

The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef

N.A.J. GRAHAM*, R.D. EVANS AND G.R. RUSS

School of Marine Biology and Aquaculture, James Cook University of North Queensland, Townsville, Queensland, 4811, Australia

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SUMMARY

What are the effects of no-take marine reserves on trophic relationships of coral reef fish? Previous studies often have lacked detailed dietary information on major predators, and have often been confounded by differences in habitat complexity between reserve and fished sites. This study investigates the effects of marine reserve protection on predator-prey interactions of coral reef fish on the inshore islands of the Great Barrier Reef (GBR). The abundance of species of prey fish of *Plectropomus leopardus* (Serranidae), a piscivore and the major target of the hook and line fisheries on the GBR, were estimated in protected and fished zones. These prey species were identified from previous detailed studies of the diet of *P. leopardus*. Fish populations and habitat characteristics were surveyed by underwater visual census. Previous studies had determined that the biomass of *P. leopardus* was 3–4 times higher in protected than fished zones in the Whitsunday and Palm Islands, central GBR, after 14 years of protection. Eight of the nine prey species had a higher density within fished zones than protected zones, six significantly so. The density of all prey fish was twice that in the fished than the protected zone ($p < 0.001$). There were no significant differences in availability of different sized refuge holes, structural complexity or live coral cover between zones. Thus, important attributes of habitat complexity did not confound the comparisons between reserve and fished zones. Finally, a significant negative correlation ($r = 0.46$) between coral trout biomass and summed prey fish biomass suggested that predation may be an important structuring process in this system. The results have implications for the conservation of fishery targets and their prey. The study highlights the potential ecosystem implications of the use of no-take marine reserves as conservation and fisheries management tools.

Keywords: predator-prey relationships, no-take marine reserves, Great Barrier Reef, coral reef fishes, habitat structure, fisheries management, trophic relationships

INTRODUCTION

No-take marine reserves are often advocated as conservation and fisheries management tools, particularly on coral reefs (Roberts & Polunin 1991; Roberts *et al.* 2001; Russ 2002). Reasonable evidence for increases in abundance of target species within no-take marine reserves relative to fished areas exists (Roberts & Polunin 1991; Polunin & Roberts 1993; Russ & Alcala 1996; Russ 2002; Halpern 2003). As the target species of fisheries are often large piscivores (Russ 1991; Jennings & Kaiser 1998), an increase in their abundance inside reserves may reduce abundance of their prey. This predation hypothesis suggests that post-settlement mortality due to piscivory largely determines patterns of abundance of adult fish (Hixon 1991). A decline in predatory fish due to fishing may result in 'prey release', in other words an increase in the species they normally prey upon (Hixon 1991; Jennings *et al.* 2001; Steneck 1998). Conversely, prey availability may limit predator growth (Hollowed *et al.* 2000) and abundance (Stewart & Jones 2001). Within reserves, an increase in predator abundance may cause a decrease in prey abundance.

Clear predator-prey responses have been described in fish-urchin relationships in the Caribbean (Hughes 1994) and East Africa (McClanahan & Shafir 1990; McClanahan *et al.* 1999). Prey release has also been documented in tropical lakes (Marten 1979) and some temperate marine systems (Estes *et al.* 1998). Although evidence of prey release in reef fish has been documented (Caley 1993; Carr & Hixon 1995; Hixon & Beets 1993; Koslow *et al.* 1988; Watson & Ormond 1994), studies are often much less conclusive (Jennings *et al.* 1995; Jennings & Polunin 1997; Russ & Alcala 1989, 1998a). This is surprising given that piscivorous fishes are probably the most significant consumers of fish biomass on coral reefs and may result in top-down control of the ecosystem (Grigg *et al.* 1984). The frequent lack of detectable trophic effects of fishing on predatory reef fish may be a result of predator-prey relationships not being as tightly coupled in some systems (Jennings & Kaiser 1998; Jennings *et al.* 2001). In complex ecosystems like coral reefs with a greater diversity of species, carnivores are often generalists and highly opportunistic in their feeding habits (Russ 1991).

Studies on the Great Barrier Reef (GBR) have demonstrated that the pomacentrid, *Acanthochromis polyacanthus*, is vulnerable to predation (Connell 1996, 1998) and its abundance is significantly negatively correlated to that of the coral

* Correspondence: Mr Nicholas A.J. Graham Tel: +44 15394 46212 Fax: +44 15394 46212 e-mail: naj_graham@hotmail.com

trout, *Plectropomus leopardus* (Serranidae) (Thresher 1983a, b). In a manipulative experiment, Caley (1993) had to remove all predators from small patch reefs to affect abundance of reef fish prey significantly. Other manipulative experiments have demonstrated predation effects on abundance of newly settled juveniles (Webster 2002; Webster & Almany 2002). However, studies explicitly addressing the trophic effects of no-take marine reserves on coral reefs are needed.

The majority of previous studies of the trophic effects of marine reserves have lacked detailed dietary and feeding rate information of the fished species (St John *et al.* 2001). On the GBR, coral trout, *Plectropomus* spp., make up a large proportion of the predatory reef fish assemblage (Goeden 1982; Newman *et al.* 1997) and are among the most popular targets of recreational and commercial fishers (Williams & Russ 1994). The diet of coral trout is known (Kingsford 1992; St John 1995). Reef topography and habitat complexity affect abundance of reef fish (Beukers & Jones 1997). The diversity, distribution and abundance of reef fishes is often influenced by the availability of potential shelter sites (Steele 1999; McClanahan & Arthur 2001) perhaps because post-settlement predation causes greater mortality in areas with less shelter (Hixon & Beets 1993; Steele 1999). However, large variations in annual recruitment of reef fish (Doherty 1991) often make studies of predation effects problematic (Russ & Alcala 1989, 1998a).

Significantly higher biomass (3–4 times) of coral trout occurs in protected than fished zones at two inshore island groups of the GBR (Williamson 1999; R.D. Evans, D. Williamson & G.R. Russ, unpublished data 2003). As other species of piscivorous reef fish do not differ significantly in abundance between fished and protected zones (R.D. Evans, D. Williamson & G.R. Russ, unpublished data 2003), a difference in predation pressure due specifically to coral trout is likely. The objective of this study was to compare the density of 11 common prey species of coral trout between the fished and protected zones at two island groups in the central section of the Great Barrier Reef Marine Park. Data on percentage live coral cover, structural complexity of the substratum and abundance of different sized refuge holes were collected to account for any effect of habitat complexity.

METHODS

Study sites

The study was carried out in the Whitsunday Islands (20°08'S, 148°56'E), which account for over one-third of all tourist visitors to the GBR annually, and the Palm Islands (18°34'S, 146°29'E) in the central section of the Great Barrier Reef Marine Park, Australia (Fig. 1). The Whitsundays consist of 53 islands, the 16 sites studied being approximately 25 km from the mainland, on the east coast of Whitsunday Island, the east and north coasts of Hook Island, and around Border Island (Fig. 1). Recreational fishing is popular on the fringing reefs, and commercial fishing,

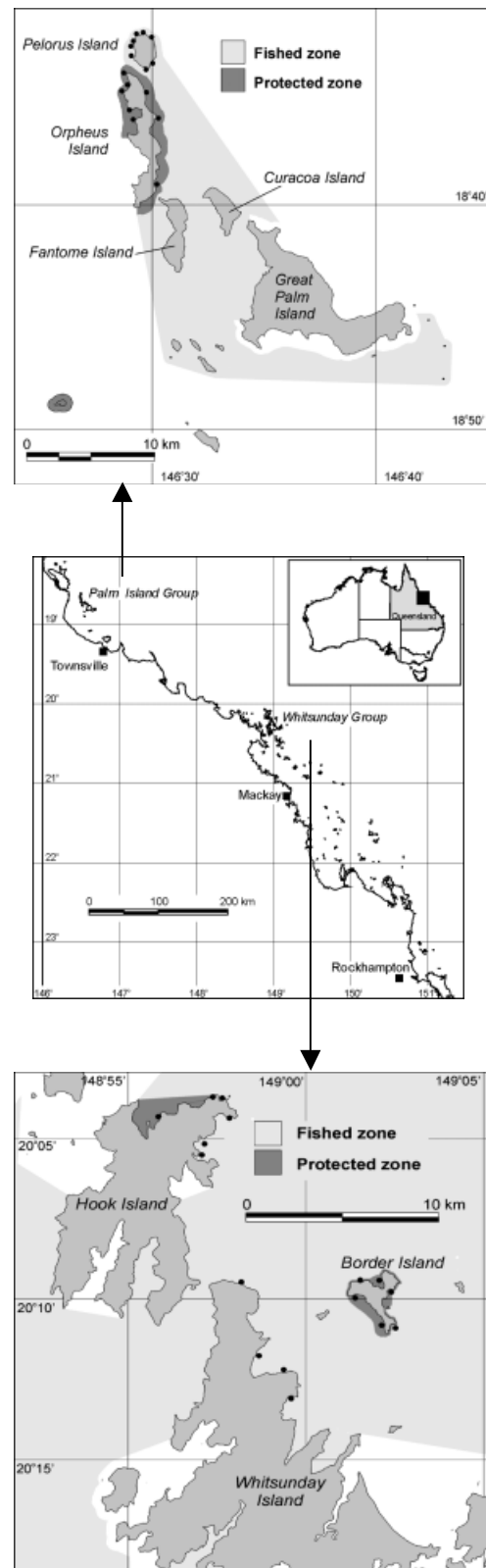


Figure 1 Map of the study areas. The study was conducted in the central Great Barrier Reef near the Townsville area. The Palm Island group is situated off Ingham. Study sites are marked with black dots. The no-take protected zone around Orpheus Island and the fished zone around Pelorus Island were surveyed. The Whitsunday Island group is situated off Airlie Beach, south of Townsville. Study sites are marked with black dots. Zoning of interest is protected and fished.

collecting, and traditional fishing, hunting and gathering occur in the area. The fringing reefs around the islands consist of a reef flat, reef crest and reef slope. The reef flat is 1–2 m in depth at mean tidal height. The reef crest is 3–4 m deep, while the slope drops away to 8–20 m in depth. The reef slope has high relief, with caves, ledges, gullies and bommies (large coral heads). The sites were selected randomly (D. Williamson, unpublished data 1999) and were at least 100 m apart. Eight sites were situated in no-take protected zones around Border Island and northern Hook Island (Fig. 1). A further eight sites were situated in fished zones along the east coasts of Whitsunday and Hook Islands (Fig. 1). Surveys were made in December 2001. The protected reefs had 14 years of zoning protection when this study was conducted.

The Palm Island group consists of nine islands approximately 15 km from the mainland. The 16 study sites in the Palm Islands were located around Orpheus and Pelorus Islands (Fig. 1). The Palm Island group is a popular destination for recreational fishers from Townsville (the largest city on the north-east coast of Queensland), Ingham and Cardwell. The aboriginal communities of Great Palm Island also fish the area. Commercial fishing, both line and trawling, occurs in the area, but largely away from the fringing reefs (Williamson 1999). The fringing reefs are similar to those of the Whitsunday group, although the topography of the reef slope has less relief, particularly on the western, sheltered side of the islands. The sites were selected randomly (Williamson 1999) and were at least 100 m apart. Eight sites were situated in the protected zone around the north-west and eastern sides of Orpheus Island (Fig. 1) and eight in the fished zone around Pelorus Island (Fig. 1). Surveys were made in April 2002. The protected reefs had 14.5 years zoning protection when this study was conducted.

Visual census of reef fishes

Five 50 m × 6 m (300 m²) replicate belt transects were censused visually at each site using scuba. Transects were laid haphazardly along the reef slope within a depth range of 7–11 m, averaging 9 m. Transects were a minimum of 5 m apart. Two fish counters (counting predators and prey separately) swam side by side along each transect whilst laying the tape, and all fish 3 m either side of the transect were recorded. A third diver followed the first two, and laid the transect tape. This third diver notified the fish counters when the 50 m census length was completed. Each transect took an average of eight minutes to complete. Benthic data were collected as the transect tapes were reeled in. As reef fishes tend to associate with refuge holes of similar size to their bodies, and may be limited by the number of these refuges available at any one site (Hixon & Beets 1993), a habitat index incorporating refuge holes was used. The number of different sized refuge holes (diameters <10 cm, 10–30 cm, 30–50 cm, 50–70 cm, 70–100 cm, >100 cm) was counted within a 1-m strip upslope of the tape for two 10-m sections (10–20 m and

30–40 m) along each transect. Percentage live coral cover was estimated every 2 m along the tapes. Each transect was assigned an arbitrary structural complexity: (1) low relief; (2) mainly rubble with sparse relief; (3) moderately complex with steepening slope; (4) complex reef structure with overhangs; and (5) steep slope with complex structure including caves and overhangs. Information on depth, visibility and speed of completion of transects was also recorded for each site.

Individuals of each of 11 prey species were selected as likely prey of *Plectropomus leopardus* on the GBR (St John 1995) and these were counted by the same observer (N.G.) along each transect. Pomacentridae, with *Acanthochromis polyacanthus* the dominant species, were the dominant family in the diet of *P. leopardus*, with Labridae, Scaridae and Caesionidae contributing a substantial portion of the diet (Kingsford 1992; St John 1995; St John *et al.* 2001). The prey species surveyed were five species of pomacentrids (*Acanthochromis polyacanthus*, *Pomacentrus moluccensis*, *Amblyglyphidodon curacao*, *Pomacentrus brachialis* and *Neopomacentrus azysron*), two species of labrid (*Thalassoma lunare* and *Halichoeres melanurus*), two species of scarid (*Chlorurus sordidus* and *Scarus rivulatus*) and two species of caesionid (*Pterocaesio trilineata* and *Pterocaesio diagramma*). All of these species were common on the fringing reefs of both the Whitsunday and Palm Islands. Precise counts were obtained for all species except *N. azysron*, *P. trilineata* and *P. diagramma*, which were encountered in such high numbers per school, that an estimate of abundance was made. A single observer (R.E.) collected data on the density and size (5 cm size classes) of predators (including *P. leopardus* and *Plectropomus maculatus*) at each site. Information is lacking on the diet of *P. maculatus*, but both species have similar feeding behaviour, and we assumed that their diets were similar.

Data analysis

Of the 11 prey species surveyed, only nine were analysed statistically. The two species of caesionid form large schools and were seen sporadically on transects. Error terms of mean density were SE throughout. Normality of data was examined with histograms and quantile–quantile (Q–Q) plots. Homogeneity of variances was tested with Levene's test. A three-factor analysis of variance (ANOVA) design (factors: zones, island groups and sites nested in combinations of zones and islands) was planned. However, assumptions of homogeneity of variance could not be met with any data transformations. This was due to large between-transect variation within sites. Therefore, the transect data were pooled at the site level, making the eight randomly selected sites in each zone at each island group the replicates.

Thus, the abundance of all nine species was analysed using a two-factor orthogonal ANOVA. The two factors were zone (protected and fished), which was treated as a fixed factor, and island group (Whitsunday Islands and Palm Islands), which was also treated as a fixed factor. There were

Table 1 Results of univariate two-factor analyses of variance on densities of nine prey fish species. Values given are F ratios (probability results given in brackets). *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns = not significant.

| <i>Variate</i> | <i>Zone</i> (1,28 <i>df</i>) | <i>Island</i> (1,28 <i>df</i>) | <i>Zone</i> × <i>Island</i> (1,28 <i>df</i>) |
|--|----------------------------------|------------------------------------|--|
| <i>Acanthochromis polyacanthus</i> | 51.79 (***) | 7.14 (*) | 4.06 (ns) |
| <i>Pomacentrus moluccensis</i> | 5.59 (*) | 0.00 (ns) | 3.29 (ns) |
| <i>Amblyglyphidodon curacao</i> | 6.52 (*) | 10.10 (**) | 0.57 (ns) |
| <i>Pomacentrus brachialis</i> | 10.16 (**) | 0.03 (ns) | 0.31 (ns) |
| <i>Neopomacentrus azysron</i> | 3.91 (ns) | 0.20 (ns) | 3.34 (ns) |
| <i>Thalassoma lunare</i> | 18.90 (***) | 2.78 (ns) | 10.00 (**) |
| <i>Halichoeres melanurus</i> | 1.04 (ns) | 19.66 (***) | 0.69 (ns) |
| <i>Chlorurus sordidus</i> | 3.42 (ns) | 1.38 (ns) | 0.52 (ns) |
| <i>Scarus rivulatus</i> | 4.45 (*) | 4.25 (*) | 1.46 (ns) |
| Summed prey | 3.46 (ns) | 0.12 (ns) | 0.65 (ns) |
| Summed prey (except <i>N. azysron</i>) | 31.80 (***) | 0.01 (ns) | 0.20 (ns) |

eight sites within each combination of zone and island group. The F ratios for the effect of zone were identical for the two-factor orthogonal ANOVA performed and the three-factor nested ANOVA originally planned (1, 28 *df*). Data for *A. curacao* and *T. lunare* were \log_{10} transformed and data for *C. sordidus* $\log_{10}(x + 1)$ transformed to meet the assumption of homogeneity of variance. Levene's test produced a probability value of 0.032 for *A. curacao* (\log_{10} transform); the significance level for this ANOVA was thus set at 0.03. Coral trout biomass data at the same sites was also analysed using a two-factor orthogonal ANOVA. Data were square root transformed to meet the assumption of homogeneity of variance.

Two-factor orthogonal ANOVAs were carried out to test if differences existed between zones in the availability of refuge holes, live coral cover and structural complexity. The hole size category <10 cm was \log_{10} transformed to meet the assumption of homogeneity of variance. Analyses of covariance (ANCOVAs) were performed on prey density, with refuge hole-size categories used as covariates both separately and for all hole sizes pooled. Biomass estimates for each species were obtained from length-weight (L–W) relationships provided in Fishbase (Froese & Pauly 2002). Where L–W relationships were not available for a particular species, a L–W relationship for a species of similar size and shape was used. A modal length was estimated for each prey species to allow estimates of biomass from density. Correlations were conducted between biomass of coral trout (*P. leopardus* and *P. maculatus* combined) and biomass of all prey fish combined at each site.

RESULTS

Eight of the nine prey species had higher mean densities in the fished zones than in the protected zones. This difference was significant for six of the species, namely *Acanthochromis polyacanthus*, *Pomacentrus moluccensis*, *Amblyglyphidodon curacao*, *Pomacentrus brachialis*, *Thalassoma lunare* and *Scarus rivulatus* (Table 1; Fig. 2). The differences for *Halichoeres melanurus* and *Chlorurus sordidus* were not statistically significant (Table 1; Fig. 2). *A. polyacanthus* and *H. melanurus* had significantly higher densities at the Whitsunday than at the

Palm Islands, while *A. curacao* and *S. rivulatus* had significantly higher densities at the Palm than the Whitsunday Islands (Table 1; Fig. 2). However, there was no zone-island interaction for any of these species (Table 1). *T. lunare* displayed a significant zone-island interaction. The difference between zones was much greater in the Palm than the Whitsunday Islands (Table 1; Fig. 2). *Neopomacentrus azysron* was the only prey species found in higher density in the protected than the fished zone, although this was not statistically significant ($p = 0.58$) (Table 1; Fig. 2).

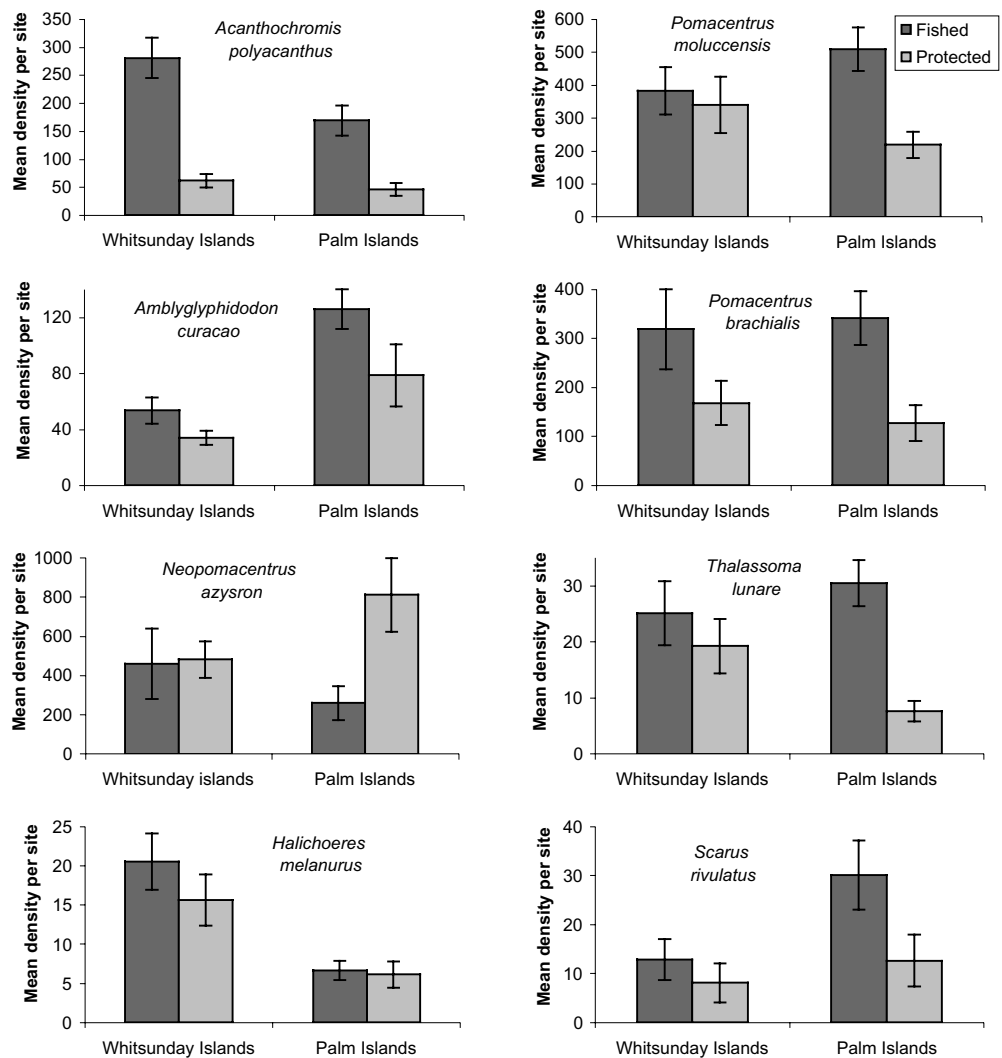
The densities of the nine prey species combined were higher in the fished than protected zones. The variation in counts of *N. azysron* was very high and, excluding this species, total density of prey species was significantly higher in the fished than the protected zone (Table 1) in both island groups (Fig. 3). Coral trout (*Plectropomus leopardus* and *Plectropomus maculatus*) biomass was significantly greater in the protected zone (9790 ± 1394 g 1500 m⁻²) than in the fished zone (3420 ± 631 g 1500 m⁻²) (two-way ANOVA, $F = 19.46$, $df = 1, 28$, $p < 0.001$; Fig. 3).

There was no significant difference in the density of any of the different sizes of refuge holes between zones (Table 2).

Table 2 Results of univariate two-factor orthogonal analysis of variance of habitat variables: different sized refuge hole categories, % live coral cover and structural complexity index. Values given are F ratios (probability results given in brackets). *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns = not significant.

| <i>Variate</i> | <i>Zone</i> (1,28 <i>df</i>) | <i>Island</i> (1,28 <i>df</i>) | <i>Zone</i> × <i>Island</i> (1,28 <i>df</i>) |
|-----------------------|----------------------------------|------------------------------------|--|
| Hole size category: | | | |
| <10 cm | 2.70 (ns) | 3.44 (ns) | 0.25 (ns) |
| 10–30 cm | 2.63 (ns) | 3.86 (ns) | 2.63 (ns) |
| 30–50 cm | 0.05 (ns) | 0.01 (ns) | 0.03 (ns) |
| 50–70 cm | 0.28 (ns) | 4.47 (*) | 0.50 (ns) |
| 70–100 cm | 0.97 (ns) | 1.93 (ns) | 2.10 (ns) |
| >100 cm | 0.01 (ns) | 0.07 (ns) | 4.60 (*) |
| % live coral cover | 0.24 (ns) | 11.18 (*) | 0.13 (ns) |
| Structural complexity | 3.25 (ns) | 0.04 (ns) | 0.51 (ns) |

Figure 2 The effect on abundance (mean per 1500 m² ± SE) of zoning at each island group for eight of the nine prey species analysed.



Refuge hole size class 50–70 cm had a significantly higher density in the Palm than in the Whitsunday Islands (Table 2), but there was no zone-island interaction. Refuge hole size class >100 cm had a significant zone-island interaction, with a greater density of holes in the protected zone than in the fished zone at the Whitsunday Islands, and the reverse pattern at the Palm Islands (Table 2). There was also no significant difference between per cent live coral cover and structural complexity between zones (Table 2). There was a significantly greater live coral cover at the Whitsunday than the Palm Islands, however there was no zone-island interaction (Table 2).

ANCOVAs (using hole sizes as covariates) only affected the outcomes of analyses of density of *P. moluccensis* and *A. curacao*. For *P. moluccensis* refuge hole size category <10 cm had a greater effect ($p = 0.0001$) than zoning ($p = 0.042$). However, the hole category <10 cm did not differ significantly between zones in this study (Table 2). Refuge hole size category 10–30 cm affected *A. curacao* densities (though not significantly, $p = 0.092$) enough to reduce the effect of zoning ($p = 0.054$). Again, a non-significant zone effect for

refuge hole size category 10–30 cm indicated that the difference in density of *A. curacao* between zones was related more to differences in predator density than to refuge hole availability.

There were significant negative correlations between coral trout biomass (*P. leopardus* and *P. maculatus*) and *A. polyacanthus* biomass ($r = 0.41$, $F = 6.12$, $df = 1, 30$, $p = 0.019$) and between coral trout biomass and summed prey species biomass (excluding *N. azysron*) ($r = 0.46$, $F = 8.12$, $df = 1, 30$, $p = 0.008$) at the site level (Fig. 4).

DISCUSSION

The results suggest a secondary effect of marine reserve protection. Eight of the nine prey species of coral trout occurred in higher densities within areas of low coral trout biomass (fished zones) than in areas of high coral trout biomass (protected zones). The largest difference in density of prey occurred for *Acanthochromis polyacanthus*, which was four times more abundant in fished than protected zones. An inverse relationship between predator (coral trout) density

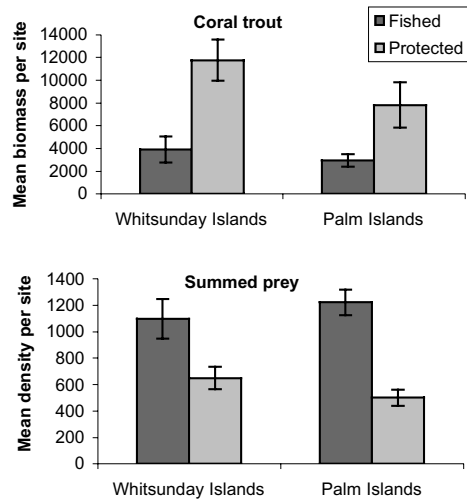


Figure 3 Mean coral trout (*P. leopardus* and *P. maculatus*) biomass (g 1500 m⁻² ± SE) between zones at each island group (top graph) and mean density (per 1500 m² ± SE) of the prey species summed together (excluding *N. azysron*) at the same sites at each island group (bottom graph).

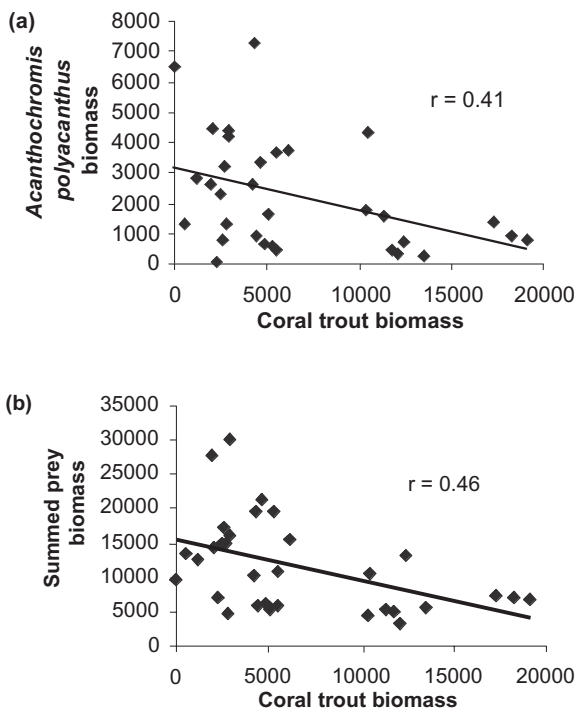


Figure 4 Plots of mean coral trout (*P. leopardus* and *P. maculatus*) biomass against (a) *A. polyacanthus* biomass and (b) summed prey (excluding *N. azysron*) biomass per site (g 1500 m⁻²)

and *A. polyacanthus* survivorship has been reported on the GBR (Thresher 1983a, b) and *A. polyacanthus* is a common prey of *Plectropomus leopardus* (Kingsford 1992; St John 1995). *A. polyacanthus* is a territorial reef fish, and is one of few coral reef fish with non-dispersive young that are tended

by their parents (Thresher 1985; Froese & Pauly 2002). They display aggressive defensive behaviour, often associated with defence of their young, towards other reef fishes and are often off the reef in the water column. This kind of behaviour could make them potentially more vulnerable to predatory attack from a piscivore such as a coral trout, thus helping explain the large differences in *A. polyacanthus* density observed between fished and protected zones in this study.

Pomacentrus moluccensis does not defend young or benthic eggs (Froese & Pauly 2002), and generally stays close to refuge holes. Although coral trout feed upon it, it is likely that a number of smaller fish predators, particularly *Cephalopholis cyanostigma*, commonly also eat it (A. Abdulla, personal communication 2002). Both *Amblyglyphidodon curacao* and *Pomacentrus brachialis* spend a large amount of time above the substratum feeding on plankton in the water column, and this potentially enhances their vulnerability to attack by coral trout.

Neopomacentrus azysron was the only species of prey that had a higher density in the protected than the fished zone, however, this was not statistically significant and was only distinct in the Palm Islands. *N. azysron* schools in great numbers and it was the only species that could not be counted reliably, resulting in reduced power to detect differences.

Thalassoma lunare and *Halichoeres melanurus* are small, relatively mobile species, potentially making them more vulnerable to predation by coral trout. *T. lunare* had a higher density at the Palm than the Whitsunday Islands, however at both island groups it occurred in highest density in the fished zone. *Chlorurus sordidus* and *Scarus rivulatus* are both relatively large, mobile species feeding on the reef flat and slope. Their mobility may make them vulnerable to predation by coral trout.

The density of eight of the prey species combined in the fished zone was twice that in the protected zone. This suggests a trophic effect of zoning, with a greater density of piscivores within protected areas causing a decrease in prey abundance, and a reduction of piscivores in fished areas resulting in prey release. However, a broader trophic effect of zoning on the wider assemblage of reef fish would likely not be detected. The reasons for this are twofold. Firstly, *P. leopardus* is the only piscivore that has a strong density and biomass difference between fished and protected zones (R.D. Evans, D. Williamson & G.R. Russ, unpublished data 2003). There is no evidence of a numerical response of other predatory reef fish to either marine reserve status or to decreases in coral trout abundance due to fishing. Secondly, only prey species specifically recorded in gut contents analysis of *P. leopardus* were censused. We acknowledge that if coral trout biomass was reduced by fishing and the remaining coral trout and/or other species of piscivores demonstrated functional responses such as increased feeding rates or prey switching, such processes would weaken the link between coral trout biomass and predation pressure outside reserves. This study does suggest however, that strengths of predator-prey

interactions may shift with marine reserve protection, even in complex reef fish communities.

A large proportion of the marine reserve literature involves spatial comparisons at one time of fished and protected sites (Russ 2002; Halpern 2003). Such comparisons are frequently confounded by differences in habitat between the fished and protected sites, and such confounding is often not accounted for (Russ 2002). The present study is a spatial comparison of fished and protected sites at one time, but there were no significant differences in abundance of refuge holes of various sizes, structural complexity of the substratum or total coral cover between fished and protected zones. Thus the probability that habitat differences could have confounded the comparison of zones was low.

Variable recruitment is characteristic of reef fish communities (Doherty 1991) and such variability often makes unequivocal detection of marine reserve or predation effects difficult (Russ & Alcala 1998a). The predator assemblages at both the Palm and Whitsunday Islands have been surveyed for 3–4 years, and the higher density and biomass of coral trout within protected zones are temporally consistent (R.D. Evans, D. Williamson & G.R. Russ, unpublished data 2003). Furthermore, the fished and protected sites at each island group were within 1–10 km (Fig. 1) of each other and were generally subject to similar current regimes. Thus, a recruitment pulse of a species in a fished zone, but not in a protected zone, was extremely unlikely. As densities of eight of the nine prey species were higher in fished than protected zones at each of two island groups, separated by 315 km, spatial differences in recruitment seems an unlikely explanation for the patterns detected. Thus, the differences in prey density between zones most likely result from differences in fishing pressure on predators.

Significant negative correlations were found between coral trout and *A. polyacanthus* biomass ($r = 0.41$) and between coral trout biomass and biomass of eight species of prey ($r = 0.46$). These correlation coefficients are confounded by other factors that influence prey abundance such as recruitment variability, habitat variability, nutrient differences, chance and any differences due to other predators. However, the present study does suggest that predation by coral trout can influence the structure of reef fish communities on the GBR.

Previous attempts to detect trophic effects of marine reserve protection and/or fishing in species-rich ecosystems, such as Indo-Pacific coral reefs, have been inconclusive. Studies in the Seychelles (Jennings *et al.* 1995), Fiji (Jennings & Polunin 1997) and the Philippines (Russ & Alcala 1989, 1998a, b) have detected little or no effect. The complexity of trophic interactions, variability in recruitment rates and a lack of dietary information have all been acknowledged as reasons for not detecting a clear effect. This study, however, suggests that if detailed dietary information on key predators is available, the study incorporates suitable habitat indices and large, consistent prior differences in density and biomass of major predators are present, then a trophic effect

of marine reserve protection and fishing can be detected at the species level.

The results of this study have relevance to density-dependent spillover (net export of adult fish; Russ 2002) of predators from reserve to non-reserve locations. Predators may be more likely to move out of reserves if density of their prey is higher outside the reserves. Such effects have been suggested by Ecopath modelling (Walters *et al.* 1999), however empirical evidence for this is sparse. Although this study is limited by the number of prey fish surveyed, it at least suggests that the basic premises of predator and prey densities exist that could enhance spillover of predatory fish from reserves. The other perceived benefit of marine reserves in terms of fisheries enhancement, is net larval export to non-reserve locations (Russ 2002). Studies have shown that increased piscivore density within GBR reserves leads to enhanced cannibalism on coral trout recruits, and so reduced survival (Ayling *et al.* 1993). In non-reserve locations, not only will cannibalism rates be reduced, but also food availability may be enhanced due to an increased density of prey fish populations. This would likely increase both survivorship and growth of the recruits of target species like coral trout, and thus enhance the associated fisheries. Studies on the effects of prey densities on adult spillover of predators and survival and growth of recruits of predatory fish in fished areas would be of particular use to understanding of the ecosystem consequences of marine reserves.

Future work on the trophic effects of marine reserves should investigate the fishery closely before designing the study. Major predators targeted by the fishery should be identified, and prey fish should be selected on the basis of detailed gut contents analysis of these predators. In this way, the likelihood of finding a predatory effect will be greatly enhanced. However, extrapolating the effect to the whole prey assemblage will remain difficult.

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