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Predators drive community structure in coral reef fish assemblages

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Abstract. The importance of top-down effects in structuring ecological communities has been widely debated by ecologists. One way in which to examine these processes is to study the secondary effects of predator removal on communities. This study examined the role of predatory fishes in structuring communities of coral reef fishes, by using a network of marine reserves (the Great Barrier Reef Marine Park) as a natural experiment. We hypothesized that reefs with high densities of piscivores (marine reserves) would have distinct fish communities from those where piscivores have been depleted through fishing, due to variation in predation pressure. We predicted that predator depletion would result in "prey release", and a corresponding increase in prey densities along a gradient of fishing intensity, causing a change in the community composition of reef fishes. To address this, fish counts and habitat surveys were conducted at four locations on the Great Barrier Reef. At each location, comparisons were made amongst three marine park zones that varied in their exposure to fishing practices; no- take marine reserves, limited fishing areas, and open fishing areas.

The density and biomass of predators varied consistently among zones at each location. Furthermore, we found strong evidence for prey release at all four locations, resulting in distinct fish assemblages amongst zones. Reefs open to fishing had much lower densities of piscivores, and higher densities of prey and herbivorous fishes compared to marine reserves. This broad pattern was consistent amongst locations, and persisted at the level of species, trophic groups, families and communities. Habitat characteristics did not vary significantly amongst zones in a consistent manner amongst locations. Although habitat relationships were strong for specialist species such as butterflyfishes, densities of predators were stronger predictors of prey density for most species, and the trophic composition of reef fish communities differed significantly amongst zones at all locations. Results from this study support the concept that top-down effects can be strong divers of prey populations and influence community structure in highly diverse systems. These data emphasize the vital role of predators, and reinforce the importance of preserving and restoring top-down trophic interactions in ecological systems.

Key words: commercial fishing; conservation and management; coral reef fisheries; coral trout; fishing impacts; Great Barrier Reef; marine reserves; natural experiment; predator-prey interactions; recreational fishing; top-down effects; trophic dynamics.

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INTRODUCTION

Predators perform crucial roles in both marine and terrestrial ecosystems, and the pervasive loss of apex predators is of global conservation concern. Major reductions in predator populations have occurred in almost every ecosystem on the planet, as a result of hunting, fishing, habitat destruction, and a myriad of other anthropogenic effects (Pauly et al. 1998, Jackson et al. 2001, Duffy 2003, Terborgh et al. 2010, Estes et al. 2011). The role of predators in structuring ecological communities has been a recurring concept in ecological theory, and the loss of predators may provide an opportunity to examine how predators shape natural systems (Terborgh et al. 2010). Reductions or removals of apex predators have caused documented changes to communities in terrestrial, freshwater, and marine systems (Beschta and Ripple 2009, Babcock et al. 2010, Estes et al. 2011). Although the nature and complexity of these changes may vary from one system to another, the ubiquity of flow-on effects demonstrates the importance of key predators in stabilising natural systems.

Top-down effects and trophic cascades

Predators may exert top-down control on ecosystems by interacting with species at lower trophic levels, primarily through predation. However, the importance of this process in structuring communities has long been debated by ecologists. Nelson Hairston proposed the "Green World Hypothesis" in 1960, suggesting that global plant biomass is controlled indirectly by predators, which limit herbivore populations (Hairston et al. 1960). Robert Paine coined the term "trophic cascade" to describe this process, through his experimental work on "keystone" predators of marine intertidal systems (Paine 1980, 1988). Trophic cascades typically involve interactions between predators, primary consumers and primary producers, and by definition must include three or more trophic levels which are connected by predation (Paine 1980, 1988, Pinnegar et al. 2000). Implicit in this concept is the notion that removal of top predators could result in changes to the community structure of an ecosystem. Such "top-down effects" from predation may be mediated by or interact with "bottom-up effects" such as variation in primary production and nutrient supply. For many systems it is likely that both top-down and bottom-up effects interact to structure communities (Hunter et al. 1997, Shurin et al. 2010). Further, variations in habitat quality may interact to either ameliorate or exacerbate top-down effects, depending on the nature of habitat associations (Wilson et al. 2008). Since overexploitation of species and habitat degradation are the leading causes of species extinctions, it is critical to determine the relative importance of top-down effects across a wide range of habitats (Dulvy et al. 2003, Wilson et al. 2008).

Although debate on the importance of top-down effects continues, there is little doubt that the "trophic downgrading" (sensu Estes et al. 2011) of ecosystems has led to significant changes in terrestrial, aquatic and marine ecosystems worldwide. Instances of trophic cascades can be found in almost all biomes, from the poles to the tropics, and can lead to landscape scale changes, demonstrating the importance of top-down effects (Shurin et al. 2010, Estes et al. 2011). For example, in the North Pacific, the collapse of sea otter populations resulted in dramatic increases in the abundance of sea urchins, and subsequent overgrazing and degradation of kelp forests (Estes et al. 1978, Estes and Duggins 1995, Estes et al. 2011). In the USA, extirpation of large predators from national parks has resulted in major impacts to plant communities through overgrazing by ungulates (Beschta and Ripple 2009). For example, loss of wolves from Yellowstone national park in the early 1900s resulted in recruitment failure for Aspen due to overgrazing by Elk (NRC 2002, Beschta and Ripple 2009). These examples demonstrate the importance of top-down effects across a wide range of ecosystems.

In marine systems, intensive fishing of apex predators has resulted in systematic reductions of predatory fish populations (Pauly et al. 1998). Globally, over 75% of fish stocks are depleted or fully exploited, and it is common practice to principally target apex predators such as tuna, billfish, and on coral reefs, groupers, jacks and snappers (GBRMPA 2009, Essington 2010, FAO 2012). This can lead to the "ecological extinction" of overharvested predators (sensu Jackson et al. 2001), with severe ecological and economic consequences (Pauly 1995, Pauly et al. 1998, Jackson et al. 2001, Estes et al. 2011). Marine reserves have been developed as a critical tool to address this issue, and some well managed reserves have been successful in restoring high numbers of piscivorous fishes through prohibition and regulation of fishing (Russ and Alcala 2004, Mumby et al. 2006, Russ et al. 2008, Babcock et al. 2010). Apart from the clear conservation benefit that this creates, this restoration of higher trophic levels means that reserves can be used as an effective comparison to adjacent fished areas, making marine reserve networks a powerful scientific tool to investigate trophic interactions (Graham et al. 2003, Micheli et al. 2005). The Great Barrier Reef Marine Park (GBRMP) has the potential be a particularly useful tool for use in such investigations.

The GBRMP is the largest network of marine reserves in the world, and is considered a well-managed and effective marine reserve network (Russ et al. 2008). On the Great Barrier Reef (GBR), densities of targeted piscivores such as coral trout and snapper are two to three fold higher in marine reserves compared to adjacent fished areas (Mapstone et al. 2004, Williamson et al. 2004). The GBRMP consists of multiple zones which vary in the fishing activities allowed within them, resulting in a gradient of fishing intensity (GBRMPA 2009). Approximately one third of the total area of the GBRMP is designated as marine reserve, and this area is representative of all major habitat types that occur on the GBR (GBRMPA 2009). The result is a well replicated suite of sites of different levels of fishing mortality, which can facilitate investigation of the ecological role of predators on coral reefs. As such, the design and effectiveness of the GBRMP makes it an ideal template on which to study the importance of top-down effects in coral reef systems.

Top-down effects in complex systems: the case for reefs

The strength of top-down effects may vary amongst reef systems depending on species diversity and the complexity of trophic interactions. On temperate reefs in Australia and New Zealand, long term studies of no-take marine reserves have demonstrated strong top-down effects of predators (Babcock et al. 2010). Inside marine reserves, re-establishment of predatory lobster and fish populations resulted in decreases in herbivores such as urchins and abalone, and a corresponding increase in macroalgal cover (Edgar and Barrett 1999, Shears and Babcock 2003, Barrett et al. 2009). In these cases, there was a strong and direct link between predators, herbivores and the benthos. Conversely, tropical systems such as coral reefs and rainforests have historically been considered unlikely to be strongly influenced by top-down effects due to their complexity and very high diversity (Strong 1992, Polis and Strong 1996). Such species-rich systems often have a high rate of omnivory, as well as ontogenetic and environmentally induced diet shifts, which can prevent the establishment of discrete trophic levels and obscure top-down effects (Polis and Strong 1996, Shurin et al. 2010). Coral reefs have a naturally high abundance and diversity of piscivorous fishes, which may constitute a significant proportion of fish biomass on protected reefs (Sandin et al. 2010). As such, there may be a high level of functional redundancy in the predator guild, and it has been postulated that removal of a predatory species may simply result in replacement by another (Shurin et al. 2010). Piscivorous fishes on coral reefs are also known to be highly opportunistic, and often include a wide variety of prey species in their diet (Kingsford 1992, Kulbicki et al. 2005). Furthermore, the complex and shelter-rich substrate of coral reef habitats may mediate predator-prey interactions, and many coral reef fishes are strongly influenced by variation in benthic habitat (Bouchon-Navaro and Bouchon 1989, Garpe and Öhman 2003, Jones et al. 2004). All of these characteristics may act to dampen top-down effects, however despite this, they have been documented in coral reef ecosystems in Kenya (McClanahan and Shafir 1990), the Caribbean (Hughes 1994), the Great Barrier Reef (Graham et al. 2003) and the Red Sea (Roberts and Polunin 1992).

Studies that have demonstrated top-down or cascading trophic effects on coral reefs thus far generally hold the common property of having urchins as the primary grazer in the system, and involve fisheries where predators of urchins such as triggerfishes, are heavily targeted (McClanahan and Shafir 1990, Hughes 1994, McClanahan 1994). In Kenya, fishing of triggerfishes has led to an increase in urchin density in fished areas, resulting in bio-erosion of coral, and an increase in filamentous algae, which is more resistant to urchin grazing (McClanahan and Shafir 1990). As such, fished areas have a lower coral cover and topographic complexity compared to marine reserves (McClanahan 1994). Conversely in the Caribbean, urchins are important in controlling macroalgae and mediating competition between coral and algae (Sammarco 1980, Hughes 1989). Fishing of both predatory and grazing fishes here has resulted in urchins being the primary regulators of algae (Hughes 1989, Hughes 1994). When urchin populations were decimated by disease, overgrowth of macroalgae followed, resulting in large declines in live coral cover (Lessios et al. 1984, Hughes et al. 2007*b*). The consistency of top-down and cascading trophic effects in systems involving fish-urchin interactions is high in both tropical and temperate systems, however studies concerning top-down effects of piscivores on prey fishes have had conflicting results (Pinnegar et al. 2000). Depletion of piscivores through fishing was found to have no detectable effect on prey fishes at spatial scales of tens of kilometers in the Seychelles (Jennings et al. 1995), Fiji, (Jennings and Polunin 1997) and the Philippines, (Russ and Alcala 1998). Conversely, greater densities of prey fishes in predator depleted areas at similar spatial scales has been found for grazing surgeonfishes in the Red Sea (Roberts and Polunin 1992), small damselfish and labrid species on the Great Barrier Reef (Graham et al. 2003), and diodontids, small labrids and pomacentrids in Kenya (McClanahan 1994). None of these studies, however, have demonstrated prey release along a gradient of fishing intensity, or assemblage level changes due to predator depletion. Furthermore, with the exclusion of Graham et al. 2003, all of these studies involve fisheries where fishes from multiple trophic levels are targeted, which can increase the difficulty of detecting top-down effects.

Although top-down effects have been difficult to demonstrate on coral reefs at large spatial scales (i.e., kilometers to hundreds of kilometers), numerous small scale studies have demonstrated the importance of predator-prey interactions in structuring fish communities. Top-down effects of piscivores on prey have been demonstrated at scales of meters to tens of meters on natural patch reefs in Moorea (Holbrook and Schmitt 2003), and on constructed reefs in the Virgin Islands (Hixon and Beets 1993), whereby prey abundance and/or species richness was highly correlated with local piscivore abundance. Experimental manipulation of small patch reefs (a few meters in diameter) through predator removal or exclusion, has similarly resulted in changes in the abundance, species richness, and mortality of prey species on reefs with natural recruitment (Doherty and Sale 1985, Caley 1993, Connell 1998), and with stocked prey (Carr and Hixon 1995). These studies have been effective in determining the importance of predators in structuring prey communities at small spatial scales, particularly in the early post-settlement stage. However, it is difficult to "scale up" the implications of such studies to a spatial scale that is ecologically relevant to both understanding population drivers of coral reef communities, and management of marine systems. At broad scales, ecological processes on coral reefs occur against a backdrop of abiotic influences such as storms, cyclones, pollution, sedimentation, and climate change impacts, which can cause significant changes to coral reefs (Rogers et al. 1983, Hughes 1994, Hughes et al. 2003, Wenger et al. 2012, Woolsey et al. 2012). Coral reefs continue to be at risk from an ever increasing number of such threats, which could affect coral reef organisms at multiple trophic levels. Understanding the relative importance of top-down effects on coral reefs is vital when considered in light of such threats, and will increase the ability of ecologists to predict the outcomes of future perturbations to coral reef communities.

The GBRMP provides a unique opportunity to study predator-prey interactions and the importance of top-down effects on coral reefs. This marine reserve network can act as a natural experiment, allowing investigation of these ecological interactions at a broad spatial scale that is both ecologically relevant, and applicable to management. We demonstrate that the GBRMP is the ideal template on which to test the importance of top-down effects on coral reefs for a number of reasons. Firstly, both recreational and commercial fisheries focus primarily on piscivorous reef fishes; herbivorous and small bodied fishes are not major targets (Taylor et al. 2010, GBRMPA 2011). This focus on removal of higher trophic levels allows investigation of top-down effects without the dampening effect of removal of lower trophic levels. Secondly, most coral reef fishes are removed by line fishing, a method that is unlikely to have large effects on habitat structure compared to other fisheries methods such as trawling, netting, or explosive fishing, so habitat structure should not vary as a direct result of fishing (Jennings and Kaiser 1998, GBRMPA 2011). As such, changes in prey assemblages across a gradient of fishing intensity can be attributed to predator removal, rather than habitat destruction. Thirdly, the zoning plan of the GBRMP was designed such that each zone contains a representative area of habitat types occurring on the GBR (GBRMPA 2009). Therefore, use of a selection of reefs/sites from within the GBR can be considered an accurate representation of processes at a broader scale. This combination of factors allows the GBRMP to be used as an excellent template for investigating the importance of top-down effects on coral reefs.

The objective of this study was to investigate the importance of top-down effects on coral reefs, using the GBRMP as a natural experiment in predator removal. The specific aims of this study were as follows:

1. Estimate the density and biomass of piscivorous fishes and their prey, across a gradient of fishing intensity.
2. Estimate the importance of top-down (predation) effects on prey fishes from a variety of trophic groups.
3. Investigate the relative importance of habitat on prey fishes, and how this may interact with top-down effects.
4. Investigate the impacts of predator removal on the trophic structure and species assemblage structure of fishes on the Great Barrier Reef.

Given the focus that recreational fisheries have on piscivorous fishes on the GBR, coupled with previously demonstrated differences in the biomass of key piscivores (Evans and Russ 2004, Russ et al. 2008), we hypothesized that patterns of predation would be significantly different amongst management zones on the GBR. Furthermore, we hypothesized that these differences in predation pressure would result in changes to prey assemblages, and that the nature of such changes would differ according to both the vulnerability of prey trophic groups to predation, and the strength of habitat associations. Small bodied prey such as pomacentrids and juvenile herbivores (e.g., scarids) feature prominently in the diet of key piscivores such as coral trout (Kingsford 1992), and as such we hypothesized that these groups would be strongly influenced by top-down effects, whilst habitat specialists such as chaetodontids would be more influenced by variation in benthic habitats, such as the cover of live coral (Bouchon-Navaro and Bouchon 1989, Fowler 1990). Finally, we hypothesized that these variations in the response of prey groups to predator removal would result in the formation of distinct fish assemblages amongst management zones at the four locations surveyed. From this, we made the following four predictions:

Prediction 1.—Depletion from fishing would result in a reduction in predator densities in heavily fished zones, and related variation in overall predator density and biomass amongst management zones.

Prediction 2.—Predator depletion would result in a corresponding increase in the density of small prey fishes such as pomacentrids and herbivorous fishes, resulting in an increase in prey densities in depleted zones.

Prediction 3.—Species that associate strongly with habitat characteristics such as live coral cover (e.g., chaetodontids) would be strongly influenced by variation in benthic habitat, and these habitat effects may diminish the importance of top-down effects.

Prediction 4.—The composition of fish communities would vary amongst management zones due to predator depletion and associated changes in prey assemblages.

METHODS

Study area

The Great Barrier Reef Marine Park (GBRMP), Queensland Australia, consists of a network of marine protected areas, and is managed through a zoning plan which designates allowable activities within each zone. Zoning of the GBRMP allowed us to study reefs with varying predator numbers and therefore with related variation in predation pressure. This study focussed on three

Table 1. Sampling design of surveys showing the zones surveyed, and nested design of reefs within zones, and zones within reefs, as well as total sites for each location.

	Zones surveyed			Sample sizes		
Location	MR	LF	OP	Reefs per zone	Sites per reef	Total sites
Capricorn Bunkers	x	x	x	2	3	18
Whitsundays	x	x	x	1	5	15
Palm Islands	x	x	x	1	5	15
Ribbon Reefs	x		x	2	2	8
Total for all locations						56

Note: Zone abbreviations are: MR = marine reserve, LF = limited fishing, OP = open.

zones that are subject to a gradient of fishing pressure: no-take marine reserves, limited fishing zones and open fishing zones. No-take marine reserves are closed to all forms of fishing at all times, and will be referred to hereafter as "marine reserves". Limited fishing zones allow limited recreational fishing (with gear restrictions) and open areas allow for both recreational and commercial fishing including line fishing, trawling and trolling (GBRMPA 2009).

Coral reefs on the GBR are subject to both commercial and recreational fisheries. The main commercial fishery operating on coral reefs with the GBRMP is the coral reef fin fishery; predominantly a hook and line fishery which operates mostly at offshore locations. There is also a substantial amount of recreational fishing activity, particularly near populated areas (Taylor et al. 2010). Both commercial and recreational fisheries largely target piscivorous reef fishes, namely coral trout (a group including seven serranid species from the genera *Plectropomus* and *Variola*), red-throat emperor (*Lethrinus miniatus*), stripey snapper (*Lutjanus carponotatus*), and a variety of other snappers and emperors (GBRMPA 2009, Taylor et al. 2012). The GBRMP was formed in 1975 to provide a network of marine reserves, and was rezoned in 2004 to increase protection to its current level, with 30% of its area now designated as no-take marine reserves (GBRMPA 2009). The majority of the marine reserves surveyed in this study had been protected for at least 25 years. With the exception of One Tree Island, and two of the marine reserve sites in the Whitsundays, marine reserves surveyed in this study were established in 1986–1988. One Tree Island was protected as a scientific research zone (no-take) in 1978, and the two Whitsundays sites were established as part of the rezoning in 2004.

Studies have shown that no-take marine reserves have been effective in re-establishing populations of targeted fishes such as piscivores (Evans and Russ 2004, Russ et al. 2008). In order to assess the importance of piscivores in structuring prey assemblages, surveys were conducted in zones within the GBRMP that were expected to vary in the density and biomass of piscivorous fishes. As fishing practices on the GBR are heavily targeted towards piscivorous fishes, we predicted that piscivore densities would vary with fishing intensity. Fish and habitat surveys were conducted within three management zones which varied in fishing intensity: marine reserves (predicted to have high densities of piscivores), limited fishing zones (predicted to have moderate piscivore densities) and open fishing zones (predicted to have low piscivore densities). To allow assessment of the spatial generality of patterns, surveys were conducted at four locations, separated by hundreds of kilometers; the Capricorn Bunkers Group in the southern GBR, the Whitsundays and Palm Islands in the central GBR and the Ribbon Reefs in the northern GBR (Appendix). Hierarchical sampling designs were used at each location to examine processes at multiple spatial scales and to provide tests for each of these levels; residual variance measured variation among replicate belt transects. Tests are provided for sites within reefs (separated by hundreds of meters to kilometers), reefs within management zones (separated by kilometers), and management zones within each location (separated by tens of kilometers; Table 1); the entire design was repeated at four locations. Sampling designs varied amongst locations according to the local zoning plan, however all three management zones were surveyed at each location with the exception of the Ribbon Reefs, which does not have limited fishing zones (Table 1). At each site, fish were counted and habitat surveyed along belt transects, as described below. Five transects (25 × 5m) were placed haphazardly along the reef crest at each site, in a depth range of 3–10 m. All fish counts and habitat surveys were conducted by a single observer for the duration of the study. Methods were tailored to test the predictions of the study as follows.

Predictions 1 and 2: Depletion from fishing would result in reduced predator densities, and a corresponding increase in prey densities in heavily fished areas.

Fish counts.—We hypothesized that fishing would cause a reduction in piscivorous fish densities, and result in a corresponding increase in prey densities along a gradient of fishing intensity. To test this, we quantified fish assemblages by surveying fishes using underwater visual census along belt transects. Surveys were focussed on estimating the density and size of piscivorous fishes as well as that of common prey groups, and herbivorous fishes. A total of 150 species were surveyed throughout the study, including large piscivores targeted by fisheries (Serranidae, Lutjanidae, and Lethrinidae), smaller meso-predators such as *Cephalopholis, Epinephelus*, and *Pseudochromis* spp. (Serranidae), and small piscivorous labrids, small prey species such as pomacentrids and chaetodontids, and larger herbivorous fishes such as scarids, acanthurids, and siganids; taxonomy was according to Randall et al. 1997. Counts were restricted to reef associated species, and did not include transient pelagic species (e.g., carangids). Transect sizes varied according to the relative densities and mobility of each species. All piscivorous fishes and mobile herbivores were counted along 25 × 5 m transects, chaetodontids and pomacentrids were counted along 10 × 5 m transects, and highly abundant and site attached pomacentrid species were counted along 2 × 10 m transects; the latter two sized transects were within the area of the 25 × 5 m transect. The size of each fish (total length) was estimated, and small fishes were placed into the following size categories: recruits (<15 mm), small (15–29 mm), medium (30–59 mm), large (60–100 mm) and extra-large (>100 mm). These methods allowed us to estimate both the density and biomass of each species.

Trophic groupings.—After all data were collected, fish were categorized into trophic groupings to allow comparisons of the trophic structure of fish assemblages among zones. These groups were as follows (number of species in parentheses): targeted piscivores (16), non-target piscivores (25), omnivorous (21), planktivorous (11), and herbivorous pomacentrids (13), corallivorous (15), and benthic feeding chaetodontids (10), and scraping (18) cropping (6), grazing (5) and farming (10) herbivores. Categorization of species into trophic groups was decided based on published accounts and personal observations of diet and feeding behavior (Ceccarelli et al. 2005, Pratchett and Berumen 2008, Green and Bellwood 2009, Froese and Pauly 2013). Targeted piscivores were defined as those species commonly targeted by either recreational or commercial fisheries, and fishes were categorized as piscivorous if fishes constituted the majority of their diet (GBRMPA 2009, 2011). Biomass estimates of each species were calculated from length estimates of fishes by using length-weight relationships provided in the online resource Fishbase (Froese and Pauly 2013).

Data analysis.—We predicted that the densities and biomass of fishes would vary among management zones and that this would be consistent by location and replicate zones within locations. Fully nested analysis of variance (ANOVA) was used to compare the density and biomass of fishes, and habitat characteristics amongst zones, reefs and sites at each location. This analysis also allowed us to use variance components to estimate the percentage of the total variation that could be attributed to different levels of the design; raw data were used to calculate variance components (Underwood and Petraitis 1993). Because the sampling design varied slightly due to the number of management zones that occur within each location, locations were analysed separately (see Tables 1 and 2). Assumptions of homogeneity of variance for ANOVA were tested using Cochran's test (Underwood 1997). Normality of the data was assessed by a visual examination of the distribution of the residuals; data were transformed when necessary. Post- hoc analyses were performed to determine how zones differed from each other using the Student-Newman-Kuels (SNK) test. Results from post hoc analyses were

Table 2. Results from ANOVAs on fish groups and habitat characteristics by location. All analyses are on density data unless otherwise specified.

	Capricorn Bunkers			Whitsundays		Palm Islands		Ribbon Reefs		
Dependent variable	Zone	Reef	Site	Zone	Site	Zone	Site	Zone	Reef	Site
df	(2, 72)	(3, 72)	(12, 72)	(2, 12)	(12, 60)	(2, 12)	(12, 60)	(1, 32)	(2, 32)	(4, 32)
Piscivores	***	NS	*	**	*	*	NS	NS	NS	NS
Targeted piscivores	***	NS	NS	***	*	**	*	*	NS	NS
Non-targeted piscivores	NS	**	**	NS	*	**	*	NS	NS	NS
Coral trout (*Plectropomus* spp.)	***	NS	*	***	***	***	NS	***	NS	NS
L. carponotatus	**	NS	NS	**	NS	*	NS	NP	NP	NP
Total prey	***	*	***	*	NS	**	NS	**	NS	NS
Pomacentridae	***	NS	***	*	NS	**	NS	**	NS	NS
Planktivorous	**	***	***	*	NS	*	*	*	NS	NS
Omnivorous	***	NS	***	*	NS	***	**	*	NS	NS
Herbivorous	**	***	***	***	NS	***	*	NS	***	*
P. moluccensis	***	NS	**	***	***	*	NS	***	***	**
P. wardi	**	**	***	***	***	**	***	**	***	NS
A. polyacanthus	NS	*	NS	**	*	***	NS	NS	NS	NS
A. curacao	**	NS	***	*	**	**	***	**	**	NS
Chaetodontidae	*	**	NS	NS	NS	**	**	*	*	NS
Total herbivores	**	NS	*	**	***	***	**	NS	NS	*
Scraping herbivores	***	*	**	***	***	NS	NS	NS	NS	NS
Grazing herbivores	***	***	***	**	NS	NS	NS	NS	NS	NS
Cropping herbivores	*	NS	*	NS	*	NS	NS	NS	NS	NS
Farming herbivores	**	***	***	***	NS	***	**	NS	***	*
Biomass- piscivores	***	NS	*	***	NS	***	***	**	**	**
Biomass- coral trout	***	NS	**	***	**	***	NS	***	**	**
Biomass- *L. carponotatus*	*	**	**	**	NS	**	*	NP	NP	NP
Biomass total herbivores	**	NS	*	NS	*	NS	NS	NS	*	*
Live hard coral cover	NS	***	**	NS	*	NS	**	NS	NS	NS
Live soft coral cover	***	**	***	***	***	***	***	NS	**	***
Algal cover	*	NS	**	NS	**	NS	**	NS	*	**
Structural complexity	*	NS	**	*	NS	**	**	***	***	**

Notes: NP = not present. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

used to group zones. Multiple analyses were done for species within each design. It could be argued that a Bonferroni correction factor should be used to readjust the critical levels of P and, therefore, minimise the possibility of Type I error (i.e., 0.05/n tests). A problem, however, is that this can greatly increase the risk of Type II error and for this reason no correction was used (Moran 2003).

Prediction 3: Species that associate strongly with habitats such as live coral would be more strongly influenced by variation in benthic habitat than by top-down effects.

Benthic habitat surveys.—To characterize the benthos and reef structure at each site, the percentage cover of benthic habitat types, as well as the rugosity and vertical relief of the substratum were estimated. These have been demonstrated to be important habitat characteristics and determinants of the distributions and diversity of many reef fishes (Luckhurst and Luckhurst 1978, Holbrook et al. 2002). All habitat data were collected along five 25 × 5 m transects at each site. Substratum cover was recorded using the linear point intercept method, which has been demonstrated to be a precise and time-efficient method for obtaining estimates of coral cover (Nadon and Stirling 2006). Cover was estimated by recording the dominant substratum at 20 to 35 points along each transect. Coral cover was recorded according to morphology, as described by Veron (2000). This included live and dead forms of the following: branching, massive, foliose, laminar, encrusting, and free living hard corals, and branching, foliose and encrusting soft corals. In order to most accurately record the available habitat types for fishes, where dead corals were covered with encrusting organisms (e.g., algae, sponges), the encrusting organisms were recorded, and dead coral was only recorded as such if it was bare. The cover of red, green and brown algae was also recorded, and separated into filamentous, branching, coralline, and macroalgae, and the cover of sand and rubble was also recorded.

As well as benthic cover, the structural complexity of reefs can be an important determinant of fish densities, as complex structures may increase the availability of shelter sites (Hixon and Beets 1993, Beukers and Jones 1998). We used two measures to estimate the structural complexity along each transect; rugosity and vertical relief. Rugosity measures give an estimate of the overall complexity of the substratum; low rugosity values indicate that the substratum is flat and homogenous with a low number of shelter sites, whilst high rugosity values indicate a complex substratum with a variety of holes and crevices, which can be used by fish for shelter sites (Nash et al. 2013). The observer was trained to accurately estimate rugosity along transects by first measuring rugosity using the traditional ball-and-tape methods (Risk 1972), and then using these values as a guide to visually estimate rugosity on subsequent reefs. These pilot studies encompassed reefs which varied in their rugosity and vertical relief, and rugosity was found to be estimated with a high level of accuracy using this method. Mean vertical relief of each transect was calculated by estimating the reef height at five meter intervals along each 25 × 5 m transect. Rugosity and vertical relief estimates were converted into categories, 1–4 for rugosity and 1–5 for vertical relief. For each site, an overall structural complexity index was calculated by multiplying the rugosity and vertical relief categories, and the index ranged from 1 (lowest) to 20 (highest). Both the structural complexity index, and the values for rugosity and vertical relief were used for analyses in this study. The structural complexity was used in Analysis of Variance to compare broad patterns of complexity amongst zones, reefs and sites, however the raw rugosity and vertical relief values were used as descriptors for the multiple regressions and BIO-ENVIRON analysis (Clarke and Ainsworth 1993) in order to get a more detailed understanding of how habitat variables influenced fish densities.

Data analysis.—We predicted that the relative importance of predators vs. habitat would vary amongst prey species, depending on the strength of their habitat associations. To test this, we used linear regression models to test the explanatory value of predator densities and habitat characteristics for a number of prey species and groups. Stepwise multiple linear regressions were used to analyse relationships between predators, prey and habitat, and determine the best combination of variables to predict prey densities. We used stepwise regression rather than multiple regressions to allow the best combination of habitat and species density variables to be determined for the regression model, allowing us to identify the most important characteristics for species/groups. The following predictor variables were used in the analysis: percentage cover of live hard coral, live soft coral, dead coral and algae, as well as vertical relief and rugosity, and densities of coral trout (*Plectropomus* spp.), *L. carponotatus*, and total piscivores. Square root and log transformations were applied to variables to meet the assumptions of normality for General Linear Models.

Prediction 4: The composition of fish communities would vary amongst management zones due to predator depletion and associated changes in prey assemblages.

We proposed that variation in the densities of predatory fishes would be a good predictor of reef fish assemblages. The trophic structure of fish assemblages amongst zones and reefs were compared using non-metric multi-dimensional scaling (nMDS) and Permutational Analysis of Variance (PERMANOVA) (Anderson 2001). All analyses were performed separately for species-level data and trophic structure. To compare the trophic structure, species were pooled into trophic groups (as described above) and the analysis was run on the pooled data. Data were square root transformed to decrease the influence of highly abundant species and matrices of similarity were calculated using the Bray-Curtis similarity coefficient. Nonmetric multidimensional scaling (nMDS) was used to produce ordinations of the rank orders of similarities amongst zones; stress levels in the nMDS were used to evaluate the robustness of the test, and were considered robust if stress was <0.2. Differences amongst zones within each location were formally tested using Permutational ANOVA (PERMANOVA), which is considered a robust method of multivariate analysis of variance (Anderson 2001). Percentage of similarity analysis (SIMPER) was used to compare the

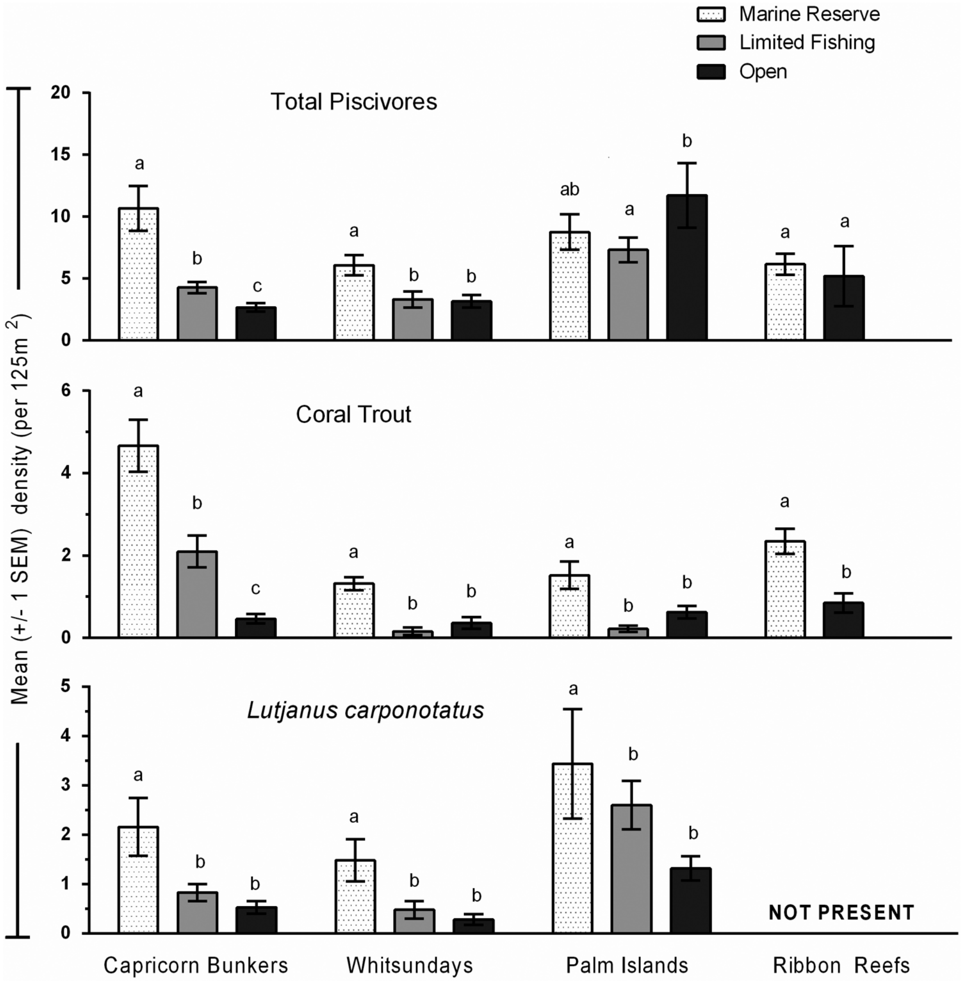

Fig. 1. Density (mean ±1 SE) of total piscivorous fishes, and key species targeted by fisheries; coral trout (*Plectropomus* spp.), and stripey snapper (*Lutjanus carponotatus*), amongst marine reserve, limited fishing and open zones at all four locations. *L. carponotatus* did not occur at the Ribbon Reefs. Letters above bars indicate groupings based on post hoc analysis: different letters indicate significant differences amongst zones.

dissimilarity of communities amongst zones, and the contribution of species and groups to this dissimilarity. BIO-ENV analysis (Clarke and Ainsworth, 1993) was used to determine the extent to which multivariate patterns of fish densities were driven by habitat characteristics, and to determine the best environmental descriptors for the biological data

RESULTS

Prediction 1: Depletion from fishing would result in variation in overall predator density and biomass amongst management zones.

Piscivores.—Piscivore densities differed significantly amongst management zones at three of the four locations across the GBR (Fig. 1, Table 2). The density of all piscivores combined was a minimum of two times greater in no-take marine reserves as compared to other zones in both the Capricorn Bunkers, and Whitsundays, whilst at the Palm Islands piscivore density was greatest in the open fishing zones, and at the Ribbon Reefs no significant differences in piscivore density occurred amongst zones. At the Palm Islands, the density of non-targeted piscivores was inversely related to targeted piscivores. Greater overall densities of piscivores in the open fishing zones

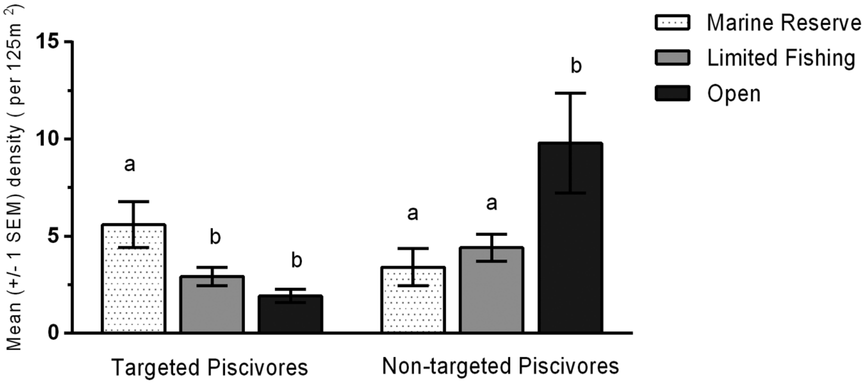

Fig. 2. Density (mean ±1 SE) of targeted and non-targeted piscivorous fishes at the Palm Islands. Letters above bars indicate groupings based on post hoc analysis: different letters indicate significant differences between zones.

at the Palm Islands occurred due to increases in species not targeted by fisheries; targeted species had significantly greater densities in marine reserves (Fig. 2, Table 2). Such patterns were not found at the other three locations. The biomass of piscivores was significantly greater in marine reserves than fished zones at all four locations (Fig. 3, Table 2). In the Capricorn

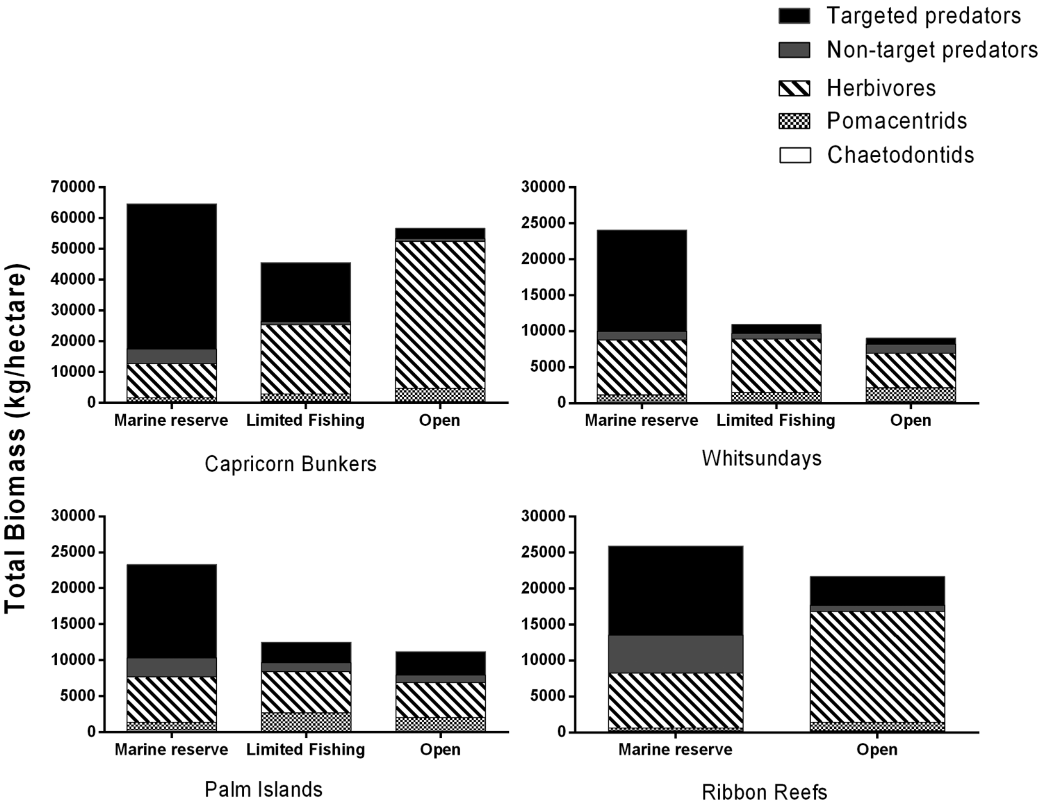

Fig. 3. Total biomass (kg/ha) of fishes amongst zones at all four locations, separated by families/trophic groups. Note the differences in axis scales amongst locations.

Bunkers, piscivore biomass decreased significantly along the gradient of fishing pressure (open < limited fishing < marine reserves). Overall, densities of piscivores varied consistently by zone, with little variation attributed to reefs within zones (0–2%). Zones explained 14–31% of the variation; variation was moderate at the site level (12–16%), and high at the residual level (56–70%), as would be expected for aggregating fish, however this did not prevent detection of significant zone effects in the ANOVA.

Coral trout.—The densities of coral trout (*Plectropomus* spp.) were up to five times greater in marine reserves compared to open zones. At all four locations, the density and biomass of coral trout was significantly greater in marine reserves than limited fishing and open zones (Figs. 1 and 3, Table 2). At the Capricorn Bunkers the density and biomass of coral trout decreased along a gradient of fishing intensity (open < limited fishing < marine reserves). Densities of coral trout overall were much greater at this location (Fig. 1, Table 2). Zoning explained a greater proportion of variance (24–44%) than either reefs (0–3%) or sites within reefs (13–28%); variation among replicates was again great (residual; 48–70%). The density and biomass of stripey snapper (*Lutjanus carponotatus*) was also greater in marine reserves in the three locations where this species occurs. Although zoning effects were significant for this species, residual variation was very high (up to 85%) due to their aggregative behavior, however little variation occurred amongst reefs and sites within zones (0–8%).

Prediction 2: Predator depletion would result in an increase in the density of small prey fishes and an overall increase in prey densities in depleted zones.

Pomacentrids.—Densities of total prey and pomacentrids were strongly influenced by zoning and had an inverse relationship to marine reserve protection; densities were significantly greater in fished zones at all four locations (Fig. 4, Table 2). At the Whitsundays, pomacentrid densities in limited fishing zones did not differ significantly from either marine reserves or fished zones, however open fishing zones had significantly greater densities compared to marine reserves. At all other locations densities were significantly greater in both limited fishing and open zones. Zoning explained 17–30% of the variation in pomacentrid density. There was little variation in pomacentrid densities amongst reefs or sites within zones (0–9%), with the exception of the Capricorn Bunkers, where densities differed significantly amongst sites, which accounted for 41% of the total variation (Table 2). There were great differences in densities among replicates, which explained 40–70% of the variation, but this did not mask zoning effects.

Pomacentrids demonstrated differences in their response to zoning when separated into trophic groups. Densities of omnivorous pomacentrids were greater in fished zones at all four locations, and increased along a gradient of fishing intensity (open < limited fishing < marine reserves), at the Capricorn Bunkers and Palm Islands (Fig. 5). Planktivorous and herbivorous pomacentrids showed greater variability in their zoning relationships. Planktivorous pomacentrids had significantly greater densities in fished zones at the Palm Islands and Ribbon Reefs, and in limited fishing zones at the Capricorn Bunkers, but showed the opposite relationship at the Whitsundays, where densities were significantly lower in limited fishing zones compared to marine reserves and open zones. Densities of herbivorous pomacentrids were greatest in limited fishing zones at the Whitsundays, and in open zones at the Palm Islands, but showed no zoning-related patterns in the Ribbon Reefs or Capricorn Bunkers (Fig. 5).

Zoning had a strong impact on densities of individual pomacentrid species (e.g., *Pomacentrus moluccensis, P. wardi, Amblyglyphidodon curacao, Acanthochromis polyacanthus*; Fig. 6, Table 2). Overall, 50% of pomacentrid species exhibited zoning-related patterns whereby they had significantly greater densities in fished zones at most locations. Species that exhibited differences made up 75% of the total pomacentrid densities, and had a strong effect on patterns for pomacentrids overall.

Chaetodontids.—Although the density of chaetodontids did differ among the fishing zones, these patterns were not consistent among the four locations. The density of chaetodontids was significantly greater in marine reserves at the Palm Islands and Ribbon Reefs compared to fished zones (Fig. 4, Table 2). At the Capricorn Bunkers densities were greatest in limited fishing zones, whilst at the Whitsundays, densities were

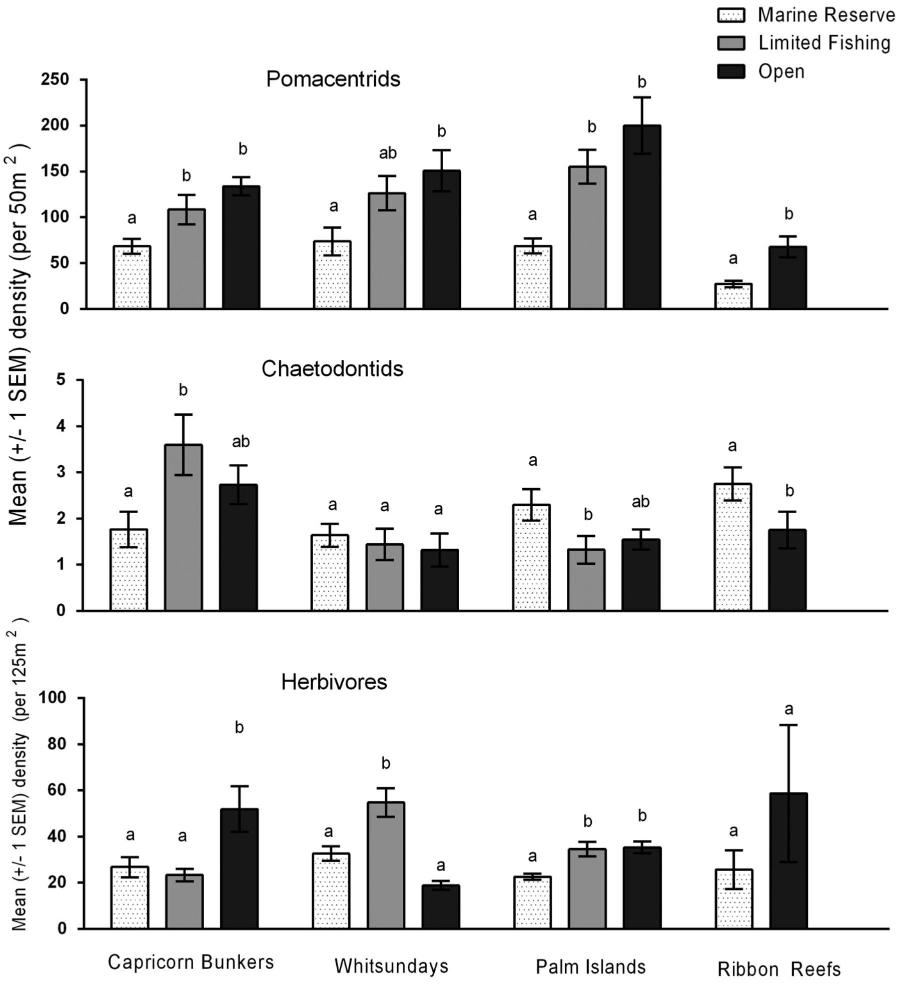

Fig. 4. Density (mean ±1 SE) of pomacentrids, chaetodontids, and herbivorous fishes amongst marine reserve, limited fishing and open zones at all four locations Letters above bars indicate groupings based on post hoc analysis: different letters indicate significant differences between zones.

very similar among zones. Densities of chaetodontids differed significantly among reefs within zones at the Capricorn Bunkers and Ribbon Reefs, where reefs were responsible for 15–24% of the total variation. Variation amongst sites was high at the Palm Islands, accounting for 21% of total variation, and was great among replicates at all locations (residual level = 65–90%).

Herbivorous fishes.—Herbivorous fishes were strongly influenced by zoning, and had greater densities in fished zones compared to marine reserves at the Capricorn Bunkers, Whitsundays and Palm Islands (Fig. 4, Table 2). At the Ribbon Reefs there was a strong trend of greater densities of herbivores in open zones, however this was not significant due to very patchy distributions, as indicated by high residual variation (85%). Patterns of variation in densities by zones differed among locations. At the Capricorn Bunkers, herbivore densities were significantly greater in open zones compared to marine reserves and limited fishing zones, and the total herbivore biomass was more than four times greater than in marine reserves (Figs. 3 and 4, Table 2). This pattern was consistent for all herbivore trophic groups (scraping, grazing, cropping and farming herbivores). At the Whitsundays, total herbivore density was greatest in the limited fishing zones, and there were no significant differences between open zones and

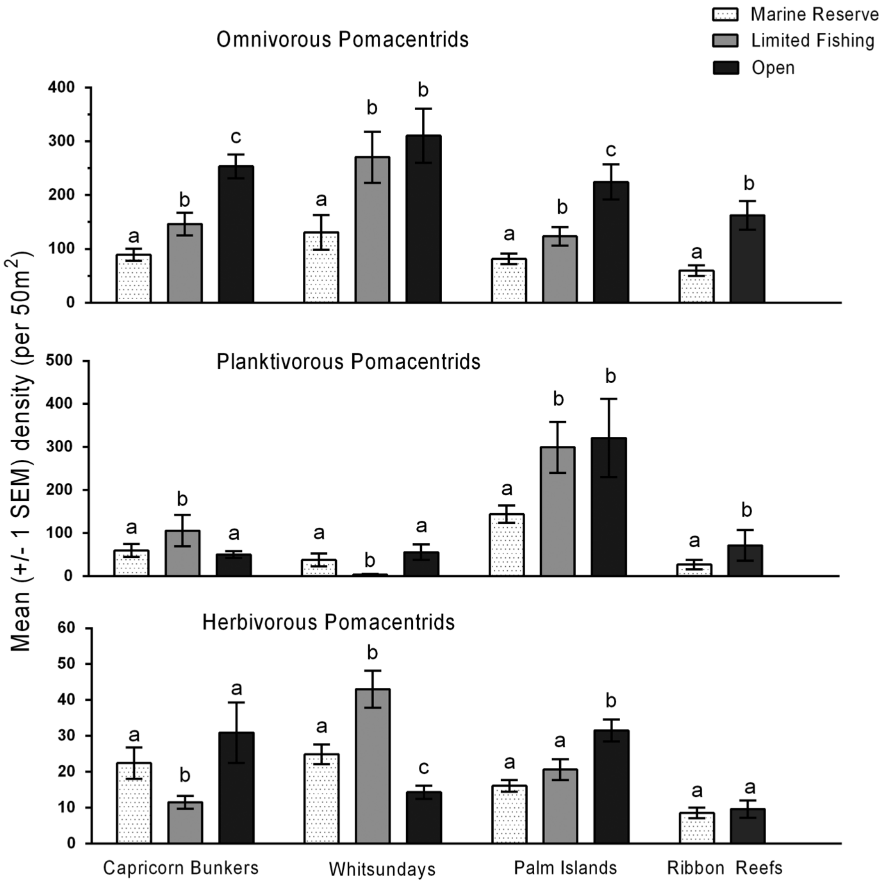

Fig. 5. Density (mean ±1 SE) of omnivorous, planktivorous and herbivorous pomacentrids amongst marine reserve, limited fishing and open zones at all four locations Letters above bars indicate groupings based on post hoc analysis: different letters indicate significant differences between zones.

marine reserves (Fig. 4, Table 2). This pattern was consistent for all herbivore groups except for cropping herbivores, but did not result in a significant difference in total biomass (Fig. 3, Table 2). At the Palm Islands, total densities of herbivores were greater in limited fishing zones and open zones, however this pattern was driven largely by farming herbivores, mostly territorial grazing pomacentrids (Fig. 4, Table 2). Densities of scraping, grazing and cropping herbivores did not differ significantly by zone, and the total biomass of herbivores was similar amongst zones (Fig. 3, Table 2). Overall, zoning effects were strong, accounting for up to 20% of total variation, whilst variation amongst reefs within zones was low (0–2%). Variation in herbivore density was great amongst sites (18–64%), and at the residual level (29–80%), due to their strong schooling behavior.

Prediction 3. Species that associate strongly with habitats such as live coral would be more strongly influenced by variation in benthic habitat than by top-down effects.

Variation in benthic cover amongst management zones.—Fishing did not have a strong effect on habitat, and no consistent patterns were found amongst management zones at the four locations. Live hard coral cover was consistent amongst all three zones at all locations. It did however, vary significantly among reefs at the Capricorn Bunkers (16% of total variation) and sites at the Capricorn Bunkers (11%) and Whitsundays (40%; Fig. 7, Table 2). There were some differences in soft coral and algal cover amongst management zones, however there was no consistent pattern amongst the four locations.

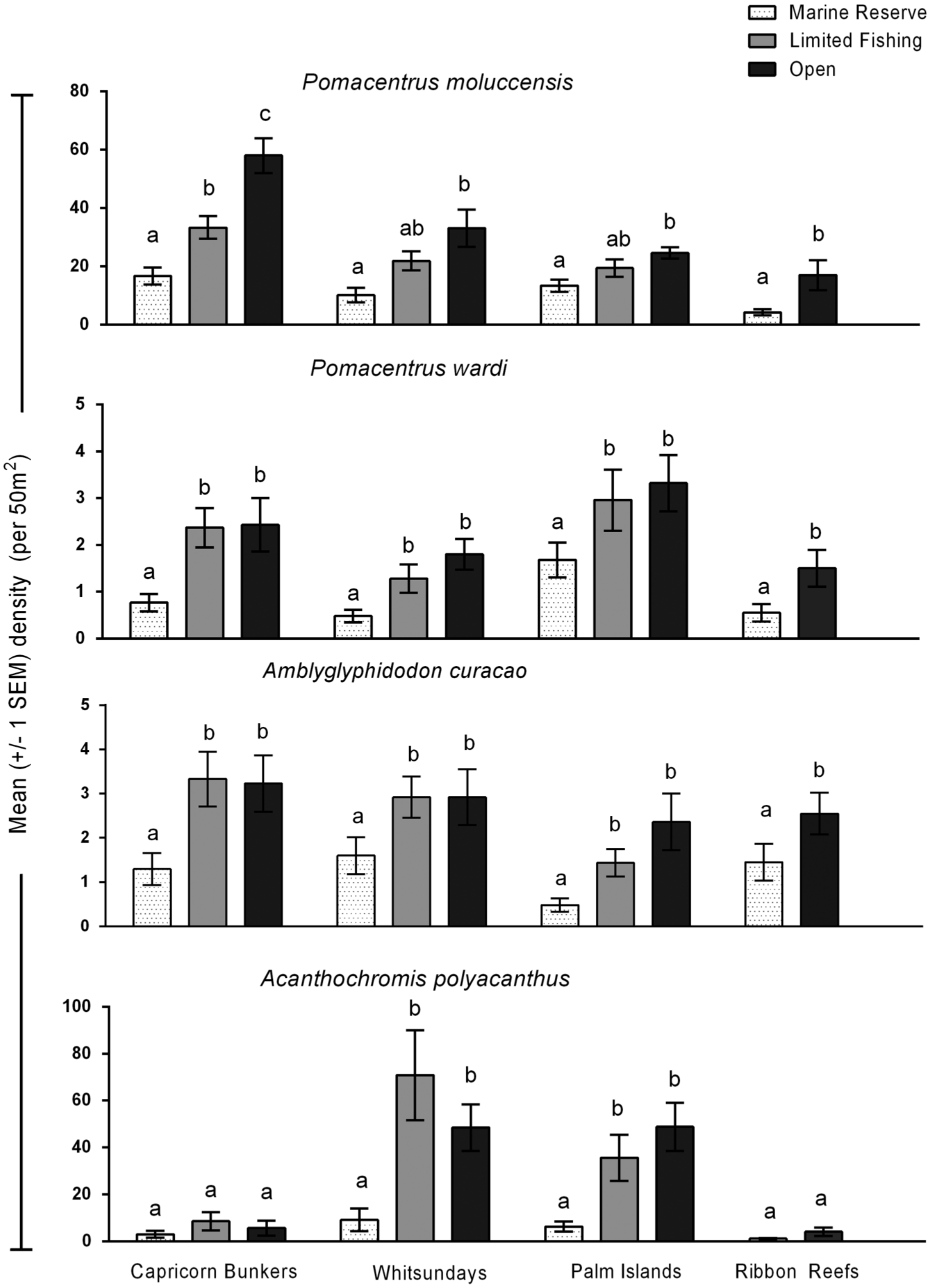

Fig. 6. Density (mean ±1 SE) of the key prey species; *Pomacentrus moluccensis, P. wardi, Amblyglyphidodon curacao,* and *Acanthochromis polyacanthus* amongst marine reserve, limited fishing and open zones at all four locations Letters above bars indicate groupings based on post hoc analysis: different letters indicate significant differences between zones.

Live soft coral cover differed by zone at all locations except the Ribbon Reefs, however patterns were not consistent amongst locations, and varied amongst reefs (20–40% of total variation) and sites (10–30%). Soft coral cover was lower in limited fishing zones at the Capricorn Bunkers compared to both marine reserves and open zones and had the lowest

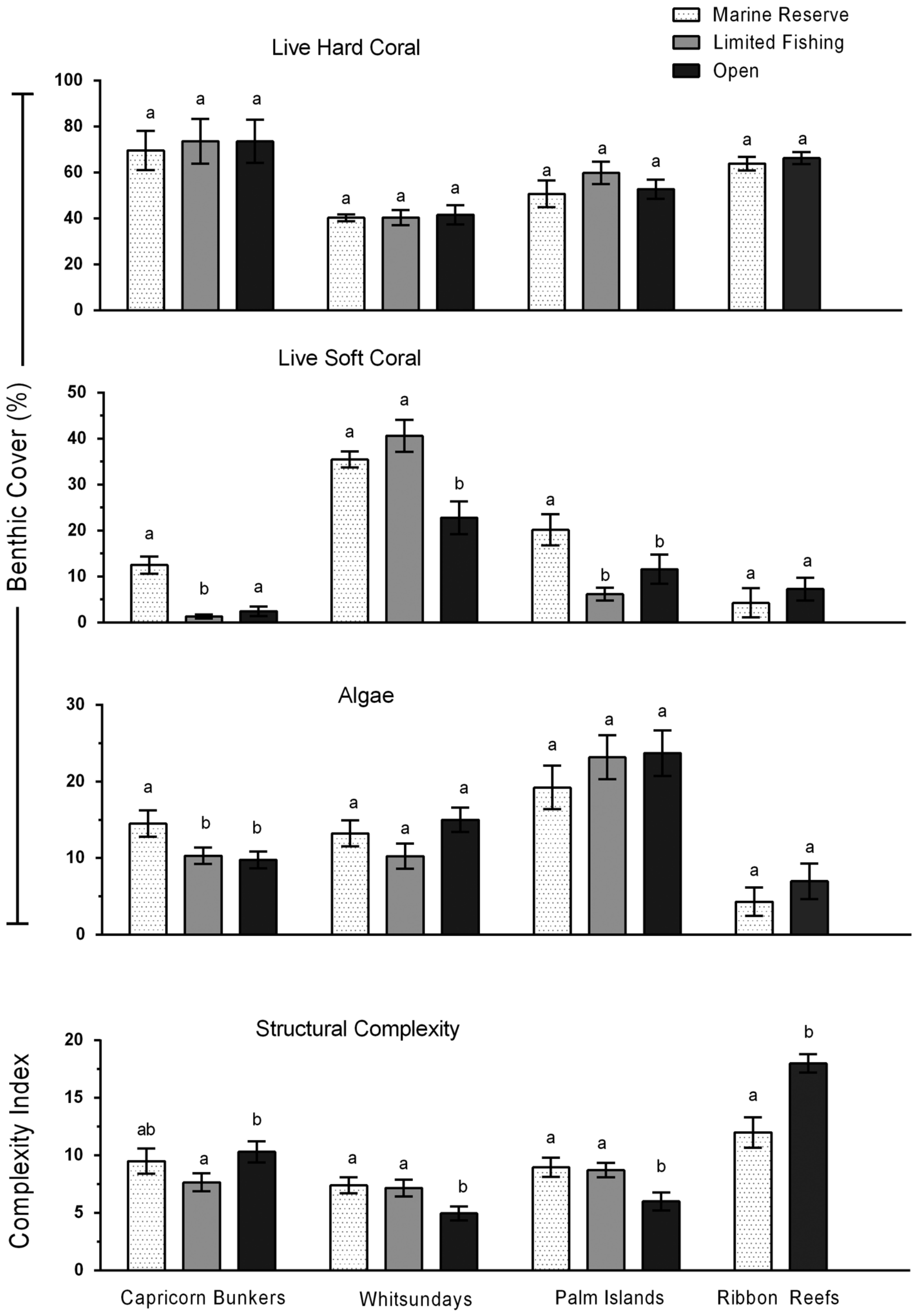

Fig. 7. Percent cover (mean ±1 SE) of live hard and soft coral and algae, and mean structural complexity (an index encompassing rugosity and vertical relief) of reefs amongst marine reserve, limited fishing and open zones at all four locations Letters above bars indicate groupings based on post hoc analysis: different letters indicate significant differences between zones.

cover in open zones at the Whitsundays. At the Palm Islands soft coral cover was lower in both limited fishing and open zones, however no zoning patterns occurred at the Ribbon Reefs (Fig. 7, Table 2). Overall, soft coral cover was much greater in the Whitsundays compared to other locations. Algae were less abundant in both limited fishing and open zones at the Capricorn Bunkers, however percentage cover did not differ significantly amongst zones at any other location. Algal cover differed significantly among sites at all locations, and variation among sites accounted for up to 85% of the total variation.

Structural complexity differed significantly amongst zones, however the nature of this varied amongst locations. At the Whitsundays and Palm Island, complexity was lowest in open fishing zones, however the opposite pattern was observed for the Capricorn Bunkers and Ribbon Reefs (Fig. 7). Structural complexity varied greatly amongst sites within reefs (up to 40% of total variation), and was lower in open zones at both the Whitsundays and Palm Islands (Fig. 7, Table 2). Conversely, At the Capricorn Bunkers and Ribbon Reefs, complexity was greatest in open zones, however was not significantly different compared to marine reserves at the Capricorn Bunkers. There was great variation in the distributions of benthic cover and structural complexity at the residual level, which accounted for 9–79% of total variation.

Habitat associations vs. predator-prey relationships

1. *Pomacentrids.*—There was a strong negative relationship between the density of predators and prey at all four locations, and predator density had more predictive value than habitat for small prey species and groups such as pomacentrids (damselfishes; Tables 3 and 4). Densities of small prey species such as pomacentrids were negatively related to densities of key predators such as coral trout (*Plectropomus* spp.), and stripey snapper (*L. carponotatus*) at all four locations (Fig. 8, Tables 3 and 4). This relationship was particularly strong at the Ribbon Reefs, where densities of total prey, and total pomacentrids were strongly negatively related to densities of coral trout (*P. leopardus, P. laevis* and *P. areolatus*), which explained 82–83% of the variation. This relationship was stronger for omnivorous pomacentrids, compared to planktivores and herbivores. Total predator density was the strongest predictor for the lemon damsel (*P. moluccensis*, 49.4%), and the density of *P. leopardus* was the strongest predictor for the spiny chromis (*A. polyacanthus*, 32.5%). At the Palm Islands, the regression model did not explain a large proportion of variation, however there was a significant negative relationship between coral trout (*P. maculatus* and *P. leopardus*) and total prey, pomacentrids (including omnivores and herbivores) *P. moluccensis* and *A. polyacanthus* (Fig. 8, Table 4). The density of *P. maculatus* explained 15–34% of the total variation for these species/groups. In the Whitsundays, the density of the stripey snapper (*L. carponotatus*) was a strong negative predictor for densities of small prey species/groups. *L. carponotatus* density was the primary predictor for densities of total prey, omnivorous pomacentrids and *P. moluccensis*, and explained 40–50% of variation (Fig. 8, Table 3). In the Capricorn Bunkers, the density of coral trout (*P. leopardus* and *P. laevis*) was the primary predictor for the density of pomacentrids (including planktivores, omnivores and herbivores). The density of coral trout explained 30−46% of the variation in density for these species/groups. Habitat variables had less predictive value for pomacentrids than piscivore densities did, and no consistent relationships with habitat were detected amongst the four locations (Tables 3 and 4). Hard coral cover was a primary predictor for total prey (31.6%), and a secondary predictor for *P. moluccensis* (31.4%) at the Capricorn Bunkers, and for *A. curacao* (17.2%) at the Whitsundays.

2. *Chaetodontids.*—Chaetodontid densities were strongly related to habitat characteristics, including hard coral, algae, rugosity and vertical relief. Hard coral cover was the primary predictor for the density of chaetodontids at the Capricorn Bunkers, Whitsundays and Palm Islands and explained 33–76% of the variation in the density of chaetodontids overall (Fig. 8, Tables 3 and 4). No strong predator-prey relationships occurred for chaetodontids, and piscivore densities held little predictive value for this group. Patterns of density for chaetodontids differed at the Ribbon Reefs, and were positively related to densities of coral trout, but not significantly related with habitat.

3. *Herbivores.*—Herbivores displayed great

Table 3. Results of stepwise multiple linear regressions on the density of prey species and groups, and herbivore functional groups for the Capricorn Bunkers and Whitsundays. Only significant independent variables and models are given. Signs for the coefficient of each independent variable are in parentheses. The r^2 values have been multiplied by 100 to represent the percentage of variation each independent variable explains. *L. carp* = *Lutjanus carponotatus*. "Coral trout" refers to the summed density of all *Plectropomus* spp.

	Capricorn Bunkers			Whitsundays		
Dependent variable	Independent variable	Partial r^2 (× 100)	Model r^2 (× 100)	Independent variable	Partial r^2 (× 100)	Model r^2 (× 100)
Total prey	Hard coral (+)	31.6	31.6	*L. carp* (−)	40.0	40.0
Pomacentrids	Coral trout (−)	36.5	36.5	*L. carp* (−)	40.7	40.7
Planktivores	Coral trout (−)	42.11	42.11	Not significant		
Omnivores	Coral trout (−)	42.7	42.7	*L. carp* (−)	24.5	24.5
				Hard coral (+)	19.5	44.0
				Coral trout (−)	13.8	57.8
Herbivores	Coral trout (−)	28.55	28.55	Algae (−)	45.2	45.2
P. moluccensis	Coral trout (−)	44.8	44.8	*L. carp* (−)	50.5	50.5
	Hard coral (+)	31.4	58.2	Coral trout (−)	16.8	67.3
P. wardi	Algae (−)	16.8	16.8	*L. carp* (−)	14.1	14.1
A. polyacanthus	Coral trout (−)	46.1	46.1	*L. carp* (−)	42.7	42.7
A. curacao	Relief (+)	15.5	15.5	Coral trout (−)	32.0	32.0
				Hard coral (+)	17.2	49.2
Chaetodontids	Hard coral (+)	76.4	76.4	Hard coral (+)	33.1	33.1
	Algae (−)	7.8	84.2	Rugosity (+)	5.7	38.8
	Relief (+)	6.5	90.7			
Total herbivores	Coral trout (−)	28.6	28.6	Algae (−)	37.0	37.0
”Grazers”	Algae (−)	24.4	24.4	*L. carp* (+)	31.7	31.7
	Dead coral	48.0	23.6			
”Scrapers”	Coral trout (−)	23.2	23.2	Dead coral (+)	21.5	21.5
	Relief (−)	23.2	46.4			
”Croppers”	Coral trout (−)	14.3	14.3	Not significant		
”Farmers”	Relief (−)	31.8	31.8	Algae (−)	42.6	42.6

Table 4. Results of stepwise multiple linear regressions on the density of prey species and groups, and herbivore functional groups for Palm Islands and Ribbon Reefs. Only significant independent variables and models are given. Signs for the coefficient of each independent variable are in parentheses. The r^2 values have been multiplied by 100 to represent the percentage of variation each independent variable explains. *L. carp* = *Lutjanus carponotatus*. "Coral trout" refers to the summed density of all *Plectropomus* spp.

	Palm Islands			Ribbon Reefs		
Dependent variable	Independent variable	Partial r^2 (× 100)	Model r^2 (× 100)	Independent variable	Partial r^2 (× 100)	Model r^2 (× 100)
Total prey	Coral trout (−)	15.5	15.5	Coral trout (−)	82.2	82.2
Pomacentrids	Coral trout (−)	16.3	16.3	Coral trout (−)	83.0	83.0
Planktivores	Not significant			Coral trout (−)	32.9	32.9
Omnivores	Coral trout (−)	33.4	33.4	Coral trout (−)	75.0	75.0
Herbivores	Coral trout (−)	20.7	20.7	Piscivores (−)	32.3	32.3
	Algae (−)	15.7	36.4			
P. moluccensis	Coral trout (−)	18.8	18.8	Piscivores (−)	49.4	49.4
P. wardi	*L. carp* (−)	16.6	16.6	Not significant		
A. polyacanthus	Coral trout (−)	23.4	23.4	Coral trout (−)	32.5	32.5
A. curacao	Coral trout (−)	17.2	17.2	Not significant		
Chaetodontids	Hard coral (+)	36.3	36.3	Coral trout (+)	35.1	35.1
Total herbivores	Algae (−)	28.0	28.0	Piscivores (+)	77.2	77.2
	Hard coral (+)	4.0	32.0			
”Grazers”	Rugosity (+)	25.6	25.6	Relief (−)	42.1	42.1
	Hard coral (−)	12.3	37.9			
”Scrapers”	Rugosity (+)	10.8	10.8	Hard coral (−)	34.1	34.1
	Relief (−)	9.2	20.0			
	Hard coral (−)	3.8	23.8			
”Croppers”	Not significant			Not significant		
”Farmers”	Rugosity (−)	29.8	29.8	Algae (+)	71.1	71.1

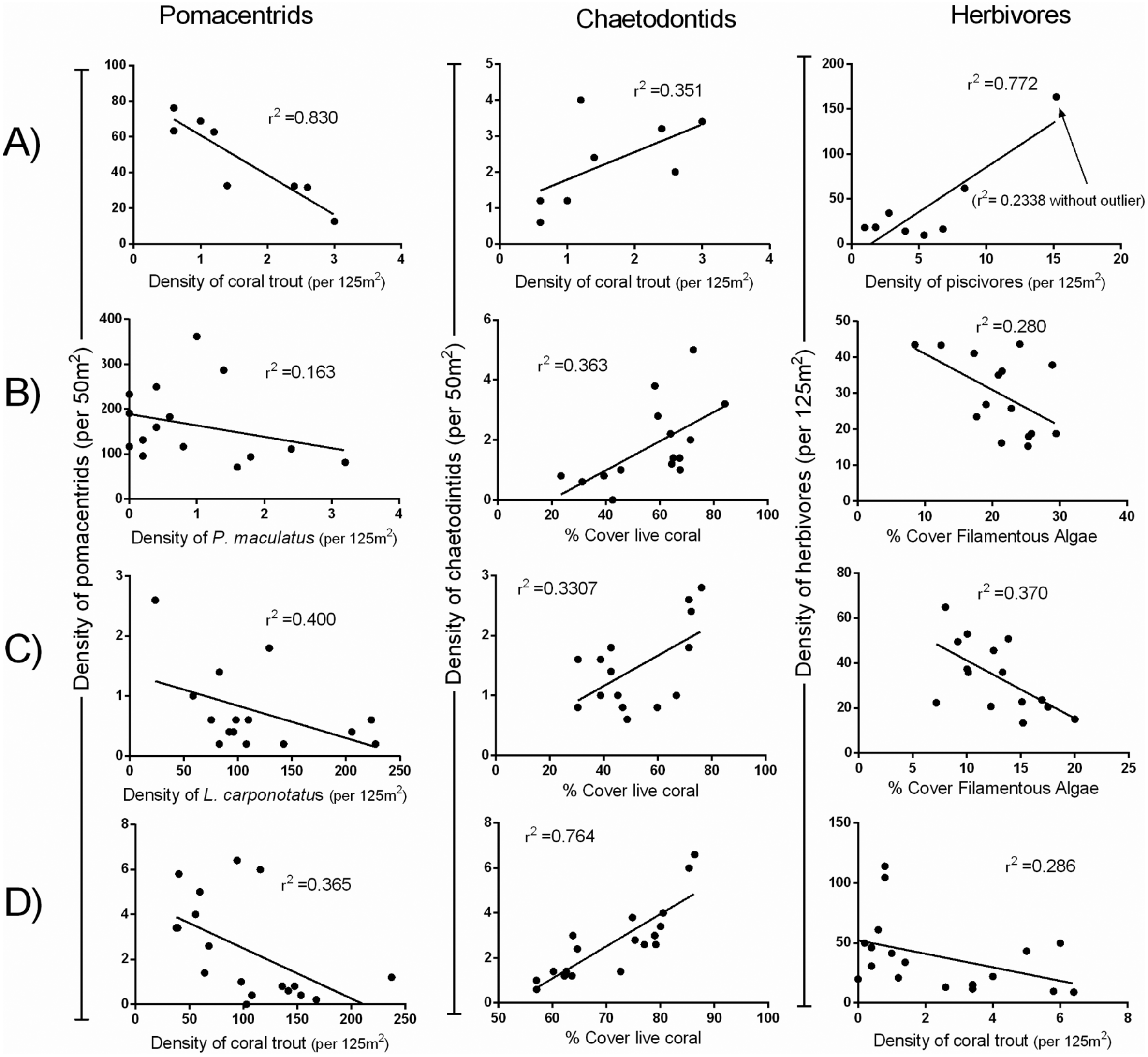

Fig. 8. Linear regressions of pomacentrids, chaetodontids, and herbivorous fishes at each location (zones pooled). A = Ribbon Reefs, B = Palm Islands, C = Whitsundays, and D = Capricorn Bunkers. Fish groups are plotted against their primary predictor from the multiple regressions models, using site means. All regressions had slopes significantly different from zero (ANOVA).

variation in patterns amongst locations, and predator densities and a variety of habitat characteristics were primary predictors for herbivore groups. At the Whitsundays and Palm Islands, the total density of herbivores had a significant negative relationship with the cover of filamentous algae, and the cover of algae was lowest where densities of herbivores were great (Fig. 8, Tables 3 and 4). At the Palm Islands there was a secondary positive relationship between herbivore abundance and live coral cover, the opposite of the pattern observed for filamentous algae (Table 4). These patterns were not consistent, however, when herbivores were analysed as trophic groups, for example only farming herbivores had a negative relationship with algae at the Whitsundays (Table 3). At the Capricorn Bunkers densities of total herbivores were negatively associated with coral trout abundance, which explained 28.6% of the variation. At the

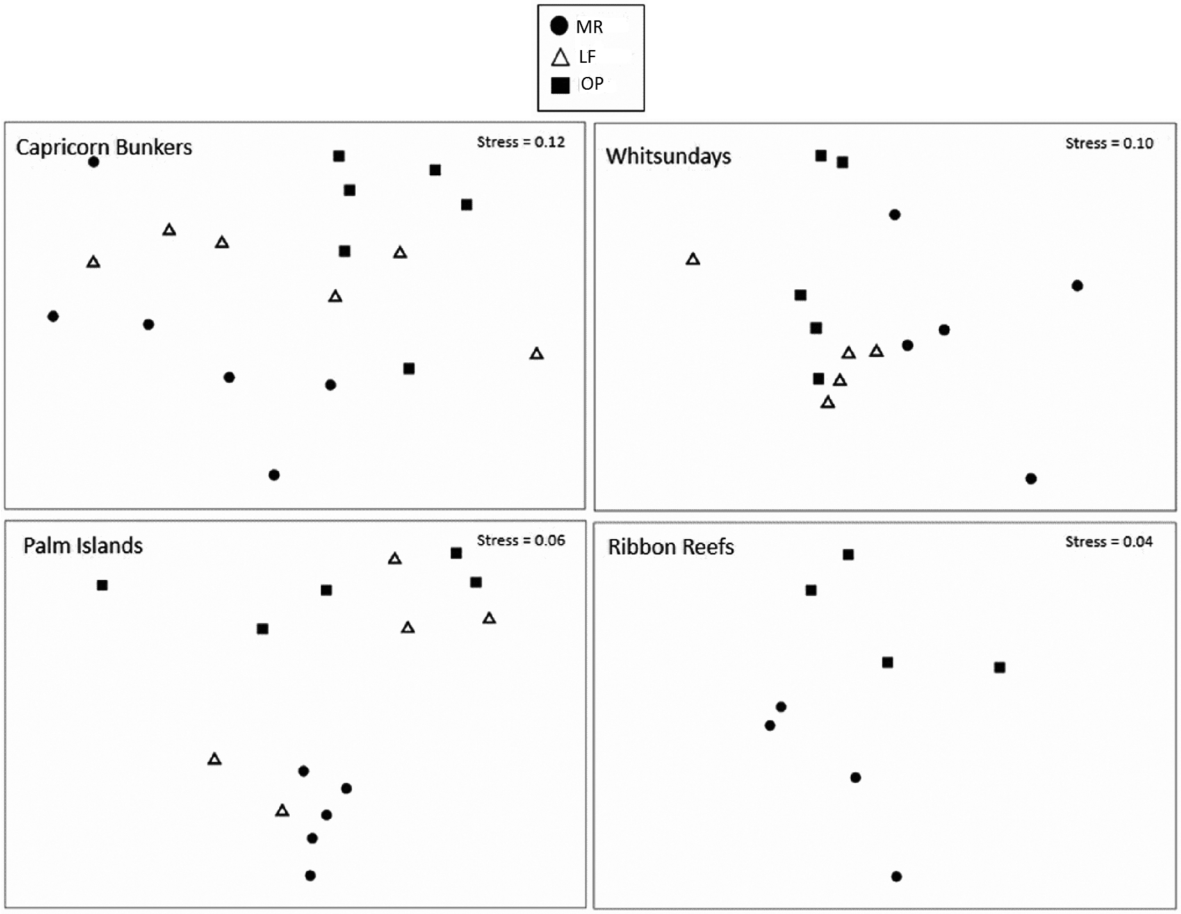

Fig. 9. Ordination plots (nMDS, nonmentric multidimensional scaling) of fish assemblages amongst marine reserves (MR), limited fishing (LF), and open (OP) zones at the Capricorn Bunkers, Whitsundays, Palm Islands and Ribbon Reefs. Symbols represent sites within each management zone, and data have been pooled into trophic groups. Stress values indicate the level of fit between the Bray-Curtis similarity rankings and distance rankings in the ordination plot. Stress values <0.2 indicate a useful ordination.

Ribbon Reefs, herbivores had a strong positive relationship with piscivores, which explained 77.2% of variation, however this pattern was mostly driven by a single site which had high densities of both predatory and herbivorous fishes; without this data point the relationship was poor ($r^2 = 0.2338$). There were no clear trends in relationships between habitat variables, predator densities and herbivore groups (grazers, scrapers, browsers and farmers). Scrapers and croppers had a negative relationship with coral trout at the Capricorn Bunkers but this was not consistent amongst locations (Tables 3 and 4). Herbivore groups were associated with a variety of habitat variables such as live coral, dead coral, vertical relief, rugosity, and filamentous algae; however no clear trends occurred amongst groups within or among locations, or within groups amongst locations and within locations.

Prediction 4: The composition of fish communities would vary amongst management zones due to predator depletion and associated changes in prey assemblages.

The structure of fish assemblages varied significantly amongst zones in the composition of both species and trophic groups (Fig. 9, Table 5). At the Capricorn Bunkers and Palm Islands, open zones had a significantly different composition of trophic groups compared to both marine reserves and limited fishing zones. This relation-

Table 5. Results of Permutational ANOVA (PERMANOVA) on fish densities by trophic groupings, and by species. Letters indicate groupings based on post hoc analysis.

Location	PERMANOVA Dependent variables	p	Post hoc analysis (groups)		
			MR	LF	OP
Capricorn Bunkers	Trophic groups	0.0092*	a	a	b
	Species	0.0006*	a	b	b
Whitsundays	Trophic groups	0.0006*	a	b	c
	Species	0.0005*	a	b	c
Palm Islands	Trophic groups	0.0110*	a	a	b
	Species	0.0004*	a	b	b
Ribbon Reefs	Trophic groups	0.0041*	a	NA	b
	Species	0.6993	a	NA	a

Note: MR = marine reserve, LF = limited fishing, OP = open. *Analysis significant ($p < 0.05$).

ship differed slightly when comparing species compositions, which were distinct in marine reserves compared to limited fishing and open zones at both locations (Table 5). In the Whitsundays all three zones had distinct species and trophic assemblages and at the Ribbon Reefs the trophic composition differed amongst zones (marine reserve and open), however the species composition did not. Variation in the trophic composition of species assemblages by zone was driven strongly by prominent pomacentrid groups such as omnivorous, planktivorous and herbivorous pomacentrids (Table 6). These three groups combined were responsible for up to 70% of the dissimilarity amongst management zones. Non-target predators (Palm Islands), and grazing herbivores such as surgeonfishes (Ribbon Reefs) were also responsible for differences amongst zones. At the species level, four common pomacentrid species (*P. moluccensis, C. atripectoralis, C. nitida,* and *A. polyacanthus*) were responsible for the majority of dissimilarity amongst zones. The relationship between habitat and the composition of fish assemblages was weak and habitat was not a significant driver of the composition of species assemblages or trophic

Table 6. Results of multivariate SIMPER analysis on the density of species and trophic groups amongst zones at each location. Dissimilarity values are the percentage dissimilarity amongst zones that were significantly different from PERMANOVA analyses. The three species/groups that were responsible for the largest amount of this dissimilarity are listed for all significant analyses.

Location	Dependent variables	Dissimilarity (%)	Top three groups/species accounting for differences	Percentage
Capricorn Bunkers	Trophic groups	22–28	omnivorous pomacentrids	31–33
			planktivorous pomacentrids	14–22
			herbivorous pomacentrids	12
	Species	56–59	*P. moluccensis*	10–12
			C. atripectoralis	7–12
			C. nitida	9–10
Whitsundays	Trophic groups	21–27	omnivorous pomacentrids	27–39
			planktivorous pomacentrids	19–22
			herbivorous pomacentrids	7–21
	Species	36–44	*A. polyacanthus*	10–17
			P. moluccensis	9–14
			C. nitida	10–13
Palm Islands	Trophic groups	21–26	planktivorous pomacentrids	40–47
			omnivorous pomacentrids	18–27
			non-target predators	8
	Species	33–38	*Neopomacentrus* spp.	14
			A. polyacanthus	8–12
			C. nitida	4–6
Ribbon Reefs	Trophic groups	56	omnivorous pomacentrids	33
			planktivorous pomacentrids	20
			grazers	9
	Species	NS†		

† NS = not significant.

groups at any of the locations. BIOENVIRON analysis indicated that habitat variables were not driving the zoning-related trends in fish assemblages. There were no significant relationships between habitat characteristics and assemblage structure, and habitat did not vary amongst zones at the multivariate level. There were no consistent patterns in the best environmental descriptors amongst locations; a combination of benthic cover and structural complexity characteristics best described the patterns of fish density, however none of these were significant.

Discussion

This study has provided strong evidence supporting the ecological importance of top-down control in ecosystems, and demonstrated the role of predatory fishes in structuring coral reef fish assemblages. These findings concur with studies from terrestrial systems (Beschta and Ripple 2009), lakes (Carpenter et al. 2010), and temperate reef systems (Edgar and Barrett 1999, Shears and Babcock 2003), which have demonstrated the role of predators in controlling populations of species at lower trophic levels. Coral reefs are complex systems, with a high degree of functional diversity and variability in trophic interactions**.** The strength and consistency of predator-prey relationships found in this study is remarkable in light of this complexity, providing strong evidence that piscivores are important in structuring prey communities.

Predictions 1 and 2:
Predator-prey interactions and prey release

Global reductions in predator populations have resulted in significant changes to ecosystems, primarily through alteration of predator-prey interactions, and subsequent flow on effects (Estes et al. 2011). In this study, we predicted that predator depletion from fishing would cause an overall reduction in piscivore densities, and a corresponding increase in prey densities along a gradient of fishing intensity. Our data provided strong evidence to support these predictions at a range of spatial scales. Prey generally had greater densities in heavily fished zones where predators were depleted, and predator density was a strong predictor of prey density for many species. As expected, coral reef fish communities were spatially heterogeneous, and varied amongst reefs and sites within management zones. These variations, however, did not prevent detection of strong zoning-related effects. Given the prevalence of significant zoning-related patterns (e.g., 29 out of 32 tests for pomacentrid species), it is highly unlikely that these results could have been due to chance; our conclusions, therefore, are robust.

Whilst changes in prey density in the opposite direction to predators suggests that predator-prey interactions are the cause, these data are correlative, and may co-vary with habitat. However we found no evidence of a consistent zoning effect on habitat at the univariate or multivariate level. Furthermore, prey release was documented along a gradient of fishing intensity for species such as damselfishes, providing strong evidence that release from predation was the likely mechanism underpinning the observed patterns. These data demonstrate the important role of top predators, and challenge the notion that top-down effects are likely to be weak in complex systems (Polis and Strong 1996, Shurin et al. 2002, Shurin et al. 2010). Findings from this study are consistent with ecological models from terrestrial, freshwater and temperate marine systems, in which top predators are considered strong regulators of community structure (Shears and Babcock 2003, Sinclair et al. 2003, Carpenter et al. 2010). Whilst top-down control has been demonstrated quite consistently in these systems, the case for coral reefs has been less clear. Data from this study supports findings from coral reef ecosystems in the Caribbean (Hughes 1994), Kenya (McClanahan and Shafir 1990) and the Red Sea (Roberts and Polunin 1992), which all demonstrated some level of top-down control by predators on coral reefs. These data also concur with and expand on the only previous study to consider such trophic interactions the on the Great Barrier Reef (Graham et al. 2003) and demonstrate that predators can have important regulatory roles in complex and diverse ecosystems.

In addition to direct effects on prey, apex predators can have a significant influence on community organization through interactions with meso-predators. The "Meso-predator Release Hypothesis" predicts that populations of small predators will increase as they are released from competition with apex predators, which can in turn affect prey species (Soule et al. 1988). Such interactions are most commonly observed for mammalian carnivores in terrestrial systems. For example, in California declines in coyote populations led to increases in native (skunks, racoons, foxes) and exotic (feral cats, opossums) meso-predators causing local extinctions of scrub-feeding birds (Crooks and Soule 1999). Similar interactions have occurred for Tasmanian devils and quolls in Australia, following the near extinction of Tasmanian devils due to a disease outbreak (Hollings et al. 2014). In this study, we found evidence to suggest that predator/meso-predator interactions occurred at the Palm Islands between large fisheries-targeted predators such as coral trout and snappers, and smaller non-target meso-predators such as small groupers and cods. Such patterns may have come about due to competitive release, or release from juvenile predation, as larger predators were removed through fishing. Fear mediated responses might also occur, as meso-predators alter their behavior in the presence of apex predators (Ritchie and Johnson 2009). Despite the fact that targeted predators and meso-predators share similar prey sources (Kingsford 1992 (*Plectropomus leopardus*), Beukers-Stewart and Jones 2004 (C*ephalopholis cyanostigma*, *C. boenak*), Feeney et al. 2012 (*Pseudochromis fuscus*)), prey release still occurred in fished areas. This suggests that overall predation pressure remained much lower in these areas, and that large targeted predators play a stronger role in regulating prey compared to meso-predators, probably due to their greater overall biomass and associated high prey consumption.

Fish populations can be regulated by a complex variety of pre-settlement and post-settlement processes including larval supply, and mortality from predation. Larval supply may be an important factor determining densities of prey, as described in the "Recruitment-limitation Hypothesis" (Doherty 1981, Doherty and Fowler 1994). Predators can influence the effect that larval supply has on populations of post-settlement fishes through mortality, and indirect effects on intraspecific and interspecific competition (Connell 1998, Holbrook and Schmitt 2002, Hixon and Jones 2005). As such, in areas of very low predator density, prey density may be strongly related to larval supply. It is possible that recruitment pulses in heavily fished areas, in combination with low piscivore densities, resulted in greater densities of prey in this study. However, it is unlikely that larval supply was a contributing factor to differences in the zoning-related patterns we observed. Considering the great variation in oceanographic processes that occur amongst the locations surveyed, it is highly unlikely that the same management zones would be subject to similar oceanographic conditions, especially considering that consistent patterns were found at locations separated by hundreds of kilometers (Wolanski 2001). Furthermore, available data indicate that densities of key predators at these locations have remained relatively stable over recent years, whereas larval supply and related recruitment is by nature highly variable (Doherty et al. 2004, Kingsford 2009). The evidence strongly suggests, therefore, that post-settlement mortality arising from predation was the primary process regulating densities of prey.

The body size and home range of prey species/groups may influence their relative susceptibility to predation. Coral reefs have a high diversity of fishes at all trophic levels, which encompass a range of body sizes which may vary in their susceptibility to predation (Munday and Jones 1998). Such diversity has been suggested to result in strong interactions between top-down effects and habitat variations, as species that grow to a larger size become less susceptible to predation, and more influenced by habitat and/or food availability (Sinclair et al. 2003). Studies in the Serengeti have demonstrated such interactions between ungulates of various sizes, and their canine and feline predators (Sinclair et al. 2003). In the present study, large herbivorous fishes such as grazers (Acanthuridae), scrapers (Scaridae) and croppers (Siganidae, Acanthuridae) had highly variable responses to habitat and predators. These herbivores are vulnerable to predation in the juvenile phase, as evidenced by high numbers of juvenile scarids in the gut contents of coral trout (Kingsford 1992), however may suffer lower overall mortality from predation compared to species with smaller maximum body sizes such as damselfishes (Hambright et al. 1991).

Home range may also influence the effect to which species are affected by either top-down or habitat effects at local scales. Many herbivorous fishes have large home ranges (Welsh and Bellwood 2012), which may make the effects of both local predator densities, and local habitat characteristics difficult to detect. This would explain the variable and inconsistent relationships with predators and habitat found for herbivores amongst locations in this study. Despite these variations, however, densities of herbivores did vary at broad spatial scales in relation to zoning and predator density, particularly at the Capricorn Bunkers where biomass increased threefold from marine reserves to open zones. This suggests that if variation in predator densities occurs at large spatial scales (e.g., depletion of predators at the reefal scale), this can influence even far ranging species with highly variable distributions.

Prediction 3:

Top-down vs. habitat effects

For many species, both top-down processes and habitat variation may interact to regulate populations, and the relative importance of each process may vary amongst species and trophic levels (McQueen et al. 1989, Brown et al. 2013). We predicted that the relative importance of top-down (predation) vs. habitat effects on prey would vary amongst species according to the strength of habitat relationships. That is, habitat specialists would be more likely to be driven by variation in benthic habitats, whilst generalists would be more strongly affected by predation. We found some evidence of this, however this varied amongst fish families. For example, within the Pomacentridae (damselfishes), the lemon damsel (*P. moluccensis*) is considered a habitat specialist that predominantly occurs on live hard coral (Booth 2002, Pratchett et al. 2012). Despite these habitat associations, densities of *P. moluccensis* were strongly influenced from the top-down, and predators such as coral trout were strong predictors for the density of this species. Conversely, chaetodontids were most influenced by habitat characteristics, and associated strongly with live hard coral, with no clear detectable predator effects. The relative importance of top-down vs. habitat effects on prey may be reliant on whether habitat is important to a species for shelter, food, or both. Both *P. moluccensis* and chaetodontids associate with live hard coral, however *P. moluccensis* relies on this resource for shelter, whilst many chaetodontids also rely on hard corals as a primary food source, as well as shelter (Pratchett and Berumen 2008). Further, their pairing behavior may also provide protection from predation (Brandl and Bellwood 2013*a*). The combined characteristics of habitat specialisation, corallivory, and pairing behavior may make these fishes less vulnerable to predation, and therefore strongly influenced by variations in benthic habitat.

Prediction 4:

Predator-prey interactions and community-level change

Changes in the abundance or distributions of apex consumers can cause major shifts in patterns of predation and alter the structure of communities (Hairston and Hairston 1997, Estes et al. 2011). Recognition of these top-down effects led to the development of broad ecological theories to describe global patterns of productivity, such as Hairston's "Green World Hypothesis" (Hairston et al. 1960). At a more regional scale, we predicted that depletion of predators on coral reefs would cause a change in the community composition of prey fishes, and we found strong evidence of this at all four locations. Marine reserves were characterized by a large biomass of piscivores, and a moderate number of herbivores and prey. With increasing fishing pressure, piscivore densities decreased and fish assemblages changed considerably. Numbers of herbivorous fishes increased up to two-fold, constituting a large amount (up to 80%) of total biomass at fished reefs in some locations (e.g., Capricorn Bunkers). Small prey fishes such as pomacentrids also increased greatly in number. From our analyses, habitat had little to do with this change in fish assemblages; instead community level changes were strongly driven by small pomacentrid species and groups. Although the importance of individual interactions between species and habitat cannot be denied, overall changes in species assemblages amongst MPA zones could not be explained by these interactions, and the representation of habitats was similar amongst sampling units. Instead, it is likely that prey release due to predator depletion is responsible for this, as evidenced by the large change in predator biomass amongst zones, and the corresponding but inverse response of prey.

Results from this study support the concept that top-down effects can be strong drivers of prey populations and community structure, even in highly diverse systems. We found evidence of top-down control at multiple spatial scales, and for a variety of prey species/groups. This study supports the findings of numerous experimental studies which have highlighted the importance of piscivores in structuring fish communities at small spatial scales (i.e., tens of meters) (Hixon 1991, Hixon and Beets 1993, Connell 1998, Holbrook and Schmitt 2003), and demonstrates that these processes can be scaled up and observed in broad scale field studies spanning kilometers to hundreds of kilometers. Species in diverse systems such as coral reefs and rainforests have evolved a remarkable variety of ecological traits and adaptations that allow them to co-exist in these environments. Prey species on coral reefs are no exception to this, and have evolved a spectacular array of physical, behavioral and physiological adaptations that help them to escape from the diversity of predatory species which threaten them. Fish may use camouflage (Feitosa et al. 2012), morphological adaptations (Lonnstedt et al. 2013, Robertson 2013), and behavioral responses such as pairing and shoaling to escape predation (Connell 2000, Brandl and Bellwood 2013*b*). They exhibit an impressive variety of escape responses, and can learn quickly about the dangers of predators and adapt their behaviors accordingly (Lonnstedt et al. 2012). Additionally, the extremely high structural complexity that coral reef mosaics exhibit supplies a seemingly infinite number of shelter holes which help prey to escape from predation (Hixon and Beets 1993, Holbrook et al. 2002). All of these factors may act to dampen top-down effects, and could prevent landscape/seascape level changes from trophic cascades occurring, as is witnessed in lower diversity systems. However, results from this study suggest that top-down effects can be strong drivers of community structure on coral reefs, and that diverse systems may not always be as resilient to trophic perturbations as was previously imagined (Polis and Strong 1996, Loreau et al. 2002).

Top-down vs. cascading effects

Although top-down effects were very strong in this study, we did not find unequivocal evidence of these effects cascading down a further trophic level and influencing habitats. Cascade effects must, by definition, involve three or more trophic levels, and generally involve changes in habitat which occur due to interactions between herbivores and predators (Paine 1980, Pinnegar et al. 2000). On the GBR, herbivorous fishes such as scarids (parrotfishes), acanthurids (surgeonfishes) and siganids (rabbitfishes) are important regulators of algal growth, and can mediate competition between algae and coral, facilitating coral survival (Mumby et al. 2006, Hughes et al. 2007*a*). Conversely, smaller herbivores such as territorial damselfishes may promote algal growth through their "farming" behavior, whereby they defend and tend to small patches of turf algae (Ceccarelli et al. 2005). Hence the role of herbivorous coral reef fishes in influencing primary production and habitat may be more complex than in other systems. In this study, relationships between piscivores and herbivores occurred whereby herbivorous fishes had greater densities in fished zones where predators were depleted, most likely due to lower juvenile mortality. At the Capricorn Bunkers, evidence for predator/herbivore interactions were further strengthened by the occurrence of direct negative relationships between piscivores such as coral trout, and densities of herbivore functional groups such as scrapers and croppers. Additionally, algal cover was significantly lower in fished areas where herbivore density was high. Hence open zones had fewer predators, more herbivores and lower algal cover, suggesting that top-down effects may be cascading down multiple trophic levels and influencing the benthos at this location. However, it should be noted that other habitat characteristics such as the cover of live soft coral also varied by zone at this location, which is unlikely to be related to herbivores, and that there was no evidence of greater live coral cover in fished areas as a result of lower algal cover. Furthermore, whilst predators had a strong negative influence on herbivores in the multiple regression models, herbivore/benthos relationships could not be consistently demonstrated in a similar manner. These data allow clear inferences to be made about the importance of top-down effects, and suggest the potential for trophic cascades involving piscivores, herbivores, and algal cover, however further studies would be required to provide a clear and direct link between herbivores and benthic cover in order to confirm these cascading effects.

This study has provided valuable insight into the importance of top-down effects on coral reef fishes. Other studies around the world have demonstrated top-down and cascading trophic effects on coral reefs, however these examples typically involve predator effects on grazing urchins, and associated changes in algal cover (McClanahan 1994, Hughes et al. 2007*a*). Prior studies that have investigated the top-down effects of coral reef fishes using in situ survey data have had varying outcomes (Jennings et al. 1995, Russ and Alcala 1998, Pinnegar et al. 2000). This study found strong, consistent evidence of top-down effects for coral reef fish at multiple spatial scales and for many species and groups, resulting in distinct fish assemblages as a function of fishing and predator removal. We suggest that the difference between the outcomes of this study and previous studies lies in the specific nature of fisheries on the GBR, coupled with the existence of a well-managed marine reserve network. Fisheries on the GBR target piscivorous fishes heavily (GBRMPA 2009, 2011), and consistent differences in piscivore numbers were found according to fishing intensity. This situation is in contrast to other studies, which have typically involved fisheries that target multiple trophic levels, and have already begun to "fish down the food web" (Pauly et al. 1998) or involve small, potentially ineffective marine reserves (McClanahan and Shafir 1990, Russ and Alcala 1998, Mumby 2006, Newman et al. 2006). Results of this study support that of Graham et al. (2003) which demonstrated changes in the density of select prey species between open zones and marine reserves on the GBR. Graham et al. (2003) found consistent trophic effects for six prey species (four pomacentrids, one labrid and one scarid), as well as a direct negative relationship between the pomacentrid *Acanthochromis polyacanthus* and coral trout, however could not extrapolate this to changes in assemblages, or prey groups overall. The present study has expanded on these initial findings, and indicates that these patterns are much more consistent amongst species, groups and locations than expected. Furthermore, we have demonstrated prey release over a gradient of fishing intensity, and over an exceptionally large spatial scale, providing strong evidence that fishing effects occur at the ecosystem level.

Marine reserve networks as scientific tools

Our results support the use of marine reserve networks as scientific tools for investigating ecological processes. In this study, fishing had a strong impact on piscivore populations, which was consistent amongst zones at all of the study locations, providing a strong background template to investigate predator-prey interactions. Trophic effects often take decades to eventuate (Babcock et al. 2010), however the majority of marine reserves surveyed in this study have been in effect for more than 25 years, and despite high natural variation amongst reefs, the effects of fishing and MPA zoning were clear for fishes from multiple trophic groups. The marine reserve network was useful as a natural experiment, and also was an effective impact study to determine the impacts of predator removal. Contrary to the typical BACI model, where sampling is done before the impact (Green 1979), we were limited to spatial inference as the zoning had been in place for multiple years. However, in our case spatial inference was very strong because the study was done at multiple latitudes over very broad spatial scales and multiple reefs with different zones within latitudes. This broad scale and nested design allowed the investigation of ecological processes at multiple spatial scales, and allowed hypotheses from experiments regarding the importance of predators to be tested in a field scenario. The enigmatic nature of predator effects is such that they are often difficult to detect without manipulation (Estes et al. 2011). In this case, fishing provided consistent manipulation of assemblages by removing piscivores at large spatial scales, however this would not have been effective if not complemented with well managed marine reserves. Given the limitations of correlation, it is doubtful that the importance of predator-prey interactions could have been detected without this manipulation. Marine reserves are beneficial for conservation, management, recreation and stewardship of our marine resources and biodiversity (Jennings 2000, Lubchenco et al. 2003, Russ et al. 2004, Russ et al. 2008), and these results suggest yet another benefit of the creation of networks of marine reserves; their ability to enhance scientific knowledge and understanding (Carr et al. 2011).

Management implications

Results from this study hold clear management implications, and reinforce the importance of ecosystem-based management of fisheries and marine reserves. Fisheries on the GBR are considered to be fairly sustainable (GBRMPA 2009, 2011), however the prevalence of trophic effects found in this study imply that this should be assessed at the ecosystem level rather than just for the targeted species. Whilst the total catch of piscivorous fishes on the GBR may be low in relation to other fisheries worldwide, fishing has caused a change in a key ecological process; predation. Ecological processes must be preserved just as importantly as species are, and overfishing can lead to "ecological extinction" of predators, a state from which it can be difficult to return (Jackson et al. 2001). Whilst at present there is probably little risk that fisheries on the GBR are approaching this point, these data indicate that caution would be judicious and that adaptation of an ecosystem level approach would be most effective for fisheries management. On the other hand, these data also highlight the effectiveness of marine reserves on the GBR in protecting both targeted species, and ecological processes. Importantly, predator-prey interactions changed along a gradient of fishing pressure at some locations in this study, highlighting the validity and utility of having limited fishing zones, which offer an intermediate level of protection, but still allow recreational fishing activities. This study is, to our knowledge, the first to demonstrate such gradient type effects.

Whilst strong trophic effects from fishing were found in this study, it is important to note that these data constitute a subset of locations, without temporal replication. The consistent patterns found in this study from four locations encompassing a large area and latitudinal range suggest that these patterns are likely to occur broadly across the GBR, however the likelihood of trophic effects occurring may differ amongst individual reefs and in part this may relate to temporal organismal trajectories relating to other impacts. The Great Barrier Reef and other reef systems are under threat from a myriad of stressors such as cyclones, nutrient runoff and sedimentation, and climate change impacts, all of which can have a strong effect on habitats and fish assemblages (Rogers et al. 1983, Hughes 1994, Hughes et al. 2003, Jones et al. 2004, De'ath et al. 2012, Wenger et al. 2012). The current state of reefs is actually the net result of a time series of events as reefs are subjected to perturbations, and decline or recover. Delays in recovery from such stochastic events could add variation to ecological processes amongst locations, especially since major disturbances such as cyclones are often latitude specific (Basher and Zheng 1995). The consistency of trophic effects and ecological interactions amongst latitudes found in this study is remarkable in light of this, however it is unknown how fisheries-related impacts may interact with other disturbances. Cascading trophic effects have been shown to develop over decadal scales, and the frequency of disturbances at some reefs on the GBR may preclude development of such interactions (Babcock et al. 2010). Future research should focus on determining the spatial and temporal generality of trophic effects, as well as their relative importance in disturbed/undisturbed reefs, in order to fully understand the implications of these patterns.

Top-down effects have been demonstrated in multiple terrestrial ecosystems, however robust predator-related effects have rarely been demonstrated in reef ecosystems. In this multi-spatial scale study we have demonstrated that top-down effects can be important drivers of community structure in complex ecosystems such as coral reefs, and that marine reserve networks can be effective tools for investigating such ecological interactions. Predator removal through fishing resulted in major trophic effects, and marine reserves were effective in restoring and maintaining top-down control. The consistency of trophic interactions found in this study provide compelling evidence of the importance of predators in ecosystems, and hold important implications for the development of ecological paradigms, as well as conservation and management.

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SUPPLEMENTAL MATERIAL

APPENDIX

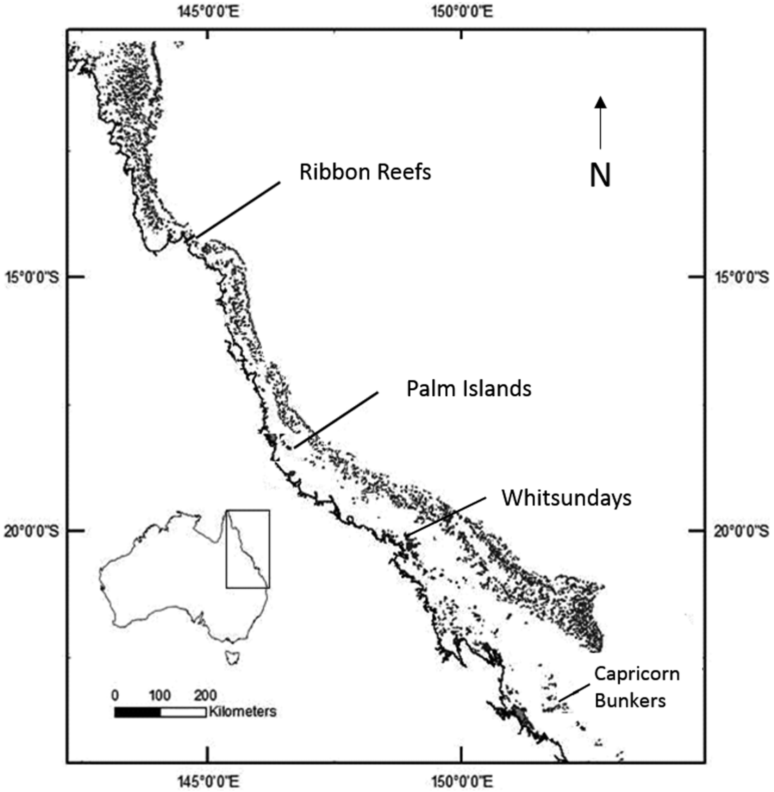

Fig. A1. Map of locations where fish/benthic surveys took place in this study, showing their location along the Great Barrier Reef on the Queensland coast.