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No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef

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SUMMARY

The application of no-take marine reserve status to an area is expected to increase abundance and average size of individuals of species targeted by fisheries. The majority of the evidence supporting such expectations still involves comparisons of abundance at the one time of sites with and without marine reserve protection. Very few studies have data on the abundance and size structure of species targeted by fisheries in an area before reserve status is applied. Quantitative estimates of density and biomass of coral trout, *Plectropomus* spp., the major target of the hook and line fisheries on the Great Barrier Reef (GBR), Australia, on inshore fringing reefs of the Palm and Whitsunday Island groups, central GBR, are provided for 3–4 years before (1983–1984), and 12–13 years after (1999–2000) the establishment of no-take reserves in 1987. Quantitative estimates of density and biomass of coral trout in areas open to fishing were also collected in 1999–2000 at these two island groups. Density and biomass of coral trout increased significantly (by factors of 5.9 and 6.3 in the Palm Islands, and 4.0 and 6.2 in the Whitsunday Islands) in the reserve sites, but not the fished sites, between 1983–1984 and 1999–2000. In 1999–2000, density and biomass of coral trout and a secondary target of the fisheries, *Lutjanus carponotatus*, were significantly higher in the protected zones than in the fished zones at both island groups. The density and biomass of non-target fish species (Labridae, Siganidae and Chaetodontidae) did not differ significantly between reserve and fished zones at either island group. This is the most convincing data to date that the management zoning of the world's largest marine park has been effective, at least for coral trout on inshore reefs.

Keywords: coral reef fishes, Great Barrier Reef, management zoning, no-take marine reserves, *Plectropomus* spp.

INTRODUCTION

Marine fisheries are showing clear signs of overexploitation (Pauly *et al.* 2002; Myers & Worm 2003). The situation is particularly serious in coral reef areas, where fish stocks are subject to unprecedented levels of exploitation because of increasing human populations and the advent of lucrative live reef fish exports to Asian markets (Polunin & Roberts 1996; Roberts 1997; Pauly *et al.* 2002; Sadovy & Vincent 2002).

Selective targeting and heavy exploitation of species of tropical reef fish at high trophic levels (for example Serranidae, Lutjanidae and Lethrinidae) is of major concern (Bohnsack 1998; Jennings & Kaiser 1998; Russ 2002; Myers & Worm 2003). Life history characteristics of such species, and the formation of seasonal spawning aggregations, make them particularly vulnerable to overexploitation (Roberts 1997; Sadovy & Vincent 2002). Decreases in the abundance, average size and biomass of predatory reef fish species, which are highly favoured targets of fisheries, are expected to be one of the most readily detectable direct effects of fishing (Myers & Worm 2003; Russ & Alcala 2003; Willis *et al.* 2003*a*). Furthermore, depletion of large predatory reef fishes can cause significant impacts upon prey species and the structure of coral reef communities (McClanahan and Muthiga 1988; Hughes 1994; Graham *et al.* 2003).

No-take marine reserves are popular for their dual potential as conservation and fishery management tools (PDT [Plan Development Team] 1990; Polunin 1990; Roberts & Polunin 1991; Roberts *et al.* 2001; Gell & Roberts 2002; Russ 2002; Willis *et al.* 2003*b*). No-take marine reserves are perceived as a means to protect marine habitats and communities, separate conflicting uses of marine resources, enhance tourism opportunities and act as reference areas for investigating fishing effects (Bohnsack & Ault 1996; Roberts 1997; Gell & Roberts 2002). Marine reserves have been widely advocated as a relatively simple and effective means of managing multi-species reef fisheries (PDT 1990; Roberts & Polunin 1991; Roberts 1997; Gell & Roberts 2002; Russ 2002). Inside no-take reserves, species targeted by fisheries are expected to increase in abundance and mean size. Eventually reserves are expected to influence fisheries outside them by becoming net exporters of biomass to fished areas (Russ 2002).

In the Great Barrier Reef Marine Park (GBRMP), Australia, about 23% of nearly 3000 individual coral reefs (approximately 4.6% of the total area of the Marine Park) are zoned as 'no-fishing' areas. Zoning plans for the GBRMP were first introduced in the southern region of the Park in July 1981, with the entire Marine Park under multiple-use zoning plans by July 1988. Williams and Russ (1994) reviewed available evidence of the effectiveness of reserve

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areas of the GBRMP (after 3–10 years of zoning) in protecting fish stocks. They found that the evidence for significantly increased densities of the major target of reef line fisheries, the coral trout (*Plectropomus leopardus*), was largely equivocal. Evidence that no-take reserves increased mean sizes and hook and line catch rates was more convincing (Williams & Russ 1994). More recent evidence also suggests that no-take zones may not have been as successful as expected in increasing density and average age of coral trout on mid- and outer-shelf reefs of the GBRMP (Zeller & Russ 1998; Adams *et al.* 2000; Ayling *et al.* 2000; Mapstone *et al.* 2003). However, experimental hook and line catch rates of coral trout are usually much higher in no-take zones than fished zones (Mapstone *et al.* 2003).

The paucity of strong reserve effects within the GBRMP could result from natural variability in the productivity of different reefs, or from relatively low fishing pressure on 'open' reefs (Williams & Russ 1994). However, measures of total mortality rates of the inshore coral trout (*Plectropomus maculatus*) (Ferreira & Russ 1992) and natural mortality rates of the common coral trout (*P. leopardus*) (Russ *et al.* 1998), suggest that this scenario is unlikely for many areas of the GBR. A third possibility is that movement of fish between reserve and fished reefs 'swamps' any effect of protection. Within the GBRMP the majority of no-take reserves protect entire reefs or clusters of reefs. Although coral trout can move considerable distances (up to 7.5 km) within reefs to reach spawning aggregation sites (Samoilys 1997; Zeller 1998; Davies 2000), Davies (2000) showed that movements of coral trout between reefs, across expanses of open sandy substrate, are unlikely. Movement of coral trout between reserve and fished reefs may occur in certain areas, but is dependent on factors such as distance between reefs and substrate composition of inter-reefal areas (Samoilys 1997; Zeller & Russ 1998).

Another potential explanation for the lack of strong reserve effects within the GBRMP is poaching (illegal fishing) on reserve reefs. Poaching can mask the effects of no-take reserves by selectively removing large fish from the population and rapidly reducing fish biomass (Russ & Alcala 2003). Some evidence suggests that poaching in no-take zones by both commercial and recreational fishers occurs in the GBRMP (Gribble & Robertson 1998; Davis *et al.* 2004). Most of the reefs on the GBR are a long distance (40–100 km) from the coast and are often hundreds of kilometres from centres of human population. This makes surveillance and enforcement of no-take zones difficult. The present study was carried out on inshore reefs (10–30 km from the coast), where recreational fishing pressure is greatest (Higgs & McInnes 2003) and surveillance is relatively effective (Davis *et al.* 2004).

The majority of studies examining the effects of marine reserves have involved spatial comparisons at one time of sites with and without reserve protection. Few studies have data on the abundance and size structure of species targeted by fisheries in an area prior to marine reserve status being applied (Jones *et al.* 1993; Russ 2002; Willis *et al.* 2003*b*). This study is one of the few conducted within the GBRMP, or elsewhere, to provide reliable data on abundance and size structure collected before establishment of no-take marine reserve status, and then collected after a substantial period of protection, to infer reserve effects. The aim of this study was to measure the effect of 12–13 years of no-take management zoning (1987 to 1999–2000) on target reef fish species on fringing reefs of near-shore island groups within the GBRMP.

METHODS

Study sites

Surveys were made on sections of fringing coral reef surrounding Orpheus and Pelorus Islands within the Palm Island group, and Hook, Whitsunday and Border Islands within the Whitsunday Island group (Fig. 1). Both of these island groups are situated within the central section of the GBRMP, Australia.

The Palm Island group (18°34′S, 146°29′E) is located approximately 15 km offshore from the Queensland coast and is made up of 10 granite-based continental islands. Great Palm Island is the largest in the archipelago, and has a resident Aboriginal community of around 3000 people. Other islands in the group are uninhabited national parks and Aboriginal land areas. A tourist resort and the James Cook University Research Station are located on the western side of Orpheus Island (Fig. 1). Except for these leases, the remainder of Orpheus Island is a national park. The local mainland council own Pelorus Island. There is a small private lease on the south-western corner of Pelorus Island that is permanently maintained by a caretaker, the remainder of the island is uninhabited. Orpheus and Pelorus Islands are separated by a channel, which is approximately 1 km wide and reaches a depth of 20–25 m (Fig. 1). The fringing reef surrounding Pelorus Island has remained open to fishing. The majority of the Orpheus Island reef area has been zoned as a protected no-take marine reserve since 1987 (Fig. 1).

The Whitsunday Island group (20°08′S, 148°56′E) includes approximately 55 granite-based continental islands, stretching between 1 km and 38 km from the Queensland coast. Several of the islands within the Whitsunday group have large tourist resorts. However, the three islands included in this study are national parks. The islands are primarily uninhabited, with the exception of a small tourist resort at the southern end of Hook Island (Fig. 1). The fringing reef surrounding Whitsunday Island and the Eastern side of Hook Island have remained open to fishing. Border Island and the northern end of Hook Island have been zoned as protected no-take marine reserves since 1987 (Fig. 1).

The fringing reefs of the Palm and Whitsunday Islands consist of a reef flat, crest and slope. The reef flat typically has a patchy cover of live coral (hard and soft), as well as expanses of dead coral, coral rubble and algal-covered rock. In most sites, the reef crest is at a depth of between 1 m and 2 m at mean tidal level. Beyond the crest, the reef slope

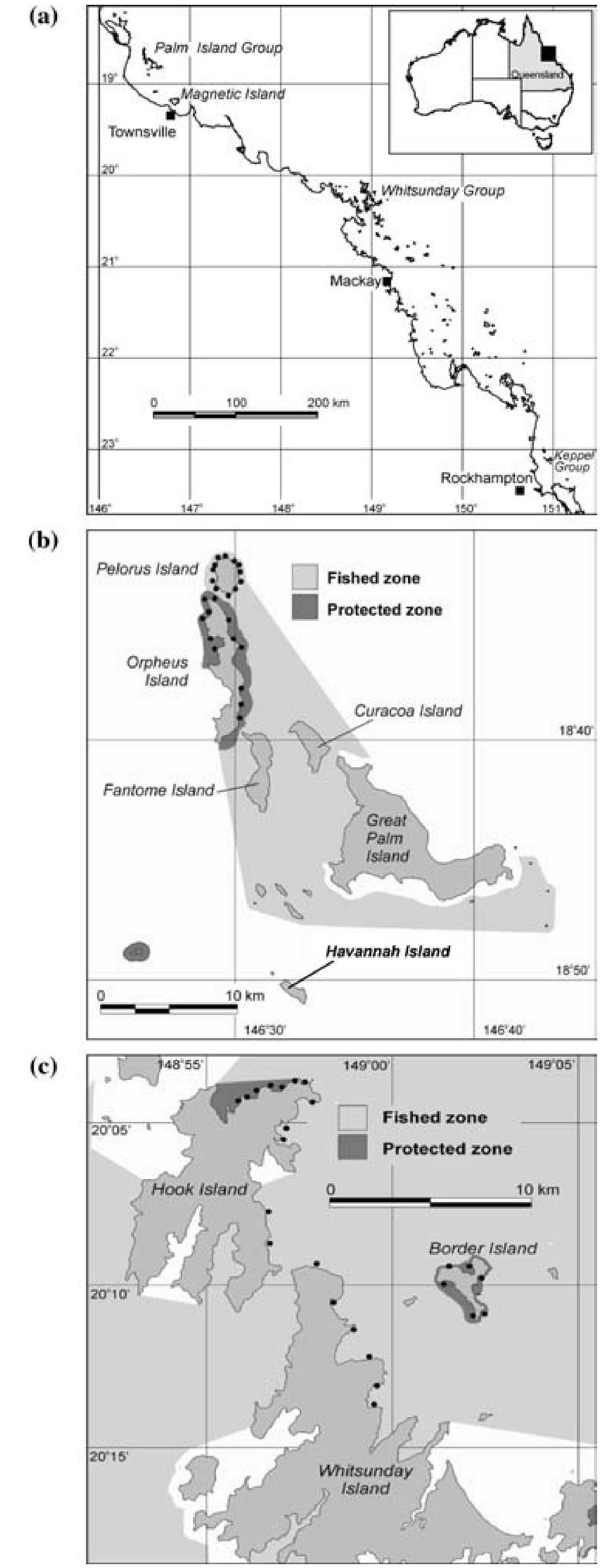


Figure 1 Maps of (*a*) the central section of the Great Barrier Reef Marine Park, (*b*) the Palm Island group and (*c*) the Whitsunday Island group, showing management zoning information. Black markers show the approximate position of sites surveyed within protected and fished zones in 1999–2000.

drops steeply to a depth of between 10 m and 20 m, where it levels out to a flat sandy bottom. In most sites, reef slope topography is complex, with many overhanging ledges and holes. Numerous bommies (distinct coral or rock outcrops) of varying sizes project from the reef slope and also rise out of deeper water beyond the base of the reef slope.

Both the Palm and Whitsunday Island groups are high-use recreational areas and are popular locations for boating, fishing and diving. There is a significant level of recreational fishing pressure (hook and line, and spear) on the fringing reefs of these island groups (Higgs & McInnes 2003). Compared with more remote areas of the GBRMP, there is a relatively high level of formal surveillance of these island groups by marine parks, fisheries, water police and coastguard vessels, and by coast watch and customs aircraft (Davis *et al.* 2004). Passive surveillance is carried out on a daily basis by local tourism operators, research station and resort staff, and by members of the community.

The current multiple-use zoning plan for the GBRMP was introduced in 1987. At the time of this study, the marine reserve areas of these fringing reefs had been formally protected for over 12 years.

Visual census of reef fishes

Fifty species of reef fish from eight families (Lutjanidae, Lethrinidae, Serranidae, Labridae, Haemulidae, Centropomidae, Siganidae and Chaetodontidae) were surveyed using a modified version of the underwater visual census (UVC) technique developed by Ayling and Ayling (1983). Using scuba, a single observer (D.H.W.) would slowly swim a 50 m transect line counting numbers and estimating the size (in 5 cm categories) of fishes within 3 m either side of the observer (a 300 m^2 survey area). A second diver would run the transect tape out behind the observer, to measure the distance covered. This method reduced disturbance to fish and minimized diver-negative behaviour of several of the surveyed fish species. All transects were conducted on the reef slope, parallel to the reef crest, at 4–12 m depth. The observer size estimation of fish was calibrated at the start of each day using wooden fish models.

The sessile benthic community was surveyed using a line-intercept method, which was conducted as each transect tape was reeled in. A point sample was taken every 2 m along each transect tape (25 samples per transect). Categories sampled were live hard coral (for example branching, bushy, tabular, massive, foliose, encrusting), soft coral, sponge, giant clams (*Tridacna* spp.), other invertebrates (such as ascidians and anemones), macro-algae and turf algae, dead coral, rock, rubble or sand. The observer visually estimated the structural complexity of the reef slope on each transect using a categorical scaling system (Table 1). Weather conditions and underwater visibility were recorded for each site. Surveys were not conducted if the underwater visibility was less than five metres.

Table 1 Categories of structural complexity of the benthic habitat, estimated visually on each transect at the Palm and Whitsunday Island groups.

Category	*Description*
1	Flat, sandy, expanses of rubble with some small scattered bommies (coral heads)
2	Bommies amongst mostly rubble and sand. Reef slope < 45°
3	Rubble amongst mostly coral bommies. Reef slope ~ 45°
4	Good reef structure with some overhangs and holes. Reef slope >45°
5	High reef complexity. Many overhangs, holes and caves. Large bommies. ~ 90° wall

Sampling design

Very few data exist on the status of fish and coral populations on fringing reefs in the Palm and Whitsunday Islands prior to the implementation of management zoning in 1987. A.M. Ayling collected data in 1983 and 1984, which has previously remained unpublished. These data provide the only reliable UVC estimates of density and size structure for coral trout (*Plectropomus* spp.) in the Palm and Whitsunday Islands prior to the establishment of the no-take protected areas. Coral trout (*Plectropomus* spp.) are the primary target species of the recreational and commercial hook and line fisheries on the Great Barrier Reef (Williams & Russ 1994). Three treatments were used to assess the effects of establishment of the no-take marine reserves on coral trout abundance: pre-protected, protected (reserve) and fished zones (non-reserve) (Table 2).

Pre-protected estimates of coral trout density and size structure were collected from the back reef slopes of Havannah and Curacoa Islands in the Palm Island group, and Border and Hook Islands in the Whitsunday Island Group. Five replicate 50 m × 20 m (1000 m^2) transects were conducted once in 1984 at two sites at each of the Palm Island group locations, and once in both 1983 and 1984 at two sites at each of the Whitsunday Island group locations (Table 2).

For sampling of the protected and fished zones in 1999–2000, six sites were randomly positioned within each of four locations in each island group (Table 2). Five replicate 50 m × 6 m (300 m^2) transects were sampled at each site in November 1999 (Whitsunday Islands) and March and June 2000 (Palm Islands). The only pre-protected (1983–1984) data available were for coral trout. Comparisons of density and biomass for species other than coral trout are thus restricted to two treatments; protected and fished, both sampled in 1999–2000.

Two weaknesses of this sampling design are acknowledged from the outset. Firstly, the 'before' data for the Palm Islands was not collected at the same islands within the Palm Island group as the 'after' data. Thus, the effect of no-take reserve protection is potentially confounded with any spatial variations between sites sampled at Curacao / Havannah with sites sampled at Orpheus/Pelorus (Table 2). This problem is not present at the Whitsunday Islands. The only way this weakness in sampling design at the Palm Islands could have been avoided was if 'before' data was collected at Orpheus and Pelorus islands during 1983–1984. A second weakness in the sampling design is that Orpheus Island has the only protected marine reserve in the Palm Island group. Thus, the location of all the protected sites on Orpheus, whilst unavoidable for the Palm Island group, could be considered pseudoreplication. The same criticism applies to the location of all the fished sites on Pelorus Island in 2000.

D.H. Williamson was unaware of the existence of the pre-protection (1983–1984) data for *Plectropomus* spp. until 2001, after the completion of sampling in 1999–2000. Thus the sampling design used to collect pre-protection data in 1983–1984 was not replicated in 1999–2000. Furthermore, in 1999–2000 we used the transect size (50 m × 6 m) shown to provide the most precise estimates of coral trout density (Mapstone & Ayling 1993).

Analysis of data

Of the 50 species of reef fish surveyed, only eleven species were analysed for the present study. These were: the coral trout species, *Plectropomus maculatus*, *P. leopardus* and *P. laevis* (Serranidae: Epinephelinae); stripy sea perch, *Lutjanus carponotatus* (Lutjanidae); red-breasted maori wrasse, *Chelinus fasciatus* (Labridae); harlequin tusk fish, *Choerodon fasciatus* (Labridae); the herbivorous rabbit fishes, *Siganus doliatus* and *S. lineatus* (Siganidae); and the butterfly fishes, *Chaetodon aureofasciatus*, *Chaetodon rainfordii* and *Chelmon rostratus* (Chaetodontidae). Of this subset, only *Plectropomus* spp. and *L. carponotatus* are sought after and captured effectively by hook and line fishing. The three species of *Plectropomus* (coral trout) were pooled, as they are equally vulnerable and equally targeted by hook and line, and spear fishing. Similarly, the two labrid species, the two siganid species, and the three species of chaetodontids were pooled to provide a group of fish that are not captured or targeted by fishing gears. Biomass estimates were calculated for *Plectropomus* spp., *Lutjanus carponotatus*

Table 2 Locations and numbers of sites used to sample coral trout density and size structure in pre-protected (1983–1984) and in the protected and fished zones (1999–2000) of the Palm and Whitsunday Island groups.

Island group	*Pre-protection 1983–1984*	*Protected 1999–2000*	*Fished 1999–2000*
Palm Islands	Havannah Island ($n = 2$)	Orpheus Island (east) ($n = 6$)	Pelorus Island (east) ($n = 6$)
	Curacoa Island ($n = 2$)	Orpheus Island (west) ($n = 6$)	Pelorus Island (west) ($n = 6$)
Whitsunday Islands	Hook Island (north) ($n = 4$)	Hook Island (north) ($n = 6$)	Hook Island (east) ($n = 6$)
	Border Island ($n = 4$)	Border Island ($n = 6$)	Whitsunday Island ($n = 6$)

and the non-target fish group using published length-weight relationships for these species (Ferreira & Russ 1992; Froese & Pauly 2002).

Univariate two-factor ANOVA was used to test for differences in *Plectropomus* spp. density and biomass between pre-protected, protected and fished zones. Factors in the analysis were zone (three levels) and island group (two levels). Because of large between-transect variation within sites, assumptions of homogeneity of variance for ANOVA could not be met with any data transformations when attempting to analyse data at the transect level. Thus, the transect data were pooled at the site level; making the 12 randomly selected sites in each zone at each island group the replicates. Thus, all variates (density and biomass of fish groups, live coral cover, structural complexity and underwater visibility) were analysed by orthogonal, two-factor univariate ANOVAs (fixed factors: zones and island groups). Cochran's test and a quantile-quantile normal plot were used to assess homogeneity of variances and normality, respectively. Analyses of covariance (ANCOVA) were performed on density and biomass of fish surveyed in 1999–2000, with live hard coral cover, live hard and soft coral cover, structural complexity and underwater visibility used as covariates. We tested for interactions between variates and covariates in the ANCOVA by examining the B-weights and beta weights. Following ANOVAs, means were compared using Tukey's HSD tests.

Density estimates of *Plectropomus* spp. and *Lutjanus carponotatus* were log $(x+1)$ transformed, and biomass estimates were square root $(x+1)$ transformed to satisfy ANOVA assumptions of normality and homogeneity of variances. Density and biomass estimates of the non-target fish group were log $(x + 1)$ transformed in order to conform to the assumptions of ANOVA.

Length-frequency distributions of *Plectropomus* spp. in protected and fished zones of the Palm and Whitsunday Island groups were compared using two-sample Kolmogorov-Smirnov tests.

Table 3 Mean density and biomass ratios for *Plectropomus* spp. in pre-protected (PP: 1983–1984), protected (P: 1999–2000) and fished (F: 1999–2000) zones of the Palm and Whitsunday Island groups.

Island group	*Comparison*	*Density ratio*	*Biomass ratio*
Palm Islands	PP : P	1 : 5.9	1 : 6.3
	F : P	1 : 3.6	1 : 6.1
	PP : F	1 : 1.6	1 : 1.0
Whitsunday Islands	PP : P	1 : 4.0	1 : 6.2
	F : P	1 : 2.7	1 : 4.1
	PP : F	1 : 1.4	1 : 1.5

Table 4 Results of two-factor univariate ANOVA on the density and biomass of *Plectropomus* spp. in the Palm and Whitsunday Island groups, in pre-protected, protected and fished zones. Numerical figures are F values. Symbols in brackets are significance levels of tests; *** = < 0.001; ns = not significant.

Source of variation	*Island group × zone (2, 54 df)*	*Island group (1, 54 df)*	*Zone (2, 54 df)*
Plectropomus spp. density	2.31 (ns)	13.98 (***)	41.09 (***)
Plectropomus spp. biomass	1.44 (ns)	3.59 (ns)	49.55 (***)

RESULTS

Effects of reserve protection on the density and biomass of *Plectropomus* spp.

In both the Palm and Whitsunday Island groups, density and biomass of *Plectropomus* spp. were significantly higher in the protected no-take reserves (1999–2000) than in pre-protection zones (1983–1984) and fished zones (1999–2000) (Fig. 2, Tables 3 and 4; Tukey's tests: protected > fished = pre-protection, $p < 0.001$ for both coral trout density and biomass at both island groups). Density and biomass estimates of *Plectropomus* spp. in fished zones (1999–2000) were slightly higher, but not significantly higher, than estimates obtained from pre-protection zones (1983–1984) at both the Palm and Whitsunday Island groups (Fig. 2, Tables 3 and 4).

In 1999–2000, the density, but not biomass, of *Plectropomus* spp. was significantly higher in protected zones of the Palm Islands than in protected zones of the Whitsunday Islands (Fig. 2, Table 5). Neither density nor biomass of *Plectropomus* spp. differed significantly between open 'fished' zones of the Palm and Whitsunday Island groups in 1999–2000 (Fig. 2, Table 5).

No significant interactions between zone and island group were detected for either density or biomass of *Plectropomus* spp. (Tables 4 and 5). There were no significant effects of benthic habitat variates on coral trout density or biomass at either the Palm or Whitsunday Island groups (Table 5).

In 1999–2000, length-frequency distributions of *Plectropomus* spp. differed significantly between protected and fished zones of the Palm Islands (two-sample Kolmogorov-Smirnov test critical value = 0.17, $p < 0.05$), but this was not the case for the Whitsunday Islands (two-sample Kolmogorov-Smirnov test critical value = 0.23, $p > 0.05$). In the Palm Island group, the modal length of fish in protected zones was 40 cm, whereas in the fished zones it was 30 cm. In the fished zones, 77% of individuals of *Plectropomus* spp. were 35 cm or less in length and, in the protected zones, 58% were 35 cm or less. In the protected zones, 18% of individuals of *Plectropomus* spp. were greater than 45 cm in length and, in the fished zones, 6% were greater than 45 cm in length (Fig. 3).

In the Whitsunday Island group, the modal length was 40 cm in both protected and fished zones. In the fished zones, 59% of individuals of *Plectropomus* spp. were 35 cm or less in length, and, in the protected zones, 42% were 35 cm or less. In the protected zones, 31% of *Plectropomus* spp. were greater than 45 cm in length and, in the fished zones, 18% were greater than 45 cm in length (Fig. 3).

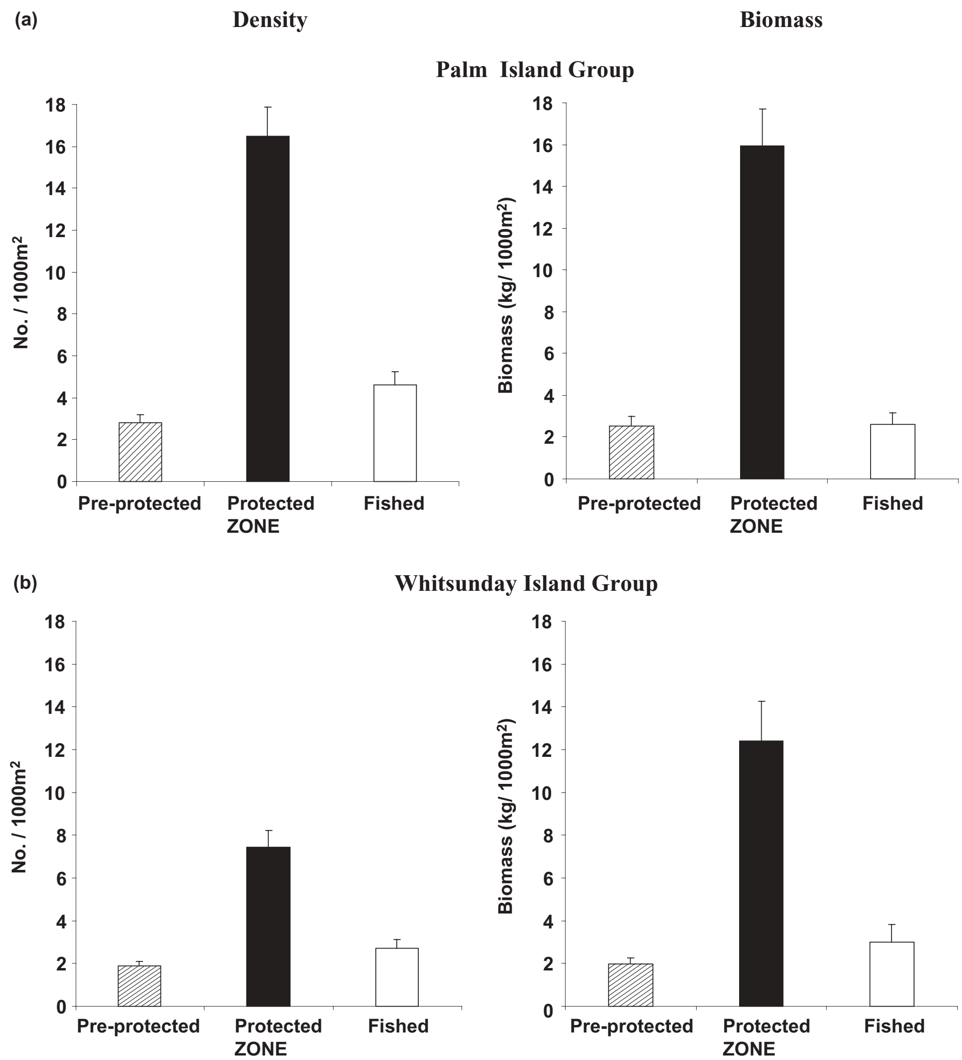
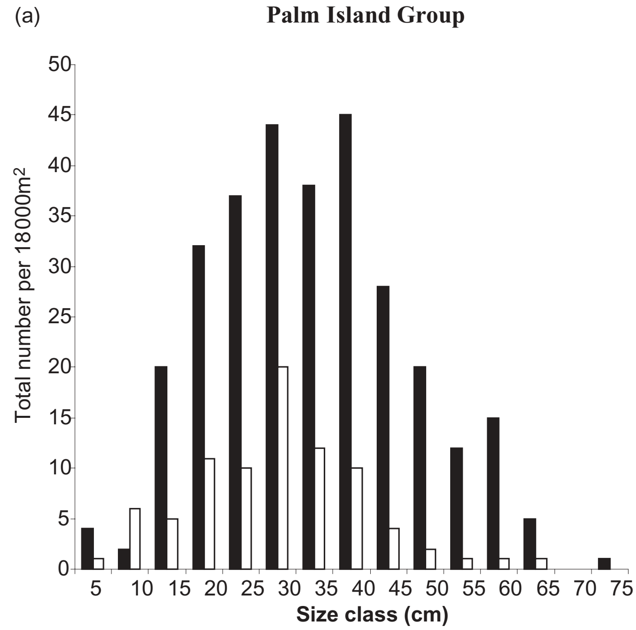


Figure 2 Mean ($\pm$ 1 SE) density (number per 1000 m^2) and biomass (kg per 1000 m^2) of *Plectropomus* spp. within pre-protected (1983–1984), protected (1999–2000) and fished (1999–2000) zones of the (*a*) Palm and (*b*) Whitsunday Island groups.

Table 5 Results of two-factor univariate ANCOVA on the density and biomass of *Plectropomus* spp., *Lutjanus carponotatus* and the non-target fish group within protected and fished areas of the Palm and Whitsunday Island groups. Covariates were live hard coral cover, live coral cover (hard and soft coral combined) and the structural complexity index. Univariate ANOVA (1,44 *df*) results for benthic variables and underwater visibility are also shown. Numerical figures are *F* values. Symbols in brackets are significance levels of tests. * = < 0.05; ** = < 0.01; *** = < 0.001; ns = not significant.

Source of variation	*Hard coral (1,41 df)*	*Hard + soft coral (1,41 df)*	*Structural index (1,41 df)*	*Island group × zone (1,41 df)*	*Island group (1,41 df)*	*Zone (1,41 df)*
Plectropomus spp. density	1.301 (ns)	0.037 (ns)	0.809 (ns)	0.825 (ns)	19.812 (***)	42.659 (***)
Plectropomus spp. biomass	0.530 (ns)	0.055 (ns)	1.221 (ns)	1.174 (ns)	1.282 (ns)	43.692 (***)
Lutjanus carponotatus density	0.013 (ns)	0.523 (ns)	0.161 (ns)	3.335 (ns)	4.456 (*)	10.678 (**)
Lutjanus carponotatus biomass	0.006 (ns)	0.282 (ns)	0.090 (ns)	2.258 (ns)	0.031 (ns)	12.486 (**)
Non-target fish, density	3.236 (ns)	3.494 (ns)	4.647 (*)	0.020 (ns)	19.418 (***)	2.474 (ns)
Non-target fish, biomass	0.885 (ns)	6.138 (*)	7.049 (*)	0.003 (ns)	37.027 (***)	3.753 (ns)
Live hard coral cover	–	–	–	6.864 (*)	0.391 (ns)	0.605 (ns)
Live coral cover (hard and soft)	–	–	–	1.995 (ns)	1.026 (ns)	7.506 (**)
Structural complexity index	–	–	–	2.074 (ns)	0.332 (ns)	4.665 (*)
Underwater visibility	–	–	–	7.102 (**)	0.789 (ns)	3.156 (ns)



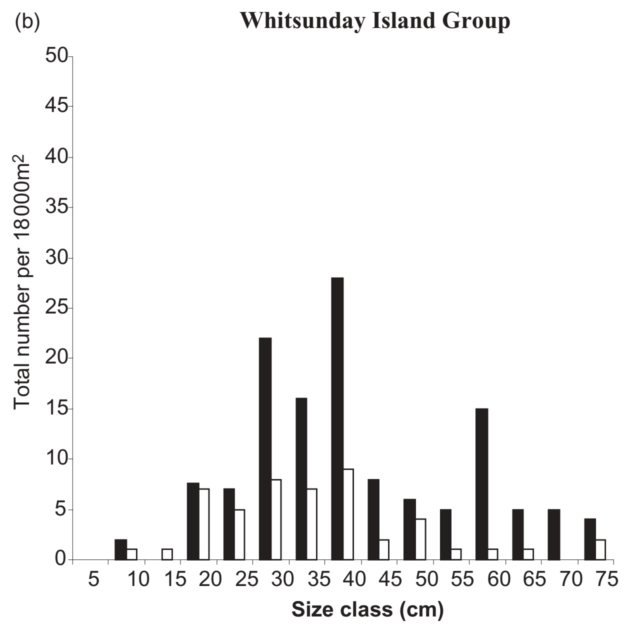


Figure 3 Length-frequency distributions for *Plectropomus* spp. within protected and fished zones of the (*a*) Palm and (*b*) Whitsunday Island groups (1999–2000). Black bars represent 'protected' zones; white bars represent 'fished' zones.

Effects of reserve protection on the density and biomass of *Lutjanus carponotatus*

In 1999–2000, density and biomass of stripy sea perch (*Lutjanus carponotatus*) were significantly higher in protected zones than in fished zones of the Palm (P:F [protected:fished] = 3.1 for both density and biomass) and Whitsunday (P:F = 1.7 and 1.9 for density and biomass, respectively) Islands (Table 5). At the Palm Island group, mean density (number of fish per 1000 m^2) was 22.7 ± 3.2 SE in protected zones and 7.3 ± 0.7 SE in fished zones. Mean biomass (kg per 1000 m^2) estimates for *L. carponotatus* at the Palm Islands were 4.8 ± 0.6 SE in protected zones and 1.5 ± 0.2 SE in fished zones. At the Whitsunday Island group, mean density (number of fish per 1000 m^2) was 11.9 ± 2.2 SE in protected zones and 6.8 ± 0.8 SE in fished zones. Mean biomass (kg per 1000 m^2) estimates for *L. carponotatus* at the Whitsunday Islands were 4.1 ± 0.7 SE in protected zones and 2.2 ± 0.3 SE in fished zones.

Density of *L. carponotatus* was significantly higher in the Palm Islands than in the Whitsunday Islands, with no significant interaction between zone and island group (Table 5). There was no significant difference in biomass of *L. carponotatus* between island groups, and no significant interaction between zone and island group (Table 5). There were no significant effects of benthic habitat variates on density or biomass of *L. carponotatus* at either the Palm or Whitsunday Island groups (Table 5).

Effects of reserve protection on the density and biomass of non-target fish species

Density and biomass of non-target fish species did not differ significantly between protected and fished zones of either the Palm (P:F = 1.0 and 0.9 for density and biomass, respectively) or the Whitsunday (P:F = 1.0 and 1.1 for density and biomass, respectively) Island groups (Table 5). At the Palm Island group, mean density (number of fish per 1000 m^2) was 85.8 ± 5.5 SE in protected zones and 83.6 ± 4.8 SE in fished zones. Mean biomass (kg per 1000 m^2) estimates for non-target fish at the Palm Islands were 15.8 ± 1.4 SE in protected zones and 16.7 ± 1.5 in fished zones. At the Whitsunday Island group, mean density (number of fish per 1000 m^2) was 58.0 ± 2.5 SE in protected zones and 55.6 ± 3.4 SE in fished zones. Mean biomass (kg per 1000 m^2) estimates for non-target fish at the Whitsunday Islands were 7.8 ± 0.5 SE in protected zones and 6.9 ± 0.5 SE in fished zones.

Density and biomass of non-target fish was significantly higher at the Palm Islands than at the Whitsunday Islands (Table 5). There were no significant interactions between zone and island group (Table 5). A significant positive relationship was detected between structural complexity of the substratum and density and biomass of non-target fish (Table 5). Live coral cover (hard and soft coral combined) had a significant positive effect on density, but not biomass, of non-target fish (Table 5).

Differences in the benthic cover and structural complexity between island groups and zones

In 1999–2000, live coral cover (hard and soft coral combined) was significantly higher in protected no-take reserves than in fished zones (Fig. 4, Table 5). Structural complexity of the fringing reef habitats was significantly higher in fished than in protected zones (Fig. 4, Table 5).

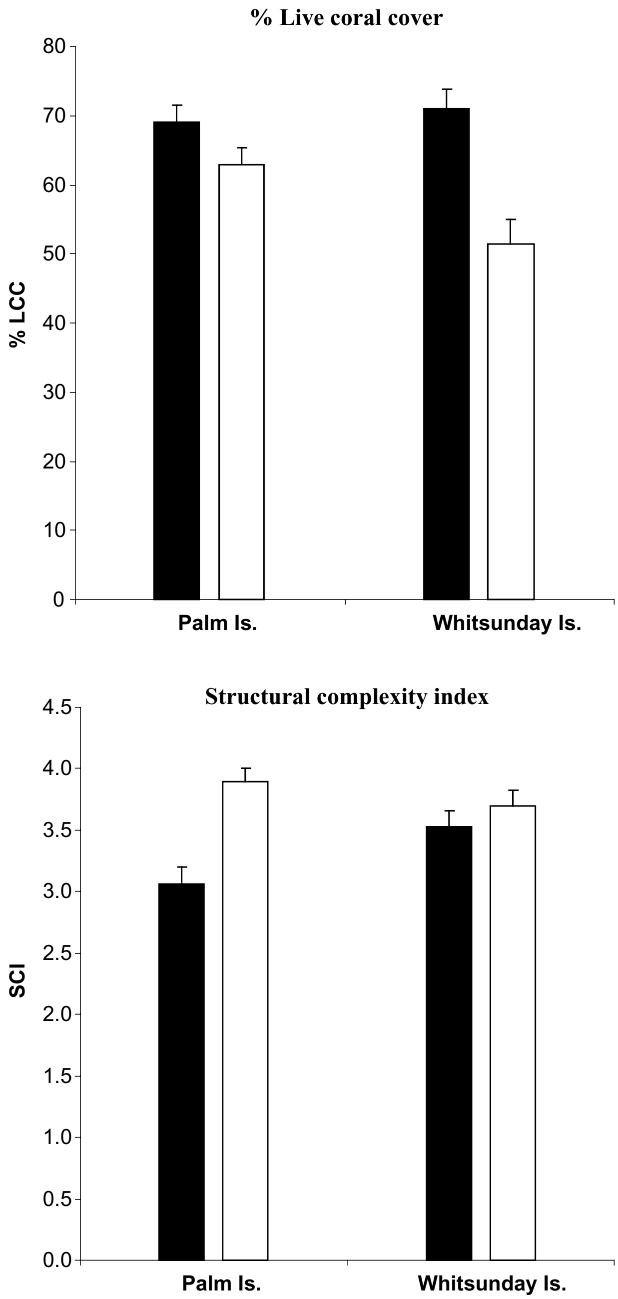


Figure 4 Mean (± 1 SE) per cent live coral cover (% LCC = hard and soft coral combined) and mean (± 1 SE) structural complexity indices (SCI) in protected and fished zones of the Palm and Whitsunday Island groups (1999–2000). Black bars represent 'protected' zones; white bars represent 'fished' zones.

Effects of underwater visibility

There were no significant differences in underwater visibility between zones or island groups during 1999–2000 sampling (Table 5).

DISCUSSION

We have demonstrated strong effects of protection by no-take marine reserves on reef fish populations of nearshore coral reefs in Australia's GBRMP. We did so by comparing abundance of the major target of the hook and line fisheries on the GBR, *Plectropomus* spp., at sites before and 12–13 years after the application of no-take marine reserve status. Few studies of the effects of marine reserves present data on abundance of target species before application of reserve status (Jones *et al*. 1993; Russ 2002; Willis *et al*. 2003*b*). The few studies in the marine reserve literature that do draw on pre-reserve data include White (1988) in the Philippines, Clark *et al*. (1989) in Florida, McClananhan and Kaunda-Arara (1996) in Kenya, Russ and Alcala (2003) in the Philippines and Roberts *et al*. (2001) in St Lucia. In most of these cases the duration of protection of the reserves was less than a decade.

Studies examining no-take reserve effects within the GBRMP are surprisingly few (see Craik 1981; Ayling & Ayling 1983, 1992; Ferriera & Russ 1995; Gribble & Robertson 1998; Zeller & Russ 1998; Adams *et al*. 2000, Ayling *et al*. 2000; Mapstone *et al*. 2003). Furthermore, the results of the few studies examining no-take reserve effects on densities of the major targets of the hook and line fisheries in this region have often been equivocal (Williams & Russ 1994; Ayling *et al*. 2000; Mapstone *et al*. 2003). The most consistent differences in population characteristics of the main target of the fisheries, coral trout, are larger average size and higher catch rates of experimental hook and line fishing in no-take than fished zones (Mapstone *et al*. 2003).

The abundance and size of large predatory reef fishes (such as serranids, lutjanids and lethrinids) are often good indicators of the effects of fishing and marine reserve protection on coral reefs (Jennings & Kaiser 1998; Russ & Alcala 2003). This study has demonstrated significantly higher abundances of coral trout (*Plectropomus* spp.) within the no-take reserves than in the pre-protection (1983) and the fished (1999–2000) areas. Furthermore, coral trout were, on average, larger and heavier inside the reserves (Fig. 3).

Density and biomass estimates obtained here for coral trout in no-take reserves of the Palm and Whitsunday Islands suggest that given time and adequate protection, target fish stocks can build up considerably within marine reserves. At some point, ecological factors such as intra- and inter-specific competition, prey availability, and niche space will govern the population carrying capacity (Jennings 2000). We cannot conclude that estimates of coral trout abundance in protected zones have reached maximum levels. Recent empirical evidence suggests that the duration to full recovery of predatory reef fish biomass inside no-take reserves may often require several decades or more (Russ & Alcala 2004).

Density and biomass estimates of coral trout were consistently higher by 2–65% (Table 3) in fished (1999–2000) than pre-protection (1983–1984) treatments. These differences may be because of the difference in the size of the sampling unit used in the 1983–1984 surveys. Pre-protection data were collected using 50 m × 20 m transects (A.M. Ayling), while data collected for protected and fished zones in 1999–2000 used 50 m × 6 m transects (D.H.

Williamson). Mapstone and Ayling (1993) showed that the wider transect can underestimate coral trout density by 50% compared to the narrower transect.

Our data suggest little change in coral trout abundance in fished areas of the Palm and Whitsunday Islands between 1983–1984 and 1999–2000. Given that the abundance of coral trout has increased considerably over this period in no-take reserves, this suggests that abundance of coral trout populations was reduced by fishing on inshore reefs, even as early as 1983–1984, before the GBRMP was established. This is not consistent with suggestions that line fishing, particularly by recreational fishers, has had little effect on reef fish populations of the GBR.

The stripy sea perch (*Lutjanus carponotatus*) is a secondary target of line fishing in this region. Most fish captured incidentally that are above minimum size limits (25 cm total length) are retained. Although not as pronounced as for *Plectropomus* spp., significant effects of marine reserve protection on abundance were detected for *L. carponotatus*. This suggests that the benefits of reserve protection extend to a range of species, beyond those most favoured and sought after by fishers.

Our results suggest that, over time, adequately patrolled and protected marine reserves will support higher density and biomass of targeted reef fish species. However, we cannot argue that these results provide unequivocal evidence that populations of targeted fish species have responded positively to marine reserve establishment, since they do not conform to a well-designed before-after-control-impact pair (BACIP) experimental design (Jones *et al.* 1993; Russ 2002; Willis *et al.* 2003*b*). The 1999–2000 data were not collected from exactly the same sites as those where the pre-reserve data from 1983–1984 were collected. This was largely unavoidable. The 1999–2000 data were collected in absence of knowledge of the pre-reserve data. The fact that the 1999–2000 data were collected from the same locations in the Whitsunday Islands occurred by chance (Table 2). Although the 1983–1984 data from the Palm Islands came from islands different from those of the 1999–2000 data, these islands are close to each other (Fig. 1) and the reef slopes at each island are similar. Thus, the study was somewhat opportunistic, rather than well designed. In addition, we did not monitor the changes in abundance in protected and fished sites regularly over the period of protection. Nevertheless, this study is the first to use reliable estimates of coral trout abundance collected before management zoning was implemented on GBR reefs.

The majority of studies examining the effects of marine reserve protection on populations and communities of coral reef fishes have involved spatial comparisons at one time of sites with and without marine reserve protection (Roberts & Polunin 1991; Russ 2002; Halpern 2003; Willis *et al.* 2003*b*). Our 1999–2000 data are of this type. However, the pre-reserve data for *Plectropomus* spp. have provided a baseline reference point from which to draw more reliable inferences.

The marine reserves within the Palm and Whitsunday Islands are some of the most adequately patrolled reserves on the Great Barrier Reef (Davis *et al.* 2004). It is known however, that some degree of poaching by recreational fishers has occurred within these reserves (Davis *et al.* 2004). Furthermore, there is evidence that poaching of reserves occurs more broadly within the GBRMP (see Gribble & Robertson 1998).

The entire GBRMP is currently undergoing a re-zoning under the GBRMP Authority's Representative Areas Programme (RAP) (Day *et al.* 2003). The recent draft plan proposes to increase highly protected no-take reserves from approximately 4.6% to 33.4% of the area of the marine park. The focus of the RAP is on protection of biodiversity and representative bioregions within the GBRMP.

This study has demonstrated the effect of no-take marine reserve status on target fish species on fringing reefs of near-shore island groups within the GBRMP. The effectiveness of marine reserve management strategies is heavily reliant on the level of public awareness, understanding and support for them. Educating the public about the purpose of zoning and the potential gains from the management strategy, plus a shift toward more community involvement in management, are of critical importance to the effectiveness of any GBRMP management strategy. The results of the present study should assist in generating greater awareness and support for no-take reserves in the GBRMP.

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