Expectations and outcomes of reserve network performance following re-zoning of the Great Barrier Reef Marine Park.

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Summary

Background

Networks of no-take marine reserves (NTMRs) are widely advocated for preserving exploited fish stocks and for conserving biodiversity. We used underwater visual surveys of coral reef fish and benthic communities to quantify the short- to medium-term (5 to 30 years) ecological effects of the establishment of NTMRs within the Great Barrier Reef Marine Park (GBRMP).

Results

The density, mean length and biomass of principal fishery species, coral trout (*Plectropomus spp.*), were consistently greater in NTMRs than on fished reefs over both the short- and medium-term. However, there were no clear or consistent differences in the structure of fish or benthic assemblages, in non-target fish abundance, fish species richness or in coral cover between NTMR and fished reefs. There was no indication that the displacement and concentration of fishing effort reduced coral trout populations on fished reefs. A severe tropical cyclone impacted many survey reefs during the study, causing similar declines in coral cover and fish density on both NTMR and fished reefs. However, coral trout biomass declined only on fished reefs following the cyclone.

Conclusions

The GBRMP is performing as expected in terms of the protection of fished stocks and biodiversity for a developed country where fishing is not excessive and targets a narrow range of species. NTMRs cannot protect coral reefs directly from acute regional-scale disturbance but, following a strong tropical cyclone, impacted NTMR reefs supported higher biomass of key fishery-targeted species, and so should provide valuable sources of larvae to enhance population recovery and long-term persistence.

Keywords

Great Barrier Reef Marine Park, management, zoning, no-take marine reserves, long-term monitoring, coral reef fishes, *Plectropomus* spp., diversity, disturbance, tropical cyclone

Introduction

Coral reefs are under increasing pressure, leading to debate about strategies to conserve biodiversity, enhance resilience, and maintain ecosystem processes in these habitats [1, 2, 3, 4]. Fully protected no-take marine reserves (hereafter "NTMRs"), defined as "areas of the ocean completely protected from all extractive and destructive activities" [5], are a widely advocated tool for conservation and management of marine systems [6, 7, 8, 9]. Historically, NTMRs were conceived as a fisheries management tool to protect exploited stocks, prevent overfishing, and mitigate habitat destruction, allowing the recovery of exploited populations once fishing pressure and associated habitat destruction cease. However, in recent decades their use has expanded to include protection of biodiversity and ecosystem processes. Whether or not NTMRs can perform these roles depends on the nature of the threats to biodiversity and the efficacy of NTMRs in countering these threats. Since NTMRs generally only eliminate extractive fishing activities, their effectiveness can vary according to size, location, and enforcement, as well as the selectivity, catch, and effort of the fishery. Hence NTMRs would only be expected to have substantial effects on fished stocks and biodiversity under certain conditions.

There is now abundant evidence that adequately protected NTMRs are effective as fishery reserves, increasing the abundance, size and biomass of species targeted by fisheries in both tropical and temperate systems [8, 10, 11, 12, 13, 14, 15, 16, 17, 18]. Importantly, NTMRs may also contribute to maintaining populations in adjacent fished areas through larval recruitment subsidies and spill-over of adult fish [19, 20, 21]. While evidence suggests that NTMRs are performing successfully as fishery reserves, key questions still remain: how much area needs to be preserved to sustain fisheries at different levels of fishing pressure and how does the spatial redistribution of fishing effort following the establishment of NTMRs affect exploited fish populations in areas that remain open to fishing?

Beyond effects on fisheries, can NTMRs effectively conserve or restore natural states of biodiversity and enhance resilience, particularly in coral reef ecosystems? The answer to this question depends largely on the socio-economic setting of the region; specifically the distribution and intensity of fishing pressure and the diversity of species exploited by the fishery [5, 22]. Where fisheries exploit a broad range of species that perform many ecological functions (e.g. Caribbean, Pacific, and South-East Asia), and in locations where destructive fishing methods are employed (e.g. dynamite, cyanide or muro-ami), NTMRs may be expected to significantly enhance biodiversity and maintain habitat condition. In contrast, in many developed countries like Australia and the USA, where only a limited range of high trophic level predatory species are targeted by fisheries and destructive fishing techniques are prohibited, enhancement of biodiversity within NTMRs may be limited and difficult to detect. For NTMRs to influence the abundance of non-targeted fish species, hard coral cover, the structure of reef fish and benthic assemblages, and biodiversity, indirect ecological processes must occur (see [4, 14, 23, 24]). Such indirect processes include trophic cascades, where targeted species exert top-down control of species at lower trophic levels, but there is little evidence of strong top-down control on species-rich coral reefs [14, 23, 25, 26]. NTMRs may protect habitat characteristics such as coral cover and benthic community composition where destructive fishing practices are used (e.g. dynamite fishing) [27], but there is little evidence that they can contribute to maintaining or enhancing coral cover in areas where less damaging fishing methods are used (e.g. Spearfishing or hook-and-line) [14, 23, 24, 28].

While the primary goals of NTMRs are to act as fishery reserves and protect biodiversity, many of the stressors degrading coral reefs – pollution, sedimentation, coastal development, and the cumulative, escalating effects of climate change, are not related to fishing. Climatic disturbance events such as cyclones, flood plumes and coral bleaching can severely degrade coral reefs and erode the accrued benefits of reserves at relatively local scales [29, 30, 31]. The frequency of extreme climatic disturbance events is predicted to increase in coming decades, and it is important to consider the role that reserve networks could play in enhancing resilience and population persistence at regional and ecosystem scales [32]. While it seems obvious that reserves can do little to mitigate against the acute impacts of severe climatic disturbances at local scales [33], this assumption has rarely been directly tested in a large, well-connected NTMR network [32].

The Great Barrier Reef Marine Park (GBRMP) includes a large-scale network of NTMRs that extends over 2000 km along the northeast coast of Australia. The GBRMP has a zoning history spanning 30 years (Supplemental Experimental Procedures), and in 2004 a new zoning plan increased the total no-take reserve area from approximately 5% to 33% of the Marine Park. The main fishery operating within the GBRMP is a hook-and-line fishery primarily targeting coral trout (*Plectropomus* spp., family Serranidae) [34]. A limited range of other reef fishes (principally from the families Lethrinidae and Lutjanidae) are not directly targeted, but individuals that are above the minimum legal length are often retained when captured [34]; here these are termed “secondary targets” (Supplementary Table S1). The GBRMP has a small and localised coastal population with moderate coastal development and has recently been exposed to a succession of severe acute disturbance events, following which the cover of habitat-forming hard corals has declined significantly on many reefs [35, 36, 37]. The majority of the recent coral loss has occurred since 2006, after multiple storms damaged large areas of the central and southern GBRMP. Most notable was severe Tropical Cyclone (TC) Hamish in 2009 (Fig. 1), which caused extensive physical damage to offshore reefs, widespread freshwater inundation of inshore reefs and localised bleaching events [38, 39].

The GBRMP is a benchmark for the implementation of networks of reserves, particularly for coral reefs, and has inspired comparable large-scale action around the world (e.g., the US west coast, Hawaii, Mediterranean, Coral Triangle Initiative). Because of its global importance as an example of the type of action that many believe is required to sustain coastal ecosystem services, there is general interest in how the GBRMP performs. However, any assessment of the performance of the GBRMP, or any other reserve network, must consider the disturbance history and socio-geographical settings of the region. NTMR networks in more degraded and heavily fished systems, such as the Caribbean or Southeast Asia, would be expected to perform quite differently from those in less degraded systems with lower fishing pressure.

Here we use two long-term datasets (2004 to 2012 and 1983 to 2012) from reefs spread over ~150,000 km^2 of the GBRMP (Fig 1) firstly to assess several key ecological measures of NTMR performance following a major re-zoning of the GBRMP in 2004 and secondly, to determine the degree to which accrued NTMR benefits were affected by a tropical cyclone. Specifically, we asked three key questions:

1. Fishery effects - were the density, length, and biomass of key targeted reef fish species higher on reefs within NTMRs than on reefs that were open to fishing?
2. Biodiversity effects - did the density of non-target reef fish species, species richness of reef fishes, hard coral cover and assemblage structure of fish and benthic communities differ between reefs in NTMRs and reefs that were open to fishing?
3. Disturbance effects - did a severe tropical cyclone affect any accrued benefits of NTMRs?

Results

1. Fishery effects

a) GBR-wide effects of reserve status

Despite variability at finer temporal (among years) and spatial (among offshore sectors and inshore island groups) scales (Supplemental Table S2, Supplemental Fig S1), the re-zoning of the GBRMP in 2004 resulted in clear GBRMP-wide increases in the density, length and biomass of the primary target of the hook and line fishery, coral trout, on NTMR reefs relative to fished reefs (Fig. 2). In inshore and offshore NTMRs, 53% and 67% of coral trout respectively were larger than the minimum legal size (38cm Total Length (T.L.)), compared with 26% inshore and 56% offshore on adjacent fished reefs (Supplemental Fig S2). On average, coral trout were 12% and 7% larger on inshore and offshore NTMR reefs respectively, compared with reefs that were open to fishing (Fig. 2). The differences in coral trout density and mean size translated into an 89% higher biomass in inshore NTMRs and an 82% higher biomass in offshore NTMRs (Fig 2). Benefits to secondary target fishes were less clear. While secondary target fishes on offshore NTMR reefs were 1% larger and biomass was 30% greater compared with fished reefs, no such differences were evident on inshore reefs (Fig. 2).

b) Historical trends

A full Before-After-Control-Impact (BACI) analysis of the effects of the 2004 re-zoning of the GBRMP was not possible, due to the lack of data from offshore reefs before 2004. However, by combining three data sets spanning 1983 – 2012 (Supplemental Experimental Procedures), we were able to put the post-2004 changes in coral trout populations into an historical context. Before the widespread establishment of the GBRMP in the 1980s, GBR-wide coral trout biomass was ~5 kg 1000 m^{-2}, subsequently declining to 1 – 2 kg 1000 m^{-2} by 1996. GBR-wide, biomass on NTMR reefs had increased to ~5 kg 1000 m^{-2} by the time the GBRMP was re-zoned in 2004, before again increasing rapidly to the highest levels recorded since the 1980s in 2008. GBR-wide biomass subsequently declined to ~5 kg 1000 m^{-2} coincident with the occurrence of Cyclone Hamish in 2009, but there was evidence for some recovery following the cyclone (Fig 3). Significantly, on reefs that were open to fishing, GBR-wide biomass remained stable or increased following the 2004 re-zoning, except after Cyclone Hamish when changes in numbers were similar to those on NTMR reefs (Fig 3). Note that the catch and effort of the GBR hook and line fishery increased from the early 1990s until 2002, declined from 2002 until 2005, then remained stable until 2012 (Supplemental Fig S3).

The overall GBR-wide time-averaged coral trout biomass was ~2.5 times higher on NTMR reefs than on those open to fishing (Fig 3). Offshore, this pattern was true for all sectors and, although the magnitude of the difference varied, the ratio of biomass in offshore NTMRs to that on fished reefs was always greater than 1.5 (Fig 3). On inshore reefs in the 1980s, coral trout biomass was generally lower than recorded offshore at that time. After 15 to 20 years of protection, biomass was greater than 1980s levels on NTMR reefs but remained similar to 1980s levels on reefs that were open to fishing (Fig. 3).

2. Biodiversity effects

There were few differences in the density of most non-target fish species, percent cover of benthic organisms and in the structure of assemblages of fishes and benthic organisms between NTMR and fished reefs. On inshore reefs, benthic foragers were 21% more abundant on reefs that were open to fishing than on NTMR reefs (Fig. 2). On offshore reefs, detritivores, omnivorous damselfishes and benthic foragers were all between 13% and 35% more abundant in NTMRs compared with fished reefs (Fig. 2). Species richness of reef fishes was 8% greater in offshore NTMRs than on fished reefs (Fig. 2), but the species that contributed most to this difference were rare (e.g. *Chaetodon bennetti, Chaetodon meyeri,* *Lethrinus ornatus, Lethrinus rubriopercularis*) and occurred in very low densities. There were no differences in cover of hard coral, soft coral or algae (Fig. 2) between NTMR and fished reefs. There was very little evidence that NTMR status affected the overall structure of the assemblages of fishes or benthic organisms on either inshore or offshore reefs (Fig. 4). NTMR zoning status accounted for <1% of the total variation in reef fish community structure, while differences among sectors or island groups accounted for 33-50% of the variation.

3. Disturbance effects on offshore reefs

In March 2009, TC Hamish tracked along much of the southern GBR (Fig. 1). In its wake there were significant declines in hard coral cover and in the density of numerous fish groups, with increases in total algal cover (turf, coralline and macro-algae) on offshore NTMR and fished reefs in the impacted region (Fig. 5). There were no substantial changes in any of these variables over the same period on more northern "control" survey reefs that were not affected by the cyclone (Fig. 5). While the density of coral trout declined on both NTMR and fished reefs in the impacted region, coral trout biomass only declined on fished reefs, with no concomitant change on NTMR reefs (Fig 5). At the same time, there was little or no change in the density and biomass of coral trout on reefs in the control region that were not affected by the cyclone (Fig. 5). There were no significant temporal changes in density or biomass of secondary target species or in total species richness of reef fish, on either NTMR or fished reefs in either the impact or control regions (Fig. 5). The density of benthic foragers and obligate corallivores declined on both NTMRs and fished reefs in the impact region but not in the control region. The density of omnivorous damselfishes and territorial farming damselfishes also declined following the cyclone, but only on reefs in the impact region that were open to fishing (Fig. 5). The density of herbivorous scrapers increased in NTMRs only, while planktivore density increased on both NTMR and fished reefs in the impacted region with no equivalent changes on reefs in the control region (Fig. 5).

Discussion

This study clearly demonstrates that the GBRMP is performing as expected, given its north-eastern Australian setting with relatively low fishing pressure and a fishery that targets a limited number of top-level predators. NTMRs established during the 2004 re-zoning of the GBRMP have yielded significant benefits for populations of targeted coral reef fishes on both inshore and offshore reefs within the first decade of protection. Substantial increases in the mean density, body size and biomass of exploited species were consistently recorded on NTMR reefs, while there were few discernible changes on reefs that remained open to fishing. Importantly, there was no indication that the density, size or biomass of targeted fish species was reduced on fished reefs as might occur from the displacement and concentration of fishing effort following the establishment of the NTMR network. Additionally, there were no differences in crude measures of biodiversity and, despite the major impacts of a tropical cyclone, the biomass of coral trout remained relatively stable on NTMR reefs, but declined on fished reefs.

The absence of data on offshore reefs from before the new zoning plan came into effect made it difficult to attribute post-2004 increases in coral trout biomass unequivocally to NTMR protection. To address this, and to place the monitoring data from 2006 to 2012 into historical context, we modelled coral trout biomass from data sets spanning thirty years collected on fished and NTMR reefs. Biomass of coral trout increased over both short (2-3 years after the 2004 re-zoning) and long (since 1996) time scales. While such results are not without precedent [12, 14, 41], increases in coral trout biomass on NTMR reefs occurred more rapidly than in the majority of previous studies. Such short term increases may reflect redistribution of biomass to the reserves following re-zoning. It is also possible that the study reefs were supporting high densities of sub-legal size (< 38 cm T.L.) coral trout prior to the establishment of reserves in 2004. Given that fish body weight generally increases exponentially with increasing length [42], the rapid biomass increases on NTMR reefs may have also been at least partly due to higher numbers of fish surviving beyond 38cm. Alternatively, the increases in coral trout biomass may simply have been a function of increasing reserve area. It is clearly not possible to apportion the contribution of these potential mechanisms to the rapid gains in coral trout biomass observed on NTMR reefs with certainty. Intuitively however, the increase in NTMR reef area from pre-2004 to post-2004, coupled with improved surveillance and enforcement of GBRMP zoning regulations and the implementation of a range of direct fishery management actions in 2004 [43] are all likely to have contributed.

While the benefits of NTMRs for exploited species were expected, an unanticipated result was that the reduction in the reef area available to fishers following the 2004 re-zoning did not reduce densities of coral trout on reefs that remained open to fishing. After an initial decline from 1980s levels, populations of coral trout on fished reefs remained stable or increased slightly from1996 until 2012, suggesting that the catch rates of the GBR Line Fishery have been sustainable since the creation of the GBRMP. The increased area of NTMRs inside the GBRMP following the 2004 re-zoning may have theoretically resulted in a "squeeze effect" [44, 45], with a relocation and concentration of fishing effort on the remaining fished reefs and concomitant reductions in the abundance and biomass of target species. The lack of evidence for such an effect in the present study suggests that fishery management actions such as the Great Barrier Reef Marine Park Structural Adjustment Package (GBRMPSAP), introduced shortly after the 2004 re-zoning, were effective in sustaining stock levels on fished reefs. The GBRMPSAP included a license buyout program, which successfully reduced the catch and effort of the coral reef line fishery from an all-time high in 2002 to lower but stable levels from 2005 onwards.

Analysis of historical coral trout biomass suggests that populations on inshore reefs had been depleted by the 1980s, before establishment of the GBRMP. The limited area of inshore fringing reef habitat is readily accessible from the mainland, so fishing effort is highly concentrated, increasing the potential for population depletion. In contrast, the area of offshore reefs is much greater, and fishing effort is more broadly distributed, so the less accessible offshore populations remained relatively lightly exploited through the 1980s [46], and supported coral trout biomass similar to levels in NTMRs today. Fishing pressure on offshore reefs increased through the 1990s [40, 47] as both commercial and recreational fishing expanded [48]. The limited historical data suggests that the number of participants in the commercial line fishery declined from 279 in 1980/81 to 176 in 1990, but there was an increase in catch from 201 tonnes 1980/81 to 1490 tonnes by 1990 [40]. This increase in the commercial catch seems the most likely explanation for the reduction in coral trout biomass we observed between the 1980s and 1995.

One of the key objectives of the 2004 re-zoning of the GBRMP was to preserve biodiversity, yet we found no large differences in coarse measures of biodiversity between fished and NTMR reefs in the present study. There was no difference in reef fish species richness between inshore NTMRs and fished reefs, and species richness was only marginally higher (8%) on offshore NTMRs than on fished reefs. This result is not surprising, as the main function of NTMRs is to reduce fishing pressure. The Reef Line Fishery operating within the GBRMP targets a narrow suite of predatory fishes and thus cannot be considered a major threat to biodiversity. In comparison, we would expect NTMRs to influence biodiversity directly in other regions of the world where fishers target a wide range of species that perform many ecological functions, often using methods that destroy coral habitat. In contrast to recent work in the Caribbean [23], our results suggest that the current levels of fishing exert little top-down control on the abundant and speciose reef fish assemblages in the GBRMP. The structure of reef fish and benthic assemblages appears to be largely driven by bottom-up processes, such as exposure, variability in larval supply and the effects of disturbances such as large-scale storms.

TC Hamish caused widespread declines in coral cover on both NTMR and fished reefs across a broad swathe of the southern GBRMP in 2009. Such broad-scale damage to habitat-forming hard corals commonly has direct effects on reef-associated species such as fishes [31], and in the months following the cyclone, commercial fishers reported that coral trout catch rates had declined [34]. Our analysis of the impacts of TC Hamish indicated that NTMR and fished reefs fared equally poorly by most metrics, including a 50% reduction in hard coral cover and in coral trout density on both NTMR and fished reefs. The reductions in coral trout density may reflect mortality or movement to less damaged reef areas [30]. There was some recovery following the storm, and the average size of coral trout was similar before and after the cyclone, which implies that relocation was more likely than widespread mortality. Such movement may be a response to the dramatic reduction in benthic habitat complexity in shallow coral reef habitats following the cyclone [49], which probably reduced prey abundance [30]. Loss of shelter may reduce the effectiveness of ambush predators such as coral trout [50], forcing them to relocate to leeward or deep water locations around the reef that were less damaged by the cyclone and still retained high levels of habitat complexity.

While coral trout density declined equally on both NTMR and fished reefs following TC Hamish, NTMRs surprisingly retained significantly greater coral trout biomass than reefs that were open to fishing. Larger fishes may be better able to withstand turbulence during cyclones, or may be less dependent on remaining reef structure after disturbances, or may have a greater capacity to move to refuge areas (e.g. deeper reef habitats) and return to shallow reef areas when conditions have settled. In any case, this finding has important implications because the retention of coral trout biomass in NTMRs following TC Hamish may speed recovery of depleted populations both inside and outside NTMRs via larval dispersal [20, 32].

Some non-target species (e. g. planktivores and scrapers) were more abundant following TC Hamish, while others (e. g. obligate corallivores and benthic foragers) declined in abundance. Such changes can be explained by increases to algal cover and reductions to hard coral cover [31, 51, 52], however there was no indication that the responses of these fishes, or algae and hard coral, differed between NTMRs and reefs open to fishing. Like other large-scale disturbances such as coral bleaching events [33], and flood plumes [30], large storms appear to swamp any differences in resistance between NTMRs and fished reefs. Marine reserves provide no direct protection from storms, flood plumes or temperature anomalies at local scales, but the establishment of a large network of NTMRs inside the GBRMP spaced over 1000s of kilometres ensured that there were protected reefs which were unaffected by TC Hamish; these remained as potential sources for reseeding damaged reefs, thereby maintaining biodiversity and the persistence of coral trout populations at regional and ecosystem scales [30].

Conclusions

The GBRMP zoning management plan appears to be performing as expected, given its geographic and socio-economic context. The expansion of NTMRs within the GBRMP, coupled with effective direct fishery management actions, have ensured adequate protection for stocks of key targeted coral reef fish species of the commercial and recreational fisheries, and have lowered overall fishery catch to what currently appears to be sustainable levels [47]. Time will tell if such levels prove to be sustainable, but if global temperatures and disturbance frequency increase in the future, we will face the prospect of having to reduce fishing pressure as target populations, both inside and outside NTMRs, suffer increasingly from non-fishery impacts. Monitoring and adaptive management would appear pertinent if we are to respond appropriately to changing conditions in the future and preserve fish stocks. There was little evidence of increased biodiversity within NTMRs compared with fished reefs, but this is not surprising given the limited range of species that are targeted by the fishery. That the devastating effects of a severe tropical cyclone affected both NTMR and fished reefs equally is a timely reminder that NTMRs are not, by themselves, the solution for the full range of threats currently afflicting coral reefs. Pollution, sedimentation, coastal development, and the escalating effects of climate change all act at regional and global scales. Should we expect NTMRs to safeguard coral reefs from these threats? An encouraging finding from this study was that NTMRs can retain some fisheries benefits in the face of strong tropical cyclones that are predicted to occur more frequently as climate change progresses [53]. The establishment of highly connected networks of NTMRs can contribute to a secure future for coral reefs, but effective measures to reduce land-based threats and to mitigate climate change will also be essential.

Experimental Procedures

1. Sampling protocols

Two systematic monitoring programs were instigated to assess the ecological effects of the new NTMRs following the implementation of the new GBRMP zoning plan in 2004. A team from James Cook University began surveying reef fish and benthic communities at three “inshore” island groups (fringing reefs on high continental islands within 30kms of the coast - Palm Islands, Whitsunday Islands and Keppel Islands – Fig. 1) in 2004 (prior to the re-zoning), while a team from the Australian Institute of Marine Science (AIMS) began surveys in five “offshore” latitudinal sectors (platform reefs >30kms from the coast - Cairns, Townsville, Pompey, Swain and Capricorn-Bunker) of the GBRMP in 2006 (Fig. 1). Both programs surveyed NTMR reefs that were paired with similar reefs open to fishing. Despite minor differences in the details of the sampling protocols, comparable methods were used to collect all data (Table 1). Further details can be found in the Supplemental Experimental Procedures.

2. Data analyses

Benthic data (hard coral, soft coral and algae) were expressed as per cent cover. On the GBR, fishers using hook and line retain all species of “coral trout” (*Plectropomus* spp. and *Variola* spp; family Serranidae) that are above the minimum legal size (38cm T.L.), so density, size and biomass estimates for all of these species were pooled. In addition, several species of “secondary targets”, which are not the main targets of fishers, are retained if caught (Supplementary Table S1). Fish surveys using Underwater Visual Census (UVC) recorded the counts and total lengths of coral trout and secondary target species on belt transects, while other reef fishes that were not targeted by fishing were only counted. All reef fish data were standardised by converting raw counts to densities 1000 m^{-2}. Biomass (kg) 1000 m^{-2} was calculated for coral trout and secondary target species from estimated fish lengths (T.L. cm) using published length-weight relationships [54, 55]. We categorised non-target fishes into functional groups (Supplemental Table S1). Further details can be found in the Supplemental Experimental Procedures.

The spatial and temporal variation in the effects of NTMRs on the density and species richness of fish taxa and the percent cover of hard coral, soft coral and algae were estimated using Bayesian hierarchical linear mixed models [56] (for details of models see Supplemental

Experimental Procedures). Inferences about specific spatial and temporal differences between NTMRs and reefs open to fishing were based on 95% Bayesian uncertainty intervals (95% U.I.) for modelled Higher Posterior Density (HPD) median effects. Differences between values for NTMR and fished reefs were then expressed as a percentage of the value on the fished reefs, such that a higher value in NTMRs compared with fished reefs would yield a positive difference, while a lower value would give a negative difference.

Offshore reefs were not surveyed systematically before the new zoning plan was implemented in 2004, thus precluding the use of BACI analysis. However, estimates of coral trout biomass were available for 187 offshore reefs over the period 1983-2012. Biomass samples from NTMRs and fished reefs in each latitudinal sector in each year were used to model trends using a Bayesian hierarchical linear mixed model. All models of biomass of coral trout were estimated using a linked, zero-inflated negative binomial model (ZINB) [57] in a Bayesian framework, using the PyMC package [58] for the Python programming language (for full model details see Supplemental Experimental Procedures). Coral trout were also surveyed on inshore reefs in the Palm and Whitsunday Islands (but not in the Keppel Islands) in the 1980s, and these estimates were compared with post-2004 values from these inshore island groups and also modelled using a linked, zero-inflated negative binomial model.

We explored the structure of reef fish and benthic communities graphically using redundancy analysis (RDA), looking for differences in assemblage structure attributable to reserve protection. Data were constrained by environmental predictors, in this case latitude (sector or island group) and zoning status (NTMR or open to fishing). The resulting variation in community structure was then partitioned among the constraining variables.

Finally, using TC Hamish as a case study, we examined the effect of a regional scale disturbance on any effects of offshore NTMRs. TC Hamish passed over reefs in the southern

Pompey, Swain and Capricorn-Bunker sectors in March 2009 (Fig. 1). We applied a BACI design to the data and used Bayesian hierarchical models described above to evaluate the effects of the cyclone on the density and biomass of coral trout, secondary target fishes, on functional groups of non-target fishes, and on hard coral cover, at NTMR and fished reefs in the affected sectors. Further details of the BACI design can be found in the Supplemental Experimental Procedures.

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Source	Spatial coverage	Number of reefs	Sites/reef	Transects/site	Data	Methods	Frequency and Use in this study
Ayling 1983 to 1986	6 sectors 11^{o} latitude	50 reefs	1 to 2 sites (140 sites in total)	10 transects (1400 transects per year in total)	Coral trout abundance & length	UVC on 50 x 10m belt transects	One off Historical modelling
James Cook University Monitoring the effects of rezoning on inshore reefs 2004 to present	3 island groups 4^{o} latitude	6 reefs	1 to 3 sites (34 sites per year in total)	5 transects (170 transects per year in total)	Fish – abundance and lengths of 190 species Benthos - % cover of hard and soft coral, algae	UVC on 50 x 6m belt transects 50 m line intercept transects. 50 points per transect	Annually Post re-zoning analysis and historical modelling
AIMS Long-term Monitoring Program 1993 to present	6 sectors 11^{o} latitude	47 reefs	3 sites (141 sites per year in total)	5 transects (705 transects per year in total)	Fish – abundance of 215 species and lengths for target species Benthos - % cover of hard and soft coral, algae Coral disease, *Acanthaster planci*, bleaching Juvenile coral	UVC belt transects: **1993-1995** 50x10m (50x2m damselfishes) **1995-present** 50x5m 50x1m damselfish **1993-2005** Video transect 40 frames Photo transects 40 frames **1993-present** 50x1m belt transect	Annually from 1993 to 2005, then biennially Historical modelling

AIMS monitoring the effects of rezoning 2006 to present	5 regions 9° latitude	56 reefs (28 reserve & non-reserve pairs)	3 sites (168 sites per year in total)	5 transects (840 transects per year in total)	As for LTMP	**2006-present** As for LTMP	Biennially since 2006 Post re-zoning analysis and historical modelling

Table 1 – methodological details for each monitoring program.

Figure Captions

FIG. 1 Map of inshore (fringing reefs on high continental islands within 30kms of the coast) and offshore (platform reefs >30kms from the coast) study locations. The track of TC Hamish is the red line, with destructive (orange) and very destructive (red) wind fields (from Australian Bureau of Meteorology). The grey horizontal dotted line delineates Control from Impact reefs used in the BACI analysis of effects of the cyclone. Reefs of the Capricorn-Bunker sector lay on the edge of the destructive wind zone but are considered to be impact reefs because they were fully exposed to the storm swell generated by the cyclone at its peak.

FIG. 2 GBR-wide effects of no-take marine reserves (NTMRs) on fishery target species, non-target fish groups and benthic organisms. Effect sizes were averaged over all surveys since the re-zoning in 2004. Data are modelled median differences between NTMRs and fished reefs with associated 95% uncertainty intervals, for inshore (open symbols) and offshore (closed symbols) reefs. Data were modelled using a Bayesian hierarchical linear mixed model and differences are expressed as a percentage of the value for fished reefs. A positive effect indicates higher values in a NTMR and statistical significance is inferred where uncertainty intervals do not intersect zero. * No results are presented for excavators and detritivores on inshore reefs as the models did not converge. ** No results are presented for inshore algae as only macro algal cover was recorded.

FIG. 3 Historical estimates of coral trout biomass in inshore and offshore NTMRs (filled symbols) and on reefs that were open to fishing (open symbols). Triangles indicate data from the dedicated post re-zoning surveys (2006 to 2012), circular symbols indicate AIMS Long Term Monitoring Program data (1995 to 2011). Sector labels are the same as in Figure 1. Data points for 2004 in the two inshore sectors (PA and WH) show coral trout biomass immediately prior to the re-zoning in 2004 but are coded according to the zones in place after 2004. Trends were modelled using a Bayesian hierarchical linear mixed model with a zero-inflated negative binomial distribution. The dark line and shaded band are the modelled medians and 95% uncertainty intervals for coral trout biomass in NTMRs, while the light line and shaded band give the same information for reefs open to fishing. Black square symbols indicate median coral trout biomass in the 1980s before the implementation of zoning on the GBR. The effect size plot (bottom right-hand panel) shows the modelled median ratio and associated 95% uncertainty intervals of coral trout biomass in NTMRs compared with fished reefs (1980s to 2012) on inshore (IN) island groups and offshore sectors. The dashed vertical line indicates equal biomass of coral trout on NTMR and fished reefs. A positive effect indicates higher values in a NTMR and statistical significance is inferred where uncertainty intervals do not intersect zero.

FIG. 4 Visualisation of the structure of the structure of reef fish and benthic assemblages on inshore and offshore reefs (2006 to 2012). The plot in each panel is based on a redundancy analysis (RDA), accounting for differences due to latitudinal sector (offshore reefs), island group (inshore reefs) and NTMR status (closed symbols = NTMR; open symbols = open to fishing). All data were standardised (row centred) prior to analysis; reef fish community data were then fourth root transformed while benthic data were square root transformed to reduce the effect of highly abundant taxa.

FIG. 5 The impacts of Tropical Cyclone (TC) Hamish on communities of fishes and benthos on offshore reefs of the GBR, based on a Before-After-Control-Impact (BACI) design applied to the MCMC samples from the Bayesian hierarchical linear mixed model for each response variable. Plots give the average differences between values from before (2006 to 2008) and after (2010 to 2012) TC Hamish (± 95% uncertainty intervals) for reefs in the impact and control zones of the GBRMP. Closed symbols indicate the average values for NTMR reefs; open symbols refer to reefs that were open to fishing. Control reefs (Cairns and Townsville sectors) were outside the destructive wind-fields of TC Hamish (Fig. 1), while impact reefs (Pompey, Swain and Capricorn Bunker sectors) were directly affected.