specific reserve characteristics examined. It is suggested that a key determinant of differences in observed responses to protection may be the intensity of exploitation outside reserves, and researchers are urged to report this information whenever possible, in order to test this hypothesis.

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References


