

# Conservation benefits of marine reserves for fish populations

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## Abstract

We synthesize the results of empirical studies of marine reserves to assess the potential benefits of protection for fish populations. Our meta-analyses demonstrate that the overall abundance of fishes inside reserves is, on average, 3.7 times higher than outside reserve boundaries. This enhancement is mainly a result of a significant increase in abundance of species that are the target of fisheries. Non-target species are equally abundant inside and outside reserves. Large-bodied species also respond more to protection, irrespective of their fishery status. Species within genera show great heterogeneity in their response to protection despite similarities in their life histories. Our study confirms that marine reserves benefit fish populations and highlights the need for monitoring prior to reserve establishment to provide more accurate, habitat-controlled studies of the effects of marine reserves on fish populations.

## INTRODUCTION

Marine reserves are used to conserve fish populations that are threatened by intensive fishing (Polunin, 1984, 1990; Bohnsack, 1990, 1998; Roberts & Polunin, 1991, 1994; Dugan & Davis, 1993; Rowley, 1994). In theory, the conservation benefits of reserves can be predicted by estimating the reductions in fishing mortality that result from the presence of the reserve and assessing how these affect the abundance and dynamics of resident fish populations (Beverton & Holt, 1957). Reductions in fishing mortality depend mainly on the area of the reserve, the movements and migrations of fish populations, the duration of protection and the relationship between reserve area and perimeter (e.g. Russ, Alcala & Cabanban, 1992; DeMartini, 1993). The response of fish populations to reduced mortality depends on life-history traits that influence the intrinsic rate of population increase (e.g. Russ & Alcala, 1998*a,b*).

In reality, the models needed to assess the conservation benefits of marine reserves are often as complex as those used for conventional fishery analysis and cannot realistically be applied to many of the fish populations that are threatened by fishing (Guenette, Lauck & Clark, 1998). Indeed, one of the advantages of reserves is that

they simplify management and reduce the enforcement costs for fish populations where little biological information is available (Bohnsack, 1998). This is one reason why they are often favoured for conservation in developing countries.

Overfishing is widespread in the developing world and many fish populations have declined sharply due to intensive fishing (Russ, 1991; Roberts & Hawkins, 1999). Conservation in these areas is particularly challenging, because many coastal dwellers rely on fishing for employment, food and income and because the data needed to implement population-based management are often inadequate or non-existent (Munro & Fakahau, 1993; Jennings & Polunin, 1996; Johannes, 1998). Moreover, it is not practical to delay conservation action until better data can be collected. For example, while several species are already threatened, a simple survey to estimate the abundance of fish at coastal sites throughout Indonesia could take 400 person-years (Johannes, 1998). If we are to act now, then we have to base the best possible conservation action on rather limited data, and must explore ways of doing this effectively.

Reserves that were established without detailed *a priori* predictions of their effects have often provided conservation benefits for fished species, such as increases in their mean size, diversity and abundance (for reviews, see Roberts & Polunin, 1991; Dugan & Davis, 1993; Rowley, 1994; Bohnsack, 1998). However, it is becoming apparent that these benefits do not apply to all species all of the time. A general synthesis is now needed to

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help us predict the circumstances in which marine reserves will be a useful conservation tool.

In this paper, we use meta-analysis to review the results of existing empirical studies of marine reserves, and attempt to make some useful generalizations about the conservation benefits of marine reserves for fishes from different families with different life histories. Life histories are likely to be a useful predictor of responses to marine reserve protection because, in theory, these should determine how populations respond to fishing mortality (Adams, 1980; Beddington & Cooke, 1983). Thus the abundance of species with late maturity, slow growth and low intrinsic rates of population increase will fall more rapidly at a given rate of fishing mortality (Jennings, Reynolds & Mills, 1998; Jennings, Reynolds & Polunin, 1999) and increase more gradually once fishing has stopped (Myers, Mertz & Fowlow, 1997). Although little is known about the detailed biology and life histories of many tropical and sub-tropical species, we can take advantage of strong empirical relationships between maturation and growth parameters in fish (Beverton & Holt, 1959; Pauly, 1980; Beverton, 1992; Charnov, 1993). An easily measured parameter such as maximum size, which tends to be negatively correlated with growth, age at maturity, reproductive output and natural mortality, may therefore be used as a surrogate for life-history parameters that are more difficult to measure.

## MATERIALS AND METHODS

### Data selection and manipulation

The abundance of fish populations inside and outside marine reserves was determined from a literature search carried out using the Scientific Citation Index (SCI), Aquatic Sciences and Fisheries Abstracts (ASFA) and GeoBase (SilverPlatter Inc.), from 1981, 1988 and 1990, respectively. All references cited in these publications were also checked, as were many relevant books on fisheries management. Additionally, a number of authors were contacted in search of grey literature, internal reports and/or unpublished data.

Datasets were included if:

1. Mean abundance (i.e. counts) and sample size (i.e. number of transects or point counts) were reported for a fish species inside and outside a marine reserve. We did not use studies that presented before–after comparisons since there were too few of them. Estimates of abundance that were aggregated by genus or family were not included. Error (SD, SEM or variance) was recorded when available.
2. The reserve was a true no-take zone, with enforcement described as being reasonably successful.
3. Data for all species that could reasonably be censused were reported (usually diurnally active, non-cryptic and reef-associated species), irrespective of their fisheries or conservation importance, or whether they were more, equally or less abundant in the reserve than elsewhere.

4. The study reported the most recent assessment of the effects of protection in a specific reserve. If there were several studies of the effects of protection in a given reserve, only the most recent data were used.

Fish species were classified as ‘target’ if they were caught deliberately by fishers outside the reserve, and as ‘non-target’ if they were not. The only life-history parameter available for all of the species included in the analyses was maximum length. Estimates of maximum length were compiled from the literature (Allen & Swainston, 1988, 1992; Humann, 1989; Randall, Allen & Steene, 1990; Randall & Heemstra, 1991; Böhlke & Chaplin, 1993; Lieske & Myers, 1994; Kuitert, 1996; Froese & Pauly, 1999).

Abundance data were converted, when necessary, to mean abundance  $\pm$  SD. A number of studies compared fish communities in two or more habitats (e.g. García-Rubies & Zabala, 1990), and data for reserve and control areas therefore appeared as two or three mean abundances. These data were aggregated into a weighted mean abundance  $\bar{X}$  for the reserves and control areas:

$$\bar{X} = \frac{\sum_{i=1}^h \bar{x}_i \times n_i}{\sum_{i=1}^h n_i}$$

where  $\bar{x}$  and  $n_i$  are the mean abundance of fish and sample size of abundance estimate in the  $i$ th habitat, respectively, and  $h$  is the number of habitats to be aggregated.

### Meta-analysis

Meta-analysis is a set of quantitative methods designed to synthesize the results of disparate studies (Hedges & Olkin, 1985). It offers several advantages over traditional, qualitative ‘vote-counting’ reviews of the literature. In particular, 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 and would normally be excluded from vote-counting 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 technique offers the possibility of weighting studies by their sample size or some measure of reliability (Cooper & Hedges, 1994; Arnquist & Wooster, 1995).

Currently, 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, Gurevitch & Rosenberg, 1997). Recently, Rosenberg, Adams & Gurevitch (1997) proposed the use of a new metric, the response ratio, which can be cal-

culated without knowledge of sample variances. The response ratio,  $RR$ , defined as the ratio of the means measured in the experimental and control area (i.e. in our study, abundance inside and outside the marine reserve), is better suited than other metrics for a study of changes brought about 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, Gurevitch & Curtis, 1999), and the natural logarithm of  $RR$  is usually recommended since it behaves better statistically (Rosenberg *et al.*, 1997). The metric we used is thus defined as:

$$\ln RR = \ln \left( \frac{\bar{X}^I}{\bar{X}^O} \right)$$

where  $\bar{X}^I$  and  $\bar{X}^O$  are the means of the abundance 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 5–200/study. Trial analyses revealed that a weighting scheme using variances generated extreme weights that did not reflect adequately the quality of abundance estimates. This problem was exacerbated by the differences in sample sizes between linear and point census methods. Moreover, half of the studies (6/12 studies) did not report variances. A more biologically meaningful weighting scheme was therefore designed based on the total area censused in each study. Each abundance estimate was weighted by  $w_j$ , which we defined as the natural logarithm of the total area covered by the census from which the estimate was obtained (see Table 1).

We first carried out a meta-analysis using all species abundance estimates to quantify the overall effect of marine protection on fish abundance. All mean effect sizes are presented back-transformed, so that they can be interpreted easily 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) and, when the number of cases in the analysis exceeded Metawin's capacity, we used specifically written routines in Matlab v.5.3 (The MathWorks Inc.).

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

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

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

To explain heterogeneity among species in their response to protection, it is possible to divide the data set into a number of biologically meaningful classes and recalculate response ratios, confidence intervals and  $Q_{wi}$  for each class. To this end, we performed four further meta-analyses to compare the responses to protection of (1) species that were and were not the target of fishing outside reserves (two classes), (2) species that belonged to different families (19 classes), (3) species that belonged to different genera (25 classes) and (4) species that differed in maximum length (seven maximum length classes: < 10 cm, 11–20 cm, 21–30 cm, 31–40 cm, 41–50 cm, 51–60 cm, > 60 cm). In (2), we restricted the analysis to the families that had five or more species representatives, whereas in (3) we included only the 25 most species-rich genera, to comply with Metawin's limit of 25 classes. This excluded 107 genera, of which 78 had only one or two representatives. Analyses (2) and (3) were also repeated, first using only species that were the target of fishing, and then only non-target species. Species ( $n = 266$ ) for which fishing information was not available were excluded from these analyses.

Differences in response to protection between classes were estimated using the statistic  $Q_b$  (Hedges & Olkins, 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 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).

The problem of non-independence of data in meta-analyses has been raised by several authors (e.g. Englund, Sarnelle & Cooper, 1999; Gurevitch & Hedges, 1999). In our data, there are four potential sources of non-independence: (i) there were often (154 out of 346 species) more than one abundance estimate per species, which were derived from separate studies, (ii) species in a reserve may respond to protection more similarly to each other than to species in other reserves, thereby increasing the possibility that large studies will unduly influence the results, (iii) the responses to marine reserve protection of individual species within a community may

not be independent due to interspecific interactions, and (iv) species with shared ancestry are likely to have similar life histories and may therefore respond in a similar way to protection. We accounted for problem (i) by running a meta-analysis using a single, randomly selected abundance estimate for each species and compared the results with a meta-analysis using the complete dataset, and for (ii) by comparing the overall response ratio obtained using the complete dataset with that generated by a partial dataset from which the largest study (McClanahan *et al.*, 1999) was omitted. We will return to the consequences of (iii) and (iv) in the Discussion, below.

## RESULTS

The literature search yielded 12 studies that provided the required data for this review (Table 1). A further 12 studies were reviewed but did not report data in a usable form, were based on an experimental design other than an inside–outside comparison, or were carried out in the same reserve as later studies (Table 2). The final dataset consisted of 575 estimates of changes in abundance for 346 fish species in 56 families.

### Overall abundance

When all species were considered, fish abundance was higher inside than outside reserves. The response ratio ( $RR = 3.72$ , confidence interval (CI) = 2.27–5.96) indicates that fish were on average more than three times more abundant in reserves than in adjacent non-reserve areas, while the confidence interval, which does not overlap 1, shows that this difference in abundance is significant. Not surprisingly, there was significant heterogeneity among species ( $Q_{wi} = 153650.65$ , d.f. = 540,  $P < 0.0001$ ), suggesting that not all species respond to protection to the same extent or in the same direction.

The studies in Table 2 reflect the same trend of increased fish abundances inside reserves found with the meta-analysis. Ten of the 12 studies that could not be meta-analysed reported higher overall abundances of fish inside reserve boundaries. In the single study that showed the opposite pattern (Bennett & Attwood, 1991), the non-reserve, control site was privately owned and had historically experienced much lower levels of fishing than the reserve site. The final study (Polunin & Roberts, 1993) did not report data in a form amenable to the calculation of overall abundances.

The two potential sources of non-independence that we tested using partial datasets appeared to have little effect overall. When the largest study in the dataset (McClanahan *et al.*, 1999) was excluded, reducing the number of abundance estimates in the analysis to 425,

**Table 1.** Summary of studies included in the analysis

Reserve	Date protection <sup>1</sup>	Area of reserve (ha)	Census method	$n^4$ (in/out)	Census area (m <sup>2</sup> )	Sites (in/out)	Replicates per site	Source
Goat Island, New Zealand	1975/13	526	Linear	85/50	8438	15/9	5–6	Cole, Ayling & Creese (1990)
Maria Island and others, Tasmania	1992/5	550 <sup>3</sup>	Linear	44/52	23 000	11/13	4	Edgar & Barrett (1999) and pers. comm. from authors
Cousin Island, Seychelles	1968/26	120	Point	80/80	12 320	5/5	16	Jennings, Grandcourt & Polunin (1995)
Banyuls-Cerbère, France, Mediterranean	1979/12	150	Linear	6/6	1200	1/1	6	Dufour, Jouvenel & Galzin (1995)
Scandola, Corsica, Mediterranean	1975/13	590/72	Linear	44/20	1280	2/1	10–12/20	Francour (1991)
Islas Medes, Mediterranean	1983/5	55	Linear	15/15	3750	3/3	5	García-Rubies & Zabala (1990)
Île de Mayote, Indian Ocean	1992/3	220	Linear	9/9	1800	3/3	3	Letourneur (1996)
Kisite & Chumbe Island, Tanzania	1974–91 <sup>2</sup> / 12–5	100 <sup>3</sup>	Linear	10/20	1500	5/10	2	McClanahan <i>et al.</i> (1999)
Kenya	1980–91 <sup>2</sup> / 12–1	25 500 <sup>3</sup>	Linear	14/20	8500	3/4	5–9	McClanahan (1994)
Barbados, Caribbean	1981/11	66	Linear	15/24	3120	5/8	3	Rakitin & Kramer (1996)
Ras Mohamed, Egyptian Red Sea	1980/11	17 100	Point	81/81	25 400– 6362 <sup>5</sup>	3/3	27	Roberts & Polunin (1992) <sup>6</sup>
Saba Island, Caribbean	1987/4	120	Point	38/41	12 250 –3060 <sup>5</sup>	8/7	5	Roberts (1995) <sup>6</sup>

<sup>1</sup>Date of protection/number of years of protection at time of study.

<sup>2</sup>Date when protection was effectively enforced.

<sup>3</sup>Various reserves close to each other.

<sup>4</sup>Number of transects or point counts.

<sup>5</sup>Two census protocols were used for different species.

<sup>6</sup>Data included in analyses of target species only.

**Table 2.** Fish abundances inside and outside marine reserves derived from studies that could not be included in the meta-analysis

Source	Reserve	Overall abundance		Reasons for exclusion and comments
		Inside	Outside	
Alcala & Russ (1990)	Sumilon & Apo Islands Philippines	36.9 t/km <sup>2</sup>	19.9 t/km <sup>2</sup>	Reported overall yields and catch-per-unit-effort before (=inside) and after (= outside) the breakdown of reserve protection
Bennett & Attwood (1991)	De Hoop, South Africa	1.82 fish/hr	2.09 fish/hr	Census by angling; recorded only species angled. Baseline monitoring prior to reserve establishment
Buxton & Smale (1989)	Tsitsikamma, South Africa	0.042 fish/m <sup>2</sup>	0.010 fish/m <sup>2</sup>	Recorded only three species
Harmelin, Bachet & Garcia (1995)	Carry-le-Rouet, France	2133 (± 1580) fish /500m <sup>2</sup>	1199 (± 898) fish /500m <sup>2</sup>	Did not census all species
McClanahan & Kaunda-Arara (1996)	Mombasa, Kenya	1424.98 (± 119.32) kg/ha	91.77 (± 8.02) kg/ha	Reported by family. Abundance translated into biomass
Samoilys (1988)	Various reserves, Kenya	31.05 fish /1000 m <sup>2</sup>	24.38 fish /1000 m <sup>2</sup>	Reported family estimates
Watson <i>et al.</i> (1996)	Shimoni, Kenya	875.8 fish /2500 m <sup>2</sup>	468.38 fish /2500 m <sup>2</sup>	Only three commercial families recorded
Bell (1983)	Banyul-Cerbère, France	655.72 fish /600 m <sup>2</sup>	318.32 fish /600 m <sup>2</sup>	Same surveyed in 1991 by Dufour <i>et al.</i> (1995)
Chapman & Kramer (1999)	Barbados Marine Reserve	94.6 fish/400 m <sup>2</sup>	54.4 fish/400 m <sup>2</sup>	Recorded only target species
Clark, Causey & Bohnsack (1989)	Looe Key, Florida	156.55 fish /176 m <sup>2</sup>	127.18 fish /176 m <sup>2</sup>	Recorded only spearfished species. Baseline monitoring prior to reserve establishment
Wantiez, Thollot & Kulbicki (1997)	New Caledonia	1.61 fish/m <sup>2</sup>	0.61 fish/m <sup>2</sup>	Although all species recorded, only some reported. Baseline monitoring prior to reserve establishment as well as control areas
Polunin & Roberts (1993)	Hol Chan, Belize & Saba Island, Caribbean	–	–	Recorded only target species. Family abundance data only, reported only when differences significant

the response ratio was slightly higher ( $RR = 4.38$ ,  $CI = 2.50-7.63$ ) and the confidence interval overlaps that obtained with the complete dataset. Similarly, when a single abundance estimate per species was randomly selected, the response ratio ( $RR = 3.20$ ,  $CI = 1.72-6.01$ ) was similar to that obtained with the complete dataset. Further analyses were therefore carried out using the complete dataset.

### Differences in response between target and non-target species

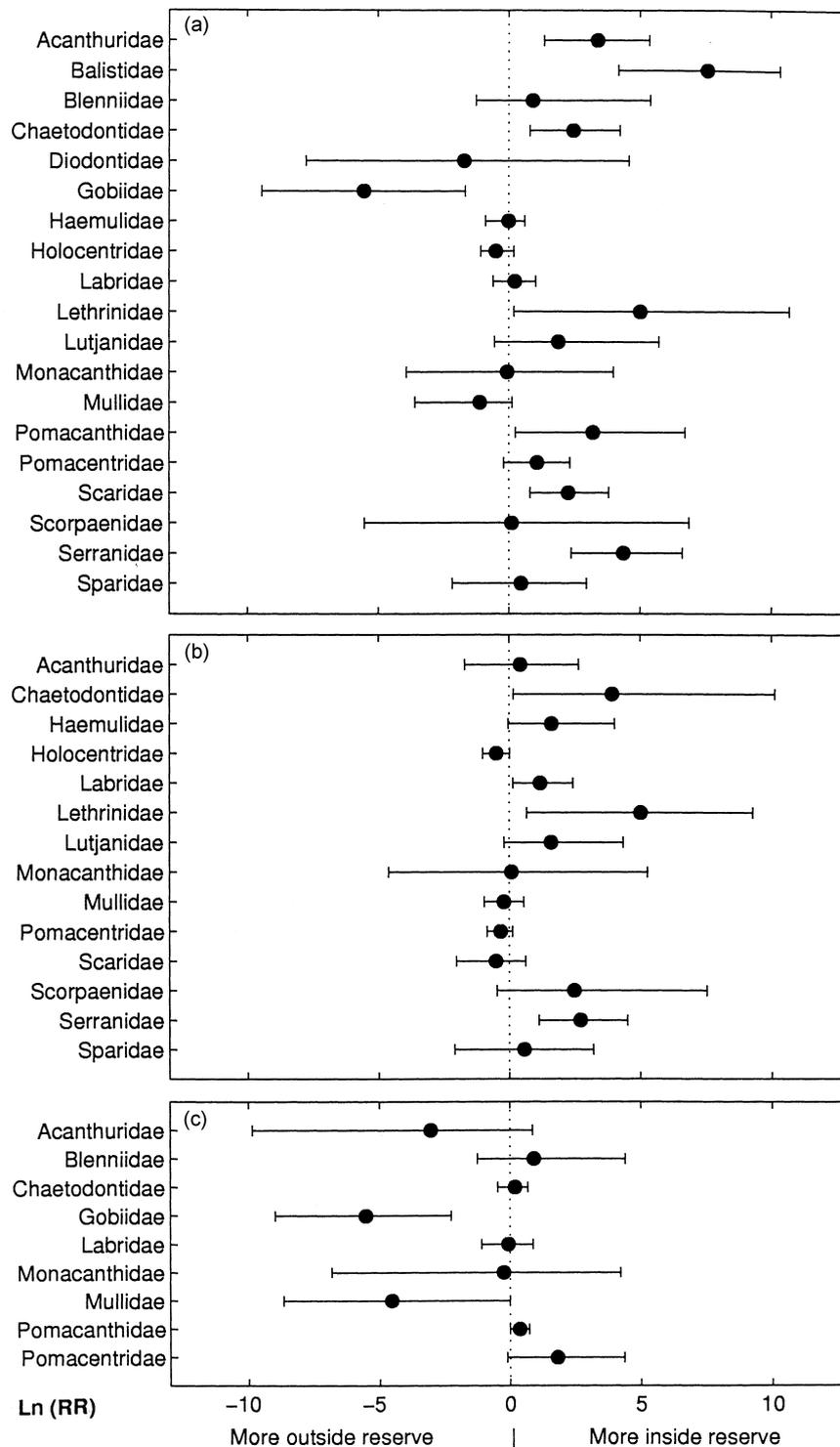
To try to explain the heterogeneity in species response, we divided species for which we had fishing information into two groups: those that were and were not the targets of fishers outside the reserve. The abundance of target species was significantly higher inside than outside protected areas ( $RR = 2.79$ ,  $CI = 1.57-5.13$ ). By contrast, the abundance of non-target species was similar inside and outside reserves ( $RR = 0.65$ ,  $CI = 0.25-1.63$ ). The overall RR value was significantly greater for target than for non-target species ( $Q_b = 1376.86$ ,  $d.f. = 1$ ,  $P = 0.008$ ). However, there was still significant heterogeneity among species within each

group (target species:  $Q_{wi} = 43496.76$ ,  $d.f. = 235$ ,  $P < 0.0001$ ; non-target species:  $Q_{wi} = 23224.43$ ,  $d.f. = 109$ ,  $P < 0.0001$ ).

### Difference in response among families

Families with five or more species in the dataset were selected for this analysis, yielding a total of 19 classes (Fig. 1, Table 3). When target and non-target species were combined, seven out of the 19 families included showed significantly higher abundances inside than outside reserves (Fig. 1). One family, the Gobiidae, showed the opposite pattern (Fig. 1). The nine families that did not show a response to protection were the Blenniidae, Diodontidae, Labridae, Lutjanidae, Haemulidae, Holocentridae, Monacanthidae, Mullidae, Pomacentridae, Scorpaenidae and Sparidae. There were significant differences in response among families ( $Q_b = 14426.64$ ,  $d.f. = 18$ ,  $P = 0.002$ ).

When the meta-analysis was restricted to target species, reducing the number of families in the analysis to 14, four families showed significant positive effect sizes with greater abundance inside reserves (Fig. 1). These include the families Chaetodontidae, Labridae,



**Fig. 1.** Response ratios (RRs) by fish families for (a) all species, (b) species that are the target of fishing and (c) species that are not fished. The number of species per family is given in Table 3. Bootstrap-generated confidence intervals are shown. The fishery status of the families Balistidae and Diodontidae was not reported, hence these families were included only in the overall analysis. See Materials and Methods for further details.

Lethrinidae and Serranidae. Other families did not respond significantly to protection (Fig. 1). Family responses were not significantly different from each other ( $Q_b = 3174.21$ , d.f. = 14,  $P = 0.14$ ). There was extensive heterogeneity in response among species within each family (all  $Q_{wi}$ ,  $P < 0.0001$ ).

By contrast, when only non-target species were included in the family analysis, all nine families showed similar or significantly lower abundances inside than outside protected areas (Fig. 1). Differences among families in their response to protection were significant ( $Q_b = 2709.97$ , d.f. = 8,  $P = 0.02$ ), and all families, except

**Table 3.** Number of species and maximum length range of families included in the analysis

Family	Common name	Number of target species	Length range (cm)	Number of non-target species	Length range (cm)	Total number of species	Length range (cm)
Acanthuridae	Surgeonfishes	18	20–70	4	19–40	45	19–100
Balistidae	Triggerfishes	0	–	0	–	10	20–75
Blenniidae	Blennies	0	–	6	15	6	15
Chaetodontidae	Butterflyfishes	4	15–30	7	11–20	31	11–30
Diodontidae	Porcupinefishes	0	–	0	–	6	45–90
Gobiidae	Gobies	0	–	7	10–18	7	6–18
Haemulidae	Grunts	11	18–65	0	–	5	23–65
Holocentridae	Squirrelfishes	5	14–25	0	–	5	14–35
Labridae	Wrasses	31	10–91	39	10–45	134	7–120
Lethrinidae	Emperors	5	40–87	0	–	5	40–87
Lutjanidae	Snappers	10	30–100	0	–	8	30–100
Monacanthidae	Filefishes	5	21–60	4	10–31	9	10–60
Mullidae	Goatfishes	10	28–50	3	32–50	13	28–50
Pomacanthidae	Angelfishes	0	–	2	15–38	10	9–40
Pomacentridae	Damsel-fishes	8	6–21	12	10–18	84	6–21
Scaridae	Parrotfishes	33	27–90	0	–	54	27–90
Scorpaenidae	Scorpionfishes	4	25–50	0	–	5	20–50
Serranidae	Sea basses	35	21–150	0	–	25	21–150
Sparidae	Porgies	20	24–200	0	–	21	24–200

Target species are those deliberately caught in fisheries outside reserves.

the Pomacanthidae ( $Q_{wi} = 2.57$ , d.f. = 1,  $P = 0.11$ ), showed heterogeneity among species (all  $Q_{wi}$ ,  $P < 0.0001$ ).

### Differences in response among genera

The 25 most species-rich genera were included in this analysis; no genus had fewer than seven species (Table 4). Overall, 10 genera were significantly more abundant inside reserves, while one (*Halichoeres*, family Labridae) showed the opposite pattern (Fig. 2). The majority of genera (14/25) did not show a significant response to protection (Fig. 2). There were significant differences among genera in their pattern of abundance ( $Q_b = 12446.05$ , d.f. = 24,  $P = 0.004$ ), and species within all genera were not homogeneous in their response to protection (all  $Q_{wi}$ ,  $P < 0.05$ ).

Among genera that included only target species, 4/17 genera were significantly more abundant inside reserves, while three genera were more numerous outside reserve boundaries (Fig. 2). More than half (10/17) of all genera showed no effect (Fig. 2). When considering non-target species, the general pattern of response was similar to that of target species, with 3/10 genera responding positively, 3/10 negatively and 4/10 showing no response to protection (Fig. 2). There was no significant difference in response among genera when only target species were included ( $Q_b = 2691.28$ , d.f. = 16,  $P = 0.35$ ); however, when non-target species were considered, different genera showed significantly different responses to protection ( $Q_b = 3305.55$ , d.f. = 9,  $P = 0.01$ ).

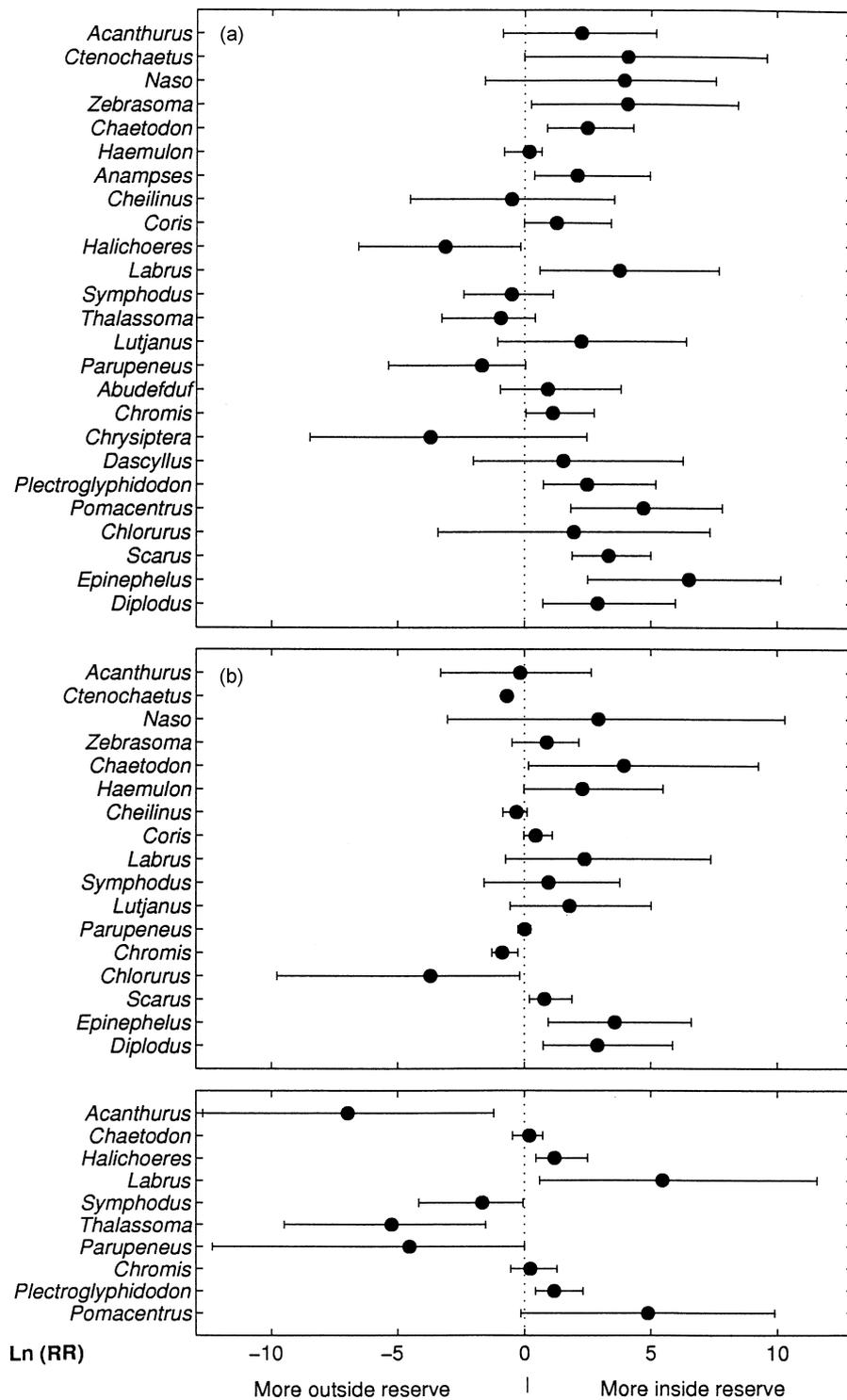
### Differences in relation to body size

To test the effect of body size on species response to protection, species were divided into seven groups according to their maximum length. When all species

are considered, 5/7 size categories show a significant and positive effect of size (Fig. 3), with the largest species exhibiting densities up to 33 times higher within than outside reserves. Response to protection increases significantly with body size (Fig. 3;  $r_s = 0.82$ ,  $n = 7$ ,  $P = 0.02$ ), although there were no significant differences in response among size classes ( $Q_b = 3735.42$ , d.f. = 6,  $P = 0.54$ ). When only target species are included, only one of the size classes shows a significant increase in abundance inside reserves (Fig. 3), but there were no differences in RR among size classes ( $Q_b = 730.30$ , d.f. = 6,  $P = 0.69$ ). For species that are not subject to fishing pressure, none of the size classes responded significantly to protection (Fig. 3) and the responses of various size classes were similar ( $Q_b = 1364.13$ , d.f. = 6,  $P = 0.28$ ). However, there was a significant positive relationship between response ratio and increasing size ( $r_s = 0.83$ ,  $n = 6$ ,  $P = 0.04$ ). In all cases, there was significant heterogeneity among species within size class (all  $Q_{wi}$ ,  $P < 0.0001$ ).

## DISCUSSION

Our meta-analyses offer the first quantitative overall estimate of the magnitude of the effects of marine reserves on fish abundance. We found that, considering all species and all reserves for which suitable data are available, fishes are 3.7 times more abundant inside than outside reserves. This increase occurs mainly because of positive responses of species that are the target of fishers. Fish species that are not targeted by fisheries show similar abundances inside and outside reserves. These results are supported by a qualitative review of studies that could not be meta-analysed (Table 2) and confirm the widely held opinion that marine reserves are beneficial to fish populations (for reviews, see Roberts & Polunin, 1991; Rowley, 1994; Bohnsack, 1998).



**Fig. 2.** Response ratios (RRs) by fish genera for (a) all species, (b) species that are the target of fishing and (c) species that are not fished. The number of species per genus is given in Table 4. Bootstrap-generated confidence intervals are shown. See Materials and Methods for further details.

Meta-analysis is increasingly used by ecologists to synthesize the results of disparate studies (e.g. Gurevitch *et al.*, 1992; Côté & Sutherland, 1997). However, the power of meta-analyses is strongly influenced by the quality of the primary data, and meta-analytical techniques do not eliminate inherent biases or fundamental

problems with these data (Hedges & Olkin, 1985). A major problem is the non-independence of data, which can affect the results of any meta-analysis (e.g. Englund *et al.* 1999; Gurevitch & Hedges, 1999). In the Materials and Methods section, above, we outlined four potential sources of non-independence that could have affected

**Table 4.** Number of species and maximum length range of genera included in the analysis.

Genus	Family	Number of target species	Length range (cm)	Number of non-target species	Length range (cm)	Total number of species	Length range (cm)
<i>Acanthurus</i>	Acanthuridae	11	21–40	2	21–23	23	21–55
<i>Ctenochaetus</i>	Acanthuridae	2	26	0	–	7	19–26
<i>Naso</i>	Acanthuridae	3	30–70	0	–	7	30–100
<i>Zebrasoma</i>	Acanthuridae	2	20–40	0	–	6	20–40
<i>Chaetodon</i>	Chaetodontidae	4	15–30	7	11–20	31	11–30
<i>Haemulon</i>	Haemulidae	8	23–43	0	–	3	23–43
<i>Anampses</i>	Labridae	0	–	0	–	7	15–22
<i>Cheilinus</i>	Labridae	4	30–45	0	–	11	17–45
<i>Coris</i>	Labridae	3	25–60	0	–	11	20–120
<i>Halichoeres</i>	Labridae	0	–	4	12–27	12	12–27
<i>Labrus</i>	Labridae	4	45–47	3	40–45	7	40–47
<i>Symphodus</i>	Labridae	10	10–35	12	10–18	22	10–35
<i>Thalassoma</i>	Labridae	0	–	2	18–25	10	14–25
<i>Lutjanus</i>	Lutjanidae	8	30–95	0	–	6	30–95
<i>Parupeneus</i>	Mullidae	4	40–50	3	32–50	7	32–50
<i>Abudefduf</i>	Pomacentridae	0	–	0	–	8	15–20
<i>Chromis</i>	Pomacentridae	4	9–16	5	11–15	19	9–16
<i>Chrysiptera</i>	Pomacentridae	0	–	0	–	9	8–11
<i>Dascyllus</i>	Pomacentridae	0	–	0	–	8	6–14
<i>Plectroglyphidodon</i>	Pomacentridae	0	–	3	10–12	9	10–12
<i>Pomacentrus</i>	Pomacentridae	0	–	2	10–12	12	15–20
<i>Chlorurus</i>	Scaridae	4	35–70	0	–	8	35–70
<i>Scarus</i>	Scaridae	20	27–90	0	–	33	27–90
<i>Epinephelus</i>	Serranidae	12	25–150	0	–	7	25–150
<i>Diplodus</i>	Sparidae	10	24–60	0	–	10	24–60

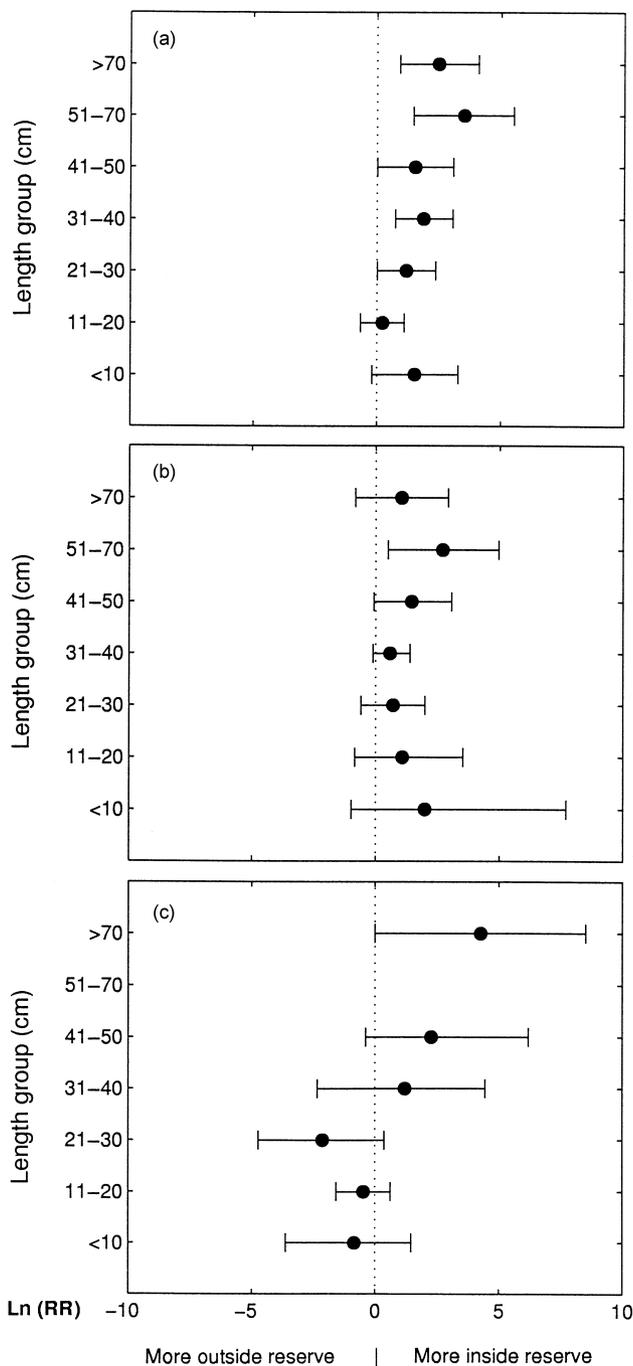
Target species are those deliberately caught by fishers outside reserves.

our data. Two sources were dealt with using analyses of partial datasets. The sources of non-independence that we could not address analytically were: first, that the responses of species to marine reserve protection may not be independent due to interspecific interactions, and secondly, that related species are not independent of each other because shared ancestry results in similar life histories, and hence similarities in response to protection. Species interactions could bias meta-analytical results if, for example, prey species showed no apparent response to protection because they suffer higher mortality in a reserve where their predators have become more abundant. While we cannot rule this scenario out, we believe that this is generally unlikely because several studies have shown that fish prey do not increase when predatory fishes are depleted (Bohnsack, 1982; Russ, 1985; Jennings & Polunin, 1997). This may be due to the considerable amount of overlap in the diet of predators, such that the impacts of individual predator species on the dynamics of their prey are minor (Hixon, 1991).

The most important source of non-independence in our meta-analyses may result from unequal phylogenetic relatedness among species. For example, the 28 species of wrasses (Labridae, Table 1) in our dataset are likely to share similar life histories. This phylogenetic non-independence could be addressed using a comparative approach (Harvey & Pagel, 1991). However, this requires that phylogenetic relationships be known, which is not the case for the majority of tropical species included in our meta-analysis. Moreover, there is currently no framework for incorporating phylogenetic techniques within meta-analyses. The combination of

these two methods would be a powerful tool for further advancing our ability to synthesize the results of disparate studies.

The link between population responses to protection and life histories is not clear. As expected, families such as groupers (Serranidae), emperors (Lethrinidae) and parrotfishes (Scaridae) responded positively to protection. These families typically have low natural mortality, late maturity, relatively long lifespan, slow to medium growth rates and large maximum size (Bannerot, Fox & Powers, 1987; Sadovy, 1996). Thus, their populations can be expected to be particularly susceptible to fishing mortality (Russ & Alcalá, 1998b). However, a similar response may also have been expected of snappers (Lutjanidae), which share similar life histories, but these did not respond significantly to protection. Among small-bodied species, there are also mixed results. Blennies (Blenniidae) and damselfishes (Pomacentridae), fast-growing species with relatively high rates of natural mortality and growth, would not be expected to benefit strongly from reserve protection and, indeed, they do not. However, similar-sized butterflyfishes (Chaetodontidae) are more abundant inside reserves. This may result from *a priori* selection of 'attractive' areas, i.e. areas with high coral cover, as reserve sites, and coral cover is positively correlated with the abundance of many butterflyfishes (Roberts & Ormond, 1987; Jennings, Bouille & Polunin, 1996; Chapman & Kramer, 1999). However, body size appears to be important. Large-bodied species generally increased more in marine reserves than smaller species. This effect appeared not to be simply confounded by the



**Fig. 3.** Response ratios (RRs) by maximum length groups for (a) all species, (b) species that are the target of fishing and (c) species that are not fished. Bootstrap-generated confidence intervals are shown. See Materials and Methods for further details.

correlation between body size and the likelihood of being the target of fishing because when target and non-target species were separated, the results held for non-target species only. However, it is very likely that these large-bodied non-target species actually experience heavy by-catch mortality.

It is notable that very few studies were based on strong experimental designs. We had to restrict our data to those

comparing abundances inside and outside reserves after protection had been implemented because the large majority of studies used this design. Few studies reported baseline abundances measured prior to reserve establishment (but see Russ & Alcala, 1998a,b; Bennett & Attwood 1991; Wantiez, Thollot & Kulbicki, 1997) or accounted for differences in habitat between the reserve and non-reserve areas (but see McClanahan 1994; Chapman & Kramer, 1999). Furthermore, few studies provided information on the period of effective protection, which could influence species responses to reserves. Table 1 reports the year of legal establishment of protection rather than effective enforcement. Studies conducted shortly after protection started may report little effect on large, slow-growing species, simply because more time is needed before they show a significant build-up in abundance (Russ & Alcala, 1998a). The few long-term studies have shown that the abundance of these species takes several years to increase after protection (Bennett & Attwood, 1991; Roberts, 1995; Russ & Alcala, 1996, 1998a). Finally, the effectiveness of protection itself is rarely reported. This effectiveness undoubtedly varied among reserves, despite our attempts to screen out studies with poor enforcement. However, the inclusion of such studies would have biased the results against our main findings.

We therefore conclude that marine reserves do generally result in increased fish abundances, and that species that are the target of fisheries, as well as large, non-target species, respond particularly well to protection. Variation among species in responses to protection can be predicted only roughly by differences in life histories, and much unexplained variability remains. The development of phylogenetic methods that can be incorporated into meta-analysis may provide a clearer insight into the link between marine protection benefits and fish life histories. More importantly, studies that include monitoring prior to reserve establishment and report abundances of all species censused are apt to yield the greatest information about why some species respond to protection more strongly than others.

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