

Adaptive management of the Great Barrier Reef: A globally significant demonstration of the benefits of networks of marine reserves

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The Great Barrier Reef (GBR) provides a globally significant demonstration of the effectiveness of large-scale networks of marine reserves in contributing to integrated, adaptive management. Comprehensive review of available evidence shows major, rapid benefits of no-take areas for targeted fish and sharks, in both reef and nonreef habitats, with potential benefits for fisheries as well as biodiversity conservation. Large, mobile species like sharks benefit less than smaller, site-attached fish. Critically, reserves also appear to benefit overall ecosystem health and resilience: outbreaks of coral-eating, crown-of-thorns starfish appear less frequent on no-take reefs, which consequently have higher abundance of coral, the very foundation of reef ecosystems. Effective marine reserves require regular review of compliance: fish abundances in no-entry zones suggest that even no-take zones may be significantly depleted due to poaching. Spatial analyses comparing zoning with seabed biodiversity or dugong distributions illustrate significant benefits from application of best-practice conservation principles in data-poor situations. Increases in the marine reserve network in 2004 affected fishers, but preliminary economic analysis suggests considerable net benefits, in terms of protecting environmental and tourism values. Relative to the revenue generated by reef tourism, current expenditure on protection is minor. Recent implementation of an Outlook Report provides regular, formal review of environmental condition and management and links to policy responses, key aspects of adaptive management. Given the major threat posed by climate change, the expanded network of marine reserves provides a critical and cost-effective contribution to enhancing the resilience of the Great Barrier Reef.

biodiversity protection | spatial planning and zoning | social and ecological resilience | coral reefs | economic cost benefit analysis

The Great Barrier Reef (GBR) is a marine ecosystem of globally significant biodiversity, exceptional environmental, cultural, social, and economic value, and extraordinary beauty. Those values are recognized in its listing as a World Heritage Area and national Marine Park. Coral reefs are exceptional reservoirs of marine biodiversity (1), but the GBR also includes a wide range of other ecosystems, from coastal seagrass beds to a wide range of diverse seafloor habitats (2). However, as for many marine ecosystems globally, those values are under serious threat from a range of human causes, with climate change at the fore (3–5). Responding to those threats demands a portfolio of diverse and adaptive conservation strategies, in turn requiring review of the effects and effectiveness of those different approaches (6–8).

The Great Barrier Reef as a Regional-Scale Case Study of Marine Reserve Management

Networks of marine protected areas are a prominent strategy in marine conservation, and current paradigms suggest numerous

benefits for biodiversity and fisheries, especially as part of an integrated package of management approaches (e.g., consensus statement in ref. 9; also refs. 3, 10). As the world's largest network of marine reserves, the GBR provides a unique opportunity to test those paradigms at large spatial scales and under best-practice circumstances, with broad relevance to the science and management of marine conservation. The Great Barrier Reef Zoning Plan 2003, implemented in 2004, serves as a benchmark for process and outcomes in marine reserve networks. Based on best-practice in design and implementation (11, 12; *SI Section 1*), it also provides the only set of comparisons, which include: (i) replication, across a large range of latitudes and other gradients; (ii) some before–after comparisons; (iii) a range of treatment levels (zones) beyond fished and no-take reserves (*Table S1*); and (iv) information on compliance and enforcement.

This review synthesizes available information, including extensive previously unpublished results and gray literature, on the effects of zoning and spatial management on the GBR, with an emphasis on the 2004 Zoning Plan and in the context of

adaptive management of the GBR Marine Park. The paper examines direct effects of the zoning on target fish and sharks on no-take and no-entry coral reefs, indirect effects on corals, crown-of-thorns starfish, and reef food webs, and effects for nonreef habitats and species of conservation concern. These ecological insights are complemented by an examination of

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compliance and enforcement within the network and social and economic costs and benefits. Finally, the implications of this information both for marine reserve management and for the science to underpin that management are discussed. Only the most significant results are included in the main paper; many results and background information on the GBR, zoning, and monitoring are included in *SI Text*.

Effects of Spatial Zoning and Marine Reserves in the Great Barrier Reef

Direct Biological and Ecological Effects of Zoning on Coral Reefs: Changes in Reef Fish and Sharks. There is now very strong evidence that no-take zones on the Great Barrier Reef benefit fish stocks within those zones. The strongest results so far come from visual surveys of abundance and size of target fish, principally coral trout (*Plectropomus* spp., the major target of line fishing on the GBR), using comparisons of fished and no-take reefs (Fig. 1) (13). Throughout this paper, “fished” is used to refer to areas legally open to fishing and does not include areas that may have illegal fishing. Monitoring has documented very fast and sustained recovery, with up to 2-fold increases in both numbers and size of fish on many no-take reefs. Significantly, this basic pattern holds across $\approx 1,000$ km north–south and for both inshore and offshore reefs, despite strong environmental differences among those reefs (Fig. S1A).

These increases appear to reflect genuine recovery of exploited fish populations on no-take reefs, rather than declines in abundance on fished reefs due to displaced fishing effort (13); note that other changes to fisheries management occurred simultaneously (14). In one of very few before–after comparisons available for GBR zoning, data from inshore reefs show that on most of those reefs, the differences primarily reflected increases in fish on protected reefs, with little decrease on fished reefs (Fig. 1A). The rate of the increases is also particularly noteworthy, with 2-fold increases in coral trout biomass appearing within 2 years of the implementation of the new zoning plan (13). Many of the protected reefs had previously been fished heavily. Although the basic pattern of elevated stocks in no-take areas was remarkably consistent, there is nonetheless notable variation between regions and cross-shelf locations, likely to reflect differences in both ecology and intensity of exploitation (15). The increased mean size of fish in no-take zones is particularly important as large fish are disproportionately more fecund and therefore contribute greatly to future fish populations (e.g., ref. 16), potentially including stocks in fished zones.

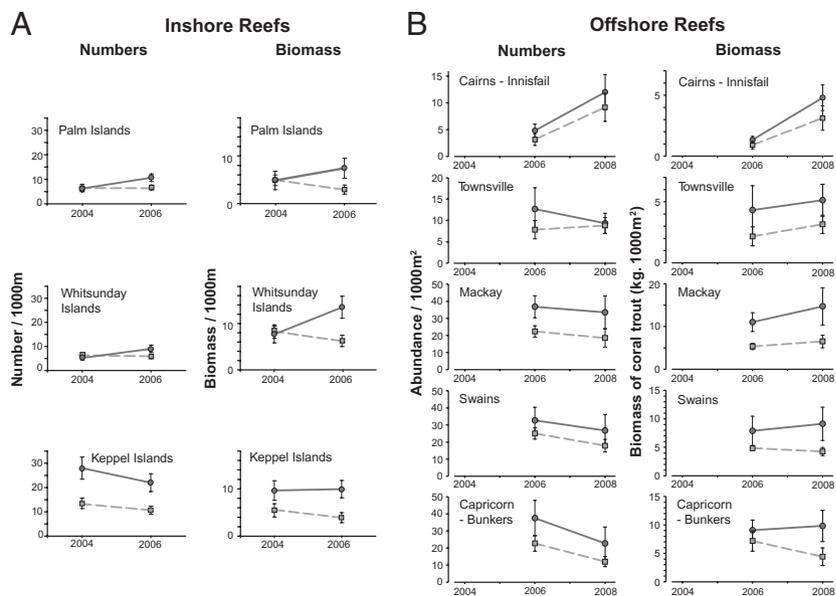


Fig. 1. Abundance and biomass of coral trout on fished and no-take reefs spread across $\approx 1,000$ km of the Great Barrier Reef (see map in Fig. S1). Solid lines are no-take zones; dashed lines are fished reefs. Data are means \pm SEM from scuba-based, visual transects of reefs zoned in 2004, updated from ref. 13. Data for inshore reefs (A) include data from before zoning implementation. Note different vertical axes and periods (dates) for A and B.

A recent series of surveys of deep, reef-base habitats also found distinct benefits to targeted fish species, using baited, remote, underwater video surveys. These patterns were strongest in coral-dominated habitats, where coral trout (*Plectropomus* spp.), red emperor (*Lutjanus sebae*), and redthroat emperor (*Lethrinus miniatus*) were all more abundant on no-take reefs. However, the patterns varied considerably among species and habitats. Differences between zones were less clear-cut than those for shallow reefs, perhaps due to lower fishing effort at these depths and/or continuity of habitat between zones, allowing fish unrestricted passage out of protected zones (17).

There is also a range of strong evidence for the benefits of no-take zones based on comparisons of zones in place before the 2004 rezoning (detailed description in *SI Section 2*; zoning history in Table S2). A large scale manipulative study of offshore reefs found that no-take reefs generally, but not always, had more, larger, and older fish for the two main target species than did reefs open to fishing (Fig. S1 B–D) (14, 15). Surveys of inshore reefs of the central and southern GBR found that coral trout and striped seaperch (*Lutjanus carponotatus*) were generally less abundant and smaller on fished reefs than on no-take reefs implemented in 1987 (Fig. S2) (18, 19). Significantly, the evidence suggests that coral trout stocks on inshore reefs generally were markedly depleted by 1984, before reserve implementation (Fig. S2).

The effects of no-entry zones are markedly stronger still than those of no-take zones. Comparing long-term (pre-2004) fished, no-take, and no-entry zones confirmed the benefits of no-take zones, but also showed that coral trout, the redthroat emperor (*L. miniatus*), and lutjanids (tropical snappers) were markedly more abundant and coral trout were larger in no-entry zones than in no-take zones (Fig. S3) (20). Although the data for no-entry zones have some limitations, this is a critical result because it raises the possibility that lower abundance in no-take zones is due to incomplete compliance (no-entry zones are much simpler to enforce, and hence have more effective compliance; further explanation, *SI Section 2*). It also suggests that baseline populations of target fish may have been significantly more abundant than previously recognized, with stocks in most areas significantly depleted in comparison with that baseline.

Populations of reef sharks, the main apex predator in coral reef ecosystems, show even stronger effects of zoning, with the largest benefits found in no-entry zones (Fig. 2). In surveys of reefs zoned before 1992, whitetip (*Triaenodon obesus*) and gray reef (*Carcharhinus amblyrhynchos*) sharks respectively were ≈ 4 and 8 times more abundant on no-entry reefs than on fished reefs in the central GBR (20). Gray reef sharks were up to 30 times more abundant on no-entry reefs than on fished reefs in the northern GBR (Fig. 2A) (21). Abundance in no-take zones was

intermediate in the central GBR (Fig. 2B) (20), but Robbins et al. (21) found numbers in no-take zones were closer to those in fished zones than no-entry zones, especially for gray reef sharks. Line fishing surveys of sharks found that catch rates of sharks on reefs historically open to fishing were less than half those on reefs that had been closed to fishing since the late 1980s (Fig. 2C) (22). Note that all three of these shark studies compared zones implemented before 1992. Surveys of deep, reef-base habitats in the southern GBR using baited underwater video found higher numbers of gray reef sharks in newly created (2004) no-take zones than fished zones (17).

The studies by Robbins et al. (21) and Ayling and Choat (20) demonstrate the value of expanding simple fished/no-take contrasts to include a range of different zones (c.f. 23 for temperate examples). Abundances in no-entry zones, markedly higher than for no-take zones, again suggest that no-take zones do not provide a reliable baseline for undisturbed shark abundances and suggest possible compliance problems (20, 21), although these interpretations again require caution (*SI Section 2*). Robbins et al. (21) also surveyed zones with limited fishing (Conservation Park), intermediate in protection between no-take zones and zones open to fishing (General Use). The effects of limited fishing zones on shark abundances were minor and not statistically significant compared to open fishing zones, although shark abundances ranked consistently higher with increased protection.

Potential Effects on Ecosystem-Wide Fish Populations. An important aspect of the effectiveness of no-take reserves is their benefits not only to fish populations *within* individual no-take reserves, but also their contributions to *overall* fish populations across the ecosystem, including both other no-take reserves within the network and contributions to fished areas. With 32% of GBR reef area in no-take reefs, and fish densities about two times greater on those reefs, fish populations across the ecosystem have increased considerably (14). Contributions beyond a reserve depend on adult and larval connectivity both among no-take reefs, and between no-take and fished reefs (e.g., refs. 7, 10, 24, 25). Although evidence exists for some export of adult fish from no-take zones to fished areas (26, 27), adult coral trout rarely move between individual coral reefs on the GBR (26, 28) and current no-take zones generally include entire reefs. The lack of adult movement between reefs clearly enhances the effectiveness and measurability of protection for fish populations within reserves. However, it also means that increased biomass of coral

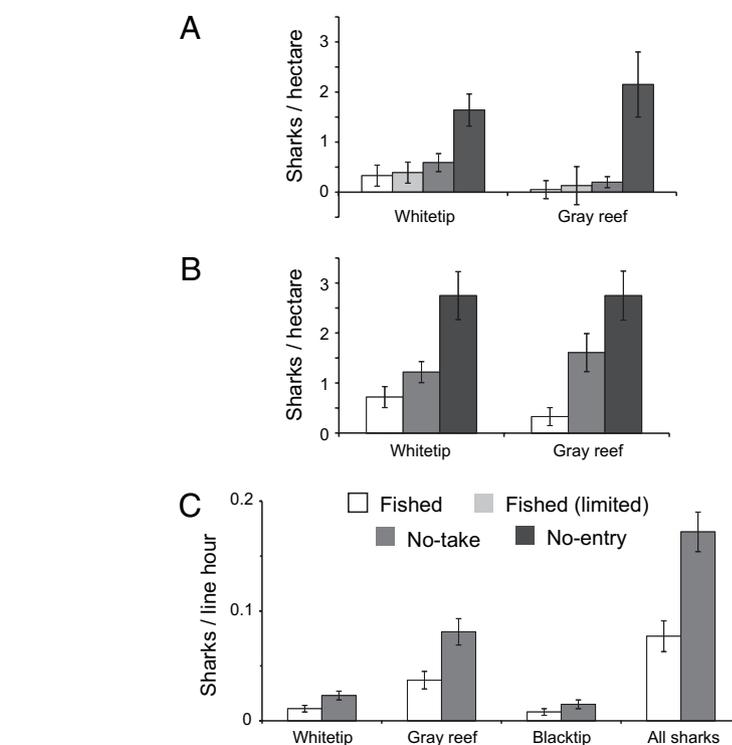


Fig. 2. Abundance of reef sharks in different zones in the northern and central GBR. Abundance of sharks based on scuba-based, visual transects for *A* (from ref. 20) and for *B* (from ref. 21). (*C*) Catch rates of sharks using commercial line fishing, disaggregated from ref. 20. All data are means \pm SEM.

trout in no-take zones will have little direct (conservation or fisheries) benefits through export of adult fishes to the two-thirds of reef area that is open to fishing.

However, reproductive output from no-take reefs may be of enormous significance, due to disproportionately higher output per unit area from the more plentiful, larger fishes in reserves (*SI Section 3*). Evidence from the GBR and elsewhere suggests that populations within marine reserves are at least partially self-sustaining between generations (29, 30), but that there is also considerable larval exchange between reefs (*SI Section 3*). Larval export from no-take zones is important both for connectivity within the no-take network and for sustaining both conservation and fishery values of the larger area of fished reefs on the GBR. The extent of such export depends on three factors: the extent of larval transport between reefs, the relative reproductive output of no-take and fished reefs, and the dispersal distances from no-take reefs to other reefs. Larval transport and relative output are considered in *SI Section 3*; for the main target species, no-take reefs likely have the capacity to provide substantial proportions of ecosystem-wide larval supply.

Recent work has recommended that networks of marine reserves should aim to preserve the natural distribution of dispersal distances and in particular maximize the proportion of reefs within 15–30 km of a

potential source reef (7, 24, 25). Spatial analysis of dispersal distances between no-take reefs suggests that the 2004 rezoning of the GBR successfully maintained the naturally occurring spectrum of dispersal distances between reefs within the no-take network (Fig. S4). Under the 2004 rezoning, the distribution of nearest-neighbor distances between no-take reefs closely matches that of all GBR reefs, and more than 99.5% of no-take reefs have a no-take reef within 14 km. Analysis of distances between no-take reefs and fished reefs show that more than 75% of fished reefs have a no-take reef within 16 km and more than 90% within 22 km, indicating that the no-take network has the capacity to provide substantial larval subsidies to the fished reefs.

Indirect Effects of Zoning on Coral Reefs: Effects on Corals, Crown-of-Thorns Starfish, and Prey Fish. Zoning benefits for target, predatory fish species are important, but the potential effects on broader biodiversity, and on reef-building corals in particular, are of greater ecological and economic significance, because the entire reef ecosystem depends on the structure provided by corals. One of the most ecologically important effects documented for GBR zoning is the decreased frequency of outbreaks of the coral-eating crown-of-thorns starfish in no-take zones (31) (Fig. 3A; pre-2004 zones; further detail in *SI Section 4*). This starfish has been the major

cause of coral mortality on the Great Barrier Reef. The relative frequency of outbreaks on midshelf reefs that were open to fishing was 3.75 times higher than that on no-take reefs. Most outbreaks occur on the midshelf region. If all reefs across the shelf were included, outbreak frequency was seven times greater on fished reefs (31).

Importantly, the reduction in starfish outbreaks appears to have direct benefits for coral populations (Fig. 3B). The cover of coral on midshelf reefs after outbreak periods appears to be markedly higher in no-take zones than in fished zones. These results are ecologically very important because they show a strong connection between a specific management strategy (reserves) and the major historical cause of mortality for reef-building corals on the GBR, with likely consequences both for overall biodiversity and for tourism value of the reefs.

Although the effect on starfish outbreaks is clear, the ecological mechanism causing this pattern remains uncertain. The major target species affected by the zoning on the central GBR are not considered to be direct predators on crown-of-thorns starfish. Sweatman (31) speculated that reductions in coral trout may cause trophic cascades, resulting in a decrease in invertebrate predators of starfish juveniles. The effects on corals (Fig. 3B) are consistent with results of independent surveys of inshore reefs (18, 19, 32) (details in *SI Section 4*, although crown-of-thorns starfish are unusual on inshore reefs). More detailed information being collected under the current zoning monitoring should help understand the where, when, and how of zoning effects on coral populations. Whatever the mechanism, reduced frequency of a major source of coral mortality will have major consequences for reef resilience.

Reserves also appear to have some impacts on food web structure on GBR coral reefs, but those impacts are not generally consistent with simplistic, top-down effects of removal of predatory fish. In particular, if abundance of prey fish depends primarily on top-down control, then recovery of fish populations within no-take zones might be expected to reduce abundance of prey fish. Although such changes have been recorded, they are far from consistent (*SI Section 4* and Fig. S5).

Nonreef Habitats and Trawling Effects.

Although nonreef habitats occupy around 95% of the area of the GBR Marine Park, and include an extraordinary diversity of habitats and taxa, only recently have there been even basic biological surveys for most of these habitats (2). For most habitats, there is negligible direct information on the biological effects of

zoning or other management initiatives (except for shoals: see below). Given this lack of biological information for seabed areas, development of the bioregions underpinning the 2004 zoning had to be largely interpolated from physical information, such as bathymetry and sediment data. However, this also prompted a major survey of seabed biodiversity, with 1,380 sites covering 200,000 km² (the Seabed Biodiversity Project, ref. 2). This new, vastly more detailed information provided the means both to assess the effectiveness of the 2004 zoning in protecting biodiversity and thereby to test the effectiveness of using physical proxies for patterns of biodiversity. Such analysis indicated that both the approach and the outcome had been very effective, substantially increasing protection at a range of levels, including species, species groups, assemblages, and habitat types (*SI Section 5*) (33). For each level, 20% or more of biomass or area was protected in zones that do not allow trawling.

The effects of prawn trawling in the GBR have been studied directly (34, 35), allowing zoning effects on trawling im-

pacts to be modeled and analyzed (35). Although potentially destructive to seabed habitats and responsible for the majority of discarded catch in the GBR fisheries (8), trawling is only allowed in 33% of the GBR Marine Park area (General Use zones). Available evidence suggests that there is relatively good compliance with zoning and that current trawling predominantly occurs within areas of seabed where scope for damage is limited. Seagrass beds in particular are not considered vulnerable (36). Pitcher et al. (35) suggested that very few species have been significantly affected by trawling and that overall management changes have largely reversed previous trends for damage to bottom habitats (further detail in *SI Section 5*). Remaining concerns about incidental catch of species of conservation concern may be partially ameliorated by bycatch reduction devices (*SI Section 5*).

The only data available for direct effects of zoning on nonreef habitats are for shoals, areas where hard substrata outcrop from the seabed in deeper water (generally >20 m). Monitoring zoning effects on these habitats involves considerable challenges, including confounded comparisons

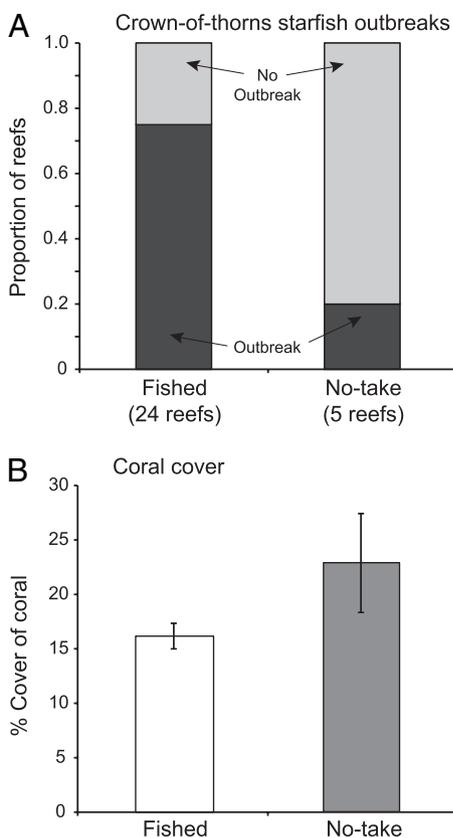


Fig. 3. Effects of zoning on coral-eating starfish and hence on coral populations. (A) Frequency of outbreaks of crown-of-thorns starfish on no-take and fished midshelf reefs in regions with active outbreaks present. Data are for 1994–2004, redrawn from ref. 31; note low numbers of no-take reefs were available pre-2004; further background in *SI Section 4*. (B) Abundance of hard corals on midshelf reefs after crown-of-thorns starfish outbreaks. Data, previously unpublished, are means \pm SEM of percent cover; details of methods in *SI Section 4*.

between zones (*SI Section 1*), lack of background information, and the need to develop new monitoring techniques (*SI Section 5*). The clearest results for shoal monitoring come from well-defined, deepwater shoals in the southern GBR, where mean abundance indices for targeted fish on no-take shoals were twice those of fished shoals, with ratios of up to 11 (Fig. S6) (37). However, some targeted species did not show benefits of protection. Results from shoals in the central GBR are less clear, largely due to the lack of clearly comparable fished and no-take zoned shoals (*SI Section 1*). In some cases, some target fish were more abundant on no-take shoals, but in other cases, the reverse was true (38).

Species of Conservation Concern: Dugong and Marine Turtles. The biology, scale of ecological function, population status, and appropriate management and monitoring approaches for dugongs (*Dugong dugon*) provide a marked contrast to those of reef-attached fish. Dugongs are considered at serious risk, have a relatively low reproductive capacity (39, 40), are highly mobile at scales greater than that of most no-take zones (41), and are considered part of a single stock in the GBR (42). Population estimates for dugong at the scales of no-take zones have high uncertainty, due to the animals' spatially heterogeneous distribution and their predominant occurrence in turbid waters, which makes them challenging to survey, even from the air (43). Thus assessment of dugong management effectiveness is more complex than simple comparisons of density within and outside no-take areas. Further background on dugong status and management are given in *SI Section 5*.

In addition to the greatly enhanced area protected by the 2004 zoning, management agencies use a suite of complementary measures to protect dugongs in the GBR. These include bycatch reduction and gear changes, a voluntary moratorium on Indigenous hunting in the southern two-thirds of the GBR, and dugong protection areas (DPAs) introduced in 1998 to protect specific areas of high conservation value (8, 40, 44, 45). Although the rezoning in 2004 protected 42% of high-priority dugong habitat in no-take reserves, doubling the previous proportion protected, this nonetheless fell short of the 50% recommended by experts as part of the Biophysical Operating Principles (45).

Overall, marine reserves and other measures appear to be providing critical but insufficient contributions to protecting GBR dugongs. A time series of aerial surveys suggests that populations on the inhabited coast are now so low that recovery will require zero human-induced mortality (40). By overlaying the population distribution models with spatial information

on ranked threats to dugongs, based on expert assessments, Grech and Marsh (46) provided a rapid assessment of risks to GBR dugong. They estimated that since the 2004 rezoning, $\approx 96\%$ of habitat of high conservation value for dugongs and 93% with medium conservation value, is at low risk from human activities (either due to spatial protection or to low levels of human activities). This is a considerable improvement on the pre-zoning situation, especially with respect to fishing bycatch (47). Grech and Marsh (46) also concluded that the protection afforded by the current ecosystem-scale network of marine reserves is limited by the inability of reserves per se to mitigate all of the factors that threaten the marine environment, including activities in the adjacent coastal catchments.

Marine turtle protection involves similar issues of scale and biology to those for dugong. Globally significant populations of several listed threatened species inhabit the Marine Park and evidence suggests populations of several species are in decline, with mortality due to fishing bycatch as a major threat. The design principles for the 2004 zoning included incorporation of marine turtle interesting (areas adjacent to nesting beaches) and foraging habitats in no-take areas, specifically including all very high-priority nesting sites and 20% of foraging areas. These principles were not fully achieved, but protection of identified interesting sites increased from 23.4 to 56.5% and foraging habitat increased from 7.1 to 29% (48, 49). Other key strategies include mandatory use of turtle excluder devices on trawl nets. A case study of iterative management responses to survey data for loggerhead turtles is given in *SI Section 5*. As for dugong, spatial zoning alone may not provide sufficient protection for marine turtles, but can be highly effective in concert with other measures.

Zoning Management, Compliance, and Enforcement. The ecological effectiveness of marine reserves depends critically on compliance, without which reserves are protected in name only. Monitoring of compliance (reviewed in *SI Section 6* and Fig. S7) provides valuable information to support and direct enforcement, but may be strongly confounded and should be integrated with data on target species, to assess the effectiveness of management. For the GBR, the combination of compliance data and the patterns of abundance of target fish between fished, no-take, and no-entry zones (Fig. 2 and Fig. S3) (20, 21) indicate that compliance with zoning regulations is not complete. That no-take zones generally achieve markedly higher fish biomasses than fished zones shows that overall compliance is considerable. However, the large differences between no-entry and no-take zones most

likely indicate significant poaching within many no-take zones (where effective enforcement is more difficult, *SI Section 6*).

Social and Economic Effects of Zoning. Importantly, the ecological benefits of the zoning appear to have only entailed limited social or economic costs, and some significant benefits. The increased abundance of corals and fish are likely to have major flow-on, long-term benefits for the major human use (tourism) and potentially for fisheries (8). Recognition of the conservation value of the zoning changes seems widespread within the broader community, even within sectors directly affected by the changes, although some concerns remain among fishers. There have of course been significant changes in locations for both recreational and commercial fishing. Available evidence on social effects is reviewed in *SI Section 7*.

The economic value of a healthy GBR to Australia is enormous, currently estimated to be about A\$5.5 billion annually and increasing steadily (Fig. 4) (50–52) (estimates only include use values and so underestimate total economic value), although comparable data are not available before 2004. The contribution to employment is estimated at 53,800 full time jobs. Tourism accounts for the vast majority of reef-based income and employment. Although such estimates are necessarily approximate, income from tourism is estimated to be about 36 times greater than commercial fishing and that ratio is increasing. Since 2005–2006, recreational use (mostly fishing) is estimated to contribute marginally more than commercial fishing. Significantly, these contributions accrue to both private industry and government sectors (through taxation and reduced unemployment welfare payments).

The major economic cost associated with the rezoning was a once-off, structural adjustment package for commercial fishing industries, which totalled A\$211 million at July 2009 [funds from Australian Government but not Great Barrier Reef Marine Park Authority (GBRMPA); data courtesy of the Department of the Environment, Water, Heritage and the Arts; also ref. 53]. In January 2004 an Australian Government policy statement was released, outlining assistance to fishers, fishing-related businesses, and fishing-dependent communities subsequent to declaration or rezoning of marine protected areas (54, 55). Estimates of likely economic impact and of financial assistance are not directly comparable (56), but a priori estimates of the costs of GBR zoning to fisheries were approximately A\$14 million per annum (gross value of production; or A\$0.5–2.59 million value added; refs. 57–59) with industry estimates as high as A\$23 million per annum (60). Review of

(Fig. 3), is especially important in demonstrating the value of reserves in maintaining ecosystem structure and function (9). Because corals construct the very habitat of coral reefs, these effects are highly relevant to long-term community structure and resilience and hence to socioeconomic value. Previous demonstrations of such benefits for no-take reserves on coral reefs have generally involved effects on fishing for herbivores and/or habitat-destructive fishing practices (e.g., refs. 63, 64), neither of which is significant on GBR reefs.

Many of the benefits of high proportions of protected habitats will not be limited to the protected zones, but may be diffused across zones, due to strong ecological connectivity between zones (e.g., highly mobile species, ecosystem-wide larval supply, and biodiversity). Benefits to fish stocks seem likely to accrue in part to the entire ecosystem, through larval subsidies (*SI Section 3*). Such ecosystem-wide benefits may be very real, but very difficult to measure reliably, as they are not amenable to simple comparisons of fished and no-take zones.

Overall, the ecological benefits appear to bring net social and economic benefits. Broad community opinion appears to support the zoning (*SI Section 7*), and the economic costs, which are being addressed through structural adjustment arrangements, are greatly outweighed by the economic benefits of a healthy reef (Fig. 4). These results show the considerable value of direct assessments of social and economic costs and benefits, assessments that are often advocated but less often implemented (9). Critics of marine reserves within the broader community and media often assert major social and economic costs of implementation. However, monitoring and survey data for the GBR suggest those costs are lower than asserted and minor compared to the social and economic values of the Marine Park. Further, understanding the costs that do occur provides insights into how they can be avoided or mitigated in the future (e.g., ensuring that fishers feel engaged in planning processes, etc., *SI Section 7*). Such lessons are valuable both for on-going management of the GBR and for the design and implementation of marine reserves elsewhere.

However, review of the GBR zoning also provides some clear cautionary insights. No-take networks alone do not provide sufficient protection for some taxa, even in a

network as extensive as the GBR. By incorporating entire reefs within protected zones, the present system provides strong protection for taxa such as coral trout, which occupy single reefs throughout their adult lives. However, taxa such as sharks, dugongs, and marine turtles, that operate over larger scales and range between protected and open zones, are likely to benefit but to a much lesser extent. As widely recommended (e.g., ref. 9), GBR zoning is complemented by a great deal of nonspatial management, including explicit management of fisheries within fished zones and bycatch reduction efforts (*SI Section 1*). The results for dugongs and marine turtles show the importance of such complementary management (*SI Section 5*).

The dramatic differences between fished and no-take zones (Figs. 1 and 2 and Figs. S1–S3), suggest that, even on one of the best managed marine systems in the world, a large proportion of reefs are significantly depleted in predatory fish and sharks. However, the stark differences between no-take and no-entry zones (Fig. 2 and Fig. S3) indicate that that depletion is much more serious than indicated by abundances in no-take zones alone, potentially affecting most reefs (no-entry zones only account for 0.2% of area). The ecological consequences of this depletion are probably exacerbated by associated depletion of by-catch species and may be more serious in terms of ecosystem structure than fisheries impacts. On this basis, the large proportion of new no-take zones, although very positive, nonetheless seems insufficient to restore ecosystem-wide stocks of target fish to undepleted levels. Interpretation of no-take reserves as baselines (c.f. ref. 9) requires rigorous compliance within those reserves: GBR no-entry zones, as “full compliance” no-take zones, are critical in preventing the shifting baseline phenomenon of perceiving depleted stocks as normal.

Effective compliance and enforcement are critical to the overall ecological effectiveness of marine reserve networks. The evidence for notable noncompliance in GBR no-take zones, although limited, is a distinct concern and demonstrates the importance of monitoring to assess compliance (above and *SI Section 6*). Even limited noncompliance may have major ecological consequences, especially because poaching in no-take zones will tend to have dramatically higher catch rates and to

catch the largest (and hence most fecund) fish and sharks (Fig. S3). Improved compliance could involve increased investment in education and awareness to improve voluntary compliance, increased investment in enforcement, and increased penalties to ensure real disincentives for noncompliance (*SI Section 6*). Given the environmental and economic value of the GBR, and the relatively minor current expenditure on zoning compliance (Fig. 4), there seems a strong case for increasing investment in compliance to protect such a valuable asset and revenue source.

In summary, the network of marine reserves on the GBR has brought major, sustained ecological benefits, including enhanced populations of target fish, sharks, and even corals, the foundation of the coral reef ecosystem. Although it is not possible to directly measure effects on seabed biodiversity, analyses indicate enhanced protection within no-trawl zones under the new network. Risk assessments even indicate some benefits to dugongs and marine turtles, despite protected zones being much smaller than the ranges of these species. These ecological benefits are likely to bring significant, long-term benefits for human uses of the Marine Park, and social and economic costs of the 2004 zoning appear limited in comparison with the large and growing economic return from a healthy GBR. Overall, the available evidence suggests that the large-scale network of marine reserves on the GBR is proving to be an excellent investment in social, economic, and environmental terms.

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