

THE IMPACT OF MARINE RESERVES: DO RESERVES WORK AND DOES RESERVE SIZE MATTER?

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Abstract. Marine reserves are quickly gaining popularity as a management option for marine conservation, fisheries, and other human uses of the oceans. Despite the popularity of marine reserves as a management tool, few reserves appear to have been created or designed with an understanding of how reserves affect biological factors or how reserves can be designed to meet biological goals more effectively (e.g., attaining sustainable fish populations). This shortcoming occurs in part because the many studies that have examined the impacts of reserves on marine organisms remain isolated examples or anecdotes; the results of these many studies have not yet been synthesized. Here, I review the empirical work and discuss the theoretical literature to assess the impacts of marine reserves on several biological measures (density, biomass, size of organisms, and diversity), paying particular attention to the role reserve size has in determining those impacts. The results of 89 separate studies show that, on average, with the exception of invertebrate biomass and size, values for all four biological measures are significantly higher inside reserves compared to outside (or after reserve establishment vs. before) when evaluated for both the overall communities and by each functional group within these communities (carnivorous fishes, herbivorous fishes, planktivorous fishes/invertebrate eaters, and invertebrates). Surprisingly, results also show that the relative impacts of reserves, such as the proportional differences in density or biomass, are independent of reserve size, suggesting that the effects of marine reserves increase directly rather than proportionally with the size of a reserve. However, equal relative differences in biological measures between small and large reserves nearly always translate into greater absolute differences for larger reserves, and so larger reserves may be necessary to meet the goals set for marine reserves.

The quality of the data in the reviewed studies varied greatly. To improve data quality in the future, whenever possible, studies should take measurements before and after the creation of a reserve, replicate sampling, and include a suite of representative species. Despite the variable quality of the data, the results from this review suggest that nearly any marine habitat can benefit from the implementation of a reserve. Success of a marine reserve, however, will always be judged against the expectations for that reserve, and so we must keep in mind the goals of a reserve in its design, management, and evaluation.

Key words: *marine reserves; reserve design; reserve effect; reserve size; trophic cascades.*

INTRODUCTION

Marine reserves (also called marine protected areas, no-take zones, marine sanctuaries, etc.) have recently become a major focus in marine ecology, fisheries management, and conservation biology. Interest stems in part from the realization that traditional forms of fisheries stock management are inadequate, as evidenced by the historical and recent collapse of many fisheries. In addition, traditional management methods such as maximum sustainable yield estimates are inadequate for addressing the multiple types of anthropogenic impacts on marine life such as over-fishing, certain fishing methods, pollution, coastal development, and other human-derived impacts. Marine reserves have been proposed as an efficient and inexpensive way to maintain and manage fisheries while simultaneously preserving

biodiversity and meeting other conservation objectives as well as human needs (Plan Development Team [PDT] 1990, Ballantine 1992, Dugan and Davis 1993, Bohnsack 1996, Nowlis and Roberts 1997, Allison et al. 1998, Lauck et al. 1998).

Despite the popularity of marine reserves as a management tool, decisions on the design and location of most existing reserves have largely been the result of political or social processes (Jones et al. 1992, Agardy 1994, McNeill 1994); until very recently, little work has been done to understand or include biological considerations in reserve placement or design. A fair amount of recent work has attempted to try to understand and quantify the biological impact of marine reserves. However, these efforts have been scattered around the world and in the scientific literature, so the results are often not easily accessible to people trying to design marine reserves. Relatively little work has been done to assess the success of reserves in general (Roberts and Polunin 1991, 1993, Jones et al. 1992,

Dugan and Davis 1993), and all of it has been anecdotal in nature. In an attempt to draw together all of these results, I have reviewed and synthesized the findings of marine reserve evaluations in order to assess the effectiveness of marine reserves. In particular, I evaluated how marine reserves have affected four biological measures (density, biomass, size, and diversity of organisms) within the reserves, and examined if reserve size influences the magnitude of these reserve effects. Specifically, I asked:

- 1) What are the impacts of marine reserves on the above four biological measures?
- 2) Is the magnitude of the effect of a reserve on biological measures related to the size of the reserve (i.e., does size matter)?
- 3) Does trophic structure change with the implementation of a reserve?
- 4) Does the goal of a reserve (e.g., fishery management vs. biodiversity conservation) influence how large a reserve needs to be?
- 5) What biases or problems exist in the current literature regarding reserve assessment and/or reserve design, and what can be done to remedy these problems?

Theoretical endeavors have produced some predictions for a few of these questions. Modeling efforts aimed at fisheries management have suggested that biomass of reproductively active fish (spawning stock biomass) should generally increase as a result of reserve protection (Polacheck 1990, DeMartini 1993, Quinn et al. 1993, Attwood and Bennett 1995, Man et al. 1995). Concomitantly, reserves are predicted to increase spill-over of fishes to areas outside of the reserve, an effect that is likely to be positively correlated with higher density of fishes inside the reserve (Russ et al. 1992, Hockey and Branch 1994). Organism size and diversity are generally assumed to follow these trends as well, since reserve protection should allow for individual organisms to grow larger (i.e., not be fished out of the system once they reach a certain size) and may also provide protection for species that are normally fished to local extinction. This review will help assess the validity of these predictions.

No direct efforts have been made to evaluate how reserve size itself affects the impact of reserves on any of these biological measures, although it is usually assumed that bigger reserves will always be "better." The literature on the theory of island biogeography (MacArthur and Wilson 1967; reviewed by Diamond and May 1976) predicts that species diversity should increase with area, and so larger reserves should contain more species. However, the theory of island biogeography does not address how reserve protection might influence species diversity at a particular location, and so few predictions can be made about how reserve size might affect the impact marine reserves have on species diversity. This review in particular addresses if reserve size affects the impact marine re-

serves might have on all four biological measures (density, biomass, size, and diversity).

Marine reserves are also predicted to lead to trophic cascade effects, in that protection from fishing may allow top predators to become more abundant in a reserve, which may in turn reduce the abundance of prey, releasing the subsequent trophic level from predation pressure, etc. (Steneck 1998; see also Sala et al. 1998). If this general pattern holds across reserves, then large increases in carnivore abundance and/or size should be associated with smaller differences or even reductions in prey populations.

Independent of the many predictions of the above models, most people simply assume that marine reserves provide the functions expected of them (such as increasing numbers of fish within and outside a reserve). Reserve success stories end up serving as the primary evidence for these assumptions, even though many examples exist where reserves did not provide the necessary functions. The main goal of this review is to evaluate the success of marine reserves in a quantitative way, and to assess what role reserve size plays in determining the magnitude of the reserve effect.

METHODS

Source selection

This review addresses the biological impacts of marine reserves and the implications of these impacts for reserve design. I limited my literature search, therefore, primarily to ecological journals. Policy and management journals, which deal with issues such as cost-efficient design, selection criteria, prioritization schemes, etc., do not include biological data and so are not relevant to this review.

I searched for empirical research in which reserves were actually surveyed. Criteria for inclusion of a study in this review were that (1) data from both before and after the creation of the reserve or from inside and outside of a reserve were reported, (2) no known harvesting occurred within the marine reserve, and (3) the observations measured at least some of the biological variables of interest. Studies examining processes only inside a reserve were not included because they did not have a control site. Similarly, I omitted surveys concerning the impact of marine reserves on fishing effort because they did not address biological measures. Finally, I looked only at no-take reserves because it allowed me to exclude fishing effort as a possible factor affecting the impact of reserves. I included work from gray literature (e.g., conference proceedings, reports, lab bulletins, etc.) if it met my criteria. Using these criteria, I found 89 empirical studies of marine reserve effect that made 112 independent measures of marine reserves (i.e., some studies examined several reserves, and some reserves were examined by several different studies). Of these 89 studies, I was able to

use 81 for qualitative analyses and 69 for quantitative analyses.

I also examined theoretical articles for predictions about how biological measures should respond to reserve protection, but only if a significant portion of the article addressed biological issues of marine reserve design. These articles often proposed models or offered reviews of specific issues (many of these I discussed in *Introduction*). Most management and policy literature addresses logistical, economic, or sociological aspects of marine reserves and was not included in this review.

Data extraction and formatting

To determine the size of a reserve, I considered only the part of the reserve that was fully protected (i.e., a no-take zone; in two cases it was a zone of no spearfishing). If the source paper did not mention the reserve size specifically, I used the World Conservation Monitoring Center's web site,¹ McArdle (1997), or communication with the authors of the studies to determine reserve size. I was unable to find sizes for five reserves and therefore only include them in my analyses of general reserve effect. The appendix lists the reserve sizes I was able to find.

Although the way in which data were reported varied among the studies of reserve effect, the type of data reported was fairly consistent. Studies examined the effect of marine reserves on the density, biomass, mean size, and diversity (measured as species richness) of organisms within the reserves, although few studies examined all four of these biological variables. The effect of the marine reserves on these measures was reported either as a qualitative trend (e.g., "fish density was higher in the marine reserve") or a quantitative difference (e.g., "lobster biomass increased 250% since the date of inception of the marine reserve"). I recorded both of these types of data as a trend of the reserve having higher values than nonreserve areas. The latter example I also recorded as a numerical difference of 3.5 (i.e., 250% equals a 3.5-fold increase).

An overall trend and the mean for all numerical values were calculated for all species examined in a given study, regardless of the number of species in each study. In five cases (Moreno et al. 1984, 1986, Castilla and Duran 1985, Cole et al. 1990, MacDiarmid and Breen 1992), several species were examined but results were presented for only one or a few species. Overall values in these cases represent only the species with reported data. Since many studies only examined a single species, overall values can represent anywhere from one to several hundred species.

In separate analyses, I examined data by functional group when it was provided. The functional groups were invertebrates, herbivorous fishes, planktivorous/

TABLE 1. Fish families and their functional group classifications.

Herbivores	Planktivores/ invertebrate eaters	Carnivores
Acanthuridae	Anthiidae	Batrachoididae
Kyphosidae	Apogonidae	Bothidae
Pomacentridae	Atherinidae	Carangidae
Scaridae	Balistidae	Carcharhinidae
Siganidae	Belonidae	Centracanthidae
Zanclidae	Caesionidae	Centropomidae
	Chaetodontidae	Coracinidae
	Clupeidae	Gadidae
	Dasyatidae	Haemulidae
	Diodontidae	Lethrinidae
	Gerreidae	Lutjanidae
	Gobiidae	Muraenidae
	Holocentridae	Pomatomidae
	Labridae	Sciaenidae
	Lagocephalidae	Scombridae
	Myliobatidae	Scorpaenidae
	Mullidae	Serranidae
	Nemipteridae	Soleidae
	Pomacanthidae	Sparidae
	Syngnathidae	Sphyrnidae
	Tetraodontidae	

Notes: These classifications are natural groupings based on those made in the reviewed literature. Mugilidae, Elopidae, Ariidae, Ephippidae, Cichlidae, and Blennidae, which were observed in a few of the studies reviewed here, do not fit well into a single category and so are not included in functional group analyses. They are included in overall values and analyses.

invertebrate-eating fishes, and carnivorous fishes (see Table 1 for fish family classifications). Data for families or species that did not fall into one of these functional groups (such as omnivores) were omitted since there were too few of these data to allow for separate statistical analyses. I treated each family (or species if the study only looked at a single or a few species) as a separate data point for analysis. This method avoided redundancy; many studies collected data for only one functional group, and if I were to sum all data for a functional group from a study and then calculate a mean, the functional group results would look very similar to the overall values. Calculating grand means of the functional-group data allowed for a more accurate picture of the effect reserve protection can have on a particular family or species, since each family or species value was recorded as a separate datum and not summed across all organisms within the same functional group within a study.

I extracted qualitative and quantitative data from the text, tables, and bar graphs presented in the articles. While data extraction from text and tables was straightforward, data extracted from graphs were slightly less precise, since these values were estimated by measuring the height of the bars against the *y*-axis. I tabulated data regardless of the reported significance values. Overall values of differences between reserve and non-reserve areas were often provided, or I calculated them

¹ URL: (<http://www.wcmc.org.uk:80/marine/data/>)

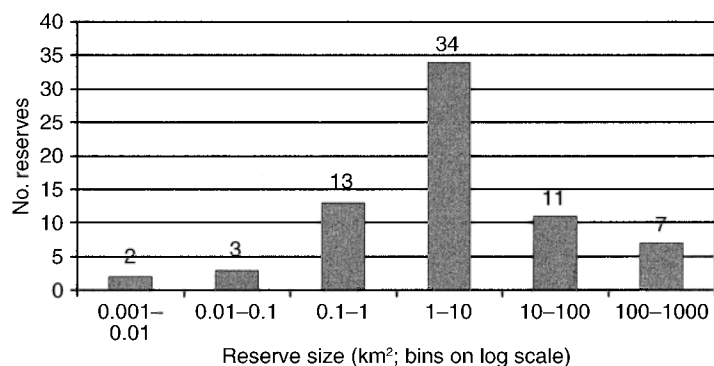


FIG. 1. Sizes of the reserves reviewed in this study. Reserve size is in square kilometers and is binned on a log scale. The range of reserve sizes is 0.002–846 km².

as the mean of the summed values for all groups or species listed. For example, Roberts (1995) lists the overall density and biomass for fish inside and outside the marine reserve in Saba, Netherland Antilles, as well as density values for several families of fish. I used the overall totals to calculate differences in biological measures as a result of reserve protection, and then calculated values for each family and averaged those to give functional group differences.

Because overall values integrate across all species studied, an extremely abundant species can disproportionately influence these overall values. For example, Cole et al. (1990) report that all but one species had higher density inside the reserve compared to outside. The one species that was very abundant, however, was much more numerous outside the reserve, and so the mean overall value ends up indicating lower density levels as a result of reserve protection. Analysis of the data at the functional group level as well as for overall values allowed this sort of "single-species" influence to be isolated. Although total density for all fish was lower inside the reserve (the entire community value), functional group analysis showed that most species had higher values inside the reserve.

Data from relevant work were occasionally described in articles that I could not obtain (Ayling and Ayling 1986, as cited in Jones et al. 1992; Spanier 1984 and Hunt et al. 1991, both cited in Childress 1997); I included these data as separate entries in my database, but only as trends (except for one datum). All studies and data used in my analyses are listed in the appendix.

Most studies compared inside vs. outside a reserve at a single point in time, and so I report these data as the ratio of these values (inside divided by outside). Several studies were able to survey an area before and after a reserve was put in place; I present these data as the ratio of after divided by before. A few studies had both before/after and inside/outside (for reference) data (Alcala 1988, Russ and Alcala 1989, 1996, 1998a, b, Alcala and Russ 1990, Bennett and Attwood 1991, Dufour et al. 1995, Edgar and Barrett 1999). For these cases, I report values as the ratio of after to before, adjusted by the difference in the reference (outside)

values over the same time period. Occasionally data were collected after protection of a marine reserve broke down (Davis 1977, Russ and Alcala 1996, 1998a). To standardize these results with the rest of the data, I report these values as if the effect were reversed. In other words, if density of a fish dropped with the loss of protection, I recorded the reserve as increasing the density of that fish.

Ratios greater than 1 represent higher levels of a biological measure within a reserve relative to non-reserve areas, while ratios between zero and one represent lower levels. If a biological measure began at or went to zero, I was unable to create a ratio and was therefore unable to use these data. To normalize the distribution of the ratios, I log-transformed the values. I use these log ratios for all analyses. In the end I back transformed ratios to aid in interpretation of the results. A reported ratio of 2.5 means that the value inside a reserve or after the establishment of a reserve was 2.5 times (or 150%) higher relative to outside (or before) the reserve.

In a few cases the trend was reported as not statistically significant, but I still used the data provided to calculate ratios. In these cases I recorded the trend as no difference but used the ratio for calculations of reserve and size effects on biological measures. For the majority of these cases the nonsignificant difference is in a negative direction; therefore, using these values can only add a slight bias against finding a positive reserve effect.

In seven cases (see Appendix), data from several noncontiguous reserves were presented as a single value. I treated these values as representing a single reserve of the summed sizes of the reserves. In only one case was the total size >30 km², and so this method should not create a bias for large reserves in my analyses of reserve size effects.

Several studies made multiple measurements in categories I did not consider in this review, such as by season ($n = 2$), depth ($n = 3$), habitat ($n = 2$), size classes ($n = 1$), or for several sites within a reserve ($n = 6$). In these cases, I averaged the values into a single value. When data for multiple years were presented, I

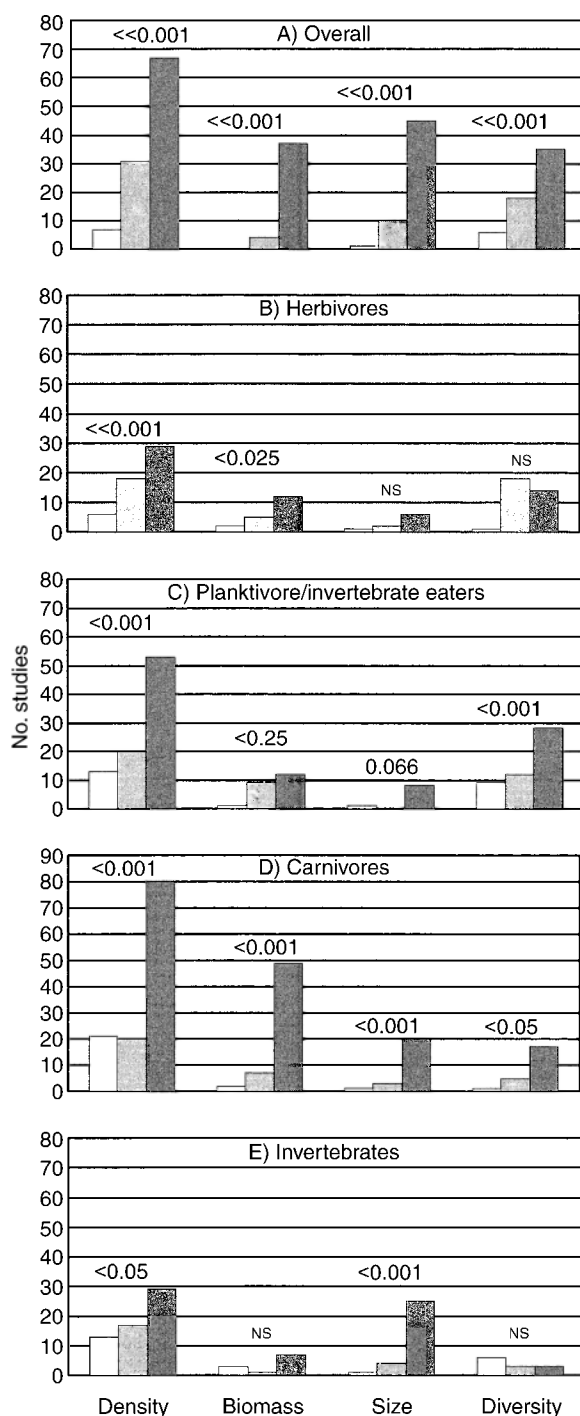


FIG. 2. Differences in biological measures (density [no./area], biomass [mass/area], mean size of organism, and diversity [total species richness]) between inside a reserve and outside a reserve (or after vs. before) for all organisms (A) and for each functional group (B–E). The numbers of independent reserve measurements that were associated with each trend are plotted for each biological measure: white bars represent lower values inside the reserve, gray bars represent no difference between reserve and nonreserve areas, and dark bars represent higher values inside the reserve. P-values above the bars are significance values for chi-square tests values

used only the data for the final year to allow for the longest time of protection and minimize the likelihood of a time effect (see *Discussion*). If reserve protection was initiated during the course of a study, then the data were treated as a before/after case.

In a few cases I needed to make minor calculations to make reported data congruent with the other studies. For example, if only a range of differences in some value was reported, I used the median of this range to approximate the mean difference. In two cases, only abundance values were given, with no reference to the area surveyed or the effort expended (Hunt et al. 1991; cited in Childress 1997, and Grigg 1994). I used these data to create ratio values, even though they might not accurately reflect the actual density of fish within the reserves. All other density values are per area or per effort.

A final difficulty arose in cases where only trends were reported and some species or families showed one trend while others showed a different trend. This occurred only three times (Duran and Castilla 1989, Bennett and Attwood 1991, Watson and Ormond 1994). In these cases, I used the trend for the majority of the species or families for overall values. For example, Watson and Ormond (1994) reported that 15 species had greater density inside the reserve, 34 showed no difference, and two showed lower density. I recorded this as a trend of no difference for overall density, even though many species did have greater numbers inside the reserve.

RESULTS

General descriptions of reserves studied

Reserve size varied over six orders of magnitude (see Fig. 1). Mean reserve size was 44.1 km², although half of the reserves were between 1 and 10 km² and the median reserve size was 4.0 km². The largest reserve (which was actually a collection of reserves) was 846 km²; the smallest reserve was 0.002 km².

The number of species surveyed in each study also varied widely, but the majority of studies fell into one of two categories: almost half of the measurements were of five or fewer species, and almost half were of 50 or more species.

The distribution between studies conducted in tropical climates and those conducted in temperate climates was fairly equal. Forty-one percent of studies were conducted in temperate regions and the rest were conducted in tropical areas. However, nearly all of the studies looked at organisms associated with reefs—coral reefs for tropical regions and rocky reefs and intertidal zones for temperate areas (although other

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for chi-square tests of differences between frequencies among observations (null hypothesis: no difference in frequency); NS, not significant.

TABLE 2. Mean squares and *F* ratios for one-way ANOVA tests of the association of mean reserve size and the three trend categories (less than, no difference, greater than) for each biological measure in each functional group.

Effect	O			C		
	df	MS	<i>F</i>	df	MS	<i>F</i>
Density	2, 97	2528.1	0.179	2, 116	2821.9	0.817
Biomass	2, 38	204 465.0	11.084	2, 53	610.8	0.044
Organism size	2, 49	594.8	0.068	2, 24	1520	0.205
Diversity	2, 56	3798.3	0.291	2, 23	119.3	1.342

Notes: *P* values for all cases are >0.07 , except for overall biomass ($P = 0.002$), suggesting that there is no effect of reserve size in qualitative changes associated with reserve establishment. Abbreviations: O = overall, C = carnivores, H = herbivores, P/I = planktivores/invertebrate eaters, and I = invertebrates.

†Only two trend categories were available for these tests.

habitats such as seagrass beds existed within these reserves).

Qualitative results

Effect of marine reserves on biological measures.—

Overwhelmingly, reserves were associated with higher values of density, biomass, organism size, and diversity of species for overall trends and for all four functional groups (Fig. 2). Invertebrate biomass and size were the only exceptions. Moreover, few reserves showed lower levels for any biological measure. This pattern is particularly striking for the analysis of all species combined (overall group; Fig. 2A): 63% of reserves had higher density (Chi-square test, $P \ll 0.001$), 90% of reserves had higher biomass ($P \ll 0.001$), 80% of reserves had larger organisms ($P \ll 0.001$), and 59% of reserves had higher diversity ($P \ll 0.001$). Only a small minority of reserves had lower values for these biological measures (7%, 0%, 2%, and 10% of reserves had lower density, biomass, organism size, and diversity, respectively). Reserves in general, therefore, usually had higher values, less often had no effect, and rarely were associated with lower values of the four biological measures.

Results are similarly striking when analyzed by functional group. For carnivorous fishes (Fig. 2D), 66% of reserves had higher density ($P \ll 0.001$), 84% of reserves had higher biomass ($P \ll 0.001$), 83% of reserves had larger organisms ($P < 0.001$), and 74% of reserves had higher diversity ($P < 0.05$). Reserves rarely were associated with lower values for any measure for carnivores; lower values occurred in only 3–17% of the cases (Fig. 2D). For planktivorous and invertebrate-eating fishes (Fig. 2C), 62% of reserves had higher density ($P \ll 0.001$), 55% of reserves had higher biomass ($P < 0.025$), 55% of reserves had higher diversity ($P < 0.005$), and 89% of reserves had larger organisms ($P = 0.066$). Although the difference in the trend for size of planktivorous fishes is not quite statistically significant, all but one of the reserves were associated with larger such organisms. For the other biological measures, only 5–18% of the reserves had lower values (Fig. 2C).

Herbivorous fishes showed similar patterns (Fig. 2B): 53% of reserves had higher density ($P < 0.01$) and 63% of reserves had higher biomass ($P < 0.05$). No difference existed between reserves and nonreserves for herbivore size or diversity; however, there was only one case of a lower value for both variables within reserves and six of nine cases showed positive differences in herbivore size. Therefore, herbivore size and diversity are usually higher or unchanged as a result of reserve protection. Herbivore density and biomass were lower in only 13% and 11% of the reserves, respectively.

Finally, for the invertebrate functional group (Fig. 2E), 50% of the reserves had higher density ($P < 0.05$) and 83% had larger organisms ($P < 0.001$), but biomass and diversity were not statistically different between reserve and nonreserve areas. Sample size for these latter two categories was fairly small ($n = 11$ for biomass and $n = 12$ for diversity), and so it is difficult to draw robust conclusions.

In summary, most of the biological measures were higher inside reserves. The next most common result was no difference from the non-reserve conditions. Rarely did reserves have lower values for density, biomass, size, or diversity, both overall and within functional groups.

The role of reserve size in determining reserve effect

I also used the qualitative data to investigate whether reserve size influences the trends seen in the previous section. For instance, were reserves that showed the largest differences more likely to be larger reserves? In all cases but one, the mean size of reserves for each of the three trend categories (less than, no difference, and greater than) for both overall and functional group categories were statistically indistinguishable (one-way ANOVA, $P \leq 0.08$ for all cases; see Table 2). This result implies that the proportional effect of a reserve is independent of reserve size.

The only case where reserve size appeared to have an effect was for overall biomass. In this case, reserves were never associated with lower biomass levels (a trend of "less than"). The mean size of a reserve in the no difference category was larger than the average reserve size in the "greater than" category (Tukey test, $P < 0.05$), but one of the three reserves in the no

TABLE 2. Extended.

P/I			H			I		
df	MS	F	df	MS	F	df	MS	F
2, 81	30.9	0.180	2, 51	67.2	0.501	2, 53	12 327	1.525
1, 17	170	2.601†	2, 17	92.3	1.456	1, 10	360.3	2.068†
1, 9	24.3	1.193†	2, 9	140.6	3.995	2, 28	256.3	1.156
2, 44	377.6	2.177	2, 30	157.5	0.792	2, 11	14 282	0.733

difference category was nearly an order of magnitude larger than all other reserve sizes.

Quantitative results

Functional group response to reserve establishment.—As expected, mean values of ratios for all biological measures in each functional group, except invertebrate biomass and size, are significantly greater than zero (two-tailed Student's *t* test, $P < 0.025$ for all cases) indicating a consistently positive effect of reserve establishment on density, biomass, size of organism, and diversity (Table 3). This pervasive positive effect can be seen clearly in Figs. 3–7, where results for each reserve are plotted against reserve area. Nearly all points in all figures lie above the log ratio = 0 line, indicating that values are almost always higher inside of reserves (or after reserve protection).

The two exceptions to this are invertebrate size and biomass. Invertebrate size inside reserves is signifi-

cantly less than zero (two-tailed Student's *t* test, $P < 0.005$), and invertebrate biomass is indistinguishable from zero (two-tailed Student's *t* test, $P = 0.053$), indicating that reserves may lower invertebrate size and have little effect on invertebrate biomass. However, invertebrate biomass values were highly influenced by extremely bimodal data and invertebrate size values were skewed by a single low datum (see Fig. 7). Removal of this single datum leads to higher mean size values roughly equal to those for all other functional groups, ~20% (a 1.2-fold increase). I discuss these factors in greater detail in the *Discussion*.

To determine if marine reserves affect functional groups differently, I tested if ratio values for density, biomass, size of organism, and diversity were different from each other. In all cases but two, ratio values of the functional groups were not statistically different from each other or from overall values (one-way ANOVA, $P > 0.13$ for all cases excluding the two excep-

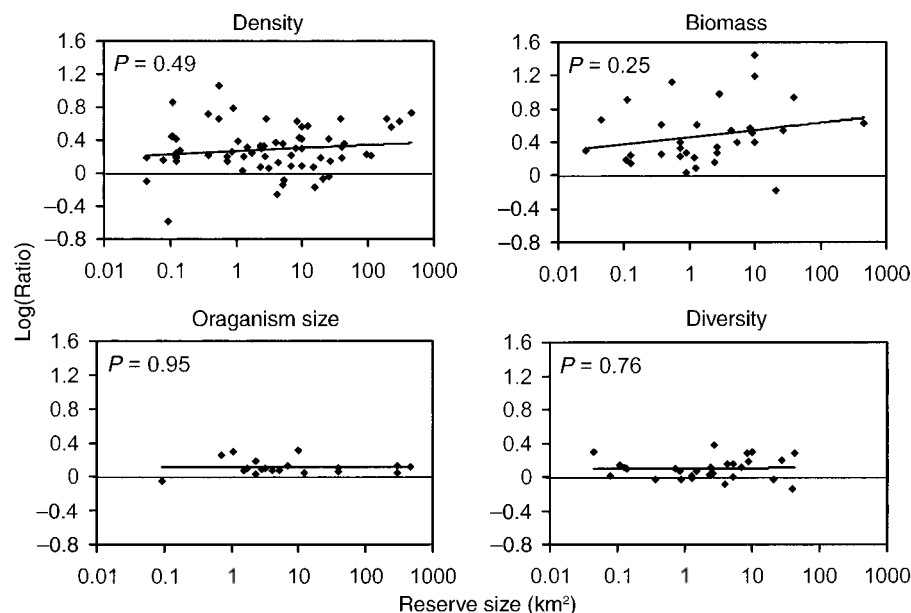


FIG. 3. Log difference ratios (inside a reserve vs. outside, or after a reserve vs. before) for each biological measure for overall values as a function of reserve size. Data are plotted as the log of the ratio vs. the log of reserve size. Because the ratio is log-transformed, lines drawn at log ratio = 0 show where reserves had no effect. Points above this line represent values greater than zero for the biological measure; points below the line represent values less than zero. In all cases except invertebrate biomass, log ratio values were significantly different from zero (Table 2). The slopes of all regression lines are not significantly different from zero (P values for linear regression analyses are in the upper left corner of each plot), indicating that reserves of all sizes showed similar proportional differences to nonreserve areas.

TABLE 3. Mean ratios of each biological measure (value inside the reserve divided by the value outside of the reserve or before the creation of the protected area), for each functional group and for all trophic groups together.

	O	C	P/I	H	I
Density	1.91 ± 0.28***	2.21 ± 5.63*	1.85 ± 0.56***	2.39 ± 2.67**	2.04 ± 6.15*
Biomass	2.92 ± 0.92***	3.12 ± 1.23***	2.38 ± 2.19**	3.33 ± 4.82**	0.25 ± 2.23
Organism size	1.31 ± 0.07***	1.31 ± 0.10***	1.23 ± 0.13***	1.52 ± 0.36**	0.80 ± 0.17***
Diversity	1.23 ± 0.07***	2.40 ± 0.43***	1.35 ± 0.37***	1.39 ± 0.27***	1.08 ± 0.22**

Notes: Values are presented as the mean (calculated from the log-transformed data, then back transformed), plus or minus the standard error (calculated from the nontransformed data). Invertebrate biomass and organism size and herbivore organism size all have six or fewer cases. Abbreviations: O = overall, C = carnivores, H = herbivores, P/I = planktivores/invertebrate eaters, and I = invertebrates. *P* values for two-tailed Student's *t* tests, testing if the mean values are equal to zero, are as follows: * *P* < 0.05, ** *P* < 0.025; *** *P* < 0.001. For invertebrate biomass, *P* = 0.053.

tions). The two exceptions are invertebrate biomass, which had lower mean values inside (or after) reserves (one-way ANOVA, *P* < 0.025), and carnivore diversity, which had much higher values than other groups (one-way ANOVA, *P* < 0.0001).

Interestingly, these results do not show a consistent pattern indicative of trophic cascades, where higher densities or biomass of carnivores would be matched by decreases in prey functional groups. In the discussion, I offer possible explanations for why trophic cascades were not obviously present here.

Effects of reserve size

Figs. 3–7 show the log of the ratio for each biological measure plotted against reserve size for overall values and for each functional group. The slopes of the regressions for all measures in all functional groups vs. reserve size are not significantly different from zero

(linear regression analysis, *P* > 0.12 for all cases; see figures for exact *P* values), indicating that reserve size has no apparent impact on proportional differences. There were only four data points for herbivore size, and so regression analysis was not possible for this case. Thus, the relative impact of reserves on all biological measures in each functional group was significantly positive, and this relative impact appears to be independent of reserve size. I discuss the implications of this in the *Discussion*.

DISCUSSION

These results demonstrate that reserves are associated with higher values of density, biomass, organism size, and diversity for overall values as well as for all functional groups. This is strong support for the many claims made that marine reserves “work.” The results of this study also support the predictions of many fisheries models; reserve protection should increase bio-

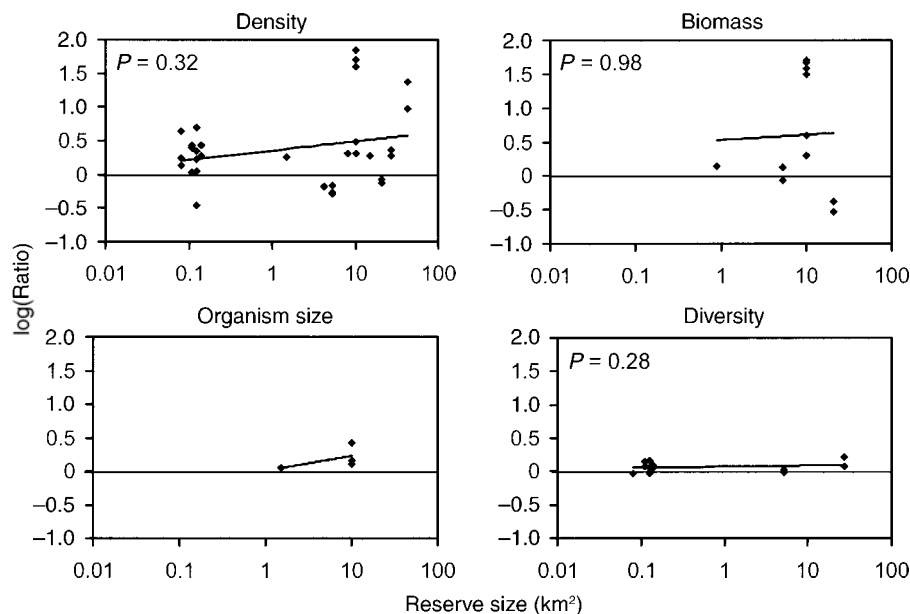


FIG. 4. Log difference ratio of each biological measure for herbivores as a function of reserve size. See Fig. 3 legend for explanation of the graphs. No *P* value is reported for organism size since there were too few data to perform a regression analysis.

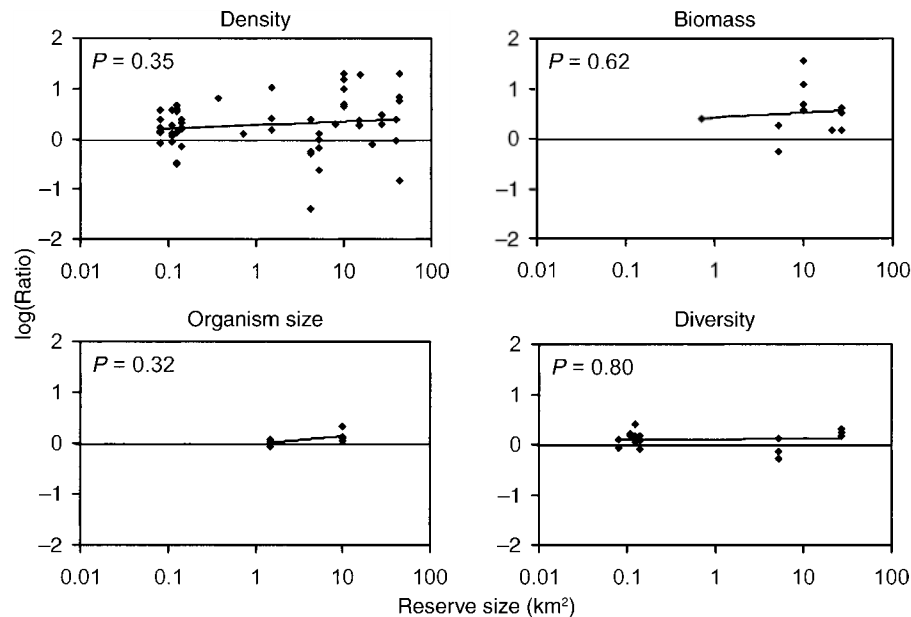


FIG. 5. Log difference ratio of each biological measure for planktivore/invertebrate eaters as a function of reserve size. See Fig. 3 legend for explanation of the graphs.

mass (Polacheck 1990, DeMartini 1993, Quinn et al. 1993, Man et al. 1995) and density (which is probably correlated to the spillover of fish to nonreserve areas; Russ et al. 1992, Hockey and Branch 1994) within a reserve. This is an encouraging conclusion in that at least some of the fishery and conservation expectations for current and future marine reserves have been met and can be realized.

These results also provide some guidelines for the magnitude of change in biological measures we can expect as a result of marine reserve protection. On average, creating a reserve appears to double density, nearly triple biomass, and raises organism size and diversity by 20–30% relative to the values for unprotected areas (see overall values in Table 3). It is important to remember, however, that these values have

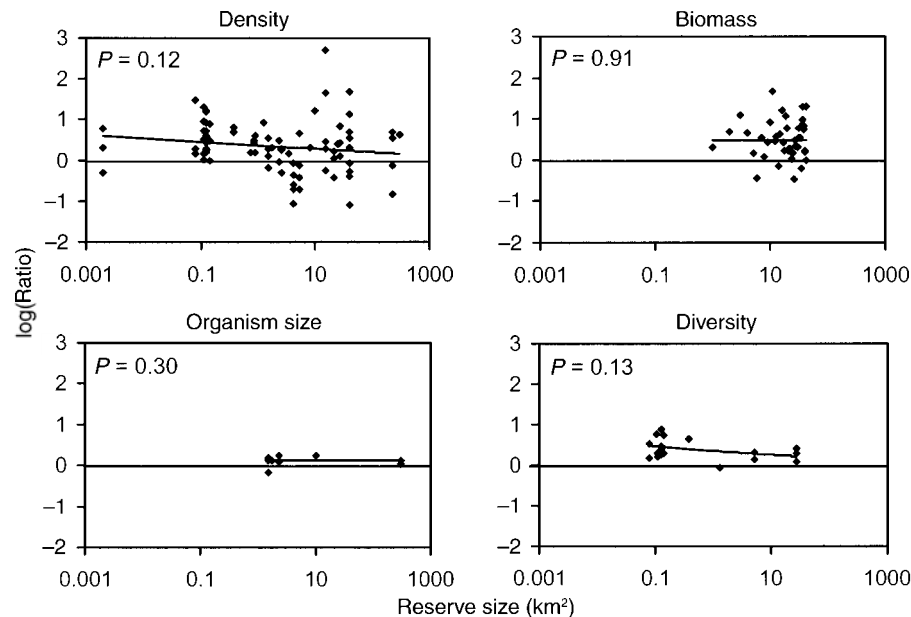


FIG. 6. Log difference ratio of each biological measure for carnivores as a function of reserve size. See Fig. 3 legend for explanation of the graphs.

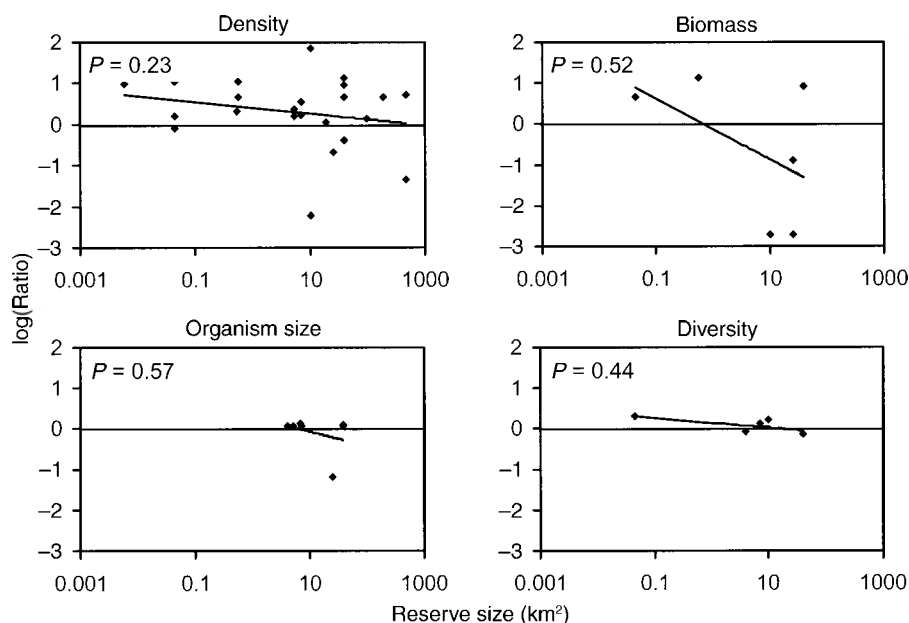


FIG. 7. Log difference ratio of each biological measure for invertebrates as a function of reserve size. See Fig. 3 legend for explanation of the graphs.

considerable variance and cannot be used to predict how a specific reserve will affect particular organisms and communities.

The results for invertebrates are less clear than for the other functional groups, but nevertheless do not detract from the general results. Invertebrate density trends and numerical values were predominantly positive, as was the case for the other functional groups. The invertebrate size results might at first glance appear to be contradictory; qualitative results showed that a vast majority of reserves held larger organisms while quantitative data imply that invertebrates are generally smaller in reserves. As was mentioned in the *Results*, however, the quantitative data were highly influenced by a single datum; removal of that datum led to new mean size values roughly equal to those for all other functional groups, about 20% higher inside the reserves. For invertebrate diversity, analysis showed that reserves were equally likely to be associated with lower, no difference, or higher trend values. However, sample size was small and the quantitative value was significantly positive, indicating that, on average, diversity will be higher inside reserves. Invertebrate biomass was lower within reserves, but as already described, these data were extremely bimodal, with reserves leading to either much higher or much lower levels of biomass. For the most part, the high values came from studies on lobsters and exploited intertidal invertebrates, while the lower values were from measurements of urchin biomass levels, which dropped within a reserve when numbers of urchin-feeding fishes increased. The implication here is that, for invertebrate biomass in particular, the effect of reserve protection will de-

pend in part on the exploitation level of the invertebrate and its position in the food chain. I discuss below other ways in which the organisms being studied might impact the way in which reserves are perceived to perform.

It is also important to distinguish between how diversity is affected by reserve protection as distinct from the other three biological measures. Diversity in this review is actually species richness, which is not measured per unit area or effort, as are density and biomass. While it is quite possible for both small and large reserves to have the same initial values of density or biomass (e.g., 2 fish/m²), larger reserves almost always initially contain more species than smaller reserves. Therefore, finding equal proportional increases in diversity for small and large reserves actually indicates a greater absolute increase in species numbers for the larger reserve. Furthermore, a single individual of a new species has a large impact on species richness measures, whereas a single individual has little impact on overall density, biomass, or organism size. Larger reserves are more likely to contain rare species simply because they encompass a greater area. In addition, diversity values will be somewhat dependent on the effort used to measure them; a long search will more likely produce a rare species than a short search. However, effort was not standardized in any way between studies.

A surprising result of this review is that the relative magnitude of the effect of a reserve on a biological measure appears to be independent of reserve size. A small reserve can double biomass per unit area just as likely as a large reserve can. This result holds even for

extremely small reserves; for example, reserves in both St. Lucia (0.026 km²) and Chile (Las Cruces: 0.044 km²) were associated with significantly larger values in the biomass and size of the organisms within the reserve compared to nonreserve areas (Castilla and Bustamante 1989, Roberts and Hawkins 1997). The reserve in St. Lucia is particularly noteworthy because even large, mobile fishes seemed to benefit from the small reserve, suggesting that small reserves can work even for mobile organisms. Furthermore, many of the small reserves were located haphazardly, yet still positively affected the organisms within them. If small reserves are more strategically placed, for example on spawning grounds or along migratory routes, their impact may be even greater.

When considering the results of this review it is extremely important to keep in mind the distinction between absolute and relative effects of reserve protection. Even small reserves appear to be able to increase density, biomass, size, and diversity of organisms, and small and large reserves can show the same proportional differences relative to nonreserve areas, but the absolute impacts of small and large reserves will be very different. For example, doubling fish numbers in a small reserve from 10 to 20 fish is substantially different from doubling the fish numbers in a large reserve from 1000 to 2000 fish, even though the relative change in density might be the same for both reserves. The goals of reserve and fishery managers often include some minimum benefit level from reserves (e.g., total catch outside the reserve, all species present and abundant enough to be self-sustaining, etc.), goals that may not be achieved if only proportional differences are considered.

Small reserves may also be insufficient for several other reasons. Alone, small reserves may not be able to provide significant export functions. This review does not examine the possibility that reserves serve as sources for unprotected areas (*sensu* Pulliam 1988), even though it is often assumed and expected that they provide this service. Models have addressed how current regimes might influence dispersal (e.g., Roughgarden et al. 1988, Roberts 1997), but only a few studies have tried to infer or measure the impact of reserves on reproductive output (Davis 1977, Davis and Dodrill 1980, Polacheck 1990, Stoner and Ray 1996, Sluka et al. 1997, Edgar and Barrett 1999; all suggest that reproductive output can be higher in reserves). An increase in numbers or size of organisms in a reserve will obviously increase reproductive output, but small reserves will only be able to increase reproductive output a small amount relative to target areas. For reserves to serve as larval sources they must be large enough to sustain themselves as well as supply the rest of the target areas.

Another potential drawback of small reserves is their susceptibility to catastrophic events. For example, if

an oil tanker runs aground near a small reserve, it is likely that the entire reserve will be impacted by the spill. If the accident occurred near part of a large reserve, on the other hand, it is possible that some of the reserve would escape harm. The unaffected part of the reserve could considerably, then, aid in the recovery process of the damaged region.

It is also possible that very large reserves (e.g., >500 km²) might provide proportionally larger values when evaluated by density, biomass, etc. If fish within a reserve use several habitats throughout their life histories, it may require a very large reserve to encompass and protect all life stages adequately. This review would most likely not be able to detect a size threshold effect such as this, since only seven of the reserves studied covered >50 km², and the only one >460 km² came from pooled data from a collection of seven smaller reserves. Furthermore, nearly three quarters of all the reserves studied covered <10 km² (see Fig. 1). Such shortcomings in the data leave open the possibility that large reserves affect biological measures in a way not detectable here. While it would be desirable to test how such a large reserve would affect such measures, the logistics of such studies would be very difficult.

An important variable not analyzed here is the role that the length of protection plays in determining the magnitude of a reserve effect. Examples exist where the magnitude of the reserve effect increased over time (e.g., Watson et al. 1996, Russ and Alcala 1998a, b). Conan (1986) described how lobster biomass initially increased over several years but then receded to original levels. In all of these cases, results would have been different had population surveys been made at a single point in time (or over a relatively brief period of time), as they were in most of the studies I reviewed here. It is difficult to determine, therefore, if the populations had actually reached equilibrium at the time of measurement. Furthermore, the impact of a reserve is certainly not instantaneous, but little is known about how long it takes for a population to reach equilibrium, or even if it ever does. I address in depth the role that length of protection plays in determining the effect of marine reserves elsewhere (Halpern and Warner 2002).

Many other variables could also influence the impact of reserves on the biological resources contained within them. Species composition (PDT 1990, Carr and Reed 1993, Ballantine 1992, 1995, 1997, Dugan and Davis 1993, Tegner 1993, Rowley 1994), the fishing intensity around the reserve (Polacheck 1990, Russ et al. 1992, Carr and Reed 1993, Rowley 1994, Nowlis and Roberts 1997), adult mobility or home range size of fish within the reserve (Kramer and Chapman 1999), and the types and quality of habitats both inside and outside the reserve (Salm and Clark 1989, Hockey and Branch 1994, Agardy 1995, Nilsson 1998) have all been proposed as variables that could be important in determining how

an organism responds to reserve protection. These sorts of observations were usually not reported in the empirical studies on marine reserves I used, and so I was unable to evaluate them here. However, these other factors should certainly be considered when setting goals and expectations for marine reserves.

Despite that many empirical studies found trophic cascade effects as a result of marine reserve protection (Kenya: McClanahan and Muthiga 1988, McClanahan and Shafir 1990, McClanahan 1994, 1995, 1997, Watson and Ormond 1994; Chile: Castilla and Duran 1985, Duran and Castilla 1989; Mediterranean: Sala et al. 1998a), this pattern did not emerge from my large-scale analyses. Instead, the densities of invertebrates, herbivorous fishes, planktivorous/invertebrate eating fishes, and carnivorous fishes all increased almost exactly the same amount (see Table 3). A possible explanation for this is that trophic cascades appear to be more likely to occur when only a small subset of a community is observed (Polis and Strong 1996). For example, in Kenya (e.g., McClanahan and Shafir 1990) the trophic cascade occurred between humans, triggerfish (*Balistidae*) and a few species of sea urchins, and was not evident in other families of fish and species of urchins that were studied. Similarly, in Chile (Castilla and Duran 1985, Duran and Castilla 1989) the cascade occurred between humans, a single gastropod, a single mussel, and algae. Thus trophic cascades may be masked when entire communities are measured. In the study by McClanahan and Shafir (1990), total fish densities as well as densities for four fish families (*Labridae*, *Balistidae*, *Diodontidae*, and *Lagocephalidae*) and urchins were measured. Urchin densities were nearly 200 times higher outside the reserve, while *Balistid* density was nearly 10-fold greater inside the reserve, exemplifying a classic trophic cascade. When all four fish families were considered (all are planktivorous fishes/invertebrate eaters), fish densities dropped to only 28% higher inside the reserve, obscuring the trophic cascade. When family or species results are incorporated into an entire functional group, as was the case here, trophic cascade effects can often become muted.

Empirical tests of the effect of reserve size are needed to test the robustness of the results suggested here. To date, only one study (Edgar and Barrett 1999) has tried to assess empirically the potential effects of marine reserve size on biological attributes of species contained within the reserves. They studied four reserves in Tasmania, three of which were ~ 0.6 km² and a fourth that was about 7 km². The largest reserve showed many significant differences relative to nonreserve areas, while the smaller reserves had only a few notable differences. For example, in the large reserve, overall fish size, density of large fish, abalone size, size of crayfish, mean plant cover, and species diversity of fish, invertebrates, and algae all increased significantly compared to control sites. In the other three sites, significant dif-

ferences were found only for density and diversity of large fish in one reserve and density of algae in another. Although the observations from the large reserve were not replicated, these results offer some empirical evidence suggesting that large reserves can provide biological functions not possible in small reserves. This conclusion is in stark contrast to the results of this review, in which even small reserves appeared to have a positive impact on most biological measures. In order to assess adequately the role of area in reserve function, a real need exists for studies that make observations in reserves of many sizes within the same biogeographic region.

Success in the design and function of a marine reserve is closely tied to the goals of the reserve. For example, fishery reserves need to increase abundance, biomass, and organism size within the reserve in order to sustain the reserve populations as well as supply the harvested areas. Conservation reserves, on the other hand, focus more exclusively on the maintenance of diversity and abundance of organisms within the reserve itself. Fortunately, marine reserves appear to lead to higher values of all of these biological measures, implying that both goals can be met with the same reserve.

The impact of marine reserves on the organisms contained within them will never be completely predictable. Variation among reserves and a level of uncertainty will always exist when examining how marine reserves affect specific biological measures. Goals set for marine reserves should account for this variation (Walters and Holling 1990, Clark 1996, Hall 1998, Lauck et al. 1998). Ultimately, though, it is encouraging to know that reserves of any size appear to function well, in terms of producing higher densities, sizes, and diversity of organisms.

Inherent problems and necessary caveats

The enormous variation in type and quality of the observations from marine reserves made it difficult to compare or analyze the results of the studies I reviewed (see also Jones et al. 1992). The primary problems include:

- 1) results are more likely to be reported for species that are actually affected by reserves (either positively or negatively) than for unaffected species, especially for single-species studies;

- 2) methodologies often differ drastically among different observations and among scientists within a study;

- 3) characteristics of reserves being studied (such as location, habitat type, current regimes, temperatures, etc.) are not the same;

- 4) observations are rarely replicated temporally or spatially (usually because there is only one reserve available for study);

5) reserves are not always adequately protected from poaching;

6) the length of protection varies among reserves;

7) numbers and types of organisms studied vary between experiments;

8) the intensity of fishing outside of the reserve may enhance or even create the perceived affect on biological measures of reserve protection.

As many have argued, the intensity of fishing occurring outside a reserve (or where a reserve is before it becomes a reserve) can have a large impact on the perceived effects of reserve protection (Polacheck 1990, Russ et al. 1992, Carr and Reed 1993, Rowley 1994, Nowlis and Roberts 1997). If an area is nearly completely fished out, the ratio of postprotection to preprotection values of abundance, biomass, etc. will be much higher than for an area that had been lightly fished (assuming all else is equal, and that new fish can be imported to the fished areas from elsewhere). It is difficult to compare fishing intensities in different parts of the world, and this can lead to inaccuracies when combining data.

The confidence in the results from any one study depend on the quality and breadth of the sampling involved, and thus can complicate comparisons across studies. As an example, conclusions drawn when comparing results from a single-species study with results from a study on 250 species suffer obvious comparison problems. Furthermore, studies that looked at only one or a few species may have missed how other species responded to reserve protection; rarely do all species respond in the same way. Future studies, therefore, should include at least a few species from all trophic levels in order to assess reserve effect accurately.

Another problem many studies face is the lack of consistency in protection level for the reserves. Even fully protected reserves often suffer some poaching (e.g., Klima et al. 1986). This potential problem was rarely quantified, largely due to difficulties in monitoring a clandestine act. Because information on actual protection level is lacking, it is difficult to know exactly how long and to what degree a reserve has been protected. Reserve effects can change over time (see Russ and Alcala 1998a, b for examples of this), so knowing the length of time protection has been in place can be a critical part of analysis. To be able to make more accurate predictions of the effect of marine reserves, actual fishing effort within reserves must be measured and accounted for (Polacheck 1990, Russ et al. 1992, Carr and Reed 1993, Rowley 1994, Nowlis and Roberts 1997) and the length of complete protection identified.

The lack of temporal and spatial replication in many of the studies further complicates interpretation of the results. Snapshots in time and space can provide clues to the effects of reserves, but it is very difficult to eliminate the possibility that observed effects were not simply a result of spatial or temporal differences, es-

pecially with inside/outside reserve studies. Before/after studies offer a possible solution to these problems and should be coupled with control observations in non-reserve areas over the same time period, across several spatial scales within a biogeographic region. However, such studies are often logistically difficult to implement.

One of the largest problems with the empirical literature on marine reserve effects is that methodologies used for different studies and the characteristics of reserves and control sites (such as substrate rugosity, depth, current regime, etc.) differ dramatically. Few people make efforts to accommodate the problems mentioned above, let alone measure the same variables in the same way. For example, sample sizes in many studies were not large enough to draw statistically significant conclusions. Other studies did not report the statistical significance of their results, even though this might have been possible. Empirical work on marine reserves needs to reflect the rigorous standards of the rest of the scientific literature.

Finally, results are often only reported when a reserve actually had an effect on an organism, whether negatively or positively. This was unlikely to be a problem for studies that looked at entire communities, but was potentially a large factor influencing single-species studies. Single-species studies can often be useful, especially for fisheries management, but it is important to remember that not every species will respond to reserve protection.

Despite these potential sources of error, my analyses uncovered clear and significant positive effects of reserve establishment on the organisms dwelling within reserve boundaries. Even the inclusion of gray literature, where many of these interpretation problems discussed above are exacerbated, did not obscure these results.

CONCLUSIONS

The most important lesson provided by this review is that marine reserves, regardless of their size, and with few exceptions, lead to increases in density, biomass, individual size, and diversity in all functional groups. The diversity of communities and the mean size of the organisms within a reserve are between 20% and 30% higher relative to unprotected areas. The density of organisms is roughly double in reserves, while the biomass of organisms is nearly triple. These results are robust despite the many potential sources of error in the individual studies included in this review.

Equally important is that while small reserves show positive effects, we cannot and should not rely solely on small reserves to provide conservation and fishery services. Proportional increases occur at all reserve sizes, but absolute increases in numbers and diversity are often the main concern. To supply fisheries adequately and to sustain viable populations of diverse groups of

organisms, it is likely that at least some large reserves will be needed.

Finally, it is paramount that we explicitly state our goals when creating marine reserves. These goals help guide the design of reserves and are critical for assessing whether or not a reserve has functioned successfully.

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APPENDIX

This appendix includes a summary of the data extracted from the literature reviewed, and the sources from where the data came.

Reserve	Size (km ²)	No. taxa	Functional group				Biological measure				Reference
			C	H	P/I	I	D	B	S	Div	
Caribbean											
St. Lucia	0.026						ND	+2	+	+	Roberts and Hawkins (1997)
Saba	0.9	40 species	×	×			ND	+1.9	+	+	Polunin and Roberts (1993)
Saba	0.9	26 species	×	×			ND	+1.09	ND	ND	Roberts (1995)
Belize	2.6	45 species	×	×			ND	+1.9	ND	+	Polunin and Roberts (1993)
Los Roques, Venezuela	4	1 species				×	+2.38		+1.17		Weil and Laughlin (1984)
Barbados	2.3	89 species					+1.16	+	+1.07	+1.06	Rakitin and Kramer (1996)
Barbados	2.3	7 species	×				+2.15		+1.53		Tupper and Juanes (1999)
Hol Chan, Belize	2.6							+2.21	ND		Roberts and Polunin (1993)
Hol Chan, Belize	2.6	19 fish families, 2 inverts	×	×	×	×	+2.1		+	+1.1	Carter and Sedberry (1997)
Half Moon Caye, Belize	39.25	19 fish families, 2 inverts	×	×	×	×	+2.07		+		Carter and Sedberry (1997)
Exhuma Sound, Bahamas	456	1 species	×				+	+4.19	+1.29		Sluka et al. (1997)
Exhuma Sound, Bahamas	456	1 species				×	+5.31				Stoner and Ray (1996)

APPENDIX. Continued.

Reserve	Size (km ²)	No. taxa	Functional group				Biological measure				Reference
			C	H	P/I	I	D	B	S	Div	
Manuel Antonio, Costa Rica	6.82	1 species					+1.65		+1.34		Ortega (1987)
SW Pedro Bank Ja- maica		13 families	×	×	×		+1.22	+1.76	+	ND	Koslow et al. (1998)
Philippines											
Sumilon	0.125	102 species	×	×	×		+1.56			+1.3	Russ and Alcala (1989)
Sumilon	0.125	overall, 4 families	×				+2.6	+1.73		+	Russ and Alcala (1996)
Sumilon	0.125	102 species	×	×	×		+1.73		+	ND	Russ (1985)
Sumilon	0.125		×		×		+1.51			ND	Alcala (1988)
Sumilon	0.125	178 species					+1.4	+1.39		+1.31	Russ and Alcala (1998a)
Sumilon	0.125	178 species	×	×	×		ND				Russ and Alcala (1998b)
Apo	0.11	overall, 4 families	×				+7.1	+8.0			Russ and Alcala (1996)
Apo	0.11	126 species	×	×	×		+2.73			+1.4	White (1988)
Apo	0.11	178 species					ND	+1.54		ND	Russ and Alcala (1998a)
Apo	0.11	178 species	×	×	×		ND				Russ and Alcala (1998b)
Apo	0.11						+2.73				Clark et al. (1989)
Pamilican	0.14	126 species	×	×	×		+1.89			+1.25	White (1988)
Pamilican	0.14						+1.89				Clark et al. (1989)
Balicasag	0.08	126 species	×	×	×		+1.45			+1.03	White (1988)
Balicasag	0.08						+1.45				Clark et al. (1989)
Sumilon "outside"	0.375	overall, 4 families	×				+5.2	+4.1			Russ and Alcala (1996)
Sumilon "outside"	0.375	178 species					ND	+1.8		ND	Russ and Alcala (1998a)
Sumilon "outside"	0.375	178 species	×	×	×		ND				Russ and Alcala (1998b)
New Caledonia											
Amedee	2.8						+4.5	+9.5		+2.43	Wantiez et al. (1997)
Signal	4.3						+1.35	+3.5		+1.42	Wantiez et al. (1997)
Laregnere	8.5						+4.29	+3.7		+1.9	Wantiez et al. (1997)
Maitre	9						+2.71	+3.21		+1.5	Wantiez et al. (1997)
Bailly	2.4						+2.0	+1.44		+1.29	Wantiez et al. (1997)
All five reserves	27	214 species	×	×	×		+1.38	+3.47		+1.57	Wantiez et al. (1997)
Fiji											
Unnamed	9.4	83 species	×	×	×		+	+			Jennings and Polunin (1996)
Great Barrier Reef											
Lizard Island	9.9	1 species					+1.2				Zeller and Russ (1998)
Boult Reef	3.42	33 species	×				+		+		Beinssen (1989)
Glow and Yankee Reefs	25.15	1 species	×				+2.58		ND		Ferreira and Russ (1995)
Heron Island Unamed on GBR	12	1 species					+3.77 ND		ND +		Craik (1981) Ayling and Ayling (1986) (in Jones et al. 1992)

APPENDIX. Continued.

Reserve	Size (km ²)	No. taxa	Functional group				Biological measure				Reference
			C	H	P/I	I	D	B	S	Div	
Red Sea											
Ras Moha- med, Sinai	21.1	45 species	×	×	×		ND (0.85)	ND (0.66)	ND	ND (0.93)	Roberts and Polunin (1992)
Ahkziv	1.5	1 species				×	+				Spanier (1994) (in Childress 1997)
Kenya											
Malindi						×	+16.57		+1.42		McClanahan and Muthiga (1998)
Malindi and Watuma	10			×	×	×	+3.58			+	McClanahan and Shafir (1990)
Malindi and Watuma	10	81 species + algae, coral	×			×	+2.6	+27.7			McClanahan (1997)
Kisite	15	51 species	×		×	×	ND	+			Watson and Or- mond (1994)
Kisite	15		×	×	×		+1.19			ND	Watson et al. (1996)
Kisite	15	23 species	×								Watson et al. (1997)
Mombasa	10	10 families + others	×	×	×		+2.0	+15.5	+2.04	+2.0	McClanahan and Kaunda- Arara (1996)
Malindi, Wa- tamu, and Kisite	25	127 species				×	ND (0.91)			+	McClanahan (1989)
Malindi, Wa- tamu, and Kisite	25	118 species	×	×	×	×	+2.27			+1.92	McClanahan (1994)
Malindi, Wa- tamu, Kis- ite, Mako Kokwe, Simam- bya, Ar- letts, and Kiwaiyu	846	188 species	×				ND	ND		+	Samoilys (1998)
Southeastern Africa											
Mayotte Is- land	5.25	239 species	×	×	×		ND (0.83)	+2.54		ND (1.01)	Letourneur (1996)
Cousin Is- land, Sey- chelles	1.2	115 species	×		×			+1.67		+	Jennings et al. (1996)
Sainte Anne	10	115 species	×		×			+2.5		+	Jennings et al. (1996)
South Africa											
De Hoop	230	10 species	×				+3.64		ND		Bennett and Attwood (1991)
Dwesa	39	8 species				×				-0.73	Hockey and Bosman (1986)
Dwesa	39	1 species				×	-		+1.16		Lasiak (1993)
Dwesa	39	1 species				×	+4.5	+8.5	+1.28		Siegfried et al. (1985)
Hluleka	4					×				-0.83	Hockey and Bosman (1986)
Isi Laka		7 species				×	-0.74			-0.63	Hockey and Bosman (1986)
Tsitsikamma	300	2 species	×				ND		+1.12		Buxton (1993)
Tsitsikamma	300	3 species	×				+4.2		+1.33		Buxton and Smalle (1989)
North America											
Naranganset Bay, RI	1.07	1 species	×		×		+2.44		+2.0		Rice et al. (1989)

APPENDIX. Continued.

Reserve	Size (km ²)	No. taxa	Functional group				Biological measure				Reference
			C	H	P/I	I	D	B	S	Div	
Hopkins, CA	2.75	10 species	×				ND (1.56)		+1.21	ND	Paddock and Estes (<i>unpub- lished data</i>)
Point Lobos, CA	3.14	10 species	×				ND (1.13)		+1.26	ND	Paddock and Estes (<i>unpub- lished data</i>)
Big Creek, CA	6.78	10 species	×				ND (1.23)		ND	ND	Paddock and Estes (<i>unpub- lished data</i>)
Edmonds Underwa- ter Park, WA	0.002	3 species	×				+		+		Palsson and Pa- cunski (1995)
Shady Cove, WA	1.71	3 species	×				+1.76		+		Palsson and Pa- cunski (1995)
Two re- serves, WA	1.712	3 species	×						+1.28		Palsson and Pa- cunski (1995)
Manele, HI	1.25						+1.06	+1.24		-0.96	Grigg (1994)
Kealakakua, HI	1.28						+1.57	+4.13		+1.02	Grigg (1994)
Huanama, Honolua, Manale, Molokini, and Kea- lakakua, HI							+1.35	+1.61	+	+1.07	Grigg (1994)
Kennedy Space Center, FL	39.6	50 species	×	×	×		+1.51			ND	Johnson et al. (1999)
Molasses Reef, FL	0.9	132 species	×				+6.1		+	-0.93	Bohnsack (1981)
French Reef, FL	0.37	132 species	×				+1.65			-0.93	Bohnsack (1981)
Looe Key Reef, FL	15.54	3 families	×		×		-0.67			+	Clark et al. (1989)
Looe Key Reef, FL	15.54	1 species				×	ND				Hunt et al. (1991) (in Childress 1997)
Dry Tortu- gas, FL	190	1 species				×	+4.5				Hunt et al. (1991) (in Childress 1997)
Fort Jeffer- son, FL	19	1 species				×	+1.55				Davis (1997)
"Prison Re- serve," B.C.		1 species				×	+1.22		+1.15		Wallace (1999)
"Ecological Reserve," B.C.		1 species				×	+1.11		ND (0.99)		Wallace (1999)
Chile											
Las Cruces	0.044	2 species				×	+10.63		+		Castilla and Duran (1985)
Las Cruces	0.044	1 species				×	+1.96	+7.26	+1.72		Castilla and Bustamante (1989)
Las Cruces	0.044	6 species				×	+			+	Duran and Cas- tilla (1989)
Las Cruces	0.044	1 species					ND	+	+		Bustamante and Castilla (1990)
Las Cruces	0.044	2 species				×	ND (0.8)		+		Oliva and Cas- tilla (1986)
Las Cruces	0.044	3 species				×		+4.67			Duran et al. (1987)
Mehuín	0.006	6 species				×	+9.56		+		Moreno et al. (1986)

APPENDIX. Continued.

Reserve	Size (km ²)	No. taxa	Functional group				Biological measure				Reference
			C	H	P/I	I	D	B	S	Div	
Mehuín	0.006	4 species				×	+		+		Moreno et al. (1984)
Montemar	0.025	1 species				×	ND	+	+		Bustamante and Castilla (1990)
New Zealand											
Leigh (Goat Island)	5.18	12 species	×			×	-0.73			+1.41	Cole et al. (1990)
Leigh (Goat Island)	5.18	1 species					+2.3		+1.17		McCormick and Choat (1987)
Leigh (Goat Island)	0.55					×	+11.25				Davis (1989)
Leigh (Goat Island)	0.55	1 species				×	+4.5	+13.05	+		MacDiarmid and Breen (1993)
Tasmania											
Maria Island	7	117 species				×	ND		+	+1.29	Edgar and Barrett (1999)
Tinderbox	0.53	117 species				×			+	ND	Edgar and Barrett (1999)
Governor Island	0.6	117 species				×				ND	Edgar and Barrett (1999)
Ninepin	0.59	117 species				×				ND	Edgar and Barrett (1999)
Spain											
Isles Medes	4.18	51 species	×	×	×		-0.55		+	+	García-Rubies and Zabala (1990)
Isles Medes	4.18	1 species				×	-0.26		-0.89		Sala and Zabala (1996)
Isles Medes	4.18	2 species				×	ND		ND		Sala et al. (1998b)
France											
Banyuls-sur-Mer	1.5	35 species	×	×	×		+2.06		+1.19	+1.17	Bell (1983)
Banyuls-sur-Mer	1.5	41 species					ND		+		Dufour et al. (1995)
Cerbère-Banyuls	6	1 species				×			+		Sasal et al. (1996)
Carry-le-Rouet	0.85	54 species		×	×		+1.78		+	+1.16	Harmelin et al. (1995)
Carry-le-Rouet	0.85	47 species	×		×		ND			+	Harmelin (1992)
Scandola	0.72	26 species		×	×		+1.6	+2.14	+1.8	+	Francour (1994)
Scandola	0.72	18 species	×		×		+1.37	+2.51		+1.24	Francour (1996)
Scandola	0.72	25 species	×		×		ND	+1.71			Francour (1991)
Unnamed in Brittany		1 species				×		ND	+		Conan (1986)

Notes: The summarized information is organized by general region of the globe in which each reserve occurs. The "outside" reserve at Sumilon in the Philippines refers to the area outside the reserve that received protection at various times (it is distinct from, but adjacent to, the Sumilon reserve). Data were occasionally reported for groups of reserves; in these cases the names of all the reserves measured are listed as one entry. The number of taxa studied in each reference gives a general idea of the breadth of each study. Although the number of species was reported in many of the reviewed studies (and therefore reported here), changes in biological measures were usually only reported at the taxonomic level of family. Functional group information describes how I was able to categorize the taxa studied and includes carnivorous fishes (C), herbivorous fishes (H), planktivorous fishes/invertebrate eaters (P/I), and invertebrates (I). An "×" indicates that data for the functional group were available from the reference. Overall values were recorded for all cases, when available, and are listed under the appropriate biological measure column. Trends are reported as +, ND, and -, corresponding to higher values, no difference in values, or lower values of a measure inside the reserve compared to outside (or after compared to before the creation of a reserve). In cases where trends were not significantly different from each other (ND) but ratio values could be calculated, biological measures are reported as ND with the ratio value in parentheses. The biological measures are density (D), biomass (B), size of the organism (S), and diversity (Div). Blank species indicate that the information was not reported in the reference and was therefore not available for analyses in this review.