REPORT

Marine reserves have rapid and lasting effects

Benjamin S. Halpern*
and Robert R. Warner
Department of Ecology,
Evolution, and Marine Biology,
University of California, Santa
Barbara, CA, 93106, U.S.A.
*Correspondence:
E-mail: halpern@lifesci.ucsb.edu

Abstract

Marine reserves are becoming a popular tool for marine conservation and resource management worldwide. In the past, reserves have been created with little understanding of how they actually affect the areas they are intended to protect. A few recent reviews have evaluated how reserves in general affect the density and biomass of organisms within them, but little work has been done to assess temporal patterns of these impacts. Here we review 112 independent measurements of 80 reserves to show that the higher average values of density, biomass, average organism size, and diversity inside reserves (relative to controls) reach mean levels within a short (1–3 y) period of time and that the values are subsequently consistent across reserves of all ages (up to 40 y). Therefore, biological responses inside marine reserves appear to develop quickly and last through time. This result should facilitate their use in the management of marine resources.

Keywords

Marine conservation, marine protected areas, marine reserves, temporal effects.

Ecology Letters (2002) 5: 361–366

INTRODUCTION

The combined problems of a global increase in fishing pressure and the recent and historical collapse of many fisheries have forced marine conservationists and environmental managers to re-evaluate traditional methods of resource management. In the last decade, marine reserves—here defined as no-take zones where it is illegal to extract organisms in any way—have become increasingly popular as an alternative to traditional management options. However, there have been few efforts to develop theory on the biological response to reserve protection, and most of this theory has focused on the effects of reserves on biomass export (effects on fisheries) and has assumed (or implicitly predicted) that biological responses to reserve protection reach an equilibrium level that remains consistent through time (Polacheck 1990; Demartini 1993; Attwood & Bennett 1995; Man *et al.* 1995). This assumption of stable post-reserve response may not be appropriate and has yet to be tested empirically.

Efforts to evaluate overall reserve performance are relatively nascent (Halpern 2002; Roberts & Polunin 1991; Jones *et al.* 1992; Dugan & Davis 1993; NRC 2001). In particular, although many reports of the impacts of marine reserves on biological measures exist, most are studies of single reserves, making it difficult to assess general trends in performance. Furthermore, the time course of changes occurring after reserve establishment have been evaluated

only occasionally, and then only for single reserves. Enough isolated studies now exist to permit a general and comprehensive assessment of marine reserve performance over time.

In a recent review (Halpern 2002) of 112 independent empirical measurements of 80 different reserves, it was found that average values of all biological measures were strikingly higher inside marine reserves compared to reference sites (either the same site before the reserve was created or equivalent sites outside the reserve). Relative to reference sites, population densities were 91% higher, biomass was 192% higher, and average organism size and diversity were 20–30% higher in reserves. Furthermore, these values were independent of reserve size, indicating that even small reserves can produce high values. These results offer evidence that marine reserves of all sizes can engender biological responses, but it is not clear how quickly these impacts occur or how long they persist.

The few existing studies that have measured temporal responses of biological communities in individual marine reserves provide no consistent pattern. Examples exist in which biological measures (density, biomass, average size, and diversity of organisms) increased within reserves through time (Castilla & Bustamante 1989; Russ & Alcala 1996; Wantiez *et al.* 1997; Russ & Alcala 1998a), showed little change over time (Roberts 1995; Sala *et al.* 1998), had values that initially climbed but then fell back to original

levels (Conan 1986; Ferreira & Russ 1995), and decreased over time (Dufour *et al.* 1995). Most of these cases represent studies of particular species or a small group of species, and so it is likely that these differences in the impact of reserves over time stem from the diverse life histories, trophic position, or degree of harvest (target vs. non-target) of the organisms studied in each case. For example, as predator densities increase due to protection, prey populations may decrease in a classic trophic cascade (Steneck 1998). Consequently, studies that focused on the response of prey species to reserve protection could find very different results from studies that focused on predator species. In the discussion we address how these species' traits may affect the results of reserve protection.

Clearly there is need for a general understanding of the temporal impacts of reserve protection. Can we expect the responses to reserve protection to accrue quickly, or must we wait a decade or more to see anything occur? Are responses to reserve protection merely a "flash in the pan", a quick response that just as quickly disappears, or can we count on the responses to reserve implementation to continue for future generations? Answers to these questions are of critical importance for management and are clearly useful to reserve designers who must face stakeholders that demand, or at least hope, that reserve protection will provide rapid and lasting effects. In this paper we address and answer these questions.

METHODS

There are two ways to review data on temporal change in reserve impact. The first is to ask whether the response overall appears to be a function of the age of the reserve. The second method summarizes studies that explicitly tracked changes in response to reserve protection through time. For the first approach, we used the database developed by Halpern (2002) of 112 independent measurements of 80 marine reserves of different ages to assess the rapidity with which reserves affect biological measures (density, biomass, average size, and diversity of organisms) and to determine how long such effects last. Studies were chosen only if they measured biological variables in a no-take reserve and included reference measurements in the site before protection or in an equivalent area outside the site. For analyses of overall response, several data came from different studies on different species but in the same reserve (for density $n = 4$, biomass $n = 3$, size $n = 0$, diversity $n = 1$). These data could still be viewed as independent (in that different species can respond differently to reserve protection), and because accounting for potential non-independence through adjustment of the degrees of freedom would only strengthen the results from our regression analyses, we report non-adjusted *P*-values.

Studies included in this review evaluated both invertebrates and fish from all trophic groups. Nearly all of the studies included in this review measured either less than five or more than 50 species. Analyses were done on the grand mean change (calculated as a relative change) in any of the four biological measures for all species within a study. Identical analyses were done for each of four groups (carnivores, herbivores, planktivores, and invertebrates; see Halpern (2002) for group classifications), but results were the same as for overall analyses and so only the overall results are presented here.

Using data for the four biological measures, we divided values inside the reserve by values from the reference site, or values after reserve protection divided by values from before protection, the latter adjusted by values from control sites if such controls existed. The $\log_{10}$ of these ratios was then calculated to normalize the distribution of the data, creating what we call an 'effectiveness index'; positive values of this index indicate higher levels of the biological measure inside reserves relative to the reference site. The value of the effectiveness index for each reserve and the associated reserve age were then used for all analyses. Details of which studies were included and the data extraction process are described elsewhere (Halpern 2002).

To assess general patterns of temporal change in biological measures, effectiveness index values were plotted against reserve age at the time of measurement. Regression analysis of these data then offers some insight into the rapidity of reserve response. A positive slope of biological measures against reserve age would indicate a gradual approach to mean values, whereas a regression slope of zero and a positive grand mean suggest that values of biological measures quickly reach mean values and then persist at those values. These data, although from a variety of reserves measured in a variety of ways (see Halpern 2002), offer an estimate of how density, biomass, average organism size, and diversity inside reserves may change through time. However, they give little insight into the initial responses to reserve protection.

For the second approach to analysing the temporal changes in reserve impact, we used data from a subset of 17 studies that report data from before and after protection was implemented. Effectiveness index values for these studies were calculated and then regression analyses of these data were performed as described above. Furthermore, studies of seven reserves also made measurements at several points in time after reserve initiation. For these data, average cumulative changes in effectiveness index values were calculated by comparing each value to initial values. Average rate of change over time was calculated by comparing each value to the previous value. Analyses of these temporal data allow for a more accurate determination of how particular biological communities respond to reserve protection over time.

RESULTS

Reserve response as a function of reserve age

At the time of evaluation, reserves varied in age from 1 to 40 y, with a mean of 11.2 y. None of the slopes of regressions of biological response vs. reserve age were significantly different from zero (linear regression analysis, $P > 0.35$ in all cases; see Fig. 1), and the grand mean for all four biological measures was significantly greater than zero (Student's t-test: density, mean EI = 0.28, $t = 8.21$, d.f. = 73, $P < 0.0001$; biomass, mean EI = 0.47, $t = 7.61$, d.f. = 33, $P < 0.0001$; size, mean EI = 0.12, $t = 5.78$, d.f. = 22, $P < 0.0001$; diversity, mean EI = 0.09, $t = 3.68$, d.f. = 30, $P < 0.001$; see also Halpern 2002). Furthermore, grand mean values of biological measures for reserves $\leqslant$ 5 y old were equal to grand mean values for all other reserves (Student's t-test, density: $t = 1.83$, d.f. = 54, $P = 0.07$; biomass: $t = 1.26$, d.f. = 26, $P = 0.22$; size: $t = 0.20$, d.f. = 14, $P = 0.85$; diversity: $t = 1.17$, d.f. = 28, $P = 0.25$). Classifying young reserves as those $\leqslant$ 5 y old allowed for at least 10 data sets for young reserves for all biological responses except average organism size, permitting an adequate statistical comparison of young vs. old reserves. Thus, while density, biomass, average size and diversity of organisms are all significantly higher inside reserves relative to reference sites (Halpern 2002), there is no indication of overall change in these values over time.

The above analyses did not account for reserve size. It is possible that reserve size affects the rate at which density, biomass, etc. respond to reserve implementation. For example, the benefits of reserve protection may accrue more slowly in small reserves because dispersing organisms (both as larvae and as adults) may not encounter the reserve as readily, or may be more likely to leave the reserve. However, we found no significant interaction between reserve size and age in their affect on biological responses inside reserves (ANOVA: density $P = 0.42$; biomass $P = 0.84$; diversity $P = 0.52$).

Temporal patterns within reserves

The foregoing analyses considered conditions inside reserves as a function of reserve age, but were not able to track changes over time in specific reserves. Analyses of data from the 17 studies that compared values of density, biomass, average organism size, and/or diversity before and after reserve protection offer more direct evidence that these biological measures respond quickly to reserve
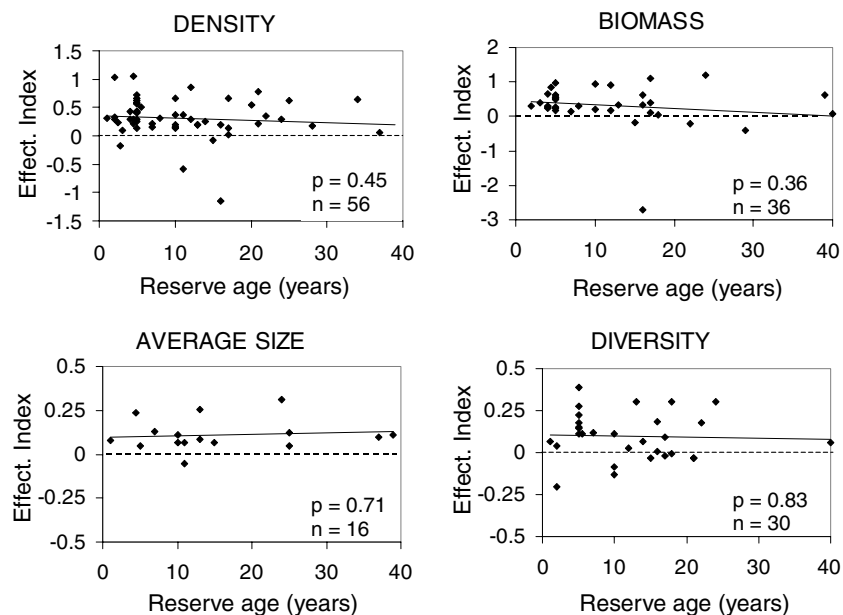

Figure 1 Log$_{10}$ ratios of values from inside a reserve vs. values from a reference site for density (no./area), biomass (kg/area), average organism size, and diversity (species richness) as a function of the age of the reserve. For the majority of cases, these data represent comparisons between values inside vs. outside the reserve. Data are plotted as the log$_{10}$ of the ratio (effectiveness index) vs. reserve age at the time measurements were made. Because ratios are log$_{10}$-transformed, at effectiveness index = 0 reserves did not differ from their reference site. Points above this line represent reserves in which the value of the biological measure was higher inside the reserve; points below the line represent reserves in which these values were lower. In all cases slopes of regression lines are not significantly different from zero (sample size and P-values for linear regression analyses for each biological measure are in the lower right corner of each plot), whereas grand mean values were all greater than zero (Student's t-test, $P < 0.025$ for all cases).

protection. In a pattern very similar to that seen above, the slope of the regression of density against reserve age was not significantly different from zero ($P = 0.68$), while the grand mean value was significantly positive (Student's t-test, mean EI = 0.26, $t = 2.60$, d.f. = 14, $P < 0.025$; see Fig. 2). Results are similar for biomass (regression analysis, $P = 0.54$; Student's t-test, mean EI = 0.46, $t = 3.05$, d.f. = 5, $P < 0.025$), but insufficient data were available from these 17 studies for analysis of temporal change in average size or diversity of organisms.

To capture the actual time course of responses inside reserves, we analysed the few examples of repeated measures within a particular reserve. Here, the rapidity of response can be gauged by comparing the rate of change of biological measures at each successive time step (either annual or biennial). If organisms respond quickly to protection, initial rates of change should be greater than later rates. For the seven studies of reserves that recorded temporal data, the rate of change for density, calculated as the ratio of the values at one time step divided by the value at the previous time step, was significantly greater for the first time step compared to all other time steps (one-way ANOVA, $P < 0.05$; see also Fig. 3A). Cumulative density ratios at each time step (values for each time step relative to initial value; Fig. 3B), and actual density trajectories (Fig. 3C) for each reserve further illustrate the very rapid responses. This pattern was not apparent for biomass and diversity, but sample sizes may simply be too small to detect a significant difference ($n = 3$ and 6, respectively). Furthermore, in all but one case the first or second time step had the fastest rate of increase (Fig. 3C).
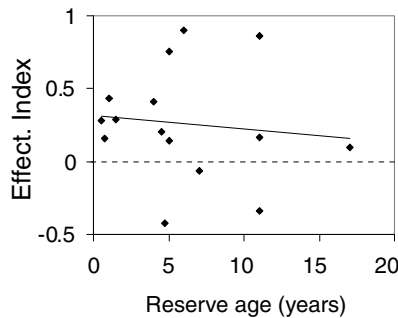

Figure 2 Log$_{10}$ ratios of values of density from inside a reserve vs. before reserve protection as a function of reserve age. In contrast to Fig. 1, these are before–after data, so each point represents the density value measured at the end of the monitoring period divided by the value measured before reserve protection. These data represent a subset of the data in Fig. 1. See legend in Fig. 1 for explanation of the specifics of the graph format. The grand mean of these data is significantly positive (Student's t-test, $t = 2.60$, d.f. = 14, $P < 0.025$) and the slope of the regression line is not significantly different from zero ($P = 0.68$).
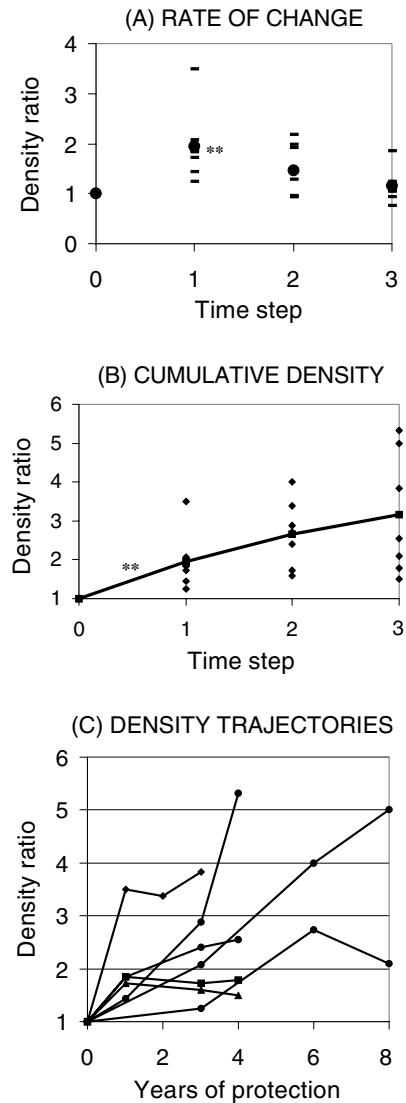

Figure 3 (A) Rate of change, (B) cumulative values of density, and (C) actual density trajectories in reserves for which successive temporal data were collected. Analyses were all done on log$_{10}$-transformed data; values were then back-transformed for presentation in these figures. For (A) and (B) time steps are primarily annual, biennial, or a mix of annual and biennial. Actual times of measurements for each reserve are shown in (C), which plots the change in density relative to time 0 through the course of each study. Time step 0 represents values from before reserve protection or shortly thereafter and a density ratio = 1 indicates no change between times or time steps. In (A), density ratios are calculated by dividing values at one time step by values at the previous time step ($t / t - 1$). The large circles represent mean values for each time step. In (B) and (C), density ratios are the value at a time step divided by the initial value at time step = 0. The line connects mean values for each time step. Values (in A) or slopes (in B) significantly different from other time steps are marked with ** in the figure (one-way ANOVA, $P < 0.05$). The greatest rate of increase in density occurs in the first time step.

DISCUSSION

Marine ecological theory does not predict how quickly communities should respond to reserve protection, although anecdotal evidence suggests that the response can occur in less than 2 y (Roberts 1995; Russ & Alcala 1998a). The consistent pattern seen in Fig. 1 suggests that biological measures likely attain near-mean values within the first 1–2 y after protection, since even the youngest reserves (6 months to 2 y) have values already at mean levels. These results are corroborated by our analyses of the studies that tracked temporal changes in reserve effect for individual reserves. Therefore, the establishment of marine reserves appears to result in significant increases in average levels of density, biomass, and likely diversity within 1–3 y, and these values persist through time. Furthermore, these results are independent of reserve size. These are very encouraging results for those facing societal and management expectations that marine reserves provide rapid and persistent biological responses.

However, it is important to realize the limitations of these results. First, we analysed mean responses, and results for a particular species will certainly depend on their life-histories (Russ & Alcala 1998b; Jennings *et al.* 1999a,b). Slow-growing, late-maturing species, and those with infrequent or highly variable recruitment levels will probably respond much more slowly to reserve protection than short-lived, fast-growing species. For example, after massive reserve closures in the Georges Bank area (located off of the New England coast), cod stocks have been slower to respond to protection, whereas scallop populations quickly grew to enormous size (Murawski *et al.* 2000). Cases such as this one highlight the importance of considering life-history traits when forming goals or expectations for reserve performance.

Second, rapidity of response of a species to reserve protection will also depend to some extent on the degree of exploitation of that species. Heavily targeted species are more likely to respond quickly to the implementation of reserves, assuming recruitment occurs at high enough levels, because the main factor limiting the population size and demography of the target species (fishing) is suddenly removed (Polacheck 1990; Carr & Reed 1993; Rowley 1994). Thus the degree of exploitation of a particular species could potentially influence conclusions about the speed (and degree) to which populations respond to reserve protection. This factor was probably not a major determinant of our results. Over half of the studies reviewed were of whole communities where both target and non-target species were surveyed. In particular, of the seven temporal studies analysed, three were of whole communities and two of these three had the second and fourth fastest initial rates of increase. It remains important, of course, to consider the degree of exploitation of a species as a potential bias in interpretations of the temporal patterns in the biological impacts of reserve protection. This issue is particularly important for conservation reserves that are intended to protect all species (targets and non-targets). Fisheries reserves, on the other hand, are primarily expected to affect particular target species. Because we analysed data for both target and non-target species, responses by target species alone to reserve protection may be even more rapid and dramatic than our results indicate.

The trophic position of a species often correlates to its life-history traits and the degree of its exploitation. Carnivores, which are most often the targets of fisheries, are also generally long-lived, slow-growing species. Therefore, one might expect that carnivores display different temporal responses to reserve protection compared to herbivores or other trophic groups. However, as we stated in the Methods, analyses showed that results for all trophic groups were equivalent to overall results and therefore to each other. Carnivores as a guild showed no distinct differences in response to reserve protection, although individual species may respond according to their life-history traits or degree of exploitation.

The results from this study indicate that some of the anticipated functions of marine reserves (e.g. species conservation, increased production) should be attained relatively quickly and persist through time. Other functions (notably the enhancement of conditions outside reserve boundaries) were not addressed in these studies but are of great importance if reserves are to be used in fisheries management. There is a real need of studies that document the export functions of reserves over time (e.g. Roberts *et al.* 2001) to see if such export mirrors the striking responses occurring within reserve boundaries shown here.

ACKNOWLEDGEMENTS

REFERENCES

Attwood, C.G. & Bennett, B.A. (1995). Modelling the effect of marine reserves on the recreational shore-fishery of the south-western cape, South Africa. *South African J. Mar. Sci.*, 16, 227–240.

Carr, M.H. & Reed, D.C. (1993). Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Can J. Fish Aquat. Sci.*, 50, 2019–2028.

Castilla, J.C. & Bustamante, R.H. (1989). Human exclusion from rocky intertidal of Las Cruces, central Chile: effects on *Durvillaea antarctica* (Phaeophyta, Durvilleales). *Mar. Ecol. Progr. Series*, 50, 203–214.

Conan, G.Y. (1986). Summary of session 5: recruitment enhancement. *Can J. Fish Aquat. Sci.*, 43, 2384–2388.

Demartini, E.E. (1993). Modeling the potential of fishery reserves for managing pacific coral reef fishes. *Fishery Bull.*, 91, 414–427.

Dufour, V., Jouvenel, J.Y. & Galzin, R. (1995). Study of a Mediterranean reef fish assemblage: comparisons of population distributions between depths in protected and unprotected areas over one decade. *Aquat. Living Resources*, 8, 17–25.

Dugan, J.E. & Davis, G.E. (1993). Applications of marine refugia to coastal fisheries management. *Can J. Fish Aquat. Sci.*, 50, 2029–2042.

Ferreira, B.P. & Russ, G.R. (1995). Population structure of the leopard coral grouper, *Plectropomus leopardus*, on fished and unfished reefs off Townsville, Central Great Barrier Reef, Australia. *Fish Bull.*, 93, 629–642.

Halpern, B.S. (2002). The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Applic.*, in press.

Jennings, S., Greenstreet, S.P.R. & Reynolds, J.D. (1999a). Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. Anim. Ecol.*, 68, 617–627.

Jennings, S., Reynolds, J.D. & Polunin, N.V.C. (1999b). Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Conserv. Biol.*, 13, 1466–1475.

Jones, G.P., Cole, R.C. & Battershill, C.N. (1992). Marine reserves: do they work? *Proceedings of the 2nd International Temperate Reef Symposium*, 29–45.

Man, A., Law, R. & Polunin, N.V.C. (1995). Role of marine reserves in recruitment to reef fisheries: a metapopulation model. *Biol. Conserv.*, 71, 197–204.

Murawski, S.A., Brown, R., Lai, H.-L., Rago, P.J. & Hendrickson, L. (2000). Large-scale closed areas as a fishery-management tool in temperate marine systems: The Georges Bank experience. *Bull. Mar. Sci.*, 66, 775–798.

NRC (National Research Council). (2001). Report of the committee on the evaluation, design and monitoring of marine reserves and protected areas in the United States. National Academy Press, Washington, DC, 288p.

Polacheck, T. (1990). Year around closed areas as a management tool. *Nat. Resource Modeling*, 4, 327–353.

Roberts, C.M. (1995). Rapid build-up of fish biomass in a Caribbean marine reserve. *Conserv. Biol.*, 9, 815–826.

Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P. & Goodridge, R. (2001). Effects of marine reserves on adjacent fisheries. *Science*, 294, 1920–1923.

Roberts, C.M. & Polunin, N.V.C. (1991). Are marine reserves effective in management of reef fisheries? *Rev. Fish Biol. Fish*, 1, 65–91.

Rowley, R.J. (1994). Marine reserves in fisheries management. *Aquat. Conserv.: Mar. Freshwater Ecosystems*, 4, 233–254.

Russ, G. & Alcala, A. (1996). Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecol. Applic.*, 6, 947–961.

Russ, G. & Alcala, A. (1998a). Natural fishing experiments in marine reserves 1983–93: community and trophic responses. *Coral Reefs*, 17, 383–397.

Russ, G. & Alcala, A. (1998b). Natural fishing experiments in marine reserves 1983–93: roles of life history and fishing intensity in family responses. *Coral Reefs*, 17, 399–416.

Sala, E., Ribes, M., Hereu, B., Zabala, M., Alva, V., Coma, R. & Garrabou, J. (1998). Temporal variability in abundance of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* in the northwestern Mediterranean: comparison between a marine reserve and an unprotected area. *Mar. Ecol. Progr. Series*, 168, 135–145.

Steneck, R.S. (1998). Human influences on coastal ecosystems: does overfishing create trophic cascades? *Trends Ecol. Evol*, 13, 429–430.

Wantiez, L., Thollot, P. & Kulbicki, M. (1997). Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. *Coral Reefs*, 16, 215–224.