Supporting Information

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SI Section 1: Management, Zoning, and Monitoring on the Great Barrier Reef

Overview of Management of the Great Barrier Reef. Management of the GBR Marine Park (GBRMP) aims for an ecosystem-based and adaptive approach to addressing the major human impacts, and, importantly, where possible aims to proactively prevent or minimize decline, as well as restore degraded or depleted ecosystem components. Management involves a cross-jurisdictional partnership between the national Australian Government and the Queensland state government, with developing co-management by Indigenous traditional owners groups. Impacts addressed include those of activities within the jurisdiction of the Marine Park, such as fisheries, tourism, and shipping, and the greater threats posed by factors external to the Marine Park, primarily terrestrial runoff from adjacent catchments, and most critically, the effects of climate change (1). Fishing is the major extractive use on the GBR, and includes a range of line, trawl, and net-based fisheries. Although fisheries are principally managed by a comprehensive series of Queensland State Government Fisheries Management Plans, managing the environmental impacts of fishing is a major purpose of GBR zoning. The coral reef hook and line fishery, the focus of many of the studies reported here, includes commercial, charter, and recreational sectors, and focuses on two main target fish, the coral trout (*Plectropomus* spp.; Serranidae) and redthroat emperor (*Lethrinus miniatus*; Lethrinidae) (2–4).

Many of the threats to the Marine Park do not respond to spatial management approaches alone, and management of the GBRMP includes a wide range of nonspatial strategies. Prominent are the Reef Rescue Plan and Reef Water Quality Protection Plan, which aim to reduce runoff of terrestrial pollutants into reef waters (www.reefplan.qld.gov.au). Other strategies include permitting, regulation, environmental impact management, specific strategies for threatened species, fishing gear restrictions (e.g., bycatch reduction and turtle exclusion devices), fish size restrictions, temporal closures (e.g., for fish spawning), licenses, commercial quotas, hook and bag limits for recreational fishers, industry codes of practice and, especially critical, education and community engagement, and collaborative partnerships with industries and between governments.

Thus spatial zoning is just one of a range of integrated mechanisms for managing the GBR, and importantly, no-take zones are just one of seven marine zones (Table S1). The 2004 rezoning of the GBR was widely recognized for achieving 33% of the area of the Marine Park in no-take zones (increased from previous 4.6%), but other significant achievements include: 66% of the area zoned as no trawling, which limits habitat destruction by fishing (increased from previous 20.6%), and the comprehensive representation of at least 20% of each of 70 different bioregions in no-take zones. The inclusion of no-entry zones has also proven invaluable in terms of information on undisturbed habitats.

Adaptive management refers to the practice of "learning by doing": that is, the regular review or monitoring of both the status of the system, and its response to management strategies, to adapt and improve those strategies (5, 6). The adaptive management cycle involves iterative planning, implementation, auditing/review of outcomes, and adaptive planning in response to review. This approach allows for the changing nature of ecosystems and the pressures on them and allows for proactive implementation without delays due to information gaps: research is combined with management, to the benefit of both (e.g., refs. 7–9). Historically, much of the management of the GBR has involved passive adaptive responses to emerging information, rather than proactively incorporating assessment of effectiveness into management actions. However, such monitoring has been explicitly implemented with the 2004 Zoning Plan and incorporated into recent management efforts to address terrestrial runoff. Active adaptive management involves deliberately manipulating management strategies for information outcomes as well as environmental outcomes. On the GBR, the "Effects of Line-Fishing Experiment" actively altered zoning status (i.e., opened and closed areas to fishing) to experimentally test zoning effects on fish stocks (4). Table S2 summarizes the history of zoning on the GBR from an adaptive management perspective.

Closing the Loop in Adaptive Management: The GBR Outlook Report. Genuine adaptive management requires more than just monitoring and assessment; it requires a mechanism to ensure feedback from that assessment into policy development (e.g., 7, 8). The key role of adaptive management on the GBR has recently been further upgraded through the implementation of the Great Barrier Reef Outlook Report, which formalizes review of the state of the GBR, and provides risk assessments and outlooks as a basis for future policy and management development. The GBR governance arrangements give effect to the goals of the Australian Government's Oceans Policy (10), and the GBR Outlook Report creates the feedback mechanism in the iterative adaptive management cycle. Required by legislation every 5 years, the first such report has just been submitted to the Australian Parliament (1) and draws extensively on much of the monitoring presented here, as well as a wide range of other, nonzoning monitoring and research. The report includes assessments of biodiversity, ecosystem health, factors affecting the Marine Park including commercial and noncommercial uses, existing protection and management, ecosystem resilience, risk analyses, and the outlook for the ecosystem. As such it provides a clear landscape for policy outcomes, although the supporting legislation requires that it stop short of specific policy recommendations.

The conclusions of the report relevant to spatial management include identification of the positive outcomes and limitations of the 2004 Zoning Plan for biodiversity protection, and its potentially critical contribution to ecosystem resilience in the face of climate change. However, it also states that important risks to the ecosystem remain from the targeting of predators (sharks), the death of incidentally caught species of conservation concern, and illegal fishing and poaching.

The recognition of potential illegal fishing and poaching stems directly from the studies of fish and shark abundances in no-entry and no-take zones reviewed in this paper (*SI Sections 2 and 6*; refs. 11, 12) and from the concerns of Aboriginal and Torres Strait Islander traditional owners about illegal hunting of dugongs and green turtles, given the critical role these large herbivores play in the ecosystem. Robust government action to address this problem would provide an especially clear and direct example of adaptive management response to scientific information.

The Objectives and Process of Zoning the GBR: The Representative Areas Program. The 2004 Zoning Plan built on more than 20 years of zoning development on the GBR (Table S2). A series of zoning plans were implemented in different regions between 1981 and 1992, with several sections zoned twice during that period (the Far Northern section was rezoned in 2002). The initiation of the 2004 Zoning Plan stemmed from assessment that the extent of protection provided for many bioregions was inadequate and even minimal (13, 14). This realization arose from ongoing improvements in scientific knowledge of biodiversity patterns and distribution in the GBR, providing a key illustration of passive adaptive management responses to review of emerging information (9, 15).

The primary objectives of the 2004 Zoning Plan, and the representative areas program that developed the plan, were to maintain biological diversity at the ecosystem, habitat, species, population, and genetic levels (13, 16). Related objectives included maintaining ecological processes and systems, allowing species to evolve and function undisturbed, providing an ecological safety margin against human-induced disasters, and establishing a solid ecological base from which threatened species or habitats can recover or repair themselves (13). The broader objectives of GBR zoning, as defined in legislation, include overall conservation, balancing protection and reasonable use, regulating exploitative use, provision of areas reserved for appreciation and enjoyment, and preservation of areas undisturbed by humans (13).

These objectives are not just aimed at conserving biodiversity or ecological processes within highly protected areas but also at protecting the integrity of the whole ecosystem, by means of increased proportions of protected areas. Thus, assessments of the effectiveness of zoning need to consider outcomes across all zones, as well as within more protected zones.

The process of developing the 2004 Zoning Plan has been documented in detail elsewhere (13–15). The process involved synthesis of scientific input and public opinion, incorporating available biological, physical, and use data, the development of explicit and transparent biophysical and social operating principles, the use of software to develop candidate zoning plans, and the incorporation of community preferences (including Indigenous groups) into a final zoning plan. Although protection of ecological processes was an explicit objective, their incorporation was largely indirect, based on patterns of species distributions or physical data, rather than explicit. New approaches are being developed to explicitly include ecological processes in conservation planning (17).

Assessing the Effects of Spatial Zoning in the Great Barrier Reef: Monitoring Objectives, Design, and Caveats. Just as management of the GBRMP involves a wide range of integrated approaches, GBR monitoring also has diverse purposes, aspects, and approaches, from assessing the overall condition of the reefs to evaluating biological and socioeconomic impacts of specific management actions. This paper focuses on the effects of zoning, but those results must be seen in the context of broader management and monitoring initiatives and strategies, especially catchment and GBR water quality monitoring (www.gbrmpa.gov.au/corp_site/key_issues/water_quality/marine_monitoring).

The primary purpose of zoning monitoring on the GBR is to assess the effects and effectiveness of zoning in achieving the goal of protecting biodiversity. However, within that goal, there are multiple objectives and approaches, ranging from direct monitoring of biological outcomes (effects on fish, corals), to simple retrospective, GIS-based accounting to assess effectiveness in achieving objectives such as representation of bioregions or connectivity. Naturally, limited funding constrains the scope and capacity of monitoring, whether ecological, social, or economic, especially given the complexity and size of the GBR ecological and social systems. Some aspects are more amenable to direct measurement than others.

A primary focus of monitoring GBR zoning has been direct comparisons of biodiversity in open (fished) and protected (no-take or no-entry) zones, as this approach is most likely to provide unambiguous results and statistical power. Further, the principal use modified by GBR zoning is fishing, so, for strategic reasons, monitoring has largely focused on abundance of target fish species, as the primary direct impact of that use on the ecosystem and food webs. However, it is important to place such results in the broader context of effects on biodiversity generally, and on patterns across the entire range of zones, because many ecological effects of zoning will not be limited to the protected zones, but diffused across zones by ecological connections (e.g., effects on highly mobile species; effects on larval dispersal). That is, many ecological benefits of the zoning simply may not be feasible to document as robust, statistical comparisons, such as contrasts between fished and no-take reefs.

In other cases, such as deepwater shoals, comparisons between no-take and open-zoned shoals are possible, but inevitably difficult and confounded, for several reasons. These habitats, little known to scientists, were identified largely by fishers, as part of the community input to the 2004 zoning process and were usually identified as preferred locations to remain open to fishing. As a consequence, many of the sites that remained open to fishers were chosen because they had more abundant fish, confounding any comparisons between zones (this was less so in the southern GBR). This problem is exacerbated by the lack of genuinely comparable habitats in no-take zones (an intrinsic problem with incorporating stakeholder preferences into reserve site selection) and the lack of suitable replicate sites in either fished or no-take zones, especially as the shoals are extremely variable in structure. Further, investigating these shoals has required initial basic description and mapping of the habitats (although this is itself of considerable value), and the development of new survey approaches (18). Shoals are generally too deep for standard, scuba-based surveys and catch-based surveys within no-take zones are not deemed feasible, in terms of political sensitivities and community perceptions of scientists fishing where others are not allowed, despite the significant benefits for fisheries science. Thus available information is based on the use of baited, remote underwater video surveys, an approach which also has limitations (18).

Socioeconomic effects in particular are not generally amenable to simple comparisons between zones. Assessment therefore hinges on analyses of temporal changes after zoning implementation, which are inevitably confounded by numerous other factors, such as other changes to fisheries management (19) or broader economic drivers such as fuel prices.

Direct comparisons of fished and no-take zones on the GBR have included comparisons not only of the effects of the 2004 Zoning Plan, but also of zones implemented before 2004. Comparisons using earlier zones are often limited by the relatively few no-take reefs, but have the advantage of longer periods since implementation, thereby allowing more time for the development of ecological consequences of protection (*SI Section 4*).

Development and design of monitoring for the 2004 Zoning Plan involved a comprehensive, multiagency workshop of reef managers and scientists, from which arose a high-level steering panel and a technical panel of expert scientists from management agencies, universities, and state and national Australian government research agencies. The technical panel considered aspects such as scientific and management needs, scientific significance, geographic spread (Fig. S1), feasibility, and funding constraints. Extensive statistical power analyses using existing information indicated that the most powerful monitoring design incorporated paired open and no-take reefs. Reef selection also prioritized inclusion of any reefs for which fish or benthos data were available before implementation of the zoning plan, because inclusion of before–after comparisons markedly enhances the power of the interpretation of results. An important outcome of the deliberations of this panel was the adaptive modification of existing broad-scale long-term reef monitoring by the Australian Institute of Marine Science. This change involved reduction from annual to biannual monitoring of existing reefs and addition of monitoring of reef pairs chosen for zoning monitoring in alternate years. The final zoning monitoring plan, which includes other fish and benthic species, as well as target fish, was then incorporated into funding programs, including the Australian Government Marine and Tropical Sciences Research Facility and Australian Research Council Centre of Excellence for Coral Reef Studies.

Community Engagement and Participation in Zoning Monitoring on the GBR. Community participation in monitoring programs can have dramatic value in enhancing uptake of scientific monitoring and management initiatives. Since implementation of the 2004 Zoning Plan, there has been increasing interest in developing community-based monitoring programs under an inclusive model that facilitates collaboration between the governments, external organizations, and local communities. In 2004, the community-based Capricorn Reef monitoring program, CapReef, was initiated by recreational fishers from the Capricorn Coast of Queensland, with seed funding from the GBRMPA, with the intention of more closely engaging community-held knowledge about local fishery resources with fisheries and other management initiatives (20). CapReef operates in collaboration with universities, state and national government natural resource management agencies, and the recreational fishing community to collect information such as recreational catch and effort; relative fish abundance; size structure of fish populations; fish spawning times and locations; expenditure on recreational fishing; and impacts of fisheries and Marine Park policy changes on fish populations and recreational fishers. CapReef also provides extensive support to scientific investigations (particularly larval dispersal studies: *SI Section 3*) undertaken by universities and natural resource management agencies (20, 21).

Surveys relating recreational catch to management changes suggest that some catch rates declined temporarily in 2004 after the zoning and simultaneous increases in size limits, but largely recovered the following year as more legal-sized fish became available (21). Data collected by CapReef have also demonstrated that recreational fishing catch and effort in the Capricorn Coast region are substantial (on par with commercial catch) and largely unaffected by bag and possession limits (22). These limits were designed to limit recreational catch, yet these results suggest that total catch from recreational fishing can expand considerably through increased participation without catch limits having effect; this amounts to a significant potential vulnerability for the fishery. CapReef has devoted substantial effort to increasing knowledge of fisheries and ecosystems in the local community, by disseminating information in easily accessible formats, including information from both professional scientific research and CapReef activities. The success of CapReef at engaging and informing the local community has prompted other communities along the Great Barrier Reef coast (with the support of the GBRMPA) to initiate their own community-based recreational fisheries monitoring programs based on the CapReef model.

SI Section 2: Direct Biological and Ecological Effects of Pre-2004 Zoning on Coral Reef Fish

Surveys of fish abundance and size on no-take and fished reefs before the 2004 zoning found generally similar effects to those found after the 2004 zoning. A large-scale manipulative study on offshore reefs (the Effects of Line-Fishing Experiment in refs. 4, 19) combined both scuba-based visual surveys and catch-based, experimental line-fishing surveys of fished and open zones over 10 years, and included manipulative changes to zoning as part of the experimental design (one of the few experimental designs to require approval by a national parliament). That study found that no-take reefs generally, but not always, had more (Fig. S1 *B* and *C*), larger and older fish for the two main target species, the common coral trout (*Plectropomus leopardus*), and the redthroat emperor (*Lethrinus miniatus*), than did reefs open to fishing. However, these differences varied considerably between sampling years and regions. Zoning had little effect in the northern GBR (Lizard Island area), and the effects of zoning were generally smaller than found in the more recent surveys (Fig. S1 and c.f. Fig. 1). Mapstone et al. (4) suggested that the lack of benefit in the north was likely due to lower fishing pressure on fished reefs, rather than ineffective no-take zones. The extent of differences between fished and no-take reefs correlated directly with the amount of fishing effort and catch. Importantly, experimental manipulations of reef zoning status and fishing effort showed that the differences were attributable to the management strategy (zoning) rather than to a priori differences between reefs. Mapstone et al. (4) concluded that no-take zones, with sufficient compliance, have the potential to sustain high biomass of reproductively mature populations despite an active fishery on the GBR. Thus the zoning strategy is considered not only to have conservation benefits but also potential benefits to the fishery.

Simulation modeling based on this study explored potential effects on fishery and conservation objectives in some detail (4, 19). The results suggest for example, that spatial closures had strong benefits for stock conservation across the entire Marine Park (i.e., fished and unfished zones combined), and that current levels of fishing effort are likely to reduce fishery performance, regardless of the proportion of no-take zones. The study emphasized the importance of minimum size limits for target fish, and effort controls, to the sustainability of the fishery.

Similar effects were observed on inshore reefs of the central and southern GBR, where surveys found coral trout (*Plectropomus* spp.) and stripey seaperch (*Lutjanus carponotatus*) were generally less abundant and smaller on fished reefs than on no-take reefs implemented in 1987 (Fig. S2; refs. 23–25; Palm Islands, Whitsunday Islands and Keppel Islands). Biomasses of coral trout and stripey seaperch were respectively 3.9 and 2.6 times greater in the protected zones than fished zones at all three island groups (24). By sourcing earlier data, Williamson et al. (25) again were able to make rare before–after comparisons, comparing abundance and biomass for 3–4 years before (1983–1984), and 12–13 years after (1999–2000) the establishment of no-take reserves in 1987. Before protection, abundances were very similar (25). Density and biomass of coral trout in the reserve sites increased, by factors of 5.9 and 6.3 in the Palm Islands, and 4.0 and 6.2 in the Whitsunday Islands, but not in the fished sites, between 1983–1984 and 1999–2000. The extent of these differences subsequently decreased, but over the subsequent 7 years abundance in no-take reserves has generally been 2- to 3-fold higher than on fished reefs (Fig. S2). The lack of a priori differences provides strong evidence that these differences are due to the protection provided by the zoning, rather than preexisting differences between reefs. It also suggests that inshore reefs were substantially depleted in abundance of coral trout when zoned in 1987.

The interpretation of markedly higher counts of target fish (Fig. S3) and sharks (Fig. 2) in no-entry zones requires some caution, because they are necessarily based on very few no-entry reefs (2 each for refs. 11, 12) that are also relatively small. Several other factors may also confound these comparisons, including decreased shyness of fish on no-entry reefs (for visual counts), or a priori higher abundance of fish in reefs zoned as no entry. Sharks and redthroat emperors also move between reefs in different zones, although this should reduce, not inflate, differences between no-entry and no-take reefs. Based on ongoing fishery catches of sharks, Heupel et al. (26) consider that Robbins et al. (11) overestimated the level of absolute declines in shark populations. Nonetheless, assuming at least some of the differences between no-entry and no-take reefs reflect zoning status, then the simplest interpretation is that abundances in no-entry zones most closely indicate true baseline abundances, and that lower abundance in no-take zones is due to infringement, in part at least. Even relatively moderate infringement may significantly affect reserve effectiveness (27). Although other interpretations are possible, from the management perspective, even suggestive evidence of widespread depletion and of infringement in no-take zones warrants very serious consideration.

With respect to shark populations in fished and no-take reefs, Robbins et al. (11) found differences between no-take and fished zones to be relatively small and not statistically significant (using visual census), whereas Heupel et al. (26) demonstrated biologically and statistically significantly higher catch rates in no-take zones. However, as Heupel et al. (26) argued, the relative abundances in these two zones are fairly similar in all three studies (fished/no-take ~30–75%), with differences in statistical significance probably reflecting sampling power (26).

SI Section 3: Larval Connectivity Within the No-Take Network and Export from No-Take to Fished Reefs

Determining the fate of larvae produced by adult populations in marine reserves has proven challenging. Preliminary studies on the GBR have provided strong empirical evidence that a significant proportion of reef fish recruitment includes individuals returning to natal reefs (28, 29). High levels of self-recruitment have also been indicated in a range of other studies in other regions (e.g., refs. 30–34), suggesting that populations in marine reserves are at least partially self-sustaining between generations. However, self-recruitment never approaches 100% on scales at which reserves are typically implemented, indicating that high levels of larval exchange also occur.

Few techniques for investigating larval transport between reefs have been applied on the scale of no-take MPA networks (35). However, recent larval tagging and genetic parentage studies suggest that larval dispersal can connect no-take reefs 20–30 km apart (36, 37). These techniques are currently being applied to measure larval export from no-take areas of some larger recreationally and commercially important fishes, and to validate biophysical dispersal models being developed for the GBR. These models incorporate the specific patterns of GBR reef bathymetry and water movements, as well as larval behavior.

The larger size and abundance of targeted fish in no-take zones has the potential to provide a major proportion of ecosystem-wide larval supply, because it is well-documented that larger fish often have disproportionately more reproductive output (38, 39). Larger fish may also produce more robust larvae (e.g., ref. 40). Female common coral trout above the size and age at recruitment to the fishery were significantly more abundant, larger, and older on reefs closed to fishing in the GBR than those on reefs open to fishing, suggesting that no-take zones are an effective insurance policy against fecundity limitation in these protogynous hermaphrodites (41).

Estimates of reproductive output for stripey seaperch on the inshore GBR found that batch fecundity per unit area increased markedly with fish size (in a power relationship), and was, on average 2.5 times, and as much as 4 times higher in no-take than fished zones (39). Although this result was only slightly larger than the underlying differences in biomass (average 2.3-fold), it is probably a conservative estimate. Egg size was also generally larger for larger fish, potentially generating greater larval survival, and larger fish may also spawn more often. Importantly, even with such relatively small increases in batch fecundity, scaling batch fecundity per unit area by approximate areas of no-take and fished reefs, would suggest that total reproductive output across all zones is likely to be higher by nearly 50% than if all reefs were open to fishing. Assuming larvae disperse evenly across zones, this would suggest that larval supply to fished zones is likely to be at least similar to that if all reefs were open to fishing. (Calculations: With relative batch fecundity per unit area for fished and no-take zones of 1 and 2.5, respectively, scaling by proportion of area in no-take and fished (0.31 and 0.69) gives total output of ~1. 5. Scaling this in turn by area, suggests that fished reefs would receive reproductive output of 1, the same as that expected with all reefs open to fishing). Research is currently underway to provide similar estimates for coral trout.

Dispersal Distance Distributions: Methods. Analysis of nearest neighbor distances for GBR reefs indicate that the reserve network has maintained dispersal distances between reefs (Fig. S4). This analysis differs from previous work (42) in comparing distances between reefs rather than between reserves (many reserve zones contain multiple reefs, skewing the distribution in the present context). Distances are measured from the centroid of one reef to the edge of the nearest neighboring reef (GIS data courtesy GBRMPA; reef boundaries delineated based on visual assessment of satellite imagery). Centroids estimated using ArcMap 9.2 (43) "shapes to centroids" function and distance measured using ArcView 3.3 (44) and Nearest Feature (45). The analysis included no-entry reefs within no-take reefs and fished reefs included zones with limited or unrestricted line fishing. Note that fished to no-take reef distances are necessarily more dispersed than distances between no-take reefs because fished and no-take reefs cannot occur within the same individual zone (imposing a minimum distance) whereas distances between no-take reefs include many pairs of reefs within the same individual zone.

SI Section 4: Zoning Effects on Crown-of-Thorns Starfish, Corals, and Reef Food Webs

Crown-of-thorns starfish outbreaks on the GBR occur as recurrent "waves," which migrate from north to south over more than a decade. The analysis in Sweatman (46) was limited to reefs in regions with outbreaks present in a particular year, to allow for differences in likelihood of outbreaks between regions and years. The analysis was also limited to reefs with a minimum of 5 years zoned as no-take, to allow ecological responses to fully develop (this precludes analysis of post-2004 effects). As the relevant zoning plans for the GBR Marine Park were fully implemented by 1989 and superseded by the new zoning plan in July 2004, this limited the analysis to data from 1994 to 2004, meaning that data were available for only a relatively small number of no-take reefs (which were much fewer before 2004) (46), introducing some uncertainty in the statistical generality of the results. Nonetheless, the difference is marked and warrants serious consideration, given the significance to reef status. It will be interesting to see whether a similar or clearer pattern emerges from the more robust proportion of new no-take zones.

Zoning Effects on Coral Cover After Crown-of-Thorns Starfish Outbreaks: Methods. If zoning effects on crown-of-thorns starfish (46) flow on to affect coral abundance, then this effect should be most evident immediately after a wave of starfish outbreaks has passed through a region, when coral recovery and any confounding effects of other disturbances should be minimal. This analysis therefore needs to take account of the episodic nature of starfish outbreaks. In the central GBR, outbreaks occur in waves that pass from north to south; in the Swains sector in the southern GBR, outbreaks have been present consistently for some time (46). The effect should also be most evident on midshelf reefs, where most outbreaks occur, and on reefs that have been protected for sufficient duration for ecological effects to develop.

This analysis is therefore based on midshelf reefs selected to have been zoned for at least 5 years (i.e., between mid 1994 and mid 2004), and within regions recently affected by starfish outbreaks. In the early 1990s, the third recorded wave of starfish outbreaks was detected in the Cooktown-Lizard Island sector in the north central GBR. Over the following decade the wave moved south. No further outbreaks were recorded in the Cooktown-Lizard Island sector after mid 2000. No outbreaks were recorded in the Cairns or Innisfail sectors after mid 2003. Starfish outbreaks were recorded in the Townsville, Cape Upstart, Whitsunday, Pompey, and Swains sectors shortly before the implementation of the second zoning plan in 2004.

Coral cover and crown-of-thorns starfish outbreak status were based on manta tow data (47) from annual surveys covering ∼10 degrees of latitude on the GBR, from the Australian Institute of Marine Science GBR Long-Term Monitoring Program. Between 40 and 137 reefs were surveyed in each year from mid 1994 to mid 2004. Reefs north of 14°S were not included in the analysis. Under the first zoning plan, only 4.5% of the GBR Marine Park was zoned as no-take, limiting the number of no-take reefs available for this analysis. To maximize this number, the analysis included any estimates of coral cover from 1 year before to 1 year after the last survey year in which starfish were recorded in a sector. For example, for the Cairns sector, analysis includes estimates of coral cover from any midshelf reefs surveyed in the period between mid 2001 and mid 2004. For reefs in the five sectors further south, the coral cover in 2004 (±1 year) was used. If a reef was surveyed more than once in that interval, the highest coral cover value was used.

These criteria yielded appropriate reef-wide estimates of coral cover for 12 no-take reefs and 76 reefs where fishing was permitted. Mean coral cover values for these groups were compared with a one-tailed t test (based on the prediction that no-take reefs have a lower frequency of starfish outbreaks and hence more coral cover). Homogeneity of variances was tested using the Brown-Forsythe test (48). Variances were not significantly different, although marginally so ($P = 0.06$), due to the large difference in number of reefs and the high variability in coral cover. However, as heterogeneity of variances with unequal sample sizes (as here) cause decreased likelihood of type I errors (49), the t test is likely to be conservative. On this basis, coral cover was significantly higher on no-take reefs in this comparison ($P = 0.0275$).

Effects of Zoning on Coral Abundance on Inshore Reefs. Williamson et al. (25) found live coral cover on inshore reefs before the 2004 zoning was significantly higher in protected no-take reserves than in fished zones (Palm and Whitsunday Islands, hard and soft coral combined) and Evans and Russ (24) found live hard coral cover was slightly higher in the protected zones of the Whitsunday and the Keppel Islands, but found the reverse pattern in the Palm Islands. Graham et al. (23) found no significant difference for the same reefs as Williamson et al. (25). As indicated in the main text, detailed interpretation of these patterns will require much more research, but that research should be much more feasible under the new zoning plan, due to the much greater replication of no-take reefs.

Effects of Zoning on Food Webs and Prey Fish. Zoning appears to have some important impacts on food web structure on the GBR coral reefs, but those impacts are not generally consistent with simplistic, top-down effects of removal of large numbers of predatory target fish. Surveys of potential prey fish on inshore reefs show highly variable patterns in space and time, but no major changes in relative abundance consistent with predator control due to establishment of no-take zones (Fig. S5*A*; also ref. 50 for a range of other families). Similar surveys of offshore reefs for two groups of potential prey fish since the 2004 zoning do not show any consistent patterns concomitant with the increases in abundance of coral trout (Fig. S5*B*); again, the results are variable with space and time.

Surveys of damselfishes (Pomacentridae) and small parrotfishes (Scaridae) on offshore reefs before the 2004 zoning found some differences between open and closed reefs, but that patterns varied regionally, through time and with species or species group. In some situations the patterns in abundance suggested that removal of a key predator (coral trout) might have led to increases in some prey on fished reefs, but the evidence was neither uniform nor convincing (4). Finally, a series of studies of inshore reefs of the Palm Islands, Whitsunday, and Keppel Islands, also found inconsistent patterns before the 2004 zoning. Evans and Russ (24) and Williamson et al. (25) found the density and biomass of nontarget fish species from the families Labridae, Siganidae, and Chaetodontidae were very similar in no-take and fished zones (24, 25). However, Graham et al. (23) in the Palm and Whitsunday Islands around the same period found that eight out of the nine prey species (based on gut samples from coral trout) surveyed had a higher density within fished zones than protected zones, six significantly so. They found the density of all prey fish was twice that in the fished than the protected zone and identified a significant negative correlation ($r = 0.46$) between coral trout biomass and summed prey fish biomass, suggesting that predation may be an important structuring process in this system.

SI Section 5: Zoning and Nonreef Habitats, Dugong and Marine Turtles

Seabed Biodiversity and Effects of Trawling. The increase in knowledge of seabed biodiversity distributions (51), provided a basis for assessing the extent of protection provided by the 2004 zoning, and the extent to which that protection had changed compared to previous zoning (52). Assessments were based on the proportion of biodiversity with more than 20% of biomass or area in zones that do not allow trawling, with biodiversity considered at four levels: (*i*) Species: the ≈850 species recorded in the surveys; (*ii*) species groups: 38 groups of species, based on correlated distributions in the surveys; (*iii*) species assemblages: 16 assemblages of relatively homogeneous species composition, with distinct differences from other assemblages; and (*iv*) biological seabed habitat types: nine broad habitat types based on similarity of species composition. Of about 850 seabed species, all were predicted to have >20% of predicted biomass in no-trawl zones after the 2004 rezoning, whereas 165 species had <20% before the rezoning; on average, biomass of each species protected increased by 30%. Of 38 groups of species, again all were predicted to have >20% predicted biomass in protected zones, whereas before rezoning 10 groups were not; average increase in protection was 27%. Of 16 species assemblages, all were predicted to have more than 20% of area in protected zones after the rezoning, whereas previously 7 were not; the average increase in protection was 36%. Finally, of nine broad seabed biological habitat types, all had 20% or more of predicted area in protected zones, compared to only five before the zoning, and the average increase in protection was 31% (52).

The effects of trawling in the GBR have been studied directly (53, 54), allowing zoning effects on trawling impacts to be modeled and analyzed (54). Trawling in the GBR is principally for prawns, is potentially directly destructive to seabed habitats, and accounts for the majority of discarded catch in the GBR fisheries (1). Trawling is limited to General Use zones, ≈33% of the area of the Marine Park (post 2004). It is neither permitted nor practical in coral reef areas and is managed by several nonspatial approaches as well as zoning. Available evidence from satellite vessel monitoring systems suggests that there is relatively good compliance with zoning, and that in fact trawling currently occurs only within a much more limited area (<15% trawled once or more per year; ≈5% trawled more than once), and avoids areas of hard seabed where damage to habitats and species is likely to be greatest (55). Pitcher et al. (54) suggested that only a small proportion of species appear likely to have been significantly affected by trawling (<5% negatively, <1% by ≈ −30%; <2% positively, only 0.2% by ≥ +50%), and only 3 of 850 bycatch species appear to have been incidentally depleted beyond mean sustainable yield. There was no evidence of species assemblages that might indicate trawl-generated ecosystem state changes. The 2004 zoning prevented future expansion of trawling, but had minimal impact on existing activity. However, other management changes (primarily a major license buyback in 2001 and penalties on transfers) reduced effort and were predicted to have arrested and reversed the previous trends for bottom habitat damage for all species analyzed (54).

Seagrass beds in particular are not considered particularly vulnerable to trawling. Only ≈14% of all deepwater seagrass habitats were trawled more than once in 2005, in part because trawlers avoid seagrass beds to limit net clogging. Available evidence suggests that, on the GBR, trawled seagrasses suffer surprisingly little damage, so that cumulative impacts may be limited (55).

Concerns do remain about incidental catch in trawls of species of conservation concern, especially sea snakes and sea turtles. Bycatch reduction devices are being successfully used to reduce the take of turtles (56) and show potential for excluding a high proportion of sea snakes from trawls (57). Thus, although trawling has had impacts, available evidence suggests they are likely to be moderate in comparison with other impacts on the GBR ecosystem, and respond to integration of spatial zoning and other management approaches (e.g., gear restrictions).

On deepwater shoals in the southern GBR, most species of target fish and sharks were more abundant on no-take shoals than on fished shoals (Fig. S6).

Further Background on Dugong Status and Management. Dugongs on the Great Barrier Reef are at serious risk, with populations in the human-populated coast (south of Cooktown) estimated to be only a small fraction of pre-European levels (58). Listed as vulnerable to extinction (59), GBR populations are globally significant to this species, an explicit reason for World Heritage listing of the GBR (60). Dugongs are, or were, the major large herbivore in the GBR ecosystem, and of high cultural value to the Indigenous peoples of the region. Native title holders are allowed to hunt dugongs, even within some no-take zones (61).

The risk assessment approach for dugong in Grech and Marsh (62) also enabled them to compare and rank risks, and hence identify the most severe risks and sites that require further management attention. The most effective reductions in risk would require four approaches to complement dugong protection areas and zoning: continuation of the moratorium by Indigenous groups on hunting, banning commercial gill netting along the populated coast, addressing the hazard of vessel strike, and reductions in terrestrial runoff from coastal catchments.

Case Study of Management Responses for Loggerhead Turtles. Nesting populations of loggerhead turtles (*Caretta caretta)* in the southern GBR appear to have benefited from iterative management responses to survey information. Populations had been declining for some time, due to combined effects of nest predation by feral foxes and drowning, apparently due to exposure to prawn trawling. Feral animal control programs have reduced egg loss due to nest predation by foxes from 90% in late 1970s–early 1980s to less than 5% egg loss since the late 1980s. Declaration of Woongarra Marine Park in 1991 precluded prawn-trawling in areas off nesting beaches, where females rest between clutches of eggs, and mandatory use of turtle excluder devices in trawl fishing has been required since 2001. This combination of spatial and other measures appears to have reversed the decline in loggerhead nesting, although concerns remain for the overall population (56).

SI Section 6: Compliance, Enforcement, and Management of Zoning

The ecological effectiveness of marine reserve networks depends critically on effective compliance and enforcement. Even a small amount of poaching can have major ecological consequences, because sharks and large fish are known to be the first to be reduced on fished reefs (27). Monitoring of recorded infringements provides critical information to support and direct enforcement (Fig. S7; ref. 63), but is often strongly confounded as indicators of actual compliance. Differences in surveillance and enforcement effort, community attitudes and awareness, and other factors mean that patterns in reporting rates may vary independently of patterns in actual infringement rates. Patterns in reporting rates may also vary differently from convictions, depending on judicial attitudes, quality of evidence, etc. Indeed, compliance, enforcement (prevention, conviction, and penalties), social behavior, and ecology (fish stocks) all interact in complex, often time-lagged ways. For this reason, compliance data alone are poor indicators of agency effectiveness and should be integrated with data on management outcomes, such as the abundance of target species. Data from no-entry zones are particularly useful indicators, because it is much simpler to effectively detect and prove illegal entry to an area than to prove illegal fishing within that area. Effective enforcement of no-take zones requires proof that fishing took place within the zone; the scale and remoteness of enforcement requirements for the GBR makes this very difficult (e.g., aerial surveillance may indicate but not prove illegal fishing).

On the GBR, direct monitoring of zoning compliance includes satellite vessel monitoring systems (VMS) for trawlers and aerial and vessel-based surveillance. Other information sources include incident reports and intelligence from fishers, tourism operators, and other park users, and the presence of discarded fishing line on reefs, or trawl tracks on the seafloor. Critically, investment in compliance includes significant investment in community education and awareness of rules, penalties, and the environmental consequences, to facilitate voluntary compliance. Anecdotal comments to compliance officers suggest an emerging ethic among fishers that illegal fishing is unfair, effectively cheating the rest of the sector.

There has only been one independent study of surveillance and illegal fishing on the GBR (63). Monitoring around two readily accessible islands on the central, inshore GBR Marine Park in 2000/2001 found that vessel-based surveillance was limited and significant but low levels of illegal recreational fishing were recorded within no-take zones. Levels decreased with increasing surveillance effort.

Detailed analysis and interpretation of the overall trends in infringements across the entire GBR Marine Park (Fig. S7) is beyond the scope of the present paper and is necessarily based on subjective interpretations by compliance officers, given a lack of relevant social monitoring. However, several illustrative points warrant mention. Increased rates of recorded infringements (e.g., 1999–2001 and 2004–2007) may reflect increases in enforcement effectiveness, due to increased investment, combined with improved strategic planning, interagency cooperation and partnerships, rather than increased rates of illegal activities. Such investment usually generates increased awareness and deterrence, generating time-lagged declines in actual infringement rates (2003/2004). Increases after 2004 (Fig. S7) also reflect the much larger area of no-take areas, increasing the likelihood of both negligent and deliberate offenses. By 2006, illegal fishing in no-take zones may have also been increasing in response to awareness of the increased fish abundances in those zones. Anecdotal reports suggest that a small minority of fishers consider the benefits of high catch rates in no-take zones makes occasional fines cost effective, depending on the level of fine. Part of the decline in recorded infringements in 2008/2009 may be due to increasingly sophisticated methods to avoid detection, an issue now being addressed. Foreign fishing vessels appeared briefly in the far north of the Marine Park in 2005/2006 targeting shark fin, as part of a widespread pattern across northern Australia. This, along with immigration incidents, generated a major national-level effort in border surveillance, largely preventing further incidents.

In concert with offense rates in the hundreds every year since 2004, the markedly higher abundance of target fish in no-entry reefs, compared to no-take zones, suggests many no-take zones on the GBR have had very real compliance issues (Fig. 2 and Figs. S3 and S7 recreational and commercial line fishing; refs. 11, 12). Compliance efforts were significantly increased after 2004, so it is possible that the patterns reflect persistent effects of previous infringements, rather than ongoing noncompliance. However, given the potential consequences of even moderate poaching, from the perspective of a management agency, even incidental evidence warrants serious attention.

SI Section 7: Social Effects of Zoning

There is only limited information currently available on the social effects of the 2004 zoning, although surveys indicate that, in 2007, no-take zones were supported by 77% of people in Queensland coastal communities, and 79% of southern Australian capital cities (64). Although these figures were down from 89% and 94% in 2006, the wording of the relevant question changed between years. There is no specific information on the effects of the zoning on Indigenous stakeholders. Anecdotal evidence suggests opinions range from strong support and engagement with the conservation benefits to opposition to perceived restrictions on traditional fishing and hunting rights. In a few isolated cases, opportunities for future development of commercial fishing enterprises in remote northern Indigenous communities have been limited by the presence of extensive no-take zones in the region.

The effects of the 2004 zoning on fishing communities are being explored in some detail through interviews and surveys with recreational fishers (n = 800; ref. 65), commercial fishers (n = 62), and charter fishing business operators (n = 41; survey methods and analyses for commercial and charter sectors are as described in ref. 65 for the recreational sector). Results available so far indicate that recognition of the importance of protecting the Great Barrier Reef is widespread among fishers, with a majority of recreational (77%), commercial (65%), and charter (85%) fishers agreeing that protecting the diversity of marine life is the most important goal of managing the Great Barrier Reef. However, there were large differences between the three sectors in support of the 2004 Zoning Plan and perceptions about the costs and benefits of the zoning changes. Three years after implementation, a majority of recreational fishers (59%) reported being supportive or strongly supportive of the plan, whereas only 18% of charter fishers and 7% of commercial fishers reported similar levels of support. The surveys also indicate that support for the plan among recreational and charter fishers has increased by about 10 percentage points in the 3 years after implementation of the plan, whereas support from the commercial sector has decreased by approximately the same amount over the same period.

Lack of support from commercial and charter fishers appears to be associated with strong beliefs that: (*i*) major rezoning of the GBR was not necessary; (*ii*) the zoning changes have had negative impacts on fishing businesses (particularly in terms of access to productive fishing areas, catch rates, and overall profitability); (*iii*) the zoning changes have not reduced the impact of fishing on the Great Barrier Reef; and (*iv*) fishers were not adequately consulted about the zoning changes. In contrast, most recreational fishers had positive beliefs about the necessity of the plan and its conservation value, and only a minority of recreational fishers reported that the zoning changes had an overall negative impact on their fishing activity. Thus levels of support were significantly higher among the recreational fishing community. However, like commercial and charter fishers, the majority of recreational fishers did not believe they were adequately consulted about the zoning changes; those who believed consultation was adequate were significantly more likely to express support for the plan (65). It is noteworthy that these concerns persist, given: (*i*) the considerable structural adjustment package, (*ii*) that zoning was not in itself intended to manage fisheries, (*iii*) that spatial closures are thought to have benefited fish stocks across the Marine Park (19), and (*iv*) that the public consultation was both very extensive (>31,000 submissions) and meticulous in analysis and application (14, 15). There is an apparent mismatch between perceptions of consultation among fishers and intensions and investment in the process.

Recreational vessel registrations in GBR coastal communities, a major aspect of the economic value of recreational fishing, show no indication of changes due to rezoning in 2004 (Fig. S8).

Redistribution of recreational fishing effort has been explored in two studies. Community monitoring data (from the CapReef program, *SI Section 1*) shows that for two recreational fishing clubs in the southern GBR, only one of nine preferred fishing sites was lost as a result of the 2004 zoning. That site accounting for 7% of fishing trips since 1996. Although catch rates declined in 2004, this coincided with an increase in the minimum legal size of fish, and catch rates recovered significantly the following year, apparently as more fish reached legal size (21).

Spatial redistribution of recreational fishing effort after the 2004 Zoning Plan has been documented using interviews with recreational fishers in the central and southern GBR. Interviews indicate that recreational fishers who lost one or more preferred fishing locations to the 2004 Zoning Plan generally compensated by shifting their fishing effort to other areas they knew to be good fishing locations, and by finding new areas that they had not exploited previously. On average, fishers' substitute locations were 27% closer to their boat ramp departure points compared with "lost" locations, resulting in a general shift in recreational fishing effort toward inshore areas. Potential consequences of these spatial changes include increased fishing pressure in the new locations, especially locations that received little exploitation previously, and reduced quality of recreational fishing experiences through increased crowding and lower catch rates. Similar surveys with commercial and charter fishers indicate that there has also been significant displacement of fishing effort by these sectors to remaining open areas (along with reduced effort due to structural adjustment); however, the patterns of displacement for commercial and charter fishers have not yet been determined. Research to estimate contributions to fished stocks by the no-take network (*SI Section 3*) should provide useful indications of the extent to which those contributions balance the displaced effort.

Even the limited social information available for the GBR zoning provides valuable insights for future management of the GBR and for implementation of reserve networks elsewhere. Fishers, especially recreational fishers, are concerned about conservation values and planning processes, as well as about direct effects on themselves. That concern can be used to generate support by enhancing awareness of the conservation value of reserves, by minimizing direct impacts on users where possible, and by ensuring that fishers *feel* engaged in the planning process.

Spatial Redistribution of Recreational Fishing Effort: Methods. Data used in this analysis were collected in conjunction with a state-wide recreational fishing survey conducted by the Fishing and Fisheries Research Centre at James Cook University. Face-to-face interviews with 132 respondents were opportunistically conducted at boat ramps and tackle shops in Townsville and Rockhampton from March 2006 to December 2007. Spatial changes in fishing locations due to rezoning were recorded on paper GBR zoning maps (scale 1:250,000) using the interview map-biography method (66, 67) and structured questions. A total of 690 current and 181 previous fishing locations were reported. Average interview length was ≈20 min and responses were validated by meetings of the CapReef program (*SI Section 1*). Maps were scanned, georectified, and entered into a geographic information system (GIS) for analyses (66, 68). Spatial analysis and mapping were conducted with ArcGIS ArcMapTM 9.2, using weighted sum and zonal statistics tools to measure and document spatial changes in fishing effort.

SI Section 8: Insights into the Science and Monitoring of Reserves

This review provides several useful insights into the challenges of monitoring marine reserves, in addition to the value of social and economic information discussed in the main text. Strategically designed monitoring projects, and well-integrated overall assessment programs are invaluable for effective adaptive management responses. In particular, simple contrasts between no-take and open areas may provide strong statistical results, but are dramatically enhanced by other comparisons, such as with no-entry reefs or other areas that benchmark compliance (11, 12). Inclusion of data from before reserve implementation is useful in unambiguously attributing causality and in demonstrating benefits of reserves, rather than losses in fished zones (25). Innovative analytical approaches are needed for ecosystem components that are not suited to simple fished/no-take comparisons, including where comparisons are confounded by a priori differences (e.g., shoals). Such situations are an unavoidable consequence of incorporating fisher's preferences into network design.

However, for many aspects of marine reserves, especially extensive networks that include little studied, nonreefal habitats, detailed or comprehensive monitoring will be impractical. Unambiguous demonstration of reserve benefits may not be feasible for those habitats, although in the absence of evidence to the contrary, it is reasonable to assume preventing damage to habitat and trophic structure will be beneficial. In such data-poor circumstances, risk assessments that integrate spatial distributions of threats and habitats can provide useful direction for management (as for dugong, ref. 62). Another important observation emerging from this review is the extent of relevant data that are not published or readily accessible. A full picture of the effects and effectiveness of zoning on the GBR has required extensive use of gray literature, previously unpublished data, and collation of separate data sources.

For monitoring to contribute to adaptive improvements in management, it should be directed to aspects with scope for practical management changes with genuine environmental consequences. For example, monitoring abundance of fish and sharks provides indications of important changes in ecological structure, changes that can be addressed through compliance and enforcement effort. Monitoring should not be directed simply at demonstrating agency effectiveness. Reciprocally, compliance and management effort should be directed to aspects where science indicates significant environmental impacts and risks.

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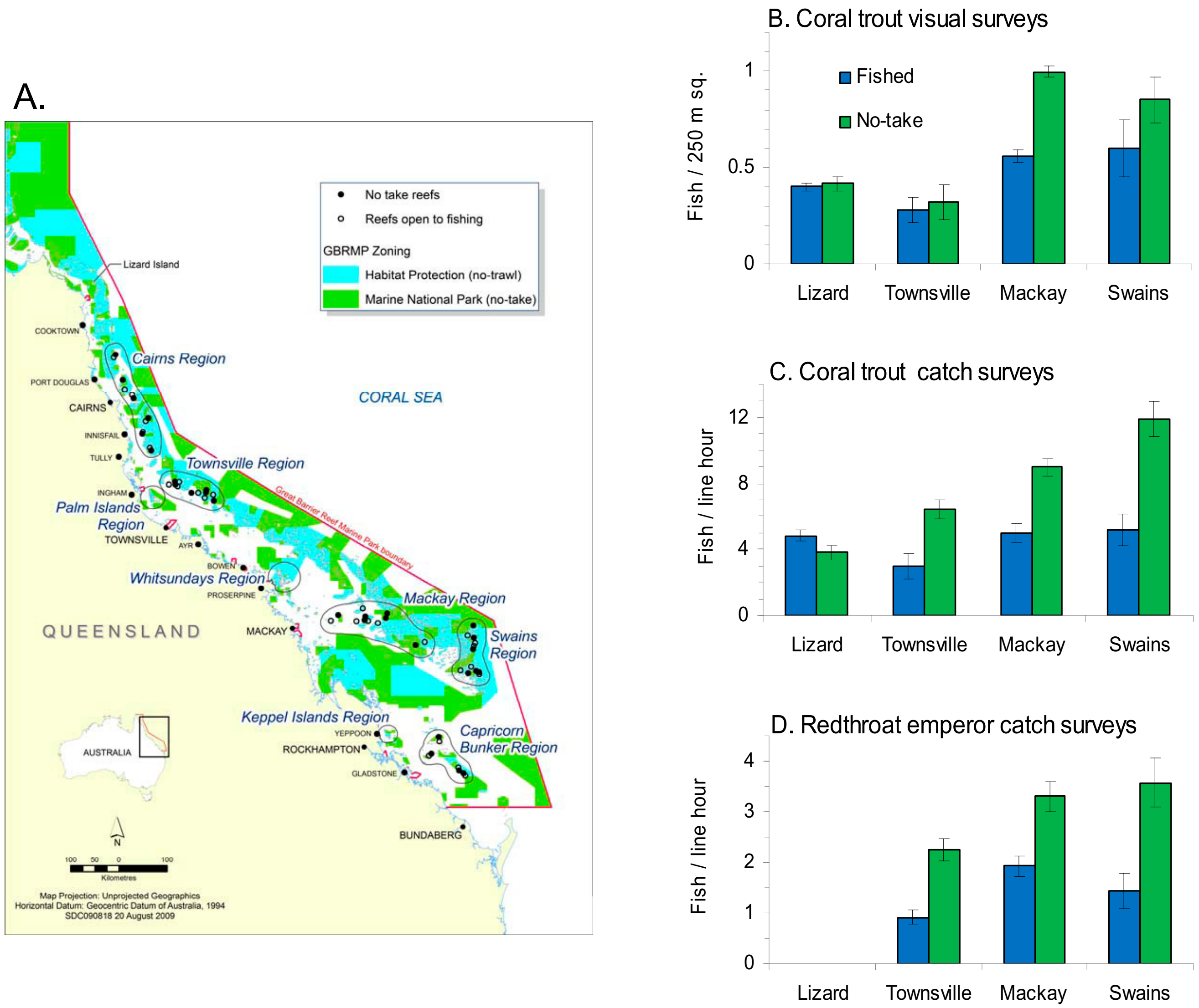

Fig. S1. (*A*) Map of the Great Barrier Reef Marine Park showing the location of study regions and study reefs for *B*–*D*. Abundance of target fish on fished and no-take reefs before the new zoning plan, showing variations between species, regions, and survey methods. Data, not previously published in this form, are from the Effects of Line-Fishing Experiment (4) and are means ±SEM from 1995 to 2000 for legal sized (>38 cm) fish. Note different vertical axis scale in *C* and *D*.

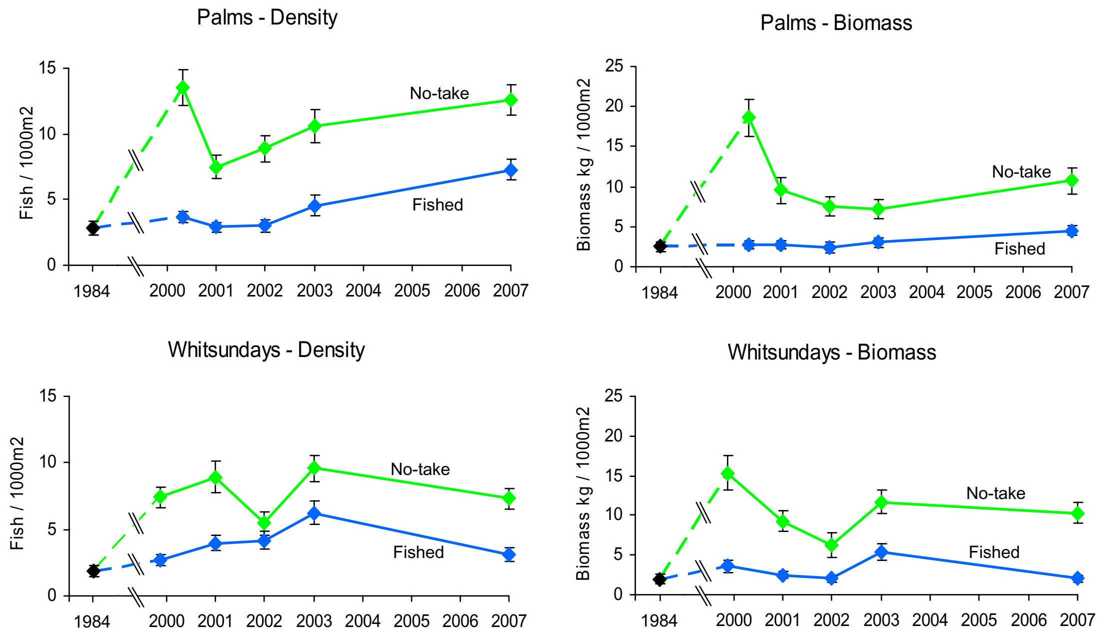

Fig. S2. Temporal dynamics in coral trout (*Plectropomus* spp.) in no-take and fished zones of the inshore Palm and Whitsunday Island groups, for zones implemented before 2004. Baseline data from 1984 were collected before the establishment of no-take zones in 1988. Data are mean (±SEM). Data previously unpublished except for 1984 and 1999/2000 redrawn from ref. 25, methods as for that paper.

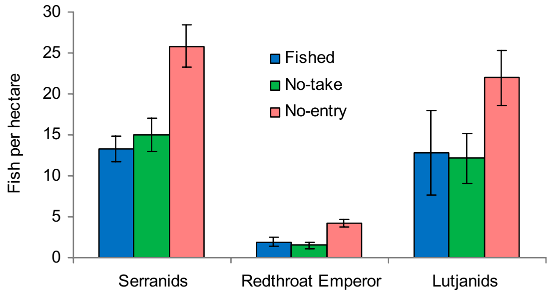

Fig. S3. Abundance of target fish in no-entry, no-take, and fished reefs in the central GBR. Serranids are predominantly coral trout; data, expanded from ref. 12, are means ±SEM, based on scuba-based, visual transects.

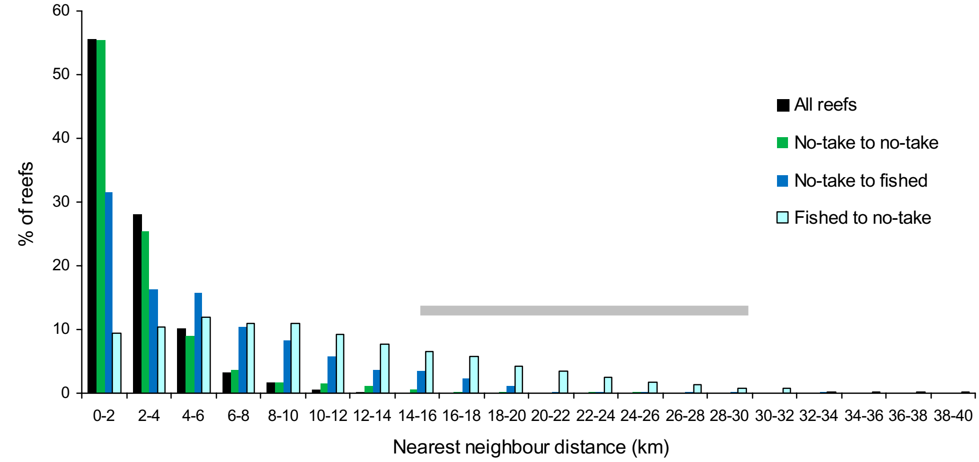

Fig. S4. Distance between neighboring reefs within the Great Barrier Reef Marine Park. Distances indicate, for each reef, the distance to the nearest reef that could contribute larvae to maintain populations on the first reef (graph truncated at 40 km). Recent studies recommend maximizing proportions of reefs within 15–30 km of potential source reefs (gray line; see text). Distance between nearest neighbor reefs for all GBR reefs (black bars; n = 3,788), indicates the natural distribution of distances. The distribution of nearest neighbor no-take reefs (green bars; n = 1,120) indicates the capacity of the network of no-take reefs to maintain larval connectivity in the absence of contributions from fished reefs (e.g., should fish stocks collapse). Distributions match closely for all reefs and the no-take reef network. The distances between each no-take reef and its nearest fished reef (dark blue bars; n = 1,120) indicate the potential for fished reefs to contribute larvae to the no-take network. Distances between each fished reef and its nearest no-take reef (pale blue bars; n = 2,681) indicate the potential for the no-take network to contribute larvae to populations on fished reefs. (N is larger for fished to nearest no-take reef because there are more fished reefs to measure from.)

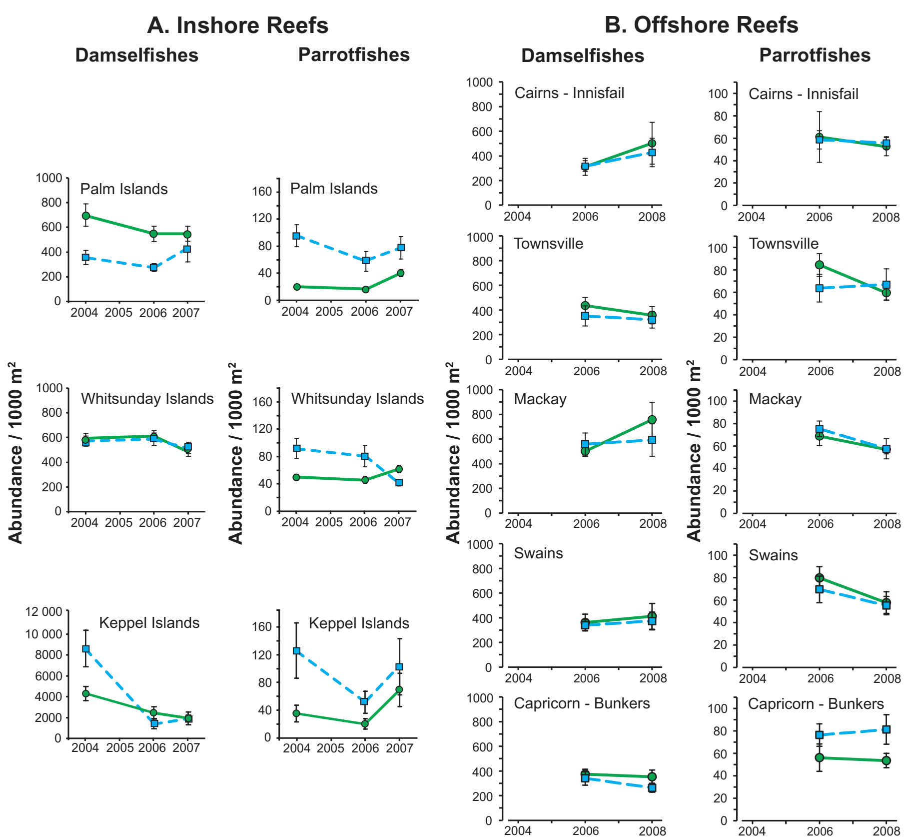

Fig. S5. Abundance of damelfishes and small parrotfishes on (A) inshore reefs and (B) offshore reefs of the GBR. Green lines are no-take zones; blue are fished reefs. Data, not previously published, are means ±SEM from scuba-based, visual transects of reefs zoned in 2004. Data for inshore reefs (A) include before data, collected immediately before implementation of the 2004 zoning. Note different vertical axis scales and different periods (dates) for A and B. Methods and analyses for A as for ref. 50 and B as for ref. 69.

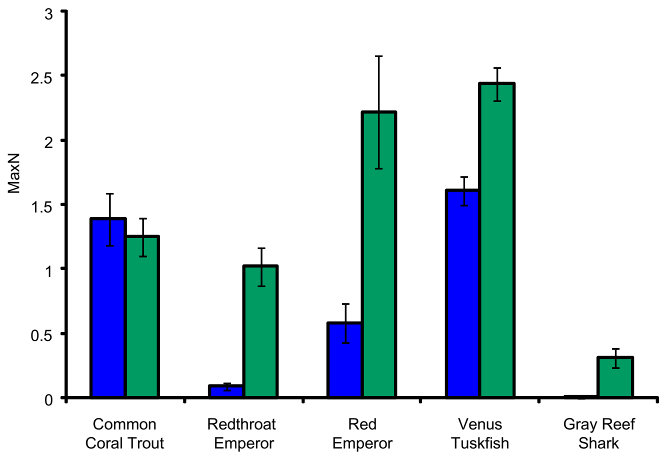

Fig. S6. Mean abundance of targeted fish and sharks on deepwater shoals in the southern GBR based on baited, remote, underwater video surveys. Data are mean ±SEM of MaxN, the maximum number of individuals observed at any moment (n = 89 and 97 surveys for fished and no-take reefs respectively; detailed methods in ref. 70).

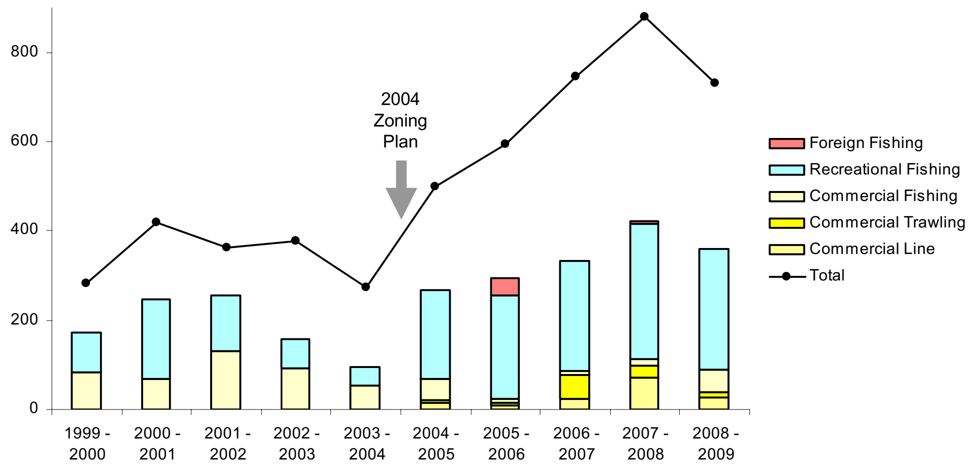

Fig. S7. Recorded compliance offenses related to zoning in the Great Barrier Reef World Heritage Area 2004–2008 (Data courtesy GBRMPA). Total figure includes nonzoning offenses. Separate data for commercial trawling and line fishing offenses are only available after 2004.

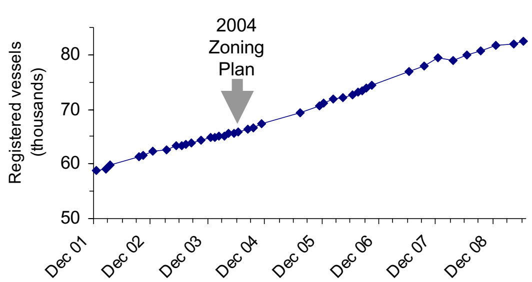

Fig. S8. Recreation vessel registrations in GBR coastal communities. Data courtesy GBRMPA and Queensland Transport.

Other Supporting Information

Table S1 (PDF)
Table S2 (PDF)