

Garry R. Russ · Angel C. Alcala

Marine reserves: long-term protection is required for full recovery of predatory fish populations

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Abstract No-take marine reserves are advocated widely as a potential solution to the loss of marine biodiversity and ecosystem structure, and to over-fishing. We assess the duration of protection required for unfished populations of large predatory reef fish to attain natural states. We have monitored two marine reserves at Sumilon and Apo Islands, Philippines, regularly for 17 years (1983–2000). The biomass of large predatory fish was still increasing exponentially after 9 and 18 years of protection at Sumilon and Apo reserves, respectively. There was little evidence that the rate of accumulation of biomass inside the reserves was slowing down even after so many years of protection. This suggests that the length of time to full recovery will be considerable. We made two assumptions in order to estimate this period. Firstly, that biomass growth will follow the logistic model. Secondly, the conservative assumption that biomass had already attained 90% of the local carrying capacity of the environments in the reserves. We conclude that the time required for full recovery will be 15 and 40 years at Sumilon and Apo reserves, respectively. Such durations of recovery appear consistent with known life history characteristics of these fish, and with empirical data on recovery rates of heavily exploited fish stocks. By the time the full fisheries or ecosystem benefits from such reserves are apparent, human populations and impacts will have doubled in much of the developing world. Thus, networks of such reserves need to be implemented immediately. Furthermore, the management mechanisms for the reserves need to be successful over timescales of human generations.

Keywords Biomass · Logistic model · Marine reserves
Predatory reef fish · Full recovery

Introduction

No-take Marine Reserves (NTMR) are places where all forms of extraction, particularly fishing, are banned permanently (Roberts and Polunin 1991; Dayton et al. 2000; Gell and Roberts 2002). This form of spatial management has been advocated as a solution to many important and pressing problems within the marine environment (Dayton et al. 2000; Gell and Roberts 2002), such as loss of marine biodiversity (Jackson et al. 2001), alteration of trophic structures (Pauly et al. 1998, 2002; Babcock et al. 1999; Castilla 1999; Jackson et al. 2001), and chronic over-fishing (Pauly et al. 1998, 2002; Hutchings 2000; Jackson et al. 2001). At the same time, NTMR may bring social and economic benefits through enhanced tourism (Dayton et al. 2000; Gell and Roberts 2002).

In the past decade, studies of NTMR have produced a burgeoning literature (e.g. Roberts and Polunin 1991; Dayton et al. 2000; Gell and Roberts 2002; Russ 2002; Halpern 2003). The main expectations of marine reserves are that they will maintain segments of populations and ecosystems in natural states. In the case of exploited stocks, it is assumed that the protection of spawning biomass will lead to net export of adults and propagules that will sustain and perhaps enhance fisheries outside reserves (Russ 2002). However, there is still a notable dearth of empirical data by which to judge these expectations (Polunin 2002; Russ 2002; Willis et al. 2003).

The literature on NTMR has concentrated on the relative merits of this approach to traditional fisheries management (Hastings and Botsford 1999; Gerber et al. 2003), the amount of area to protect (e.g. Sladek-Nowlis and Roberts 1999; Gerber et al. 2003) and the optimal placement of reserves (e.g. Gell and Roberts 2002; Gerber et al. 2003). However, a simple, albeit critical, question

G. R. Russ (✉)
School of Marine Biology and Aquaculture, James Cook
University,
4811 Townsville, Queensland, Australia
e-mail: Garry.russ@jcu.edu.au
Fax: +61-617-47251570

A. C. Alcala
Silliman University Angelo King Center for Research and
Environmental Management, Silliman University,
6200 Dumaguete City, The Philippines

that is rarely asked is what duration of protection is required for populations in NTMR to return to virgin states, as far as this is possible when the majority of other places remain disturbed by humans? A common message found in the literature is that the abundance of target species often increases rapidly following establishment of marine reserves (Roberts 1995; Halpern and Warner 2002). For example, a recent review of 112 independent measurements of 80 reserves (Halpern and Warner 2002) concluded 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 years) period of time and that the values are subsequently consistent across reserves of all ages (up to 40 years)". Few (only seven) of these studies were monitored over time. Most of these few monitoring studies were of less than 4 years' duration. McClanahan (2000) predicted that >30 years might be required to achieve full recovery of an important food fish on Kenyan coral reefs. The question of time required for full recovery remains an open one, with few longitudinal studies, and an emphasis, to date, upon single snapshots taken shortly after the removal of the human disturbance factor (Russ and Alcala 1996a, 2003; Kelly et al. 2000; Jennings 2001; Russ 2002).

We have been monitoring populations of exploited coral reef fish regularly in two small marine reserves in the Philippines that have been protected for longer than most other NTMRs in the world. Here, we present data from 17 years to ask "what duration of protection from fishing will be required for the biomass of large predatory reef fish within these reserves to reach a stable state reflecting their local carrying capacities?"

Materials and methods

The study was conducted in the central Philippines at Sumilon Island (9°21'N, 123°23'E) and Apo Island (9°4'N, 123°17'E). Sumilon Island is a coralline island of 0.23 km², surrounded by a fringing coral reef of 0.5 km² to the 40 m isobath. Apo Island is a mainland island of 0.7 km² surrounded by 1.06 km² of fringing coral reef to the 60 m isobath (0.7 km² to the 20 m isobath). Russ and Alcala (1996a) provide a detailed description of the study sites. Sumilon Island had a 0.75 km-long marine reserve (approximately 25% of the coral reef area) established on its western side in December 1974. The area of the reserve to 500 m from shore is 37.5 ha. Apo Island had a 0.45 km-long marine reserve (approximately 10% of the coral reef area) established on its south-eastern side in late 1982. The area of the reserve to 500 m from shore is 22.5 ha. At Sumilon reserve, a complex history of management (Russ and Alcala 1999) allowed 13 measurements of fish biomass at durations of reserve protection ranging from -3 (i.e. fished for 3 years after reserve status removed) to 9 years over the period 1983–2000. At Apo reserve, 13 measurements were taken at durations of reserve protection ranging from 1 to 18 years over the same period. Estimates of fish biomass were made at each reserve in December or November of each year from 1983 to 2000 except for the years 1984, 1986–87 and 1996. This resulted in 13 measurements of biomass over the period 1983–2000. Six 1,000 m² replicate areas of reef slope were surveyed by Underwater Visual Census (UVC; Russ and Alcala 1996a) in the two reserves (2 or 6–17 m depth) and at two fished control sites (9–17 m) at each island on each sampling occasion. Four data points collected for the Sumilon

Island control site (1988, 1990, 1991 and 1992) were omitted. During this period, fishing was banned at this site and the biomass of predatory fish increased (Russ and Alcala 1996a, 2003). The areas censused represented 100% and 40%, respectively, of the shallow reef slopes (reef crest to 17 m) of the Apo and Sumilon reserves. The observer (G.R.R.), the method of UVC and the position of the replicates were the same in all years. All individual fish in the families Serranidae (Epinephelinae), Lutjanidae, Lethrinidae and Carangidae were counted in each replicate, and their total lengths (TL) estimated to the nearest 5 cm. Fish <10 cm TL were not counted. We treat these four families as a guild of large predatory reef fish. Length-weight relationships were used to convert density and size-structure data into biomass (Russ and Alcala 1996a).

An exponential model best described the relationship between biomass per unit area (B_t) and duration of protection (t) at each island (Russ and Alcala 2003). Eventually, however, biomass should asymptote as the local carrying capacity of the reserves is reached. We made two assumptions in order to estimate the duration of protection required to attain this asymptote. Firstly, that biomass growth will follow the logistic model. Secondly, that biomass has already attained 90% of the local carrying capacity of the environments in the reserves. We believe that the latter assumption is conservative, given that there is little evidence in the empirical data of a slow down in the rate of biomass accumulation in either reserve (see Fig. 1). We defined the carrying capacity of the local environment as the biomass at which the per capita population growth rate of this guild of predatory fish is zero. We assume that the biomass of the guild of large predatory reef fish will follow the same pattern of growth as that for a single-species population. In order to estimate the duration required for these fish to attain the carrying capacity of their environment, we used a non-linear estimation to find the best-fitting logistic growth models. The model is $B_t = K [1 + e^{-r(t+t_0)}]^{-1}$, where B_t is biomass (g/m²), K is carrying capacity, r is the intrinsic rate of natural increase, t is duration of protection and t_0 is the theoretical time at which biomass is zero (Kaufman 1981). The parameters to be estimated in this model are K , r and t_0 . Attempts to estimate K from the data provided unrealistically high values, since the increase in biomass with reserve protection was still in an exponential phase (Fig. 1). We set K at 20 g/m² at Sumilon reserve and 25 g/m² at Apo reserve, by assuming that the maximum observed biomass was 90% of the local K at each reserve. We argue that these are realistic but conservative estimates of K . The estimates are similar to reliable estimates of 25–30 g/m² for these families of reef fish collected by UVC from reefs closed to fishing for 7 to 15 years on the relatively lightly fished Great Barrier Reef (GBR) of Australia (Newman et al. 1997, central GBR; Russ, Zeller, Hatcher and Williamson, unpublished data from Lizard Island and the Palm Islands).

Results

The best-fit models of change in biomass of large predatory fish with years of reserve protection were $B_t = 2.71 \times e^{0.19t}$ ($r^2 = 0.82$) for Sumilon reserve and $B_t = 1.94 \times e^{0.13t}$ ($r^2 = 0.86$) for Apo reserve (Russ and Alcala 2003). These exponential models explained 14% and 11% more of the variance than linear models of biomass per unit area (B_t) against duration of protection (t) at each island. Biomass of large predatory fish was still increasing exponentially after 9 and 18 years of protection in Sumilon and Apo reserves, respectively (Fig. 1). Biomass of these fish ranged from 1.4 to 17.8 g/m² at Sumilon reserve, and 1.3 to 22.7 g/m² at Apo reserve (Fig. 1). There was no significant relationship between biomass of large predatory reef fish and time during the time that Sumilon nonreserve (control site) was open to fishing (Fig. 1;

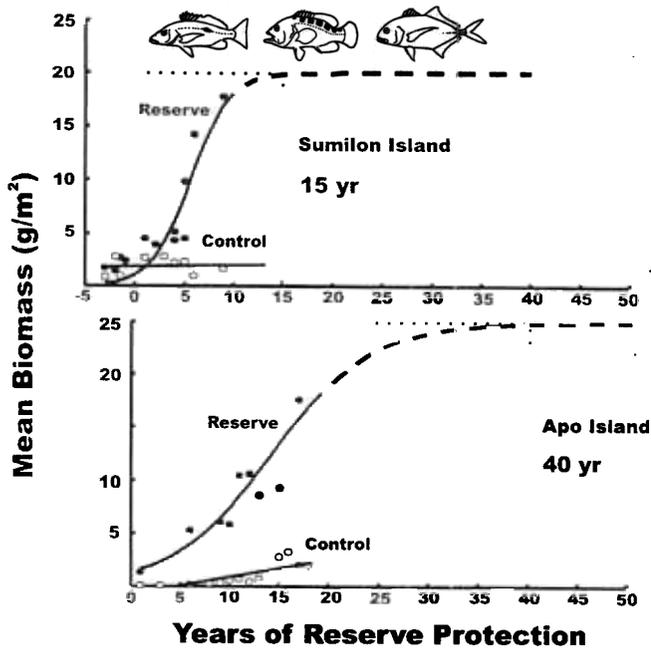


Fig. 1 Best-fit logistic growth models fitted to mean biomass per unit area against years of reserve protection for Sumilon and Apo reserves, Philippines over the period 1983–2000. *Black points* reserves; *open points* control (fished) sites. *Dashed portion* of best-fit logistic model is the prediction beyond the data to carrying capacity (K). These K values were arbitrarily set 10% above empirically observed maxima of biomass at each reserve (20 and 25 g/m^2 at Sumilon and Apo reserves, respectively). Negative values on the x -axis at Sumilon reserve is time open to fishing immediately following cessation of protection. Biomass accumulation over time was close to zero at the control site at Sumilon Island. Biomass had a slow but significant linear increase at the control site at Apo Island during the study. Asymptotes of large predator biomass are predicted at 15 years of reserve protection at Sumilon reserve, and 40 years of reserve protection at Apo reserve

$B_t = 0.01t + 1.87$; $r^2 = 0.003$). Biomass remained around 2 g/m^2 for most of this time (Fig. 1). At the Apo control (fished) site, biomass of large predatory reef fish remained below 1 g/m^2 for the majority of the 17-year study. However, there was a significant positive linear relationship between biomass and time at Apo nonreserve (Fig. 1; $B_t = 0.16t + 0.70$; $r^2 = 0.640$).

The best-fit logistic population growth models were $B_t = 20 \times [1 + e^{-0.51(t-5.63)}]^{-1}$ for Sumilon reserve and $B_t = 25 \times [1 + e^{-0.20(t-14.29)}]^{-1}$ for Apo reserve (Fig. 1). These best-fit models suggest that large predatory fish would reach >99% of carrying capacity in 15 years at Sumilon Reserve and 40 years at Apo Reserve (Fig. 1).

Discussion

Our results show that the biomass of fish targeted by fisheries can increase exponentially when protected inside no-take marine reserves (Fig. 1; Russ and Alcala 2003). The exponential pattern of increase does not necessarily mean that the absolute rate of increase is high. The exponents of the relationships for both reserves are well

below unity when time is measured in years (0.19 for Sumilon, 0.13 for Apo). Furthermore, the exponential pattern of increase implies that, on average, the initial rate of build up of biomass will be slow. Our data suggest that the duration of continuous, successful protection to attain the expected full ecosystem and fishery benefits of reserves will be measured in time scales of 15–40 years for large predatory reef fish.

We have made two assumptions in order to reach this conclusion. The first assumption, that the pattern of biomass buildup inside the reserves will eventually conform to logistic population growth, is consistent with basic population ecology (Begon et al. 1996). The second assumption, that biomass has already attained 90% of the local carrying capacity (K) of the environments in the reserves, requires justification. There are three possible interpretations of how our empirical results relate to potential K (L. Crowder, personal communication): that local K has not yet been reached; that it has been reached and not detected; or that it has been exceeded and is about to return to K , and this has not been detected. However, the rate of increase in biomass with years of protection does not appear to be slowing (Fig. 1). Thus, the first possibility is the most probable. We suggest the assumption that our data represent 90% of K is conservative, and somewhat arbitrary. Any percentage less than this increases the predicted time to full recovery considerably.

If 90% of carrying capacity has been attained already, some could argue that such a level of recovery was adequate. Given the shape of the logistic curve, the extra duration of protection required to proceed from 90% to full recovery may not be an important consideration in practice. We have two responses to such arguments. Firstly, marine reserves are often proposed as mechanisms to allow ecosystems to attain natural states (Dayton et al. 2000; Gell and Roberts 2002; Pauly et al. 2002). Evidence is emerging from marine reserve research that effective, long-term protection can lead to recovery of community and ecosystem function (Castilla 1999). It could be argued that until these important predators in coral reef systems recover fully, ecosystems would not have fully recovered. The abundance of predators close to the top of the trophic structure of coral reefs may be a proxy for the status of the ecosystem (Jennings and Kaiser 1998). Secondly, we stress that it took almost 10–20 years to attain the levels of recovery we have observed already, and we still cannot recognize a clear asymptote of large predator biomass. This stresses the main point of this paper—that times to full recovery will be considerable.

At both reserves, biomass of large predatory fish rose sharply near the end of this study (Fig. 1). These rapid increases were caused by good recruitment and growth of individual fish. Such rapid increases may unduly influence the shape of the fitted logistic curves. In particular, they will influence the t_0 , and perhaps the length of time at which the asymptote is reached. It is thus possible that this duration to full recovery may be over-estimated at Apo. However, from a precautionary viewpoint, the duration

estimated at Sumilon is likely to be a minimum time for recovery of this guild.

Jennings (2001) reviewed patterns of population recovery in marine reserves. He identified the main factors that would affect rates of recovery: initial population size, intrinsic rate of population increase (r), the nature of the stock-recruitment relationship, metapopulation structure, the success of individual recruitment events, and the extent of reduction of fishing mortality (F) in the reserve. Initial biomass of local populations was small at the start of the recovery process in this study (Fig. 1; $<1.5 \text{ g/m}^2$ at both reserves). The intrinsic rates of local population increase (r), calculated from our empirical data, would be considered low for Apo reserve (0.20) but high for Sumilon reserve (0.51) (Jennings 2001). High values like that at Sumilon may be possible in small patches of the metapopulation, over certain periods of time. We have no empirical data on the stock-recruitment relationships of large predatory reef fish at the scales of our study sites, nor at the metapopulation scale. Our assumption is that the populations at the two islands are "open" (Caley et al. 1996) and represent a small spatial component of a larger metapopulation. Furthermore, we cannot say if the period of study represented a "typical" period with respect to recruitment at each reserve. Recruitment pulses (rapid addition of individuals to the population by the process of settlement and survival to 10 cm TL) did affect rates of recovery of large predatory fish substantially, but such events were more common at Sumilon reserve (Russ and Alcala 1996a, 2003). Fishing mortality is rarely measured in reserves and fished sites over time, but can be inferred to differ based on knowledge of the effectiveness of protection. The effectiveness of protection of the two reserves over the relevant periods has been well-documented (Russ and Alcala 1999).

Our results are consistent with expectations based on life history characteristics. Maximum potential longevity of many species of large predatory reef fish, and many species of coral reef fish in general, range from 15–45 years (e.g. Cappo et al. 2000; Choat and Robertson 2002). Most species of coral reef fish have highly variable recruitment, with very large year classes often appearing as infrequently as every 5–10 years (Doherty 1991, 2002). Furthermore, once such fish have recruited, the maximum rates of biomass gain may not occur until the fish reach 2–4 years of age (Russ and Alcala 1996a). The exponential increase in biomass in our reserves is driven largely by a higher survivorship of recruits and the rates of increase in body mass with fish age. There is no suggestion that an increase in biomass within the reserves led directly to increased recruitment within the reserves. However, a recent study has demonstrated "self recruitment" of a coral reef fish at the scale of an individual reef (Jones et al. 1999). It is possible that the observed rates of biomass build-up may have been reduced due to very high harvest rates on Philippine coral reefs, reducing recruitment magnitude and frequency at the scale of the self-contained breeding populations (McManus 1997). We have no evidence to suggest that small-scale movements of fish

into the reserve areas (Jennings 2001) influenced the patterns of biomass buildup. In theory, adult fish may show net movement into reserves when the reserves are first closed ("spill-in"). This could be a behavioural response of the fish to avoid areas disturbed by fishing. We have no evidence for this occurring at either of our reserves. It is actually possible that the rates of biomass build-up may have been reduced by spillover (net export of adults) due to the small size of the reserves (Alcala and Russ 1990; Russ and Alcala 1996b). In fact, we have argued elsewhere (Russ and Alcala 1996b) that the gradual linear increase in biomass of large predatory fish in the Apo nonreserve site (Fig. 1) may have been influenced by spillover from the reserve.

Only one other study (McClanahan and Kaunda-Arara 1996) has monitored rates of biomass increase of large predatory fish (Lethrinidae) inside a reserve over a period of >5 years. These authors reported a 2.2-fold increase in biomass of lethrinids over 6 years in the Malindi Marine National Park in Kenya. Roberts et al. (2001) reported a 3-fold increase in biomass of five families of commercially targeted fish inside five reserves over a 5-year monitoring period in St Lucia. No empirical data appears to be available, as yet, to demonstrate biomass of large predatory fish reaching an asymptote (K) within any marine reserve (Russ 2002). Our conclusions are consistent with those of Kelly et al. (2000), who reported sustained rates of increase in abundance of lobsters in New Zealand marine reserves up to 21 years old. Our conclusions are also consistent with the suggestion of McClanahan (2000) that recovery times of an important reef fish predator on Kenyan coral reefs, *Balistapus undulatus*, may be >30 years. McClanahan (2000) based this conclusion largely on comparisons of abundance and predatory impact of this species in marine parks of different age at the one time.

Our conclusions are also consistent with a recent analysis of recovery rates of a wide range of teleost fish following stock-wide declines in abundance caused by fishing (Hutchings 2000). Hutchings reported that many of the 90 stocks he studied had experienced little, if any, recovery as much as 15 years after 45–99% reductions in reproductive biomass of the stock. Hutchings concluded that the time required for recovery appeared to be considerable.

The data reported here are not consistent with the conclusions reached recently by Halpern and Warner (2002). They suggested that abundance (density, biomass) often reached mean levels in reserves within short (1- to 3-year) periods of time, and that these values were subsequently consistent across reserves of all ages (up to 40 years). The vast majority of the studies they reviewed were spatial comparisons of reserve and fished sites at one time. Such spatial comparisons at one time are often confounded by choice of reserve site (reserves are often placed where fish densities and diversities are high to begin with) and habitat (reserves are often placed where benthic habitat is of good quality, and thus fish abundance is high). Furthermore, the regression analyses they used

were confounded by differences in poaching histories of the reserves, and would probably have little statistical power to detect rates of temporal change. Such problems will be present irrespective of the life history characteristics of the target species. Thus, the paucity of temporal monitoring studies available to Halpern and Warner (2002) make their generalizations about rates of change with time problematic. In the present study, the biomass buildup showed no sign of reaching a "mean level" in such a short period as 1–3 years.

Marine reserves are considered potentially useful tools for future management of fisheries (Roberts and Polunin 1991; Gell and Roberts 2002; Russ 2002) and maintenance of biodiversity and ecosystem structure (Castilla 1999; Dayton et al. 2000; Gell and Roberts 2002; Pauly et al. 2002). Marine reserves are one of the few viable management options for fisheries and biodiversity maintenance in developing nations (Polunin 1990; Roberts and Polunin 1991; Russ 2002). During the 15–40 years required to attain full effectiveness of this management tool, the human population of the Philippines will double (National Statistics Office of the Philippines, Population census, 1 September 1995, <http://www.census.gov.ph/data/sectordata/pop0.html>). The fishing pressure on Philippine coral reefs, and in many other reef systems in the developing world, is considered unsustainable now (McManus 1997). The potential success of marine reserves as a fisheries management tool is still the subject of intense debate in the ecological literature (e.g. Sale and Cowen 1998; Dayton et al. 2000; Roberts et al. 2001; Hilborn 2002; Polunin 2002; Russ 2002; Gerber et al. 2003; Willis et al. 2003). Even if marine reserves were successful in this context, can they be implemented before large-scale fisheries collapses occur?

Protecting marine reserves successfully for 15–40 years is an inter-generational human problem. We argue that marine reserves must be implemented immediately, even if for no other reason than as an insurance policy against future fisheries collapses (Bohnsack 1998). Community-based management or co-management (Russ and Alcalá 1999) provides the best hope of establishing marine reserves for long enough to perhaps prevent overexploitation of marine resources in developing nations on a massive scale.

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