



Conservation benefits of no-take marine reserves outweigh modest benefits of partially protected areas for targeted coral reef fishes

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Abstract Inshore coral reefs support unique ecosystems that are subject to a variety of threats and disturbances. Marine protected areas are powerful conservation tools and often include zones which vary in the level of fishing restriction, including fully protected (no-take) zones, partially protected zones (limited fishing), and less protected “open” fishing zones. Here, we compare outcomes from fully protected, partially protected, and “open” fishing zones on inshore fringing reefs of the Great Barrier Reef with a history of cyclone-induced habitat disturbance. Biomass of target and non-target fish groups, along with the coral cover and structural complexity of benthic habitats, was compared among zones. There was a strong positive effect of full protection from fishing on targeted fish biomass, and a comparatively modest effect of partial protection, even in areas where spearfishing was prohibited. Fully protected zones supported more than three times the biomass of highly targeted coral trout (*Plectropomus* spp.) compared to open fishing zones, and more than twice the biomass observed in partially protected zones. Similar outcomes occurred for primary targets collectively; conversely, there were no zoning-related differences for non-target fishes. Structural complexity was a consistent positive driver of fish biomass for all fish groups and

among all zones. Notably high target fish biomass occurred at NTMR sites with the highest structural complexity, highlighting the importance of both habitat and protection in supporting population hotspots for targeted reef fishes.

Keywords Coral reef habitats · Coral trout · Fishing · Fisheries management · Marine protected areas structural complexity

Introduction

Inshore coral reefs are unique habitats that provide a range of essential ecosystem services and hold significant conservation value. Their coastal location makes them important economically, socially, and culturally and also increases their exposure to a range of anthropogenic stressors (Wenger et al. 2015; Lam et al. 2018; Ceccarelli et al. 2020). Inshore reefs are often subject to significant recreational fishing pressure and have high exposure to coastal runoff and associated increased sediment, pesticide and nutrient loads (Brodie et al. 2012; Hall et al. 2021). They support distinct fish and coral assemblages, with strong connectivity to a range of other habitats in the seascape mosaic, such as mangroves, seagrass meadows, and macroalgae beds (Williams and Hatcher 1983; Sievers et al. 2020; Hall and Kingsford 2021). Such coastal mosaics may be considered key priority areas for conservation and management.

Physical disturbances such as storms and cyclones can be major drivers of the composition of coral reef habitats (Lam et al. 2018). Tropical cyclones present an acute physical disturbance that can abruptly reduce the cover of corals and subsequently diminish the structural complexity of reef habitats (Woolsey et al. 2012; Ceccarelli et al. 2016; McClure et al. 2019). Structural complexity can have a

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strong influence on the characteristics of fish assemblages; complex habitats positively influence both abundance and species richness (Friedlander et al. 2003; Nash et al. 2013; Hall and Kingsford 2021). For smaller and/ or juvenile fishes, the prevalence of complex coral forms such as branching corals is critical to provide microhabitats such as the interstitial space between branches (Beukers and Jones 1998; Wilson et al. 2008; Pratchett et al. 2012). For larger-bodied fishes, complex macro-habitat features such as caves, overhangs, and large tabulate corals form critical habitats (Connell and Kingsford 1998; Kerry and Bellwood 2012; Nash et al. 2013) and may hold particular importance from a management perspective, since these fishes constitute the majority of commercial and recreational fish catch (Boaden and Kingsford 2015; Webley et al. 2015).

Coral reefs provide for rich fisheries resources and may be subject to significant fishing pressure (Cinner 2014). Implementation of marine park zoning has been effective in reducing the impacts of fishing on coral reefs in a range of regions globally (e.g. Mumby et al. 2006; McClanahan et al. 2007; McCook et al. 2010; Russ and Alcala 2010). In the Great Barrier Reef Marine Park (GBRMP), implementation of no-take marine reserves (NTMRs) has resulted in dramatic increases in the biomass of fisheries targets (Russ et al. 2008; McCook et al. 2010; Boaden and Kingsford 2015). Effectively enforced NTMRs may provide a range of benefits: they provide a sanctuary for targeted species, protect key ecological processes such as predation and herbivory, and can directly benefit fisheries through larval export or spillover (Gell and Roberts 2003; Russ et al. 2004; Harrison et al. 2012; Edgar et al. 2014; Boaden and Kingsford 2015). Less certain, is the extent to which marine reserves provide resilience against impacts such as coral bleaching, floods, and cyclones, and correspondingly how habitat declines from these impacts may influence zoning outcomes (Jones et al. 2004; Graham et al. 2011; Mellin et al. 2016). Some studies have demonstrated enhanced recovery of coral communities within NTMRs after disturbance (Mumby and Harborne 2010; Mellin et al. 2016), whereas others have documented disturbance-related habitat declines for fish and corals in both fished and unfished zones (Jones et al. 2004; Wenger et al. 2015). From this, it is clear that a detailed understanding of habitat characteristics in the context of region-specific disturbance histories is needed to fully appreciate zoning outcomes.

Most research on marine protected areas (MPAs) is focussed on NTMRs; however, most MPAs consist of a range of zones that vary in their level of protection (Denny and Babcock 2004; Zupan et al. 2018). Partially protected areas (PPAs) are prevalent in MPAs and generally allow for limited fishing to occur, with the aim of providing some protection through restrictions on fishing effort (Hall et al. 2021). These zones are often situated close to the mainland shore, to allow

access by small fishing vessels, and are prominent on inshore reefs. Studies on the benefits of PPAs have had dichotomous outcomes, and there is ongoing debate regarding their conservation value (Lester and Halpern 2008; Sciberras et al. 2015; Hall et al. 2021; Turnbull et al. 2021). A number of empirical studies have demonstrated some benefits of PPAs in protecting fisheries targets on tropical (Frisch et al. 2012; Bobiles and Nakamura 2019; Hall et al. 2021) and sub-tropical (Harasti et al. 2018) coral reefs. Conversely, others have found no benefit of PPAs above less regulated open fishing zones (Lester and Halpern 2008; Turnbull et al. 2021). On the central GBR, some prior studies have demonstrated conservation benefits in PPAs for targeted fishes (Boaden and Kingsford 2015; Hall et al. 2021). There is conflicting evidence, however, as to whether Special Management Area (SMA) PPAs that prohibit spearfishing can provide better protection than regular Conservation Park Zone (CPZs) PPAs that do not (Frisch et al. 2008; Hall et al. 2021). A clearer understanding of the region-specific efficacy of PPAs is needed and will be of particular importance in high-use regions such as inshore reefs.

This study focussed on evaluating the effects of long-term implementation of marine park zoning in an economically and ecologically important area of the central GBR: the Whitsundays and Mackay region. The area has been subject to a history of physical and environmental disturbances such as cyclones and floods, resulting in significant impacts to coral reef habitats among sites within the region (Williamson et al. 2019; Ceccarelli et al. 2020). This history of disturbance allowed us to examine the ecological effects of different management zones on coral reef fishes, and how they may be influenced by variation in the composition and structure of benthic habitats.

The aims of the study were to:

1. Assess the effects of zoning on the biomass of target and non-target fishes;
2. Evaluate the relative efficacy of PPAs in mitigating fishing impacts, through comparison with adjacent NTMRs and Habitat Protection Zones (HPZs);
3. Compare outcomes of two kinds of PPAs, that either allow (regular CPZs) or prohibit (Special Management Area CPZs) recreational spearfishing;
4. Examine the effect of habitat composition and structural complexity on fish biomass, and how this may influence zoning outcomes.

Methods

Great Barrier Reef Marine Park

The Great Barrier Reef Marine Park (GBRMP) is a multiple use marine park with different zone types which allow

varying levels and kinds of fishing activities. Approximately one-third of the GBRMP is zoned as no-take marine reserves (NTMRs; “green zones”), where fishing is prohibited (Day et al. 2019). Habitat protection zones (HPZs; “blue zones”) are less restrictive open fishing zones and allow for a range of fishing activities (excluding trawling). Partially protected areas (PPAs), or “yellow zones” provide intermediate protection from fishing through limits on fishing gear and effort; for example, line fishing is allowed with one hook/line per fisher, but large mesh netting trawling, and dive-based harvest and collection are prohibited (Day et al. 2019; Hall et al. 2021). In this study, we include two kinds of PPAs: regular Conservation Park Zones (CPZs) and Special Management Area (SMA) CPZs. Both have the aforementioned fishing limitations, but regular CPZs allow for snorkel-based recreational spearfishing, which is prohibited inside SMA CPZs (Hall et al. 2021). The two yellow coloured zones are differentiated from each other on zoning maps by a pink hashed line around the SMA region (Fig. 1).

Study area and sampling design

The study area comprised two regions of the inner-shelf of the central GBR: the Whitsundays and Mackay region (Fig. 1). Each region includes a number of inshore continental islands with fringing coral reef habitats; these islands are known to have a varying cover of soft and hard corals, along with turfing algae and macroalgae (Williamson et al. 2019). The area was impacted by Cyclone Debbie (Category 4) in 2017, which caused physical significant damage to reefs, resulting in declines in live coral cover, especially on exposed sides of islands (Williamson et al. 2019; Ceccarelli et al. 2020). As such, variation in coral cover and habitat complexity among sites is likely to be strongly influenced by previous exposure to cyclone impacts (Williamson et al. 2019; Ceccarelli et al. 2020). Both regions are popular fishing areas, especially for recreational fishing, which is mostly reef based. Recreational and (to a lesser extent) commercial fishing are prevalent in the area and predominantly focussed on reef habitats. The Whitsundays is a popular area for tourism (e.g. diving, snorkelling, sailing), with regular tourist visitation of the islands and sites included in the study.

To examine the effects of zoning on fish and benthic habitats, we surveyed sites across three zones within each of the two study regions. Both regions have fully protected NTMRs, open fishing HPZs, and either regular CPZs (spearfishing allowed; Mackay region) or SMA CPZs (spearfishing prohibited; Whitsundays region). For the purposes of statistical analysis (detailed below), both CPZ types were considered a single level of the factor “zone”. A balanced design was utilized to compare the three zone types within each region, with six sites surveyed within each zone, resulting in 18 survey sites per region, and 36 sites total (Fig. 1).

Sites were selected to encompass fringing reef habitats around islands and were distributed across a number of islands within each region (Fig. 1). Surveys were conducted in September 2020.

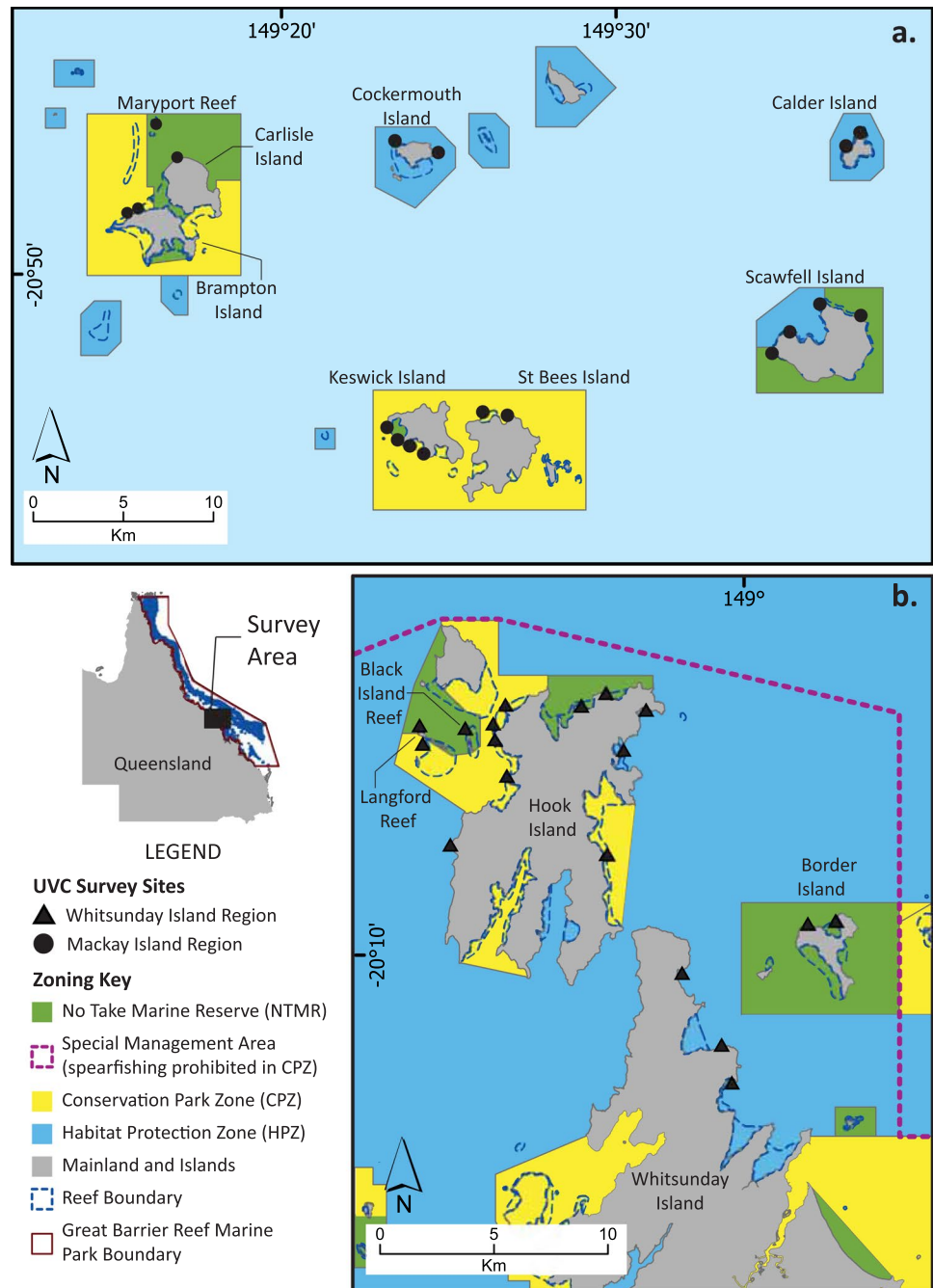
Fish and benthic surveys

At each site, fishes were surveyed along four 50×5 m belt transects placed parallel to the reef crest along a depth range of 6–16 m mean tide level (MTL); average depth was 9.7 m. The number and size (to the nearest 5 cm) of fishes were estimated using underwater visual census (UVC) along each transect by a single experienced fish observer on SCUBA. The size (total length) of each individual was then converted to biomass using published length/weight relationships (Kingsford 2009; Froese and Pauly 2021) to obtain biomass estimates per species for each transect. The fish observer also estimated a complexity score for the reef habitat along each transect, which captured both rugosity and vertical relief. Complexity scores were estimated as a continuous range of values, scaled from one to four, with increasing values representing greater complexity. For example, scores close to one represented an essentially flat surface with no real habitat attributes, and a score of four represented the presence of highly complex structures, with diverse habitat features such as overhangs, caves, and bommies. Complexity scores were estimated by a trained and experienced observer and were similar in approach to that used by numerous previous studies (e.g. Williamson et al. 2014; Hall and Kingsford 2021). Benthic habitats were surveyed along a 2-m wide belt along the centre of each transect by a second diver who recorded imagery from the benthos using a GoPro camera. Footage from each transect was then analysed by randomly selecting 15 “quadrants” (i.e. points in time) from the video, and recording benthic substratum at 12 points within each quadrat. The resulting 180 points per transect were used to estimate percentage cover and gave a 95% chance of detecting benthic taxa with >2% cover (Green 1979; Moynihan et al. 2022). Benthic substratum was categorized into broad categories of hard coral, soft coral, algae, and sand/rubble. The cover of live hard and live soft coral, along with the structural complexity score, was selected as key habitat attributes for analyses.

Fish groups

To differentiate the effects of zoning from other influences, both target and non-target species were surveyed. Primary targets were defined as those species most likely to be captured and retained by recreational and commercial fishers in the region; all primary target species had a maximum size greater than the minimum legal size limit for fisheries (Supp. Table S1). Coral trout and stripey snapper are

Fig. 1 Map of Underwater Visual Census (UVC) survey sites of fish and benthic habitat in **a** Mackay Island region, and **b** Whitsunday Island regions. Colours indicate the Great Barrier Reef Marine Park management zones



key fisheries species that are abundant in the region, and likely to be caught and retained. As such, they were analysed separately, to infer zoning effects specific to these species, and were also included in the primary targets group for all analyses. Three species of coral trout were observed: (*Plectropomus leopardus*, *P. maculatus*, and *P. laevis*) and were grouped collectively as “coral trout” (*Plectropomus* spp.), since they are all very similar species that are key fisheries targets (Emslie et al. 2015; Hall et al. 2021). Primary targets were all medium to large-bodied piscivores

or benthic foragers, so a similar suite of non-target fishes was also surveyed to enable comparisons of non-target and targeted fishes among zones (Supp. Table S1). Non-target species were defined as such if their size maximum did not exceed the minimum legal limit for fisheries, and/or if they were considered undesirable as a fisheries target (based on the available literature and discussions with relevant experts Webley et al. 2015; Hall et al. 2021). The resulting species list for target and non-target fishes included all species of Serranidae, Lutjanidae, Lethrinidae and Haemulidae, as

well as large mobile wrasses from the genera *Choerodon*, *Cheilinius* and *Hemigymnus* (Supp. Table S1).

Analysis

Mixed effects models were conducted to analyse differences in fish biomass between regions and among zones. Separate models were run for each fish species/ group as follows: coral trout (*Plectropomus spp.*), stripey snapper (*Lutjanus carponotatus*), pooled primary targets, and pooled non-targets. All analyses were conducted using R (v.4.1.0, R Development Core Team, 2020). Models were fit in the frequentist method for model and variable selection and then run in the Bayesian framework for interpretation and analysis of results. Region and zone were included as fixed factors, with Site as a random factor. All models were fitted using a hurdle gamma distribution with a log link function, to account for the large number of zero values. Habitat covariates (complexity, live hard coral, and live soft coral) were also considered in the model selection process. Every combination of region, zone, hard coral, soft coral, and complexity was explored in both additive and interactive models. The final model output was identified as the most parsimonious model and was selected by comparing Akaike information criteria values (AICc), examination of DHARMA residual diagnostic tests (v. 0.4.3) for goodness of fit, and use of the *vif* function from the *car* package to confirm no collinearity of factors.

The Bayesian hierarchical model was fit using the ‘brms’ package (v. 2.15.0). Model selection informed by the frequentist approach was further evaluated in the Bayesian format, where region, zone, and complexity (the most informative habitat variable) were explored as additive and interactive models. Bayesian models were fit with flat, uninformative priors using the following parameters: Chains = 3, Iterations = 5000, warmup = 2000, thin = 5. Model convergence and diagnostics were assessed to confirm even mixing of chains, no autocorrelation, and appropriate effective sampling size and efficiency. Model outputs reported median posterior estimates and the 95% and 50% highest posterior density (HPD) credible intervals. Strong evidence for an effect (i.e. inferred significance) is determined when 95% credible intervals do not cross zero. The package *emmeans* (v. 1.6.2.1) was used to for pairwise comparisons, and to estimate biomass ratios between regions and among zones. Ratios were calculated as the first model estimate divided by the second (e.g. NTMR: HPZ = NTMR estimate/HPZ estimate).

The probability of biomass differences between zones was obtained from the modelled dataset; where ratio differences were summarized for > 1.0 (one zone having greater biomass than the other zone), > 1.5 (one zone having a 1.5 times or more the biomass of another zone), and > 2.0

(one zone having 2 times or more the biomass of another zone). The *gather_emmeans_draws()* function was used to compile the comparisons of predicted biomass estimate values per contrast (i.e. among zones) for all draws (samples of the chains). For each model, 1800 estimates were calculated (3 chains, 5000 iterations, 2000 warmup, 5 thin. $3 * ((5000 - 2000) / 5) = 1800$ estimates). From these, a proportion value was calculated by identifying the number of contrast comparisons that had selected differences in biomass estimate values. For example, calculating the number of draws where NTMRs had biomass estimate values greater than 1.5 times that of HPZs provided a probability (percentage) value for the ratio comparison of > 1.5. In this study, strong evidence of an effect was defined as probability values greater than 95% (Hannan et al. 2021). Meaning more than 95% of the 1800 estimates had the relevant ratio value (e.g. > 95% certainty that zone A has at least 1.5 times the fish biomass of zone B). Moderate evidence of an effect was defined for probabilities between 80 and 95% (e.g. 80–95% certainty that zone A has at least 1.5 times the fish biomass of zone B). Probability values less than 80% were considered to have no evidence of an effect.

Results

Fish assemblages

A total of 34 fish species within the survey groups were observed across the two regions: nine species of primary targets and 25 non-target species (Supp. Table S1). Primary targets were a mix of species from families Labridae, Lethrinidae, Lutjanidae, and Serranidae. The most abundant and commonly encountered primary target species was *L. carponotatus* (stripey snapper), which occurred on 73% of transects (Fig. 2 and Supp. Table S1). Two species of *Plectropomus* were commonly observed: *P. maculatus* (barcheek coral trout), and *P. leopardus* (common coral trout), which occurred on 62% and 63% of transects, respectively (Fig. 2 and Supp. Table S1). Blue spotted coral trout (*P. leavis*) also occurred but were rare, with only three individuals observed. Non-target fishes consisted of smaller species of Labridae, Lethrinidae, Lutjanidae, and Serranidae, as well as four Haemulidae species (Supp. Table S1). The two most abundant non-target species were *Lutjanus vitta* (brownstripe snapper), and *Diagramma pictum* (painted sweetlips) which both occurred in groups and were patchily distributed, occurring on only 20% of transects. *Choerodon fasciatus* (harlequin tuskfish) was the most commonly encountered non-target species, occurring on 76% of transects (Supp. Table S1).

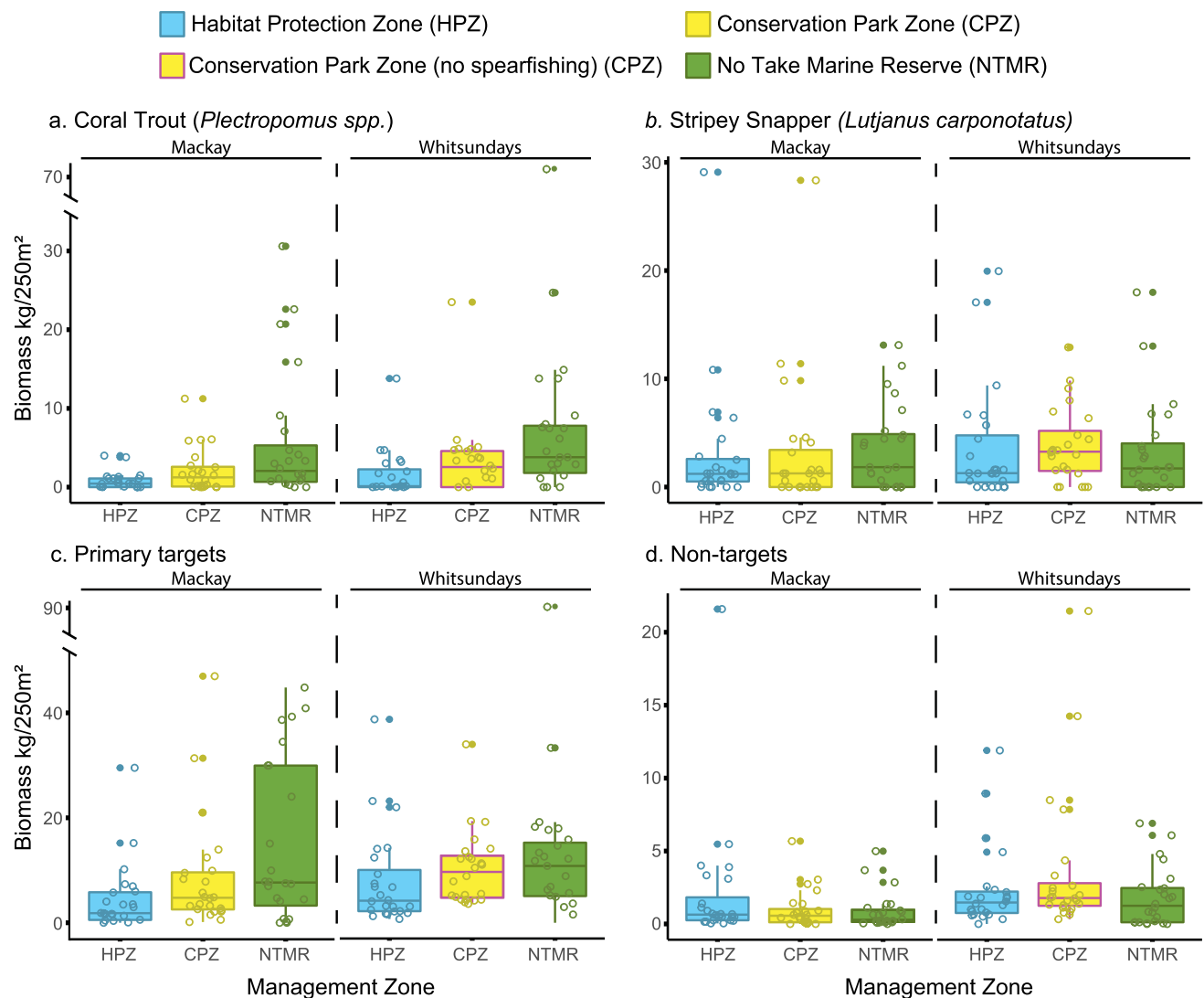


Fig. 2 Box plots of raw data for fish biomass (kilograms per 250-m²) between Mackay and Whitsunday regions and among different management zones for **a** Coral trout (*Plectropomus* spp.), **b** Stripey Snapper (*Lutjanus carponotatus*), **c** Primary targets and **d** non-targets. The

pink border on the CPZ zone in the Whitsundays indicates that spearfishing is prohibited. Filled points are outliers in the boxplot, and open circles are the raw data points of individual transects

Benthic habitats

Benthic habitats varied among sites but showed no consistent trends among zones (Fig. 3). Live hard coral cover and structural complexity were mostly consistent among zones and between regions. A notable exception was for HPZs in the Whitsundays region (Fig. 3), which had the lowest median complexity and live hard coral cover, driven by particularly low values in cyclone-exposed sites. There was, however, considerable overlap in the range of values in Whitsundays HPZs with other zones and with the Mackay region. For both regions, all three habitat attributes were highly variable within zones; live hard coral cover ranged from 3 to 52% (site means), and live soft coral cover ranged

from 0.7 to 26% (site means; Fig. 3). Both regions had some sites with very low coral cover; however, the Mackay region had greater maximum values for hard coral compared to the Whitsundays region (Fig. 3). Complexity varied greatly by site, with a similar range of values for both regions (Fig. 3).

Fish biomass models

For all four models (coral trout, stripey snapper, primary targets, and non-targets), initial model exploration found no evidence of an interaction between fixed factors (region, zone), and an additive model was selected as most parsimonious after model comparison (Supp. Table S2). Structural complexity was consistently identified as the most

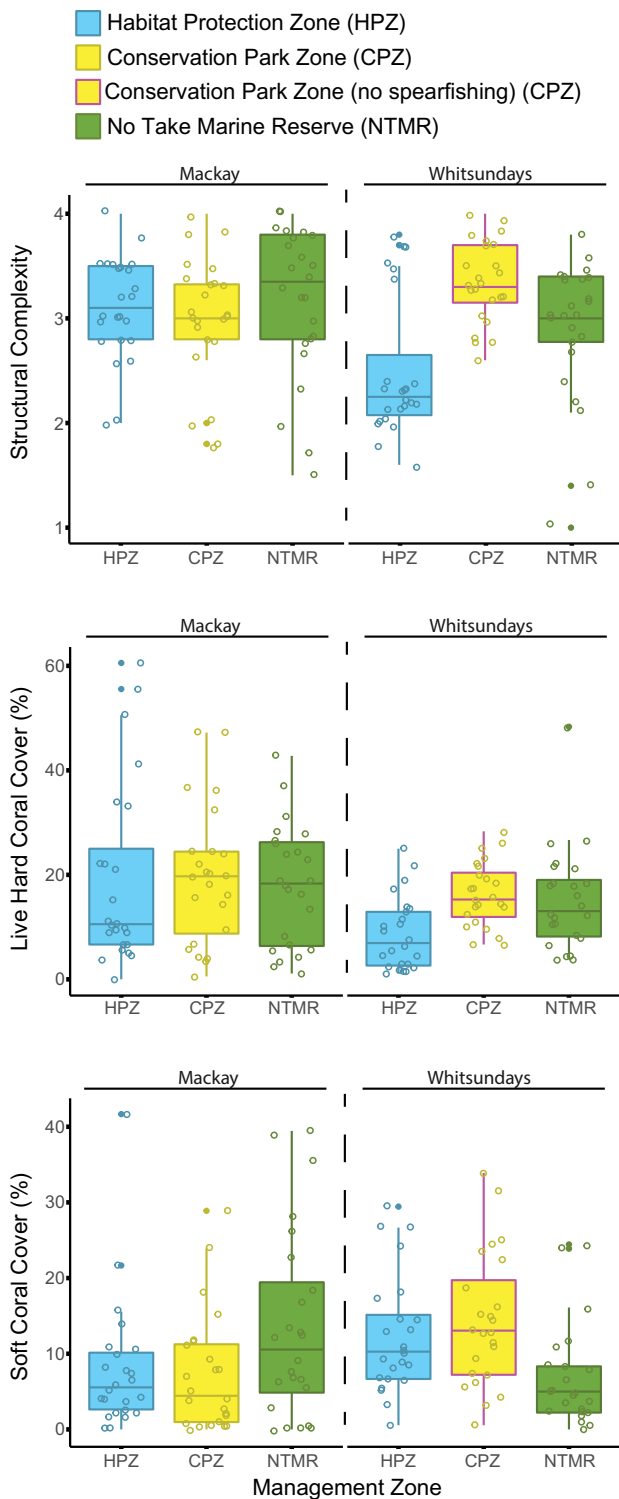


Fig. 3 Box plots of raw data for structural complexity estimates of the benthos, hard coral cover, and soft coral cover among management zones in Mackay and Whitsunday regions. The pink border on the CPZ in the Whitsundays indicates that spearfishing is prohibited. Filled points are outliers from the boxplot, and open circles are the raw data points

informative habitat variable in model selection. Complexity was explored as both additive and interactive with region and zone. The best-fit models for all species groups included complexity as an additive variable. When complexity was included as an interactive variable, the model did not meet the requirements of the diagnostic checks. Inclusion of additional habitat covariates (live hard and soft coral) did not improve the models; therefore, complexity was the only habitat covariate used in the final models. All four models were additive, where region, zone, and complexity were fixed factors, and site was included as a random intercept factor (Supp. Table S2).

Zoning and regional effects

There was clear evidence of a positive effect of zones on fish biomass for unfished NTMRs, which supported greater biomass of coral trout and primary targets compared to both other zones (Table 1, Fig. 2). For both fish groups, there was a trend for increasing biomass with increasing protection from fishing (i.e. HPZ < CPZ < NTMR; Fig. 2), and the greatest magnitude of effect occurred when comparing fully protected NTMRs with HPZs (with the lowest level of protection from fishing; Table 1). The magnitude of effect was also greater for comparisons of NTMRs with partially protected CPZs than it was when comparing CPZs with HPZs, indicating that full protection in NTMRs provided the most powerful benefits for fished species (Table 1). There were large regional differences for coral trout and non-targets, which both had greater biomass in the Whitsundays compared to Mackay (Table 1). Coral trout and non-targets, respectively, had an estimated ≈ 2.28 times and ≈ 2.82 times the biomass in the Whitsundays compared to Mackay. No such trend occurred for stripey snapper and primary targets (Table 1).

Coral trout

Of all the species groups, coral trout (*Plectropomus spp.*) exhibited the greatest zoning-related response. There was a clear positive effect of protection from fishing in NTMRs; where biomass was greater in NTMRs compared to both HPZs and CPZs (Table 1 and Fig. 4). Estimated coral trout biomass in NTMRs was 3.65 times that of HPZs, and 2.13 times that of CPZs (Table 1). There was greater than 95% probability (strong evidence) of higher biomass in NTMRs compared to HPZs across all ratio contrasts, and an 86% probability (moderate evidence) that coral trout in NTMRs would have > 1.5 times the biomass of CPZs (Table 2). There was some evidence to suggest a positive effect of partial protection from fishing in CPZs, although the magnitude of effect was comparatively modest. While there was no evidence of a difference in coral trout biomass from pairwise

Table 1 Pairwise comparisons of region (A) zone (B) and complexity (C) for biomass of fish species/groups

Response	Comparison 1	Comparison 2	Estimated difference (kg/250m ²)	Lower HPD	Upper HPD	Comparison Ratio
<i>(A) Region</i>						
Coral Trout (<i>Plectropomus spp.</i>)	Whitsundays	Mackay	3.17	0.64	5.75	2.28
Stripey Snapper (<i>Lutjanus carponotatus</i>)	Whitsundays	Mackay	0.83	-0.86	2.74	1.25
Primary Target Species	Whitsundays	Mackay	3.60	-0.20	7.77	1.50
Non-Target Species	Whitsundays	Mackay	1.62	0.55	2.96	2.82
<i>(B) Zone</i>						
Coral Trout (<i>Plectropomus spp.</i>)	NTMR	HPZ	5.03	1.80	8.88	3.65
	NTMR	CPZ	3.66	0.26	7.44	2.13
	CPZ	HPZ	1.38	-0.42	3.27	1.72
Stripey Snapper (<i>Lutjanus carponotatus</i>)	NTMR	HPZ	0.43	-1.84	2.78	1.12
	NTMR	CPZ	0.39	-1.73	2.73	1.11
	CPZ	HPZ	0.01	-2.02	2.36	1.00
Primary Target Species	NTMR	HPZ	6.70	1.67	12.56	2.08
	NTMR	CPZ	5.22	-0.56	11.11	1.66
	CPZ	HPZ	1.60	-2.07	5.57	1.25
Non-Target Species	NTMR	HPZ	-0.88	-2.40	0.42	0.57
	NTMR	CPZ	-0.44	-1.88	0.62	0.74
	CPZ	HPZ	-0.44	-2.07	1.11	0.79
<i>(C) Complexity</i>						
Coral Trout (<i>Plectropomus spp.</i>)	1	3	-2.59	-3.89	-1.21	0.34
	1	4	-5.44	-9.77	-1.98	0.20
	3	4	-2.84	-5.94	-0.75	0.58
Stripey Snapper (<i>Lutjanus carponotatus</i>)	1	3	-3.09	-3.99	-2.25	0.16
	1	4	-8.63	-13.02	-5.20	0.06
	3	4	-5.53	-9.01	-2.49	0.40
Primary target species	1	3	-6.73	-9.13	-4.78	0.26
	1	4	-15.57	-22.94	-8.29	0.13
	3	4	-8.78	-14.77	-4.16	0.51
Non-target species	1	3	-0.96	-1.67	-0.18	0.42
	1	4	-1.90	-3.90	-0.16	0.27
	3	4	-0.91	-2.22	-0.03	0.65

Values are modelled predicted median estimates from planned comparisons from the Bayesian hierarchical linear mixed effects models. Estimated difference values are the difference in biomass between the first and second comparison. If positive, the first (left hand) comparison has a greater biomass estimate. If negative, the second (right hand) comparison has the greater biomass estimate. A. Regional comparisons between Mackay and Whitsundays (zone and complexity at median). B. Management zone comparisons (region and complexity at median). C. Complexity comparisons (zone and region at median). *NTMR* no-take marine reserves, *CPZ* conservation park zone, *HPZ* habitat protection zone. Lower and upper highest posterior density (HPD) intervals are the 95% credible interval. Comparison ratio is the average ratio of median biomass estimates between comparisons 1 and 2. Significant differences are inferred (at the 0.05 level) when upper and lower HPD intervals do not cross zero (bolded rows)

tests between CPZs and HPZs (Table 1, Fig. 4), there was still a 94% probability (moderate evidence) that CPZs would have greater coral trout biomass (ratio ≥ 1.0) compared to HPZs (Table 2). There was, however, no evidence for CPZs to have greater than 1.5 times the biomass of coral trout compared to HPZs, indicating that the magnitude of the effect is likely to be fairly low. The spread of biomass values for coral trout was greatest in Whitsundays, which had notable outliers with extremely high biomass (up to 70 kg/250m²; Fig. 2a and Fig. 4). These occurred where coral trout were

congregating on individual coral bommies in locations with high structural complexity (e.g. Black Island Reef; Fig. 1).

Stripey snapper

There was no evidence of a zoning or regional effect for biomass of stripey snapper (*L. carponotatus*; Table 1, Fig. 4). Estimated biomass ratios were similar between regions (ratio = 1.25) and among zones (ratios = 1.00–1.12), and biomass was quite consistent

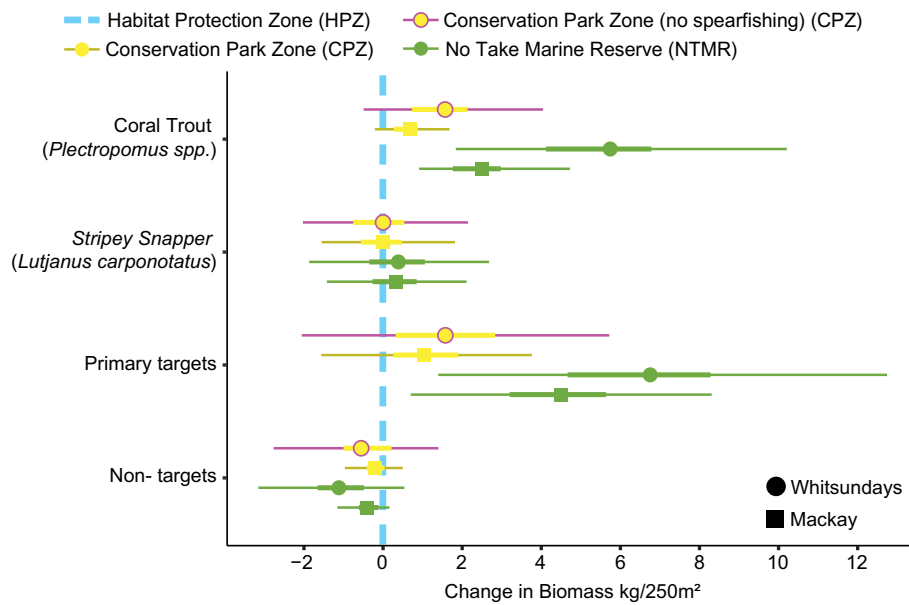


Fig. 4 Effect sizes for pairwise comparisons among management zones between Mackay (square) and Whitsunday (circle) regions for each fish species group. The pink border on the CPZ in the Whitsundays indicates that spearfishing is prohibited. Comparisons are median differences in fish biomass (kilograms per 250-m²) between CPZ and NTMR zones compared to HPZ zones (reference HPZ line).

Circles and squares are median posterior density estimates from Bayesian linear mixed effects models with 50% and 95% credible intervals (CI). Positive values indicate higher biomass in a zone compared to HPZs. Negative values indicate lower biomass compared to HPZs. Evidence of significance can be inferred when 95% (CI) do not cross the vertical dotted line (HPZ zone)

Table 2 Probability of differences in predicted median biomass of fish groups between management zones

Ratio	Contrasts	Coral trout (<i>Plectropomus spp.</i>)		Stripey snapper (<i>Lutjanus carponotatus</i>)		Primary targets		Non-targets	
		Prob	Evidence	Prob	Evidence	Prob	Evidence	Prob	Evidence
> 1.0	NTMR-HPZ	100%	Strong	66%	None	100%	Strong	9%	None
	NTMR-CPZ	99%	Strong	64%	None	97%	Strong	21%	None
	CPZ-HPZ	94%	Moderate	50%	None	81%	Moderate	27%	None
> 1.5	NTMR-HPZ	99%	Strong	18%	None	89%	Moderate	1%	None
	NTMR-CPZ	86%	Moderate	16%	None	64%	None	3%	None
	CPZ-HPZ	66%	None	9%	None	25%	None	6%	None
> 2.0	NTMR-HPZ	96%	Strong	3%	None	56%	None	0%	None
	NTMR-CPZ	58%	None	3%	None	23%	None	1%	None
	CPZ-HPZ	34%	None	1%	None	4%	None	1%	None

Values display the per cent probability (prob) of the first management zone having a certain per cent of biomass compared to the second zone. Contrasts are presented for a ratio of > 1.0 (some difference in biomass between zones), > 1.5 (one zone has 1.5 times or more the biomass of the other), and > 2.0 (one zone has at least twice the biomass of the other). Probability values are categorized as providing strong evidence (95–100%), moderate evidence (80–94%), or no evidence (None: < 80%) of a difference between zones, for each ratio. NTMR no-take marine reserve, CPZ conservation park zone, HPZ habitat protection zone

among sites overall (Fig. 2). There was no evidence for a difference in biomass among any of the zones; probability values for zone comparisons were all < 70% (Table 2). *Lutjanus carponotatus* had fairly uniform biomass (mean

3.4 kg/250m² ± 0.4 SE), with the exception of two notable outliers (in CPZ and HPZ sites) where they were observed in large groups of up to 50 individuals (biomass 28–29 kg/250m²; Fig. 2b).

Primary targets

Zoning had strong evidence of an effect for primary targets, with the magnitude of difference among zones less than that observed for coral trout (Table 1, Fig. 4). The largest differences were evident between NTMRs and HPZs (Fig. 4), where NTMRs had strong evidence of greater (2.08 times) estimated fish biomass compared to HPZs (Table 1). This difference in biomass was driven strongly by coral trout species, however, smaller species such as tuskfishes (*Choerodon cyanodus* and *C. schoenleinii*) and lethrinids (e.g. *Lethrinus laticaudis*) also contributed to the trend (Supp. Table S1). *Lutjanus carponotatus* biomass had little influence on zoning trends for primary targets since their biomass was similar among zones (Figs. 2 and 4). Although median biomass values in NTMRs were greater than CPZs (ratio = 1.66), there was substantial overlap in the range of values (Figs. 2, 4 and Table 1). Biomass did not differ between CPZs and HPZs, and estimated modelled ratios were similar (ratio = 1.25; Table 1). When comparing NTMRs with other zones (HPZs and CPZs) based on probabilities, strong evidence of an effect was only found for biomass ratios > 1.0 (e.g. that NTMRs had more biomass than the other zones), but not for ratios > 1.5 or > 2.0. (Table 2). There was moderate evidence for a biomass ratio of > 1.0 between CPZs and HPZs, but no evidence of a greater difference, indicating a modest effect of zone (Table 2). The Whitsundays had an estimated 1.50 times the biomass of primary targets compared to Mackay (Table 1).

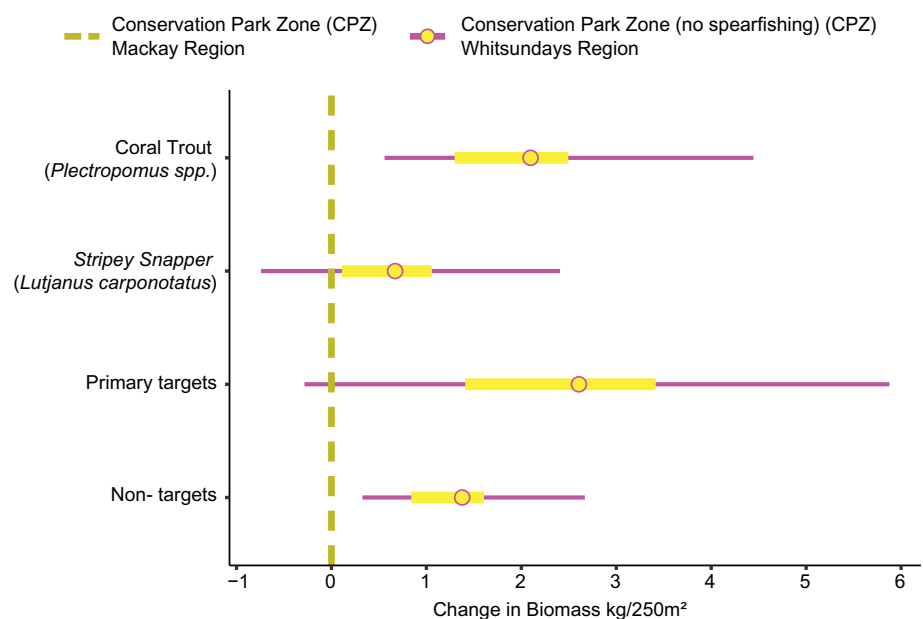
Non-targets

Non-target fish species showed no evidence of an effect of zone (Fig. 4, Table 2), but did have evidence of a strong effect of region (Table 1). Regional differences were strongest for non-targets; the Whitsundays had on average 2.82 times the biomass of non-target fish species compared to Mackay (Table 1). There was no evidence of an effect of zone when comparing probability outcomes from the model; probability values were below 30% for all zone comparisons and ratios (Table 2).

Comparison of PPA types

There was no clear evidence of a difference in biomass between Whitsundays SMA CPZs (no spearfishing) and Mackay regular CPZs (spearfishing allowed) for targeted fishes. Although pairwise model comparisons showed that both coral trout and non-targets had greater biomass in Whitsundays CPZs compared to Mackay CPZs, both groups also had strong regional effects with greater biomass in the Whitsundays region overall (Fig. 5 and Supp. Table S3). Average biomass values for coral trout were lower in Mackay CPZs ($1.7 \text{ kg}/250\text{m}^2 \pm 0.39\text{SE}$) compared to Whitsundays ($2.6 \text{ kg}/250\text{m}^2 \pm 1.5\text{SE}$); however, this was mostly due to one outlier site (Langford Reef) with high biomass; this reef has split CPZ/NTMR zoning (Figs. 1 and 2). Further, there were no strong differences between CPZs and HPZs for coral trout biomass in either region, indicating a similar magnitude of effect of CPZs in both regions (Supp. Table S3). Stripey snapper and primary targets had similar (overlapping) biomass in the two CPZ types (Fig. 5). This collective evidence

Fig. 5 Effect sizes for pairwise comparisons of fish biomass in conservation park zones (CPZs) between regions. Whitsundays CPZs (yellow circles, pink lines) prohibit spearfishing activities, compared to Mackay CPZs (reference yellow dotted line) which allows spearfishing. Comparisons are median posterior density estimates of fish biomass (kilograms per 250-m^2) from Bayesian linear mixed effects models with 50% and 95% credible intervals (CI). Positive values indicate higher biomass in the Whitsundays CPZ compared to Mackay CPZ. Evidence of significance (at the 0.05 level) can be inferred when 95% (CI) do not overlap and/or do not cross the vertical dotted line



suggests that a regional effect was likely the cause of differences in biomass between the two PPA types.

Effects of structural complexity

Structural complexity had a positive effect on fish biomass for all species groups (Fig. 6, Supp. Table S2), and the slope of complexity ranged from ≈ 1.3 – 1.8 (Supp. Table S2). Biomass values for all groups increased with increasing complexity of habitats in both the Whitsundays and Mackay region (Fig. 6). For all fish species/groups, low complexity (score 1) sites had less than a third of the biomass compared to high complexity (score 4) sites (Table 1). The

strongest relationship with complexity was observed for stripey snapper, with a $1.8 \text{ kg}/250\text{m}^2$ increase in biomass for every 1.0 unit increase in complexity (Supp. Table S2). Although interactions were not modelled in these data, the relationship between complexity and fish biomass did vary by zone for coral trout and primary target species (Fig. 6). In both instances, the greatest fish biomass was observed in NTMRs in locations with the highest structural complexity, though there was high variability among sites (Fig. 6). This suggests that the magnitude of the effect of complexity was often greatest in NTMRs. For example, coral trout (*Plectropomus* spp.) biomass for sites in NTMRs with high or very high structural complexity (scores 3–4) was on average

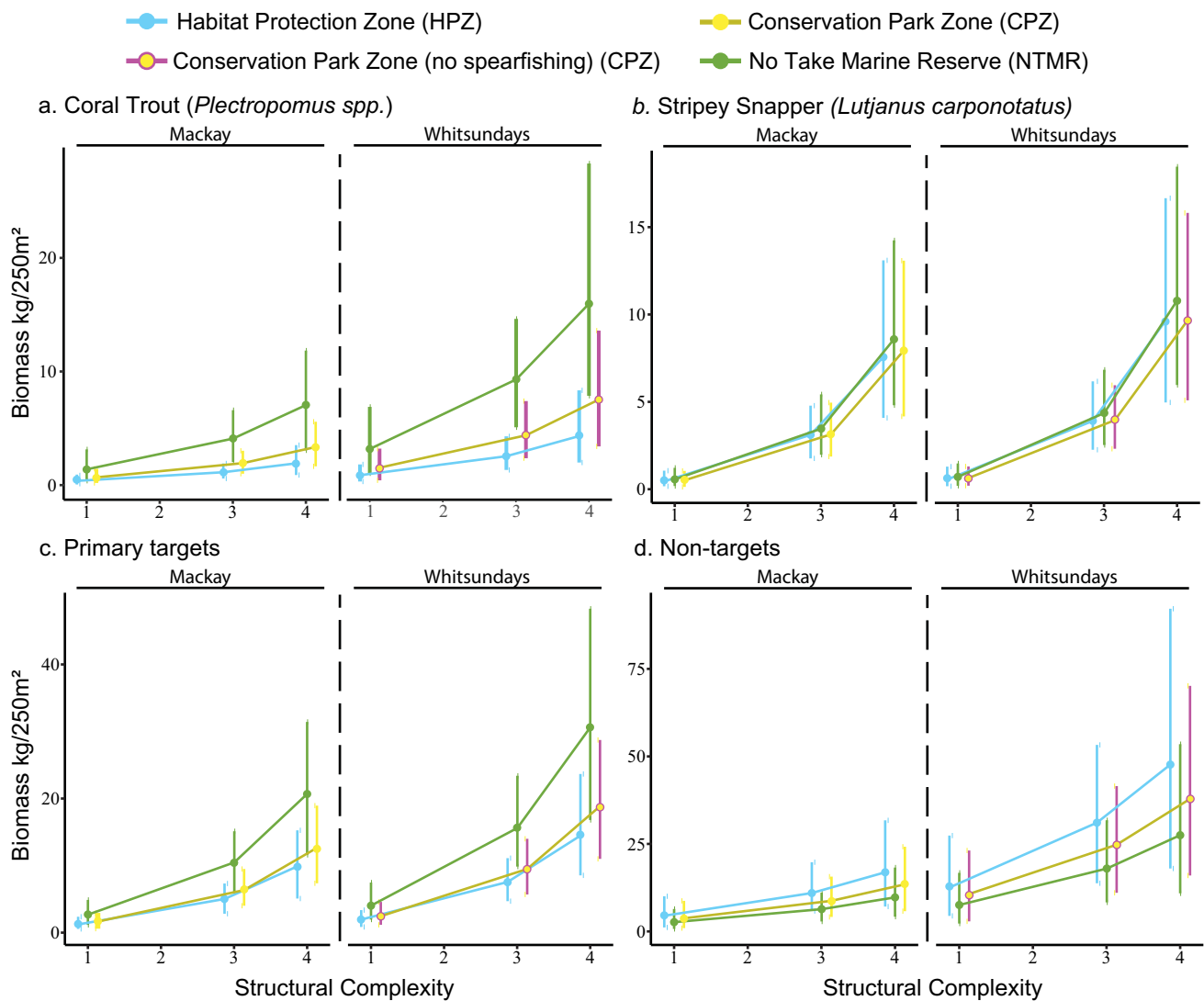


Fig. 6 Modelled changes in fish biomass (kilograms per 250-m^2) with structural complexity in Mackay and Whitsunday regions, compared among management zones. Structural complexity was modelled at the minimum (1.0), mean (3.0), and maximum (4.0) values observed in the raw data. The pink line on the CPZ zone in the Whitsundays indicates that spearfishing is prohibited. Circles are the average median biomass from modelled estimates, and error bars are 95% credibility intervals from Bayesian generalized linear mixed effects models

sundays indicates that spearfishing is prohibited. Circles are the average median biomass from modelled estimates, and error bars are 95% credibility intervals from Bayesian generalized linear mixed effects models

≈3.8 times greater than the biomass of NTMR sites with low complexity (score 1). Comparatively, in fished zones, biomass in high/very high-complexity sites was ≈1.5 (CPZs), and ≈1.0 (HPZs) times greater than low complexity sites. This trend was not evident for stripey snapper, which had a similar magnitude of response for all zones, or for non-targets, where the strongest response tended to occur in HPZs (Fig. 6).

Discussion

Our results demonstrate the importance of marine parks in providing conservation benefits for coral reef fishes and in particular highlight the pivotal role that no-take zones play in mitigating fishing impacts. No-take marine reserves (NTMRs) supported a much greater biomass of targeted fishes compared to both other fished zones in our study regions, and there was strong evidence to conclude that variation among zones was the result of fishing effects. Differences between fished and unfished zones only occurred for targeted species, and the strongest effects occurred for the most highly targeted taxa (coral trout), indicating that the effect size of zoning differences was strongly related to fishing pressure. Although some previous studies (e.g. Hall et al. 2021; Hall et al. 2022) have demonstrated benefits from partial protection from fishing on coral reefs, it was clear in this case that the strongest outcomes were achieved for target species only when full protection was provided by management zones. We surveyed multiple zones in the region, along a spectrum of protection: fully protected (NTMRs), partially protected (CPZs) and less regulated open fishing zones (HPZs). For all taxa, the difference between full and partial protection was of greater magnitude than the difference between partial protection and open fishing zones. Thus, the provision of full protection in NTMRs was clearly irreplaceable in these inshore reef habitats.

Structural complexity was a consistent positive driver of fish biomass for all fish species/groups across all three zones. All fish groups had strong evidence of a positive relationship with complexity, regardless of their zoning relationships. For example, stripey snapper (*L. carponotatus*) had the strongest positive relationship with complexity, but no evidence of zoning relationships, whereas coral trout (*Plectropomus* spp.) were strongly influenced by zoning, but also had strong evidence of a positive relationship with complexity. There was high variation in the magnitude of this effect (Fig. 6), i.e. not all high-complexity sites supported particularly large numbers of fishes. This variability may be due to the influence of other factors (e.g. benthic composition, recruitment) at these sites. Our results align with a number of previous studies demonstrating the importance of highly complex habitats for large-bodied piscivorous and

carnivorous fishes, which may be more strongly influenced by habitat complexity than by coral cover (Connell and Kingsford 1998; Emslie et al. 2008; Kerry and Bellwood 2012; Hall and Kingsford 2021). Although the cover of live hard and soft corals is undoubtedly important for a range of coral reef fishes (Wilson et al. 2008; Coker et al. 2014; Darling et al. 2017), macro-scale complexity features such as caves and overhangs can provide critical habitat features for larger-bodied fishes (Kerry and Bellwood 2012; Nash et al. 2013).

Although the presence of no-take zones may not always directly influence benthic habitats, the occurrence of optimal habitats within NTMRs may have positive synergistic effects. Notably, we found a trend for complexity effects to be of a greater magnitude in NTMRs compared to other zones. Areas of particularly high complexity attracted large groups of fishes, especially when these hotspots occurred inside NTMRs. For example, a single high-complexity bommie at Black Island Reef in the Whitsundays supported 13 coral trout, most of which were large (> 500 mm). Similar aggregations of coral trout have been observed at high complexity “hotspots” elsewhere on the GBR (e.g. One Tree Reef; Connell and Kingsford 1998). The Whitsundays region has a documented history of severe decline in coral cover, particularly due to recent cyclone impacts (Williamson et al. 2019; Ceccarelli et al. 2020). Given this, any remaining high-complexity habitats that have been minimally impacted during such disturbance events may form important post-disturbance refuges for populations of targeted fishes (Williamson et al. 2014). The ability to recover from impacts may be also helped by the life history characteristics of many of the target species. For example, coral trout have a relatively short life span (maximum 15 years) compared to many other serranids and may reach reproductive maturity as young as two years of age (Kingsford 2009). Our outcomes indicate that a strong history of protection, coupled with the presence of complex habitats, can be pivotal for supporting healthy and productive numbers of ecologically and commercially important coral reef species.

The value of partially protected marine areas as a conservation tool is widely debated (Lester and Halpern 2008; Zupan et al. 2018; Hall et al. 2021; Turnbull et al. 2021). Here, we found some evidence that limiting fishing inside PPAs provided a benefit for targeted fishes, but acknowledge that the magnitude of this effect is likely to be modest. There was a gradient effect in coral trout biomass, which was intermediate in CPZs compared to NTMRs and HPZs. However, biomass in partially protected CPZs was more similar to open fishing HPZs than it was to fully protected NTMRs. Thus, there appears to be a modest benefit to increasing protection levels from minimal (in HPZs) to moderate (in CPZs), and a much greater benefit to further increasing from partial to full

protection (in NTMRs). This outcome differs to previous studies on coral reefs of GBR (Frisch et al. 2012; Boaden and Kingsford 2015) and in sub-tropical regions (Harasti et al. 2018), where fisheries target abundance and/or biomass was significantly greater in PPAs compared to open fishing areas. In the present study, it is possible that the history of habitat disturbance to the region affected the ability for more subtle zoning effects (i.e. partial protection) to be detected. However, our outcomes do concur with studies of PPAs in temperate (Turnbull et al. 2021) and sub-tropical (Malcolm et al. 2018) habitats where PPAs were found to be of minimal benefit from a social and ecological perspective.

We hypothesized that prohibiting spearfishing inside CPZs may infer additional benefits for target species, but found no compelling evidence to support this premise. A comparison of the two CPZs did show greater coral trout biomass in Whitsundays (no spearfishing) CPZs compared to Mackay (spearfishing allowed) CPZs; however, this trend was strongly influenced by a single outlier site in Whitsundays (Langford Reef), located on a reef with split CPZ/NTMR zoning. Further, a similar trend also occurred for non-target fishes, and both groups had a strong trend for greater biomass in the Whitsundays region overall. As such, the difference between CPZs most likely occurred to the regional effect rather than an effect of spearfishing. Spearfishing can be highly selective and therefore has the potential for strong impacts on key fisheries targets (Frisch et al. 2008). Studies of tropical and temperate reef fishes have shown the benefits of prohibiting spearing for fisheries targets (Frisch et al. 2012; Curley et al. 2013). On the GBR, two studies examining the impacts of spearing on inshore reefs have had differing outcomes, with one (Frisch et al. 2012) showing a significantly greater biomass of coral trout in SMA CPZs compared to regular CPZs, and another (Hall et al. 2021) showing no difference between the two zones. We propose that, in our study area, the lack of an effect of SMA (no spearfishing) CPZs, and small effect size of CPZs overall may be due to high visitation by tourists and other recreational users. Recreational fishing is thought to be popular in the area, particularly in the Whitsundays region, which receives heavy tourist visitation (Webley et al. 2015). Indeed, during our surveys, we observed large amounts of derelict fishing gear in many CPZ sites, suggesting substantial line fishing activity (Williamson et al. 2015). As such, the extent of recreational line fishing effort may be high compared to commercial fishing, resulting in minimal differences in fishing effort between CPZs and HPZs. Our outcomes suggest PPAs may be of limited utility in such high-use areas, emphasizing the importance of full protection inside NTMRs in the region.

Management implications

Our results hold important management implications that relate to both marine park zoning, and the preservation of coral reef habitats. The dual benefits of protection from fishing, alongside the presence of optimal habitats, may be critical in creating biomass hotspots, particularly for commercially and ecologically important species such as coral trout (Boaden and Kingsford 2015). Such hotspots may be an important source of larval export, and therefore benefit populations in the broader region (Harrison et al. 2012). Coral reefs face an ever-increasing range of threats, including coral bleaching, disturbance from cyclones and severe storms, and runoff/pollution (Hughes 2008; Brodie et al. 2012; Hughes et al. 2017). Management of coral reef ecosystems must therefore take into account the ongoing presence of such threats, and where possible, minimize their impact and facilitate recovery. For managers focussed on optimizing conservation outcomes in MPA systems, there are two clear and relevant implications from this study. Firstly, the placement of NTMRs within MPA systems may be of greatest benefit when located in areas that have important habitat attributes such as high structural complexity. And correspondingly, protection or restoration of coral reef habitats may be most beneficial (at least for target species) when undertaken in zones protected from fishing.

Although this study compared the three zone types only at one point in time, our results do concur with temporal studies in the Whitsundays region showing persistent benefits of NTMRs over HPZs in supporting coral trout biomass over a period of 23 years (Williamson et al. 2019). Further, our data expand upon this existing knowledge by incorporating a broader study area (including the Mackay region), and through the inclusion of PPAs in zoning comparisons. Our data highlight the ability for reserve effects to persist for over three years after significant habitat disturbance, emphasizing the importance of a history of long-term protection inside NTMRs. The ongoing recovery trajectories of these reefs, however, are unknown and will be an important component of ongoing research and monitoring. Although our study was limited to a single region of the GBR, we provide clear evidence of the critical nature of protection inside marine reserves on coral reefs, an outcome which is relevant to coral reefs, and indeed many marine ecosystems, globally. The preservation of species, ecosystem processes, and ultimately coral reef ecosystems inside protected reserves is and will continue to be, an essential component of marine conservation and management.

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Declarations

Conflict of interest This research was carried out under an approved animal ethics permit # A2438. The authors have no competing interests to declare that are relevant to the content of this article.

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