Evaluating the relative conservation value of fully and partially protected marine areas

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Abstract
The establishment of marine protected areas (MPAs), particularly of no-take areas, is often viewed as a conflict between conservation and fishing. Partially protected areas (PPAs) that restrict some extractive uses are often regarded as a balance between biodiversity conservation and socio-economic viability. Few attempts have been made to generalize the ecological effects of PPAs. We synthesized the results of empirical studies that compared PPAs to (i) no-take reserves (NTRs) and (ii) to open access (Open) areas, to assess the potential benefits of different levels of protection for fish populations. Response to protection was examined in relation to MPA parameters and the exploitation status of fish. Our syntheses suggest that while PPAs significantly enhance density and biomass of fish relative to Open areas, NTRs yielded significantly higher biomass of fish within their boundaries relative to PPAs. The positive response to protection was primarily driven by target species. There was a large degree of variability in the magnitude of response to protection, although the size of the PPA explained some of this variability. The protection regime within the PPA provided useful insights into the effectiveness of partial MPAs. We conclude that MPAs with partial protection confer advantages, such as enhanced density and biomass of fish, compared to areas with no restrictions, although the strongest responses occurred for areas with total exclusion. Thus, MPAs with a combination of protection levels are a valuable spatial management tool particularly in areas where exclusion of all activities is not a socio-economically and politically viable option.

Keywords Exploitation status, fish, marine protected areas, MPA design, protection level, weighted meta-analysis

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FISH and FISHERIES

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Introduction

Much of the world’s oceans are affected by human influence with over a third strongly impacted by multiple anthropogenic drivers (Halpern et al. 2008). Much of this impact is aggregated in coastal regions, and overfishing and habitat degradation are among the most pervasive impacts (Jackson et al. 2001; Dulvy et al. 2003; Genner et al. 2010). Such impacts have led to recognition of the need for increased protection of the marine environment, and many coastal nations have moved towards increasing the proportion of their seas encompassed by marine protected areas (MPAs) (Cicin-Sain and Belfiore 2005; Wood et al. 2008).

Marine protected areas have been primarily advocated for the conservation and maintenance of sensitive marine habitats and associated species (Roberts et al. 2001; Willis et al. 2003). Increasingly, the use of MPAs has been recognized as an essential fisheries management tool both to limit direct effects on target species and to enhance production indirectly through, for example, protection of essential fish habitat and promotion of the export of adults and larvae to adjacent areas (Lindeman et al. 2000; Murawski et al. 2000; Gell and Roberts 2003). In addition to direct protection of specific species, MPAs facilitate an ecosystem-wide approach to conservation and fisheries management, by providing broader protection to local habitats and ecosystems (Browman and Stergiou 2004; Sissenwine and Murawski 2004).

No-take marine protected areas, often called marine reserves, where all extractive uses (e.g. fishing) are prohibited, have been shown to provide a number of benefits. Such benefits include increased biomass and density of species within (Garcia-Rubies and Zabala 1990; García-Charton et al. 2004; Guidetti et al. 2005) and outside the no-take area boundary (McClanahan and Mangi 2000; Stobart et al. 2009; Goni et al. 2010), enhanced reproductive output (Planes et al. 2000; Goni et al. 2003) and re-established community and habitat structure (Castilla 1999; Shears and Babcock 2002). Despite these benefits, the prohibition of all extractive activities in certain areas can have short-term negative socio-economic impacts (Richardson et al. 2006) through the loss of or increased travelling time to fishing grounds, and decreased overall catches (Fiske 1992; Jones 2001), and may consequently be harder to implement and enforce. Partially protected marine areas with less restrictive regulations that seek a balance between the conservation of biodiversity and continued use of the area may be a more viable management strategy. Additionally, partial fisheries closures that restrict activities such as commercial fishing with bottom-towed gear but allow others such as fishing with static gear may reduce conflict among users with competing interests (e.g. Blyth et al. 2002).

The reported effectiveness of partially protected marine areas for fisheries and ecosystem restoration is highly variable. Whereas some studies have recorded enhanced abundance and reproductive potential for exploited species (Pipitone et al. 2000; Beukers-Stewart et al. 2005) and recovery of community and habitat structure inside partially protected areas (PPAs; Murawski et al. 2000), others did not detect benefits over unprotected fished areas (Piet and Rijnsdrop 1998;
Denny and Babcock 2004). Very few attempts have been made to generalize the ecological effects of PPAs to date. To the best of our knowledge, the study by Lester and Halpern (2008) is the only other review that examines the impact of partial protection conferred by PPAs. However, whereas Lester and Halpern (2008) included only studies that compared variables (density, biomass, size, species richness) in no-take reserves (NTR), PPAs and open access (Open) areas (i.e. NTR vs. PPA vs. Open), here, we synthesize data on the performance of MPAs from studies that have made direct comparisons between (i) PPAs and Open areas and/or (ii) PPAs and NTRs in addition to a combination of all three levels of protection (NTR vs. PPA vs. Open). This wider literature search captured examples of specific fishing gear exclusion areas conferring partial protection that have been compared with open access areas but not to a NTR. This allowed a more in-depth examination of the benefits of MPAs conferring partial protection relative to unprotected areas for fish populations.

Species may respond differently to protection depending on the intensity of exploitation to which they are subject to outside the MPA (Williamson et al. 2004; Tetreault and Ambrose 2007; Watson et al. 2009). Therefore, we also examined whether the response to protection differed for target and non-target fish species. Previous quantitative syntheses of fish populations in no-take marine reserves (NTRs) have linked the heterogeneity in response to protection among reserves to a number of MPA characteristics such as duration of protection and size of the MPA (Micheli et al. 2004; Claudet et al. 2008; Lester et al. 2009; Maliao et al. 2009; Molloy et al. 2009; Vandeperre et al. 2011). Therefore, we investigated whether parameters such as the protection regime within the PPA, the age and size of the MPA and the distance of the reference area to the MPA border influenced the magnitude of response to protection. Insights into the effect of such characteristics are fundamental for the development of a more general understanding of the factors that underpin the effectiveness of a PPA.

Methods

We used systematic review methodology (Pullin and Stewart 2006; Higgins and Green 2008) and meta-analysis (Arnot and Wooster 1995; Gurevitch and Hedges 1999) to examine the magnitude of the response of fish to protection inside PPAs relative to NTRs and to Open areas (the review protocol and full systematic review are available online at www.environmentalevidence.org/SR79.html). The systematic review approach provides a comprehensive and robust assessment and summary of available evidence used to inform evidence-based decision-making (Gates 2002; Roberts et al. 2006). An advantage over conventional reviews is that systematic reviews follow a strict methodological protocol that involves the critical appraisal of study methodology prior to their inclusion in the analysis. This minimizes the chance of bias and improves transparency and reliability of the findings of the review (Stewart et al. 2005).

Data selection

We searched peer-reviewed scientific literature and grey literature (up until the end of February 2011) to compile a database of studies that documented the biological effects of NTRs and of PPAs on fish density and biomass (refer to Table 1 for definitions). The search was conducted in multiple electronic databases and the internet (including organizational websites) using a range of Boolean search terms that included the terms ‘Marine Protected Area’, ‘partially protected area’, ‘fishery reserve’, ‘marine area closure’, ‘gear restriction zone’, ‘buffer zone’, ‘marine sanctuary’, ‘marine reserve’ and ‘no-take area’ to capture the diverse range of terminology that has been used in the literature to refer to marine protected areas. The full list of the search term combinations by source is given in Appendix S1. The bibliographies of articles included in this review and other relevant review articles were also searched.

We retained studies if they explicitly compared (i) a NTR to a PPA, or (ii) a PPA to an Open area, or (iii) a combination of all the three levels of protection (NTR vs. PPA vs. Open). For studies that compared a NTR with PPA, these were included in the quantitative analysis only when the two were established at the same time or within 2 years of each other. Furthermore, studies that examined any of the combinations (i) to (iii) were only included if mean, sample size values (e.g. number of transects or point counts) and an appropriate error measure (SD, SEM, variance, 95% CI) were reported for fish taxa. These values were extracted as presented from tables or within
text. When values were presented in figures, these were extracted using the data extraction software TechDig v.2. When several studies reported on the effects of protection for the same MPA, we retained the most recent study unless the studies measured different metrics (i.e. density, biomass) or presented data at different levels of aggregation (e.g. total or individual species mean values). Studies that presented data aggregated for several MPAs with different characteristics (e.g. Friedlander et al. 2003) were not included. A complete list of studies included in this study, together with details of the MPA characteristics, the study survey design and methodology and metrics (density, biomass) measured are given in Appendix S2 and S3.

Data handling
Whenever a study reported paired inside–outside estimates from more than one MPA, each pair was included separately in our database (e.g. Nardi et al. 2004; Walsh et al. 2004; Link et al. 2005; Friedlander et al. 2006, 2010; Tuya et al. 2006). When data were reported from two or more MPAs but one control area (e.g. La Mesa and Vacchi 1999; Miller et al. 2005; Tupper 2007; Di Franco et al. 2009; Jaworski et al. 2010), data estimates within each MPA were included separately and compared with the same control. Because the resulting density or biomass ratios for the MPAs were not independent, we repeated all analyses using average estimates for the MPAs sharing the same control and report the results only when they differ from the analyses that included them separately. When there was more than one sampling event after MPA establishment, the most recent sampling event, representing the longest duration of protection, was used. This avoids analytical problems associated with temporal autocorrelation. However, when the data were collected within the same year (most frequently over different seasons), a composite effect size was used for subsequent analysis to eliminate any seasonal effects associated with the timing of sampling. Similarly, mean data presented for different depths within the same MPA were aggregated into a composite effect size using a fixed-effect model, whereby the weight assigned to each subgroup effect size was equal to the inverse of the within-subgroup variance (Borenstein et al. 2009).

Data appraisal
Ecosystem processes are spatially and temporally variable at multiple scales, and these variations can obscure the detection of the effects of protection (García-Charton and Pérez-Ruzafa 1999). Before–after control–impact (BACI) studies that account for both spatial and temporal variability in the environment, thus allow for unambiguous inference about the effect of protection. We attempted to explore the influence of experimental design on the magnitude of the response to protection by running a sensitivity analysis using all studies and only those with BACI design. However this was not possible as the majority of studies were based on an After Control–Impact design (see Appendix S2 and S3; systematic review report at www.environmentalevidence.org/SR79.html). The variation in habitat characteristics between protected and unprotected areas is critical in making any meaningful comparisons of the protection effect (Willis et al. 2003; Anderson and Millar 2004; García-Charton et al. 2004; Claudet et al. 2011). Accordingly, we conducted a sensitivity analysis parallel to the main analysis to examine

Table 1 Definition and abbreviation of terms describing different levels of protection.

<table>
<thead>
<tr>
<th>Abb.</th>
<th>Term</th>
<th>Definition</th>
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<tbody>
<tr>
<td>MPA</td>
<td>Marine Protected Area</td>
<td>Discrete geographical areas of the sea that are protected by spatially explicit restrictions designated under international, national, tribal or local laws to enhance long-term conservation of natural resources therein</td>
</tr>
<tr>
<td>NTR</td>
<td>No-take reserve</td>
<td>MPAs where all anthropogenic activities are excluded, apart from scientific research</td>
</tr>
<tr>
<td>PPA</td>
<td>Partially protected area</td>
<td>MPAs whereby regulations restrict some extractive uses but permit others</td>
</tr>
<tr>
<td>Open</td>
<td>Open access area</td>
<td>Areas outside the MPA that are open to fishing</td>
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Table 1: Definition and abbreviation of terms describing different levels of protection.
the influence of including the ‘habitat-confounded studies’ on the overall magnitude and direction of protection effect and report the results for the sensitivity analyses when the two differed. ‘Habitat-confounded studies’ refer to those studies where habitat variation in terms of features such as substratum type, substratum composition and complexity, rugosity and exposure, was reported to be significantly different for the studied locations inside and outside the MPA.

Meta-analysis

We used a weighted meta-analytical approach to investigate the response of fish to protection and to explicitly examine heterogeneity among MPAs. The natural logarithm transformed response ratio, LnRR (Hedges et al. 1999) was used as the effect size, which is better suited than other metrics for a study of changes brought about by protection because it is designed to quantify the proportionate change that results from the intervention (Goldberg et al. 1999; Hedges et al. 1999). LnRR was used instead of RR because it linearizes the metric so that changes in the denominator and numerator are treated equally and yields better sampling distributions (Hedges et al. 1999). The response ratio is defined as the ratio of the mean density or biomass estimate measured inside and outside the MPA (Hedges et al. 1999):

\[
\text{LnRR} = \ln\left(\frac{\bar{X}_{\text{PPA}}}{\bar{X}_{\text{Open}}}\right)
\]

Effect sizes are commonly weighted to ensure a greater contribution of the most robust studies. Robustness is usually based on (inversed) sample variance (Rosenberg et al. 2000); therefore, we estimated the variances associated with the response ratio (\(V_{\text{LnRR}}\)) (Hedges et al. 1999) as:

\[
V_{\text{LnRR}} = \frac{\text{SD}_{\text{PPA}}^2}{n_{\text{PPA}}(\bar{X}_{\text{PPA}})^2} + \frac{\text{SD}_{\text{Open}}^2}{n_{\text{Open}}(\bar{X}_{\text{Open}})^2}
\]

where \(\bar{X}_{\text{PPA}}\) and \(\bar{X}_{\text{Open}}\) are the mean density or biomass in the PPA and the Open area, SD\(_{\text{PPA}}\) and SD\(_{\text{Open}}\) are the standard deviation associated with \(\bar{X}_{\text{PPA}}\) and \(\bar{X}_{\text{Open}}\), \(n\) is the sample size for estimation of the mean (i.e. the number of hauls or transects or point counts sampled). Similarly, the effect size and the variance for comparison of the NTRs and PPA were calculated by replacing PPA with NTR and Open with PPA in the equations above.

We calculated a weighted summary effect size (\(\text{LnRR}_{\text{w}}\)) across the different MPA case-studies by conducting a random effects meta-analysis using the DerSimonian-Laird estimator method (Gurevitch and Hedges 1999; Hedges et al. 1999; Rosenberg et al. 2000):

\[
\text{LnRR}_{\text{w}} = \frac{\sum_{i=1}^{k} W_i \text{LnRR}_i}{\sum_{i=1}^{k} W_i}
\]

where \(\text{LnRR}_i\) and \(W_i\) are the effect size and weight (inverse variance) associated with each MPA included in the analysis, respectively, and \(k\) is the number of MPAs.

Positive values of the summary effect size (\(\text{LnRR}_{\text{w}}\)) indicate greater density or biomass inside the PPA relative to the Open area, or inside the NTR relative to the PPA. Negative values indicate the opposite. The summary effect size (\(\text{LnRR}_{\text{w}}\)) is considered to be significantly different from zero (i.e. there is a significant either positive or negative effect of protection) when the 95% confidence interval (CI) does not overlap zero (or 1 after back-transformation). All effect sizes reported in the text (as opposed to those shown in figures and tables) are presented back-transformed, so that they can be interpreted easily as the ratio of density or biomass inside and outside the MPA.

MPA-level analyses

To quantify the overall effect of marine protection on fish assemblage density and biomass, we carried out a meta-analysis using effect sizes calculated for MPAs that reported total mean values, or mean values for a sizeable proportion of the fish fauna surveyed (i.e. when the data were reported for 10 or more species or for more than 75% of the total catch of all fish counts). Separate meta-analyses were carried out using density and biomass estimates to quantify the effect of (i) partial protection over no protection and of (ii) full protection over partial protection in terms of each of these measures of MPA effectiveness.

Furthermore, we investigated the influence of a number of MPA characteristics on the response of the fish assemblage to protection. This analysis was only conducted for studies that compared a PPA to an Open area, as the number of studies that compared a NTR to a PPA was too small to
conduct robust analysis (biomass: $k = 6$ case-studies; density: $k = 9$ case-studies). We used the QM statistic to examine differences in the response to protection among categories of categorical variables and to test model fit for continuous variables (Rosenberg et al. 2000). The following variables were examined: MPA age (number of years between MPA enforcement and survey); size of the PPA (log$_{10}$-transformed); and PPA protection regime, which we described here as the combination of fishing activities prohibited and permitted inside the partially protected area. Based on the information extracted on the type of activities prohibited within the PPA (Appendix S4), PPAs were divided into: (i) 'indiscriminate' PPAs, if they prohibit fishing activities that are damaging to bottom habitats and non-target species (e.g. scallop dredging, bottom trawling) and (ii) 'discriminate' PPAs, if they prohibit activities which affect particular target species but not the surrounding environment (e.g. seine nets, long lines, spearfishing).

'Indiscriminate' PPAs may exhibit smaller responses to protection than 'discriminate' PPAs as habitat recovery will have to occur before some species’ populations can begin to recover. Alternatively, the prohibition of fishing with highly destructive bottom-towed gear in 'indiscriminate' PPAs compared with the prohibition of fishing with less environmentally damaging gear in 'discriminate' PPAs may lead to a stronger response to protection for 'indiscriminate' PPAs. Furthermore, based on information on the permitted activities inside the PPA (Appendix S4), we subdivided 'discriminate' PPAs into those that allow some commercial and/or artisanal fishing inside the PPA, from those that allow recreational fishing or fishing for subsistence purposes only. This categorization serves as an indication of the intensity of use by the different user groups permitted to fish inside the PPA. Fishing practices permitted inside 'indiscriminate' PPAs were carried out on a commercial scale. Therefore, PPAs were categorized into three discrete groups based on their protection regime: (a) 'indiscriminate, commercial' (IdC); (b) 'discriminate, commercial' (DC); and (c) 'discriminate, recreational' (DR) (refer to Appendix S4 for full details on the ‘protection regime’ classification scheme).

Methodological variation among studies may have a strong impact on the results obtained. Different methods of surveying fish density and biomass were used among studies included in meta-analyses. For example, fish surveys inside and outside protected areas were undertaken using underwater visual census (UVC) by belt transect, UVC by baited underwater video, or experimental fishing by trawling. These can lead to large differences in the overall area sampled. In addition, the distance between protected and control sites varied to a large degree. Processes such as fish ‘spillover’ and increased fishing activity near the MPA border following its establishment (known as ‘fishing the line’) (Stobart et al. 2009) mean that variation in the distance of the control area from the MPA among studies may impact results. To account for these issues, we examined (i) the relationship between effect size and the total area surveyed inside and outside the MPA and (ii) the influence of the proximity (measured as the minimum distance in km) of the Open control sites to the PPA border on effect size.

The relatively small numbers of MPAs did not permit the construction of models with multiple variables, therefore, weighted simple mixed effects regression models were used throughout the analyses. Furthermore, sample sizes limited the number of variables examined in the analyses. We prioritized variables according to their likelihood of influencing MPA performance and also on their relative importance to policy and MPA management. Therefore, although the effect of variables such as geographical location and substrate type would have been interesting to examine, these were not included in the analyses so as to avoid statistical issues related to data dredging and data mining.

Species-level analyses: exploitation status

A considerable proportion of studies in our database presented mean and variance values for one or more individual species, rather than fish assemblages, and we included these studies in separate meta-analyses to determine the effect of (i) partial protection over no protection and of (ii) full protection over partial protection. Examination of effects at the species rather than assemblage level allowed assessment of how the ‘exploitation status’ of species, that is, whether targeted or not by fisheries, determined the efficacy of protection. For these analyses, ‘target species’ is taken to refer to those species that are primarily sought by fishermen in a particular fishery and are the subject of directed fishing effort. ‘Non-target species’ denotes species for which fishing gear is not specifically
set, although the possibility that these species are accidentally caught as by-catch cannot be ruled out. In the analysis comparing NTRs with PPA, we further subdivided ‘target species’ into those that were protected in both the NTR and the PPA (‘target-protected species’, TP) and those that were protected by the NTR but still permitted to be fished inside the PPA (‘no-take reserve protected species’, NTP).

Individual species ln-transformed response ratios ($\text{LnRR}_j$) were calculated for each MPA using species density or biomass estimates inside and outside the MPA. When a species was absent either inside or outside the MPA (i.e. the density or biomass estimate was zero), the species was removed from the analysis as it was not possible to use the natural logarithm of effect sizes involving abundance estimates of zero. Preliminary trials in which values of 0.001 and 0.0001 were added to all abundance estimates for each species resulted in an unrealistic overestimated weighted effect size for those species that were absent either inside or outside the protected area. As the effect sizes of individual species within a MPA are unlikely to be independent of each other, a single effect size measure for each ‘exploitation status’ category within each MPA was generated to handle non-independence of data (Raudenbush et al. 2000; Hedges et al. 2010). Individual species response ratios ($\text{LnRR}_j$) were therefore averaged to produce a single study-average effect size for each exploitation category (i.e. $\text{LnRR}_T$, $\text{LnRR}_T$, $\text{LnRR}_{\text{NTP}}$, $\text{LnRR}_{\text{NT}}$). The variance associated with the single study-average effect size was calculated using (Borenstein et al. 2009):

$$\text{var} \left( \frac{1}{m} \sum_{i=1}^{m} \text{LnRR}_i \right) = \left( \frac{1}{m} \right)^2 \text{var} \left( \sum_{i=1}^{m} \text{LnRR}_i \right) = \left( \frac{1}{m} \right)^2 \left( \sum_{i=1}^{m} V_{\text{LnRR}_i} + \sum_{i 
eq j} r_{ij} \sqrt{V_{\text{LnRR}_i} V_{\text{LnRR}_j}} \right)$$

where $\text{LnRR}_i$ is the individual species’ response ratio, $V_{\text{LnRR}_i}$ and $V_{\text{LnRR}_j}$ are the within-study variance for species $i$ to $j$, $m$ is the number of species within each ‘exploitation status’ category and $r$ is the correlation coefficient that describes the extent to which the means of two different species co-vary.

Because the correlation coefficient among species within a study was never reported, a range of correlation coefficient values were used in the calculation ($\rho = 0, 0.2, 0.5, 0.8, 1$), and the analyses repeated for each value of $r$. As the results did not differ significantly for the different values of $r$, we present data for $r = 0.5$. Categorical meta-analysis was conducted between ‘exploitation status’ categories using the $Q_M$ statistic (Rosenberg et al. 2000) to determine whether the between-group responses were significantly different.

Finally, as for the fish assemblage analyses, we examined the influence of a number of MPA characteristics on the response of target species to protection. As the overall response to protection was not significantly different between ‘target-protected species’ (TP) and ‘no-take reserve protected species’ (NTP), we pooled the effect sizes from these two subcategories for the analysis of MPA characteristics on target species response. The sample sizes for the ‘non-target’ species categories were too small to allow further analysis.

Analyses were conducted using the software package Metawin (v. 2.0: Rosenberg et al. 2000) for calculation of effect size and within-study variance and in R using the metaphor package (Viechtbauer 2010) for the random effects meta-analyses.

Results

The literature search generated 4851 potentially relevant articles. After screening using the study inclusion criteria, a total of 40 studies were found to be relevant and provided the required data for inclusion in the meta-analysis. Many studies were not included in the review because the study design lacked an appropriate comparator or because the study compared a NTR to an Open area only. Studies were excluded when the
activities prohibited and/or allowed within the MPA were not described clearly such that it was difficult to decide whether the MPA was a NTR or a PPA. A list of excluded studies and the reasons for exclusion from our meta-analysis is available at www.environmentalevidence.org/SR79.html (Additional file 5).

The 40 studies retained for the meta-analysis, provided data on fish population measures for 63 MPA case-studies, of which 51 were used to assess the effect of partial protection over no protection and 22 were used to assess the effect of full over partial protection. The majority of PPAs included in the analysis of partial and no protection were based in North America and Europe. The age of the PPAs in this data set ranged between 2 and 61 years and the size of the PPA ranged between 0.14 and 11 980 km². Most of the studies comparing NTRs to PPAs were based in Europe, and these were mainly characterized by a zonation scheme, whereby the NTR and the PPA (sometimes referred to as buffer zone) are adjacent to each other. The age of the MPAs in this data set ranged between 2 and 25 years. The size of the NTR ranged between 0.13 and 30 km² and that for the PPA between 4.5 and 609 km². Additional information on MPA characteristics, survey design and methodology and metrics (density, biomass) measured for each MPA are given in Appendix S2 and S3.

Comparison of partially protected vs. open access areas

Effect of protection

Overall, fish assemblage density and biomass were significantly higher inside the PPAs than in the Open areas. Fish density was on average 22% higher within PPA boundaries (sensitivity analysis: weighted summary effect size, RR = 1.22, confidence interval (CI) = 1.02–1.48), and biomass was 51% higher in the PPA than in the Open areas (main analysis: RR = 1.51, CI = 1.23–1.84) (Fig. 1).

Examination of individual species that have been aggregated according to their fisheries’ exploitation status revealed that target fish species had significantly higher density (sensitivity analysis: RR = 1.65, CI = 1.32–2.03) and biomass (main analysis: RR = 1.49, CI = 1.19–1.88) inside the PPAs than in the Open areas (Fig. 1). In contrast, no significant effect was detected for non-target species (Fig. 1). Despite this difference in result, a direct comparison of the magnitude of response to partial protection between the target and non-target species categories was not significant for both measures (density (sensitivity analysis): QM = 1.53, d.f. = 1, P = 0.22; biomass (main analysis): QM = 0.32, d.f. = 1, P = 0.57).

Correlates of response to protection

Several potential effect modifiers were tested in an attempt to explain the variability in effect sizes between MPAs. To examine whether the response to protection was influenced by the type of fishing activities prohibited and permitted within the PPA, we conducted a categorical meta-analysis for the effect of ‘protection regime’ on fish assemblage and target species. Of the six comparisons between PPAs and Open areas conducted for fish assemblages (three types of protection regime for each of density and biomass), only one (biomass for the ‘discriminate, commercial’ DC category) showed a significant difference (Fig. 2). Comparison of the response to partial protection among the three protection regime categories examined was not significantly different for fish assemblage density (sensitivity analysis: QM = 0.63, d.f. = 3, P = ...
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Figure 2 Mean response ratio (LnRR) based on density (●) and biomass (■) data in the partially protected area and the open access area (partial: open) for each ‘protection regime’ category (IdC: indiscriminate, commercial; DC: discriminate, commercial; DR: discriminate, recreational). Results are shown for the entire fish assemblage and for fisheries’ target species only. Sample size (i.e. the number of PPAs) for each ratio is shown in parentheses. The vertical dotted line at (LnRR) = 0 represents equal fish density or biomass inside and outside of the PPA; (LnRR) > 0 means more fish inside the PPA; (LnRR) < 0 means fewer fish in the PPA.

0.73) or biomass (sensitivity analysis: $Q_M = 2.01$, d.f. = 3, $P = 0.37$). We emphasize, however, that the results for this effect modifier on assemblage data should be interpreted with caution owing to the small number of PPA case-studies within each category, which reduced the robustness of the reported average effect size (Fig. 2).

When the analysis was carried out on those studies that provided data for target species, density and biomass were significantly greater (on average twice as high) in the PPAs that allow fishing on a recreational basis or for subsistence (DR) relative to the Open area (density (main analysis): $RR_{DR} = 1.79$, CI = 0.76–1.79; biomass (main analysis): $RR_{DR} = 1.16$, CI = 0.72–1.86) (Fig. 2). Nevertheless, the magnitude of response to protection did not differ significantly among the three protection regimes for target species density ($Q_M = 3.74$, d.f. = 3, $P = 0.15$) and was marginally non-significant for target species biomass ($Q_M = 5.89$, d.f. = 3, $P = 0.05$).

The meta-regression analyses revealed a negative relationship between effect size and the size of the PPA for fish assemblage biomass (Table 2, Fig. 3). The slope suggests an average decrease in assemblage biomass relative to Open areas, of 17% for every ten-fold increase in PPA size. The response to protection of target species was not significantly related to PPA size (Table 3); however, the plots for the log-transformed PPA size indicate that the density and biomass of the target species inside the PPA became comparable with or less than those in the Open area (i.e. effect sizes approached zero or became negative, respectively) for PPAs larger than 1000 km² (Fig. 4).

Whereas the effect sizes for fish assemblage density and biomass were not significantly related to the age of the MPA (Table 2), the biomass of target fish species inside the PPA showed a slight (~3%) but significant reduction relative to the Open area upon increasing the duration of protection (slope = −0.03, CI = −0.06 to −0.003, Table 3, Fig. 4). The response to protection for target fish density was not significantly related to the age of the MPA (Table 3).

The relationship between effect size and the distance of the Open area to the PPA border was not significant for fish assemblages or for target species (Tables 2 and 3). It is worth mentioning that for the majority of PPAs (15 of 18 cases), the sites sampled within the Open area were within 1.2 km (range: 0.02–1.2 km) of the PPA boundary, and among these PPAs, the effect size was reasonably heterogeneous ($RR$ range: −0.5 to 2) (Figs 3 and 4). The difference in the survey methodology represented here by the total survey area was not significantly related to the fish assemblage or the target species response to protection (Table 2).

Comparison of no-take reserves vs. partially protected areas

Effect of protection

Fish assemblage density was on average 11% higher in NTRs relative to PPAs, but the differ-
ence was not significant (main analysis: $RR = 1.11$, CI = 0.86–1.43) (Fig. 5). In contrast, assemblage biomass was significantly higher, with 92% more biomass in NTRs than PPAs (main analysis: $RR = 1.92$, CI = 1.28–2.89) (Fig. 5).

Table 2 Summary of the weighted simple random effects meta-regression models for each of the four moderator variables on fish assemblage density and biomass effect sizes comparing partially protected areas to open access areas (partial:open). Results presented are for the sensitivity analysis (i.e. habitat-confounded studies were removed from the analysis).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Moderator variable</th>
<th>No of MPAs</th>
<th>Slope [95% CI]</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density</td>
<td>Age (yrs)</td>
<td>17</td>
<td>−0.004 [−0.03 to 0.01]</td>
<td>0.71</td>
</tr>
<tr>
<td>Density</td>
<td>Log (size) (km²)</td>
<td>17</td>
<td>0.04 [−0.12 to 0.2]</td>
<td>0.63</td>
</tr>
<tr>
<td>Density</td>
<td>Log (distance) (km)</td>
<td>15</td>
<td>−0.23 [−0.65 to 0.19]</td>
<td>0.98</td>
</tr>
<tr>
<td>Density</td>
<td>Survey area (m²)</td>
<td>16</td>
<td>0.002 [−0.65 to 0.19]</td>
<td>0.28</td>
</tr>
<tr>
<td>Biomass</td>
<td>Age (yrs)</td>
<td>18</td>
<td>0.006 [−0.007 to 0.02]</td>
<td>0.41</td>
</tr>
<tr>
<td>Biomass</td>
<td>Log (size) (km²)</td>
<td>18</td>
<td>−0.17 [−0.29 to −0.04]</td>
<td>0.01</td>
</tr>
<tr>
<td>Biomass</td>
<td>Log (distance) (km)</td>
<td>15</td>
<td>−0.13 [−0.31 to 0.06]</td>
<td>0.18</td>
</tr>
<tr>
<td>Biomass</td>
<td>Survey area (m²)</td>
<td>15</td>
<td>−0.24 [−0.51 to 0.03]</td>
<td>0.18</td>
</tr>
</tbody>
</table>

Bold values significance $r^2 = 0.26$, $p = 0.01$.

Figure 3 Plots of the relationship of fish assemblage response ratio (partial:open) with PPA age (yrs), log-transformed PPA size (sq-km), distance of the Open area to the PPA boundary (Dist. PPA to Open (km) and log-transformed survey area (sq-m)) for density (a, b, c, d) and biomass (e, f, g, h) data. Size of the circles is proportional to the weight of the study.
The biomass of target and non-target species was on average higher in NTRs than PPAs, but this increase was only significant for ‘no-take reserve protected species’ (NTP), that is, for fisheries’ target species that are protected inside the NTR but not in the PPA (main analysis: $RR_{TP} = 1.30$, CI = 0.97–1.73; $RR_{NTP} = 1.32$, CI = 1.04–1.68; $RR_{NT} = 1.63$, CI = 0.83–3.22, Fig. 5). For density,

**Table 3** Summary of the weighted simple random effects meta-regression models for each of the three moderator variables on fish target species density and biomass effect sizes comparing partially protected areas to open access areas (partial:open). Results presented are for the main analysis (i.e. all studies were retained from the analysis as no influence of the habitat-confounded studies was found on the overall effect of protection).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Moderator variable</th>
<th>No of MPAs</th>
<th>Slope [95% CI]</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density</td>
<td>Age (yrs)</td>
<td>33</td>
<td>$-0.1 [-0.03 to 0.02]$</td>
<td>0.45</td>
</tr>
<tr>
<td>Density</td>
<td>Log (size) (km²)</td>
<td>24</td>
<td>$-0.2 [-0.44 to 0.03]$</td>
<td>0.09</td>
</tr>
<tr>
<td>Density</td>
<td>Log (distance) (km)</td>
<td>20</td>
<td>$0.04 [-0.02 to 0.11]$</td>
<td>0.21</td>
</tr>
<tr>
<td>Biomass</td>
<td>Age (yrs)</td>
<td>15</td>
<td>$-0.03 [-0.06 to -0.003]$</td>
<td>0.03</td>
</tr>
<tr>
<td>Biomass</td>
<td>Log (size) (km²)</td>
<td>17</td>
<td>$-0.07 [-0.25 to 0.11]$</td>
<td>0.44</td>
</tr>
<tr>
<td>Biomass</td>
<td>Log (distance) (km)</td>
<td>14</td>
<td>$0.007 [-0.05 to 0.06]$</td>
<td>0.81</td>
</tr>
</tbody>
</table>

Bold values significance $r^2 = 0.22$, $p = 0.03$.

**Figure 4** Plots of the relationship of target species’ response ratio (partial:open) with PPA age (yrs), log-transformed PPA size (sq-km) and distance of the Open area to the PPA boundary (Dist. PPA to Open (km) for density (a, b, c) and biomass (d, e, f) data. Size of the circles is proportional to the weight of the study.
the response to full protection was positive for the two target species categories, but negative for non-target species (Fig. 5). However, none of the differences in the number of individuals between the NTRs and the PPAs were significant. The magnitude of response did not differ significantly among the three ‘exploitation status’ categories, neither for density nor for biomass (sensitivity analysis: density; $Q_M = 3.01$, d.f. = 3, $P = 0.22$; main analysis: biomass $Q_M = 0.36$, d.f. = 3, $P = 0.83$). We emphasize, however, that this result should be interpreted with caution owing to the small number of MPA case-studies within each category, which reduces the robustness of the summary effect sizes (Fig. 5).

Correlates of response to protection

The age of the MPA, the size of the NTR relative to the PPA (size ratio) and the distance between the NTR and PPA did not explain a significant amount of variation in target species density or biomass effect sizes among MPAs (Table 4). Nonetheless, it appears that on increasing the size of the NTR relative to the PPA, the density and biomass of target fish species becomes comparable between the two areas, and in some MPAs, the effect size goes to negative (i.e. NTR < PPA) (Fig. 6).

Discussion

Our synthesis suggested that while PPAs significantly enhance the density and biomass of fish relative to Open areas, NTRs generally produced greater increases in fish numbers and yielded significantly higher biomass of fish within their boundaries relative to PPAs. The positive response to protection, whether full or partial protection, was primarily driven by target fish species. The response for non-target species was more variable, although this was the ‘exploitation status’ category for which we had the least data. There was a large degree of variability in the magnitude of response to protection for all response variables. The factors determining such variation were

![Figure 5](image-url) Mean response ratios ($\ln(\text{RR})$) of fish assemblage and ‘exploitation status’ categories using density and biomass data for no-take reserves compared with partially protected areas (no-take:partial). Error bars represent the 95% confidence interval. NT refers to ‘non-target species’, TP to ‘target, protected species’, NTP to ‘no-take reserve protected species’. Sample size (i.e. the number of MPAs) for each ratio is shown in parentheses. The vertical dotted line at ($\ln(\text{RR}) = 0$ represents equal fish density or biomass inside the NTR and the PPA; ($\ln(\text{RR}) > 0$ means more fish inside the NTR; ($\ln(\text{RR}) < 0$ means fewer fish in the NTR.

<table>
<thead>
<tr>
<th>Fish target species</th>
<th>Ln Response ratio (no-take:partial)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Response variable</td>
<td>Moderator variable</td>
</tr>
<tr>
<td>Density</td>
<td>Age (yrs)</td>
</tr>
<tr>
<td>Density</td>
<td>Size ratio (NTR:PPA)</td>
</tr>
<tr>
<td>Biomass</td>
<td>Age (yrs)</td>
</tr>
<tr>
<td>Biomass</td>
<td>Size ratio (NTR:PPA)</td>
</tr>
<tr>
<td>Biomass</td>
<td>Log (distance) (km)</td>
</tr>
</tbody>
</table>

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generally unclear although the size of the MPA explained some of this variability. Examination of the protection regime within the PPA provided novel insights into the efficacy of partial MPAs for conservation and management.

Marine protected areas may meet their objectives in a number of ways without necessarily excluding all extractive activities; habitat protection can be achieved by exclusion of benthic gears (e.g. Fogarty and Murawski 1998; Beukers-Stewart et al. 2005; Smith et al. 2008), avoidance of conflict can be achieved by spatial segregation of uses (e.g. Pipitone et al. 2000; Blyth et al. 2002), sustainable exploitation or recovery of over-exploited fish stocks can occur within gear-specific exclusion areas (e.g. Murawski et al. 2000; Fisher and Frank 2002). We have thus synthesized data for studies that have examined effects of partially protected MPAs relative to open access areas to further increase our understanding of the potential value of those MPAs within which an attempt is made to strike a balance between allowing user access and achieving management and conservation measures. We found significantly higher density and biomass for fish inside the PPA relative to open access areas, and this positive response was mainly driven by target species of commercial importance. Severe reductions in the spawning stock biomass of species exposed to high levels of fishing mortality, reduces the ability of fish populations to recover after populations decline (Hutchings 2001). It follows then that the reduction or elimination of fishing mortality following the effective implementation of a MPA is expected to increase population density and biomass as stocks recover from exploitation. Our finding that target species benefit from partial protection suggests that well-managed PPAs with some restrictions on use are a valuable tool to conserve target fish species, given that the species are effectively protected under the protection regime in place. For example, Lester and Halpem (2008) point out that failure to document significant effects (in terms of density and biomass) for PPAs over Open areas may have resulted from the fact that in most of the studies they reviewed, target species were targeted in both open access

Figure 6 Plots of the relationship of target species’ response ratio (no-take:partial) with MPA age (yrs), size ratio (NTR: PPA), log-transformed distance between NTR and PPA borders (km) for density (a, b) and biomass (c, d, e) data. Size of the circles is proportional to the weight of the study.
and PPAs. We have accounted for this potential source of variation in our analysis, by keeping target species that are protected by both the NTR and the PPA (TP) separate from those not entirely protected in the PPA (NTP). Indeed, we found significantly higher fish biomass inside the NTR relative to the PPA for NTP species but not for TP species.

Although PPAs showed positive effects on fish compared with Open areas, we found that the protection provided by NTRs resulted in greater benefits compared with PPAs. Interestingly, the response to full protection (no-take:partial) was higher for fish biomass ($RR = 1.92$) than for density ($RR = 1.11$). One possible explanation for this difference is that the density of individuals is susceptible to stochastic recruitment events, which may show less relationship with protection level than the combination of recruitment, growth and survival which ultimately results in enhanced biomass. The high positive response observed for fish biomass provides evidence towards the protection benefit of fully protected areas from size-selective fishing or accidental catch.

While our finding that the effect of protection was higher for NTRs than for PPAs is in agreement with that found by Lester and Halpern (2008), they report significantly higher difference between NTRs and PPAs for density ($RR = 1.79$) but not for biomass ($RR = 1.22$). An important difference between our synthesis and that by Lester and Halpern (2008) is that whereas our study focussed on fish species only, Lester and Halpern (2008) integrated data across broad taxonomic groups (fish, invertebrates, algae) with different life history (e.g. growth rate) and ecological characteristics (e.g. larval dispersal potential, adult mobility). Therefore, for example, the sessile nature and the relative low mobility of some species (e.g. urchins, gastropods, corals, sponges) included in Lester and Halpern (2008) might have resulted in the smaller differences in density that they observed between NTRs and PPAs. By contrast, the higher mobility of fish between the NTR and the PPA might have resulted in the smaller differences in the number of individuals between the two protected areas examined in the studies included in our analysis.

In addition to the ‘exploitation status’ of individual fish species, we found that the ‘protection regime’, which defined the amount of protection afforded to target species by the PPA, was a key determinant of the magnitude of MPA efficacy. Of the three categories of protection regime, our analysis revealed that the magnitude of response to partial protection was the largest for PPAs that excluded commercial fishing with mid-water gear but permitted fishing on a recreational basis. Such protection regimes typically exist in tropical and subtropical regions. Interestingly, such protection resulted in greater positive response than those MPAs (typically found in temperate regions) which excluded bottom-towed gear but allowed fishing with mid-water gear (e.g. nets and long lines) or static gear (e.g. pots, traps). This is perhaps counter-intuitive given the well-recognized negative impact of towed bottom fishing gear on biota and habitat (Collie et al. 2000; Kaiser et al. 2006; Hinz et al. 2009). However, MPAs that excluded bottom-towed gear were typically established to protect large mobile demersal fish such as cod (Gadus morhua, Gadidae), haddock (Melanogrammus aeglefinus, Gadidae), silver hake (Merluccius bilinearis, Merlucciidae) and saithe (Pollachius virens, Gadidae) (e.g. Link et al. 2005; Dimech et al. 2008; Jaworski et al. 2010), which are likely to experience less benefits from protection (e.g. compared with reef-associated species) due to their high mobility and dispersal distances. Additionally, benthiopelagic species that rely on benthic invertebrates for their food might take longer to respond to protection as habitat recovery following disturbance by bottom-towed gear will have to occur before these species can begin to recover.

The relationship between the response to protection and different MPA characteristics including the age and size of MPA and distance to MPA was complex and variable. Nevertheless, a number of observations are worth highlighting about the influence of MPA size on effect size. Interestingly, our study revealed a trend towards a reduction in the density and biomass difference between NTRs and PPAs for target species upon increasing the size of the NTR relative to the PPA. The size of the NTRs ranged between 0.1 km$^2$ and 30.5 km$^2$ and that for the PPAs ranged between 1.9 km$^2$ and 140.1 km$^2$ for case-studies comparing NTRs to PPAs. In 10 of 11 cases, the NTR was <80% the size of the PPA. The larger proportion of species afforded protection upon increasing the size of the NTR should lead to greater spillover of adult biomass in areas outside the NTR. Given that in the majority of MPAs included in the data set, the NTR and the PPA were adjacent to each other (due to zonation scheme), it is plausible
to assume that some of the biomass accrued in NTR ends up in the PPA as a result of spillover (estimated a range of spillover distances between 800 m and 1500 m (Goni et al. 2006; Harmelin-Vivien et al. 2008; Halpern et al. 2010).

Equally interesting, we found that increasing the size of the PPA, in particular above 1000 km², reduced the effectiveness of partial protection relative to no protection for fish assemblages as well as for target species. This was somewhat surprising given that previous theoretical and empirical studies have shown that larger MPAs are more effective at increasing biodiversity and density of commercial species (Hastings and Botsford 2003; Roberts et al. 2003; Claudet et al. 2008). It is not unrealistic to assume that non-compliance and infringement of regulations are more likely in large than in small MPAs (Chiappone and Sullivan-Sealey 2000). The size of the PPAs in the data set comparing PPAs to Open areas ranged between 1.5 km² and 11 980 km², and although a single instance of illegal fishing in a small PPA can have a more damaging effect than in a large PPA, it is more likely that the frequency of illegal fishing is higher in large PPAs. This may explain the lower effectiveness of protection that we observed for PPAs over 1000 km² in size. Another possible explanation for this result is the inadequacy of the sampling effort. Among the studies included in our analysis, the majority (24 of 27) surveyed an area equivalent to <1% of the total area of the PPA. The proportion of area surveyed for MPAs larger than 20 km² was only 0.1% of the MPA area, suggesting that the sampling effort for large MPAs may have inadequate power to detect subtle changes in density or biomass between the protected and unprotected areas.

It needs to be emphasized that the MPA-related covariates examined in this meta-analysis explained only a small proportion of the total variability (\(r^2 = 0.17–0.26\)) whenever significant relationships occurred, indicating that the heterogeneity in effect size among MPAs is also influenced by other factors not investigated in this study. These factors could be related to the biological and ecological characteristics of different species (Tuya et al. 2006; Smith et al. 2008; McLean et al. 2010) as well as to the nature of the physical environment and habitat within the MPA (Link et al. 2005; Jaworski et al. 2010). The historical levels of exploitation in the MPA and the range and relative intensity of exploitation activities in reference fished areas are two further key factors affecting MPA performance. For example, Edgar et al. (2009) found low level of change for fish between the MPA and fished areas because pre-existent fishing pressure across the region was low and historically depressed stocks only slightly. Conversely, McLean et al. (2010) found very little change between protected and unprotected populations of *Lethrinus harak* even after 15 years of protection because previously high levels of exploitation combined with low recruitment years for this species led to large reductions in the abundance of this species across the region. In their study of the efficacy of the Invertebrate no-take reserve (PPA) at Santa Catalina Island, California, Iacchei et al. (2005) recorded a 3% increase in lobster (*Panulirus interruptus*) density in the MPA relative to a recreationally fished control area, but found a 57% increase when compared with a commercially fished area. These examples serve to show the importance of including exploitation intensity inside and outside the MPA for a more within-context interpretation of the efficacy of MPAs. This factor remains somewhat overlooked in most studies including those reviewed in this study.

It is a challenge to balance the uncertainty surrounding the results of meta-analysis against their potential impact when considering management implications. Throughout the study selection process, as specified by the systematic review methodology, we have applied stringent study inclusion and quality assessment criteria in the hope of providing the best quality evidence for evaluating the efficacy of MPAs. We have thus excluded studies where enforcement of the MPA was described as poor or degrading during the time of survey (e.g. Acosta 1999; Floeter et al. 2006) and have controlled for the influence of habitat confounding (as a result of habitat differences between the protected and control areas at baseline) by running a sensitivity analysis, that excluded habitat-confounding studies (e.g. Miller et al. 2005; Monaco et al. 2009), alongside the main analysis. As the primary objective of this study was to examine the effectiveness of different levels of protection in a MPA, we excluded studies that did not provide a clear description of the protection regime inside the MPA (e.g. McClanahan and Muthiga 1988; Ohman et al. 1997; Lipej et al. 2003) or that provided data from full and partial protection mixed...
together (e.g. sampling from within the integral reserve and the buffer zone treated together as ‘protected’ in the results: García-Charton et al. 2004; Guidetti et al. 2005). When comparing fully protected and partially protected MPAs, we excluded studies where the two MPAs were established more than 2 years apart (e.g. Jennings et al. 1996; Denny and Babcock 2004; McClanahan et al. 2006; Jack et al. 2009) as we did not want duration of protection to confound the effect of protection from different levels of protection. We did not include de facto MPAs (i.e. areas around oil platforms or areas ‘protected’ because of their inaccessibility) (e.g. Roberts and Polunin 1992; Schroeder and Love 2002; Duineveld et al. 2007), as our search terms were specific to capture ‘true’ MPAs (i.e. those designated under some legislation). As part of the study quality control, we have undertaken a weighted meta-analytical approach to factor in for sample size and within-study variance in the overall effect of protection and have thus excluded studies that did not provide sample sizes and variance measures (e.g. Ault et al. 2006). While acknowledging that these strict criteria might have led to some information loss and a reduction in the pool of available studies (in particular for comparison of no-take reserves to PPAs), we believe that there is little benefit in including biased or confounded studies. A valid constraint that needs to be acknowledged in our analyses, however, is that density and biomass comparisons were based on single snapshot data sets after MPA establishment. Only a handful of studies included in this analysis were based on strong experimental designs such as BACI and beyond-BACI studies (Underwood 1992; Guidetti 2002) (see Appendix S2 and S3). Ecosystem processes are spatially and temporally variable at multiple scales, and these variations can obscure the detection of the effects of protection (García-Charton and Pérez-Ruzafa 1999). Hence, while acknowledging the time constraints and increased financial costs associated with BACI empirical studies, we advocate that the controversy as to whether any differences are a consequence of protection or are merely coincidental can only be satisfactorily addressed by further monitoring incorporating assessment of change from baseline conditions. For further discussion on the key challenges and limitations met in this review, the reader is referred to the systematic review report available at http://www.environmentalevidencejournal.org/content/2/1/4.

This study allowed us to address an important question for managers and policy-makers of whether PPAs are an effective management option for conservation and fisheries compared with fully protected and unprotected areas. These results suggest that NTRs provide some benefit over less protected areas; nevertheless, the significant ecological effects of PPAs relative to Open areas suggest that PPAs are a valuable spatial management tool particularly in areas where exclusion of all extractive activities is not a socio-economically and politically viable option. Change in the distribution of fishing effort could result in economically negligible net benefits (Jones 2008) or may be detrimental to habitats previously undisturbed by anthropogenic activities (Dinmore et al. 2003). Hence, while acknowledging that MPAs are not a panacea for conservation and fisheries management, under the right conditions, which may include additional reduction of fishing effort in fishing grounds surrounding MPAs, or a network of MPAs that allow a mix of protection levels, or involvement of multiple stakeholder groups during the designation process, MPAs are valuable tools for the preservation and enhancement of fish populations.

Acknowledgements

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Anderson, M.J. and Millar, R.B. (2004) Spatial variation and effects of habitat on temperate reef fish assem-


No-take vs. partial MPAs  M. Sciberras et al.


Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Search terms.

Appendix S2. Summary of studies used in the assessment of partial protection over no protection (PPA vs. Open).

Appendix S3. Summary of studies used in the assessment of full protection over partial protection (NTR vs. PPA).

Appendix S4. MPA ‘protection regime’ categories.