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

Article *in* Proceedings of the National Academy of Sciences · February 2010

DOI: 10.1073/pnas.0909335107 · Source: PubMed

J. Howard Choat
James Cook University

Richard Evans
Marine Science Program

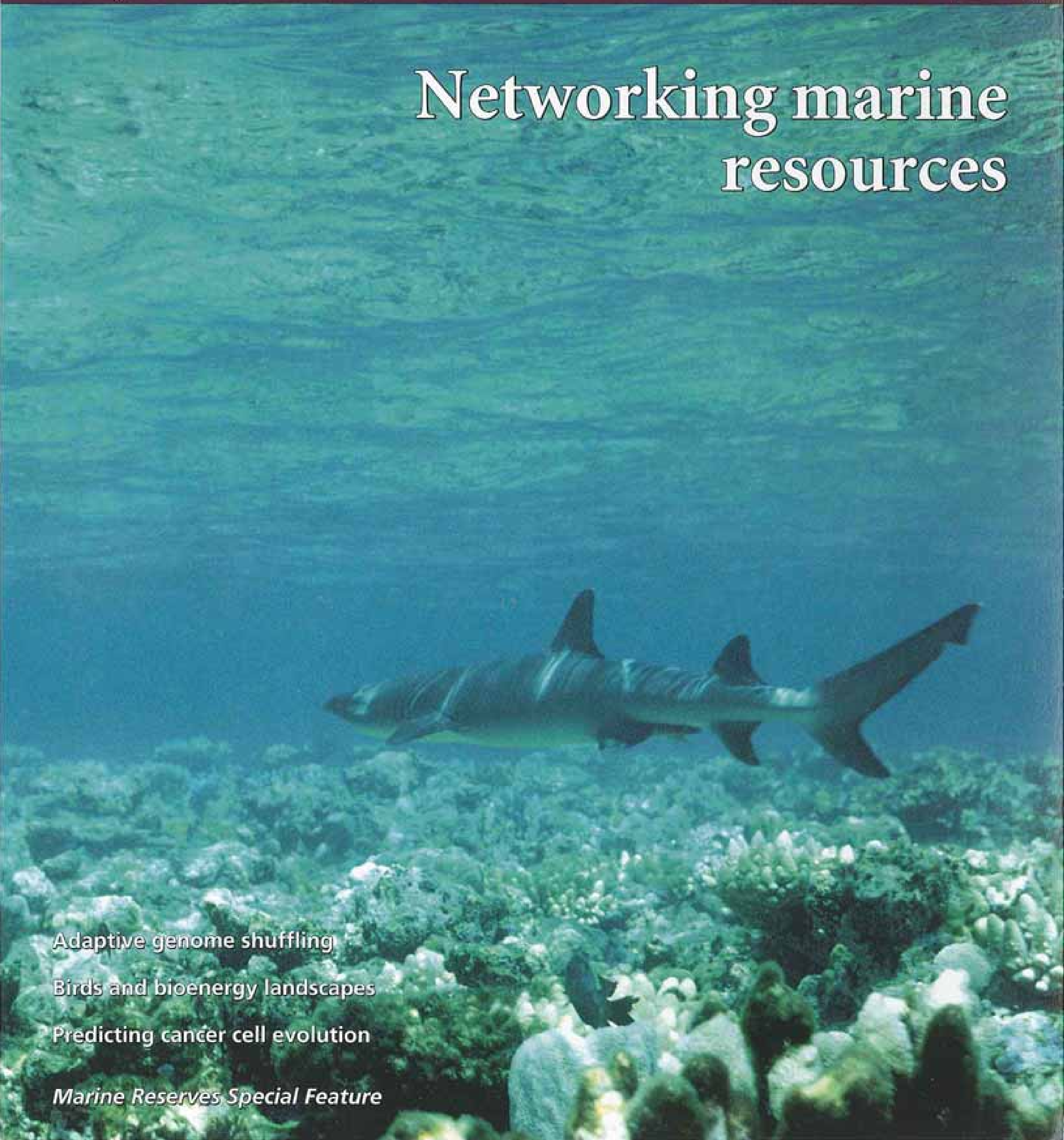
Débora M. De Freitas
São Paulo State University

Michelle R Heupel
University of Tasmania

October 26, 2010 | vol. 107 | no. 43 | pp. 18233–18742

PNAS

Proceedings of the National Academy of Sciences of the United States of America www.pnas.org



Networking marine resources

Adaptive genome shuffling

Birds and bioenergy landscapes

Predicting cancer cell evolution

Marine Reserves Special Feature

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

Laurence J. McCook[a,b,1], Tony Ayling[c], Mike Cappo[d], J. Howard Choat[e], Richard D. Evans[b,e,2], Debora M. De Freitas[b,f], Michelle Heupel[f], Terry P. Hughes[b], Geoffrey P. Jones[b,e], Bruce Mapstone[g], Helene Marsh[f], Morena Mills[b,e], Fergus J. Molloy[a], C. Roland Pitcher[h], Robert L. Pressey[b], Garry R. Russ[b,e], Stephen Sutton[f], Hugh Sweatman[d], Renae Tobin[f], David R. Wachenfeld[a], and David H. Williamson[b,e]

[a]*Great Barrier Reef Marine Park Authority,Townsville, Queensland 4810, Australia;* [b]*Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia;* [c]*Sea Research, Hideaway Bay, Queensland 4800, Australia;* [d]*Australian Institute of Marine Science, Townsville, Queensland 4810, Australia;* [e]*School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia;* [f]*School of Earth and Environmental Sciences, James Cook University, Townsville, Queensland 4811, Australia;* [g]*CSIRO Marine and Atmospheric Research, Hobart, Tasmania 7001, Australia; and* [h]*CSIRO Marine and Atmospheric Research, Cleveland, Queensland 4163, Australia*

Edited by Steven D. Gaines, University of California, Santa Barbara, CA, and accepted by the Editorial Board January 29, 2010 (received for review August 20, 2009)

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

Author contributions: L.J.M., T.A., M.C., J.H.C., R.D.E., D.M.D.F., G.P.J., B.M., H.M., M.M., F.J.M., C.R.P., R.L.P., G.R.R., S.S., H.S., R.T., and D.H.W. designed research; L.J.M., T.A., M.C., J.H.C., R.D.E., D.M.D.F., T.P.H., G.P.J., B.M., H.M., M.M., C.R.P., R.L.P., G.R.R., S.S., H.S., R.T., and D.H.W. performed research; L.J.M., T.A., M.C., J.H.C., R.D.E., D.M.D.F., M.H., G.P.J., B.M., H.M., M.M., F.J.M., C.R.P., G.R.R., S.S., H.S., R.T., and D.H.W. analyzed data; and L.J.M., T.A., M.C., J.H.C., R.D.E., D.M.D.F., M.H., T.P.H., G.P.J., B.M., H.M., M.M., F.J.M., C.R.P., R.L.P., G.R.R., S.S., H.S., R.T., D.R.W., and D.H.W. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. S.D.G. is a guest editor invited by the Editorial Board.

[1]To whom correspondence should be addressed. E-mail: l.mccook@gbrmpa.gov.au.

[2]Present address: Western Australian Fisheries and Marine Research Laboratories, Department of Fisheries, Perth, WA 6920, Australia.

This article contains supporting information online at www.pnas.org/cgi/content/full/0909335107/DCSupplemental.

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 ≈1,000 km north–south and for both inshore and offshore reefs, despite strong environmental differences among those reefs (Fig. S1*A*).

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. 1*A*). 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.

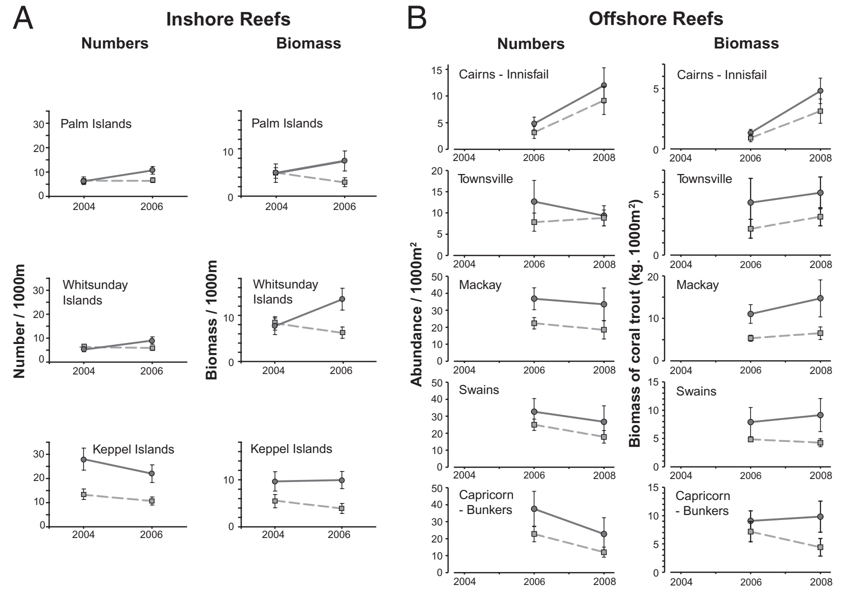


Fig. 1. Abundance and biomass of coral trout on fished and no-take reefs spread across ≈1,000 km of the Great Barrier Reef (see map in Fig. S1). Solid lines are no-take zones; dashed lines are fished reefs. Data are means ±SEM from scuba-based, visual transects of reefs zoned in 2004, updated from ref. 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 stripey 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 red-throat 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. 2*A*) (21). Abundance in no-take zones was intermediate in the central GBR (Fig. 2*B*) (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. 2*C*) (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.

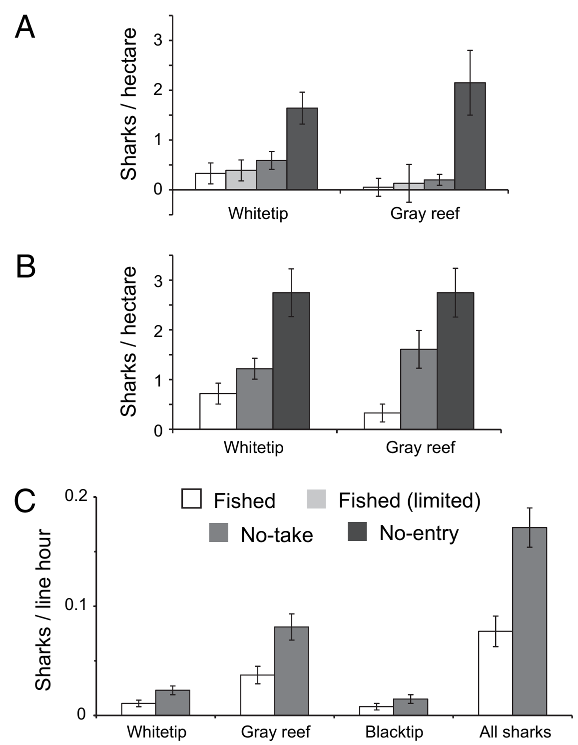


Fig. 2. Abundance of reef sharks in different zones in the northern and central GBR. Abundance of sharks based on scuba-based, visual transects for *A* (from ref. 20) and for *B* (from ref. 21). (*C*) Catch rates of sharks using commercial line fishing, disaggregated from ref. 20. All data are means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

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 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. 3*A*; 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. 3*B*). 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. 3*B*) 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).

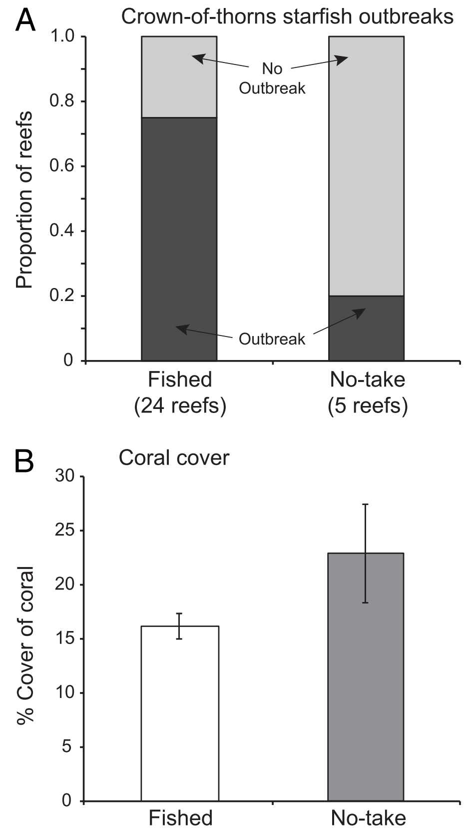


Fig. 3. Effects of zoning on coral-eating starfish and hence on coral populations. (*A*) Frequency of outbreaks of crown-of-thorns starfish on no-take and fished midshelf reefs in regions with active outbreaks present. Data are for 1994–2004, redrawn from ref. 31; note low numbers of no-take reefs were 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 ±SEM of percent cover; details of methods in *SI Section 4*.

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 km^2 (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 impacts 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 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, ≈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 prezoning 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 internesting (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 internesting 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 the initial business exit component of this package suggested a number of potential changes to improve outcomes and cost effectiveness (61) and a further review is currently underway. Given the considerable final investment, more cost-effective environmental and socioeconomic outcomes might have been achieved if initial strategic planning had been able to formally incorporate social and economic information, the need for industry structural adjustment, and cross-jurisdictional coordination of economic impacts (56).

Evidence for economic effects on businesses in the recreational fishing industry is very limited, but does not indicate major impacts. For example, recreational vessel registration data show no sign of changes due to the zoning plan (Fig. S8).

Expenditure on zoning enforcement, and on overall Marine Park management, has been relatively stable, with only minor increases in 2004 (~32% and 15%, respectively) in response to the more than 7-fold increase in highly protected zones (Fig. 4*B*; excludes special initiatives). Estimated current investment in field management and compliance is A$47 per km^2 no-take zone per year, plus an estimated A$30 per km^2 per year for surveillance by the Australian Customs (Coastwatch). Implementation of the new zoning plan involved a once-off communication and awareness program of A$4.3 million over 5 years funded under a special initiative by the Australian Government (data courtesy GBRMPA, all figures in Australian dollars).

Importantly, expenditure on zoning and on overall management of the Marine Park are relatively minor when compared to the estimated economic value of the GBR (Fig. 4*A*). Proportional to economic returns, since 2004 annual investment in overall management of the Marine Park has been consistently less than 0.9% and decreasing, and expenditure on field management (predominantly zoning compliance) has been consistently less than 0.3% and decreasing (strictly such comparisons should use net value of the GBR, rather than gross output values, but net measures are not available; precise allocation of zoning and other field management costs is not possible). Even the costs of structural adjustment only amount to about 3.9% of the economic returns from the GBR in a single year (2006–2007 financial year).

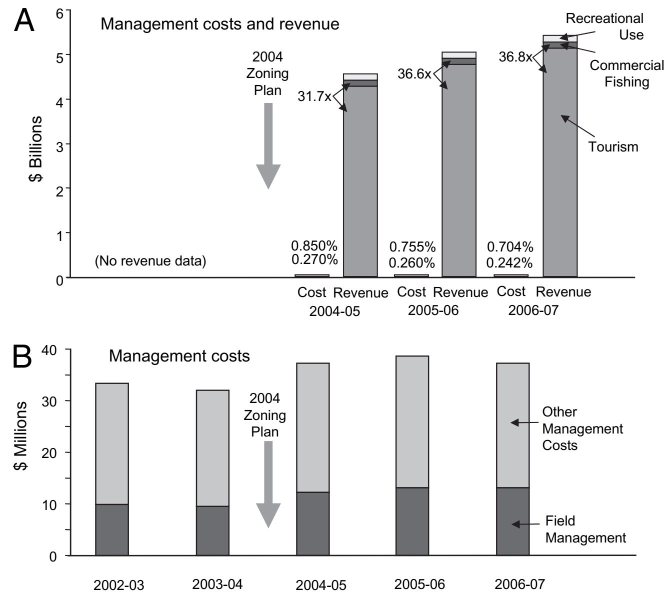


Fig. 4. Economic costs and benefits for the Great Barrier Reef. (*A*) Economic value of the GBR to the Australian economy (50–52), compared to expenditure on management of the Great Barrier Reef Marine Park (65–67). Tourism provides the vast majority of economic benefits (numbers indicate ratio of tourism to commercial fishery estimates). Percentages above costs give expenditure as percentage of revenue, respectively, for overall expenditure on management of the Marine Park and for field management. (*B*) Costs of field management (including enforcement) and other management of the GBR (65–69). All values in Australian dollars.

Marine Reserve Paradigms: Insights from the Great Barrier Reef

Overall, zoning of the GBR marine reserve network appears to be making major contributions to the protection of biodiversity, ecosystem resilience, and social and economic values of the GBR Marine Park. The breadth and regional scale of these benefits provide important validation and extension of emerging ideas about the value of reserve networks (e.g., consensus statement in ref. 9), particularly given that the GBR is the first large network designed systematically at a regional scale and provides scope for rigorous comparisons (12, 62) (see Introduction and *SI Section 1*). The results demonstrate the value of reserves both for active restoration of ecosystem structure (e.g., the widespread recovery of depleted fish stocks within the new no-take network), and for preventing ongoing degradation (the stated primary goal of the 2004 zoning; e.g., reduced coral mortality). However, it must also be emphasized that the GBR sits within an exceptional context, in terms of biogeography, scale, governance, and economics, so that emerging lessons should not be assumed relevant across all circumstances. For example, the extent of the 2004 zoning network may not be feasible in regions that lack centralized governance arrangements or that lack resources for effective enforcement. Further, this paper focuses on the effects of zoning, but those results must be seen in the context of broader, complementary management and monitoring initiatives (see below). Insights into the specific scientific challenges of assessing the effects of marine reserves are discussed in *SI Section 8*.

The breadth and extent of benefits reflect very well on the scientific and engagement processes involved in the development and implementation of the 2004 Zoning Plan (11), especially the value of larger reserve size and high proportion of overall area in reserves to provide margins of error. For example, the protection of natural patterns of reef separation (Fig. S4) was not incorporated in the design in its own right, but is an outcome of the robust and comprehensive design principles (11). Similarly, comprehensive protection of minimum levels of seabed biodiversity (*SI Section 5*) is an outcome of those same principles and demonstrates the effective use of physical data as proxies where prior knowledge of biodiversity is limited. The benefit to the entire ecosystem of enhanced fish populations, or reduced coral mortality, clearly increases with increased proportional area of reserves.

Scientifically, effects such as increased biomass of target fish in protected areas are not novel. However, results from the GBR demonstrate those benefits over larger scales and provide concrete examples of the value of monitoring for evaluating management effectiveness and for community acceptance (8, 9) (*SI Sections 1 and 7*). The breadth and scale of GBR monitoring also illustrate the considerable variability inherent in the effects of reserves, variability among regions (Fig. 1 and Fig. S1 *B* and *C*) and among species with different life-history traits or vulnerability to fishing (e.g., target fish cf. sharks and dugongs cf. prey species). Reserve effects also depend strongly on the extent of fishing pressure and compliance within a region.

The demonstration of indirect benefits on corals, through crown-of-thorns starfish

(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.

ACKNOWLEDGMENTS. The assistance and data provided by the Great Barrier Reef Marine Park Authority (GBRMPA) and numerous staff is greatly appreciated. S. Gaines, K. Grorud-Colvert, S. Lester, N. Stoeckl, J. Quiggan, and G. Lange provided valuable comments. The authors acknowledge the traditional owners of the sea country of the Great Barrier Reef. Shoals monitoring results are courtesy of the Marine and Tropical Sciences Research Facility (MTSRF) and especially P. Speare, M. Stowar, and P. Doherty. This work was supported by a Pew Fellowship in Marine Conservation (to L.Mc.C.), the Australian Research Council Centre of Excellence for Coral Reef Studies, the MTSRF/Reef and Rainforest Research Centre, the GBRMPA, and the Australian Institute of Marine Science. The Effects of Line Fishing Experiment was supported by the Cooperative Research Centre for the Great Barrier Reef, the Fisheries Research and Development Corporation, the GBRMPA, Queensland Fisheries Management Authority, Commonwealth Scientific and Industrial Research Organisation Marine and Atmospheric Research.

1. Roberts CM, et al. (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295:1280–1284.
2. Pitcher CR, et al. (2007) *Seabed Biodiversity on the Continental Shelf of the Great Barrier Reef World Heritage Area: CRC Reef Research Task Final Report* (CSIRO Marine and Atmospheric Research, Cleveland, QLD).
3. Hughes TP, et al. (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933.
4. Hoegh-Guldberg O, et al. (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742.
5. Wilkinson C (2008) *Status of Coral Reefs of the World: 2008* (Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville).
6. McCook LJ, et al. (2007) Ecological resilience, climate change and the Great Barrier Reef. *Climate Change and the Great Barrier Reef*, eds Johnson J, Marshall P (Great Barrier Reef Marine Park Authority, Townsville), pp 75–96.
7. McCook LJ, et al. (2009) Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. *Coral Reefs* 28:353–366.

8. Great Barrier Reef Marine Park Authority (2009) *Great Barrier Reef Outlook Report* (Great Barrier Reef Marine Park Authority, Townsville).
9. Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: the emerging science of marine reserves. *Ecol Appl* 13:S3–S7.
10. Russ GR (2002) Marine reserves as reef fisheries management tools: yet another review. *Coral Reef Fishes Dynamics and Diversity in a Complex Ecosystem*, ed Sale PF (Academic Press, San Diego), pp 421–443.
11. Fernandes L, et al. (2005) Establishing representative no-take areas in the Great Barrier Reef: Large-scale implementation of theory on marine protected areas. *Conserv Biol* 19:1733–1744.
12. Hughes TP, et al. (2007) Adaptive management of the Great Barrier Reef and the Grand Canyon World Heritage Areas. *Ambio* 7:586–592.
13. Russ GR, et al. (2008) Rapid increase in fish numbers follows creation of world's largest marine reserve network. *Curr Biol* 18:R514–R515.
14. Mapstone BD, et al. (2008) Management strategy evaluation for line fishing in the Great Barrier Reef: Balancing conservation and multi-sector fishery objectives. *Fish Res* 94:315–329.
15. Mapstone BD, et al. (2004) *The Effects of Line Fishing on the Great Barrier Reef and Evaluations of Alternative Potential Management Strategies* (CRC Reef Research Centre, Townsville) , Technical Report No. 52.
16. Birkeland C, Dayton PK (2005) The importance in fishery management of leaving the big ones. *Trends Ecol Evol* 20:356–358.
17. Cappo M, MacNeil A, Stowar M, Doherty P (2008) *The Influence of Zoning (Closure to Fishing) on Fish Communities of the Deep Reef Bases of the Southern Great Barrier Reef Marine Park. Part 1. Baited Video Surveys of the Pompeys, Swains, and Capricorn-Bunker Groups off Mackay and Gladstone. Report to the Marine and Tropical Sciences Research Facility* (Reef and Rainforest Research Centre Limited, Cairns and Australian Institute of Marine Science, Townsville).
18. Williamson DH, Russ GR, Ayling AM (2004) No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environ Conserv* 31:149–159.
19. Evans RD, Russ GR (2004) Larger biomass of targeted reef fish in no-take marine reserves on the Great Barrier Reef, Australia. *Aquatic Conservation* 14:505–519.
20. Ayling AM, Choat JH (2008) *Abundance Patterns of Reef Sharks and Predatory Fishes on Differently Zoned Reefs in the Offshore Townsville Region* (Great Barrier Reef Marine Park Authority, Townsville) , Research Publication No. 91.
21. Robbins WD, Hisano M, Connolly SR, Choat JH (2006) Ongoing collapse of coral-reef shark populations. *Curr Biol* 16:2314–2319.
22. Heupel M, et al. (2009) Effects of fishing on tropical reef associated shark populations on the Great Barrier Reef. *Fish Res* 95:350–361.
23. Guidetti P (2006) Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. *Ecol Appl* 16:963–976.
24. Jones GP, et al. (2007) Larval retention and connectivity among populations of corals and reef fishes: History, advances and challenges. *Coral Reefs* 28:307–325.
25. Almany GR, et al. (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs* 28:339–351.
26. Zeller DC, Russ GR (1998) Marine reserves: Patterns of adult movement of the coral trout *Plectropomus leopardus* (Serranidae). *Can J Fish Aquat Sci* 55:917–924.
27. Zeller D, Stoute SL, Russ GR (2003) Movements of reef fishes across marine reserve boundaries: Effects of manipulating a density gradient. *Mar Ecol Prog Ser* 254:269–280.
28. Davies CR (2000) *Inter-Reef Movement of the Common Coral Trout Plectropomus leopardus* (Great Barrier Reef Marine Park Authority, Townsville), Research Publication No. 61.
29. Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. *Nature* 402: 802–804.
30. Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. *Curr Biol* 15:1314–1318.
31. Sweatman H (2008) No-take reserves protect coral reefs from predatory starfish. *Curr Biol* 18:R598–R599.
32. Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environ Conserv* 30:200–208.
33. Pitcher R, Venables B, Browne M, Doherty P, De'ath G (2007) *Indicators of Protection Levels for Seabed Habitats, Species and Assemblages on the Continental Shelf of the Great Barrier Reef World Heritage Area. Report to the Marine and Tropical Sciences Research Facility* (Reef and Rainforest Research Centre Limited, Cairns).
34. Poiner IR, et al. (1998) The environmental effects of prawn trawling in the far northern section of the Great Barrier Reef Marine Park: 1991-1996. (CSIRO and Queensland Department of Primary Industries, Cleveland, QLD), Final Report to GBRMPA and FRDC.
35. Pitcher CR, et al. (2008) Recovery of seabed habitat from the impact of prawn trawling in the Far Northern Section of the Great Barrier Reef Marine Park. (CSIRO, Cleveland, QLD).
36. Coles R, Grech A, Dew K, Zeller B, McKenzie L (2008) *A Preliminary Report on the Adequacy of Protection Provided to Species and Benthic Habitats in the East Coast Otter Trawl Fishery by the Current System of Closures* (Department of Primary Industries and Fisheries, Brisbane).
37. Stowar M, et al. (2008) *Influence of Zoning on Midshelf Shoals from the Southern Great Barrier Reef. Report to the Marine and Tropical Sciences Research Facility* (Reef and Rainforest Research Centre Limited, Cairns).
38. Speare P, Stowar M, Johansson C (2008) *Temporal Monitoring of Northern Shoals off Cardwell and Townsville. Report to the Marine and Tropical Sciences Research Facility* (Reef and Rainforest Research Centre Limited, Cairns).
39. Marsh H, Eros C, Corkeron P, Breen B (1999) A conservation strategy for dugongs: Implications of Australian research. *Mar Freshw Res* 50:979–990.
40. Marsh H, De'ath G, Gribble N, Lane B (2005) Historical marine population estimates: Triggers or targets for conservation? The dugong case study. *Ecol Appl* 15: 481–492.
41. Sheppard J, Preen AR, Marsh H, Lawler IR, Jones RE (2007) Movement heterogeneity of dugongs, *Dugong dugon* (Müller) over large spatial scales. *J Exp Mar Biol Ecol* 334:64–83.
42. McDonald B (2006) Population genetics of dugongs around Australia; Implications for contemporary management. PhD thesis (James Cook University, Townsville).
43. Pollock K, Marsh H, Lawler I, Alldredge M (2006) Modelling availability and perception processes for strip and line transects: An application to dugong aerial surveys. *J Wildl Manage* 70:255–262.
44. Marsh H (2000) Evaluating management initiatives aimed at reducing the mortality of dugongs in gill and mesh nets in the Great Barrier Reef World Heritage Area. *Mar Mamm Sci* 16:684–694.
45. Dobbs K, et al. (2008) Incorporating dugong habitats into the marine protected area design for the Great Barrier Reef Marine Park, Queensland, Australia. *Ocean Coast Manage* 51:368–375.
46. Grech A, Marsh H (2008) Rapid assessment of risks to a mobile marine mammal in an ecosystem-scale marine protected area. *Conserv Biol* 22:711–720.
47. Grech A, Marsh H, Coles R (2008) A spatial assessment of the risk to a mobile marine mammal from bycatch. *Aquatic Conservation* 18:1127–1139.
48. Dobbs K, et al. (2007) Incorporating marine turtle habitats into the marine protected area design for the Great Barrier Reef Marine Park. *Pac Conserv Biol* 13:293–302.
49. Dryden J, Grech A, Moloney J, Hamann M (2008) Rezoning of the Great Barrier Reef World Heritage Area: Does it afford greater protection for marine turtles? *Wildl Res* 35:477–485.
50. Access Economics Pty Ltd (2006) *Measuring the Economic and Financial Value of the Great Barrier Reef Marine Park* (Great Barrier Reef Marine Park Authority, Townsville).
51. Access Economics Pty Ltd (2007) *Measuring the Economic and Financial Value of the Great Barrier Reef Marine Park, 2005-06* (Great Barrier Reef Marine Park Authority, Townsville).
52. Access Economics Pty Ltd (2008) *Economic Contribution of the GBRMP, 2006-07* (Great Barrier Reef Marine Park Authority, Townsville).
53. Department of the Environment Water Heritage and the Arts (2008) *Annual Report 2007-08* (Department of the Environment, Water, Heritage and the Arts, Canberra).
54. Department of the Environment and Heritage (2005) *Annual Report 2004-05* (Department of the Environment and Heritage, Canberra).
55. Australian Fisheries Management Authority (2004) *Environment Update 21* (Australian Fisheries Management Authority, Canberra).
56. Department of the Environment and Heritage (2006) *Review of the Great Barrier Reef Marine Park Act 1975, Review Panel Report* (Department of the Environment and Heritage, Canberra, Australia).
57. Hand T (2003) An economic and social evaluation of implementing the representative areas program by rezoning the Great Barrier Reef Marine Park: Report on the revised zoning plan. Submitted to the Australian Parliament, (P. D. P. Australia Pty Ltd. and Great Barrier Reef Marine Park Authority, Townsville).
58. Great Barrier Reef Marine Park Authority (2003) Explanatory statement: Great Barrier Reef Zoning Plan 2003. Submitted to the Australian Parliament, (Great Barrier Reef Marine Park Authority, Townsville) . Available at http://kurrawa.gbrmpa.gov.au/corp_site/management/zoning/rap/rap/pdf/ES_25-11-03.pdf; accessed July 2009.
59. Bureau of Rural Sciences (2003) *Implementing the Representative Areas Program in the Great Barrier Reef Marine Park - BRS Assessment of Potential Social Impact on Commercial Fishing and Associated Communities* (Bureau of Rural Sciences, Canberra).
60. Minnegal M, Dwyer PD (2008) Mixed messages: Buying back Australia's fishing industry. *Mar Policy* 32: 1063–1071.
61. Fisheries Economics Research Management Pty Ltd (2007) *A Review of the Business Exit (Licence Buyout) Assistance Component of the Great Barrier Reef Marine Park Structural Adjustment Package, Final Report* (Department of Environment and Water Resources, Canberra).
62. Leslie HM (2005) Synthesis of marine conservation planning approaches. *Conserv Biol* 19:1701–1713.
63. Mumby PJ, et al. (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311: 98–101.
64. McClanahan TR, Muthiga NA, Maina J, Kamukuru AT, Yahya SAS (2009) Changes in northern Tanzania coral reefs during a period of increased fisheries management and climatic disturbance. *Aquatic Conservation* 89:161–182.
65. Great Barrier Reef Marine Park Authority (2005) *Annual Report 2004–2005* (Great Barrier Reef Marine Park Authority, Townsville).
66. Great Barrier Reef Marine Park Authority (2006) *Annual Report 2005–2006* (Great Barrier Reef Marine Park Authority, Townsville).
67. Great Barrier Reef Marine Park Authority (2007) *Annual Report 2006–2007* (Great Barrier Reef Marine Park Authority, Townsville).
68. Great Barrier Reef Marine Park Authority (2003) *Annual Report 2002–2003* (Great Barrier Reef Marine Park Authority, Townsville).
69. Great Barrier Reef Marine Park Authority (2004) *Annual Report 2003–2004* (Great Barrier Reef Marine Park Authority, Townsville).

Supporting Information

McCook et al. 10.1073/pnas.0909335107

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

Table S1: Spatial zoning within the Great Barrier Reef Marine Park

GBRMPA Zone / (Terminology for this paper)	Activities	% area 2004	% Previous
General Use **(Open / Fished)**	All reasonable uses: trawling and large mesh gill netting allowed.	33.8%	77.9%
Habitat Protection **(Open / fished)**	**Trawling prohibited**, large mesh gill netting allowed.	28.2%	15.2%
Conservation Park	Gill netting and trawling prohibited; limited fishing and collecting allowed.	1.5%	0.6%
Buffer	Fishing limited to trolling for pelagic fish only.	2.9%	0.1%
Scientific Research	Extractive use prohibited without the GBRMPA's permission except some types of Scientific Research.	0.05%	0.01%
Marine National Park **(No-take)**	Extractive use prohibited without the GBRMPA's permission.	33.3%	4.6%
Preservation **(No-entry)**	Access prohibited without the GBRMPA's permission.	0.2%	0.1%
Commonwealth Islands	Extractive use prohibited without the GBRMPA's permission in waters surrounding the islands.		

Consistent colour-coding is used throughout GBRMPA publications and maps to indicate different zones. Further detail available at: www.gbrmpa.gov.au/corp_site/management/zoning

Table S2: Chronology of zoning and related monitoring on the Great Barrier Reef

Date	Implementation	Monitoring
1975	Great Barrier Reef Marine Park and GBR Marine Park Authority created;	Australian Institute of Marine Science (AIMS) created;
1981-1992	Implementation of initial zoning schemes;	
1980s, 1990s		A range of surveys of biodiversity distributions, especially corals and fish;
1986		Crown-of-thorns starfish surveys begun (AIMS);
1993		AIMS GBR Long Term Monitoring Program begun;
1990s-early 2000s		Effects of trawling study (53);
		Effects of line fishing study (4);
		Monitoring of inshore fish (23-25);
1998	Representative Areas Program for new zoning commenced;	
2003-2006		GBR Seabed Biodiversity surveys (51);
2004	New Zoning Plan implemented;	Initial monitoring;
	Education and surveillance/ enforcement programs;	
2006-2008		Post-zoning monitoring (e.g. 69);
2009	GBR Outlook Report 2009 submitted to Parliament (1).	

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.

1. Great Barrier Reef Marine Park Authority (2009) *Great Barrier Reef Outlook Report* (Great Barrier Reef Marine Park Authority, Townsville).
2. Higgs JB (1996) *A Review of Published Fisheries Dependent and Independent Surveys of the Recreational Great Barrier Reef Line Fisheries and Demersal Reef Fish Stocks. Report to the Queensland Fisheries Management Authority* (CRC Reef Research Centre, Townsville).
3. Mapstone BD, McKinlay JP, Davies CR (1996) *A Description of the Commercial Reef Line Fishery Logbook Data Held by the Queensland Fisheries Management Authority. Report to the Queensland Fisheries Management Authority* (CRC Reef Research Centre, Townsville).
4. Mapstone BD, et al. (2004) *The Effects of Line Fishing on the Great Barrier Reef and Evaluations of Alternative Potential Management Strategies* (CRC Reef Research Centre, Townsville), Technical Report No. 52.
5. Holling CS (1978) *Adaptive Environmental Assessment and Management* (Wiley, New York).
6. Walters CJ, Hilborn R (1978) Ecological optimization and adaptive management. *Annu Rev Ecol Syst* 9:157–188.
7. Holling CS (2004) From complex regions to complex worlds. *Ecol. Soc* 9:11.
8. McCarthy MA, Possingham HP (2007) Active adaptive management for conservation. *Conserv Biol* 21:956–963.
9. Hughes TP, et al. (2007) Adaptive management of the Great Barrier Reef and the Grand Canyon World Heritage Areas. *Ambio* 7:586–592.
10. Commonwealth of Australia (1998) *Australia's Oceans Policy (Canberra)* (Department of the Environment Water, and the Arts, Canberra).
11. Robbins WD, Hisano M, Connolly SR, Choat JH (2006) Ongoing collapse of coral-reef shark populations. *Curr Biol* 16:2314–2319.
12. Ayling AM, Choat JH (2008) *Abundance Patterns of Reef Sharks and Predatory Fishes on Differently Zoned Reefs in the Offshore Townsville Region* (Great Barrier Reef Marine Park Authority, Townsville), Research Publication No.91).
13. Day J (2002) Zoning: Lessons from the Great Barrier Reef Marine Park. *Ocean Coast Manage* 45:139–156.
14. Fernandes L, et al. (2005) Establishing representative no-take areas in the Great Barrier Reef: Large-scale implementation of theory on marine protected areas. *Conserv Biol* 19:1733–1744.
15. Olsson P, Folke C, Hughes TP (2008) Navigating the transition to ecosystem-based management of the Great Barrier Reef, Australia. *Proc Natl Acad Sci USA* 105: 9489–9494.
16. Great Barrier Reef Marine Park Authority (2003) *Explanatory statement: Great Barrier Reef Zoning Plan 2003.* Submitted to the Australian Parliament (Great Barrier Reef Marine Park Authority) Available at http://kurrawa.gbrmpa.gov.au/corp_site/management/zoning/rap/rap/pdf/ES_25-11-03.pdf; accessed July 2009.
17. Pressey R, Cabezza M, Watts M, Cowling R, Wilson K (2007) Conservation planning in a changing world. *Trends Ecol Evol* 22:583–592.
18. Mapleston A, Begg G, Ballagh A, Goldman B, Williams A (2006) *Monitoring the Effects of Rezoning on Nonreef Habitats of the Great Barrier Reef: Identifying Locations and Harvested Species of Interest* (CRC Reef Research Centre, Townsville).
19. Mapstone BD, et al. (2008) Management strategy evaluation for line fishing in the Great Barrier Reef: Balancing conservation and multi-sector fishery objectives. *Fish Res* 94:315–329.
20. Sawynok W (2007) *What is CapReef?* (CapReef, Rockhampton, Australia).
21. Platten J, Sawynok W (2006) *The Effects of Management Changes on the Catches of Two Deep-Sea Fishing Clubs in Central Queensland* (CapReef, Rockhampton, Australia).
22. Sawynok W, Platten J, Parsons W (2009) *How Much Fishing Effort Is There 2005-2009?* (CapReef, Rockhampton, Australia).
23. Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environ Conserv* 30:200–208.
24. Evans RD, Russ GR (2004) Larger biomass of targeted reef fish in no-take marine reserves on the Great Barrier Reef, Australia. *Aquatic Conservation* 14:505–519.
25. Williamson DH, Russ GR, Ayling AM (2004) No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environ Conserv* 31:149–159.
26. Heupel MR, et al. (2009) Effects of fishing on tropical reef associated shark populations on the Great Barrier Reef. *Fish Res* 95:350–361.
27. Little L, et al. (2005) Effects of size and fragmentation of marine reserves and fisher infringement on the catch and biomass of coral trout, *Plectropomus leopardus*, on the Great Barrier Reef, Australia. *Fish Manag Ecol* 12:177–188.
28. James MK, Armsworth PR, Mason LB, Bode L (2002) The structure of reef fish metapopulations: Modelling larval dispersal and retention patterns. *Proc R Soc B Biol Sci* 269:2079–2086.
29. Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. *Nature* 402:802–804.
30. Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402:799–802.
31. Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: Open or closed? *Science* 287:857–859.
32. Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. *Curr Biol* 15:1314–1318.
33. Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science* 316:742–744.
34. Saenz-Agudelo P, Jones GP, Thorrold SR, Planes S (2009) Estimating connectivity in marine populations: An empirical evaluation of assignment tests and parentage analysis under different gene flow scenarios. *Mol Ecol* 18:1765–1776.
35. Jones GP, et al. (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenge. *Coral Reefs* 28:307–325.
36. Planes S, Jones GP, Thorrold SR (2009) Larval dispersal connects fish populations in a network of marine protected areas. *Proc Natl Acad Sci USA* 106:5693–5697.
37. Thorrold SR, Jones GP, Planes S, Hare JA (2006) Transgenerational marking of embryonic otoliths in marine fishes using barium stable isotopes. *Can J Fish Aquat Sci* 63:1193–1197.
38. Goeden GB (1978) A monograph of the coral trout, *Plectropomus leopardus* (Lacepede). *Qld Fish. Serv. Res Bull (Sun Chiwawitthaya thang Thale Phuket)* 1:1–42.
39. Evans RD, Russ GR, Kritzer JP (2008) Batch fecundity of *Lutjanus carponotatus* (Lutjanidae) and implications of no-take marine reserves on the Great Barrier Reef, Australia. *Coral Reefs* 27:179–189.
40. Berkeley SA, Hixon MA, Larson RJ, Love MS (2004) Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29:23–32.
41. Adams S, Mapstone BD, Russ GR, Davies CR (2000) Geographic variation in the sex ratio, sex specific size, and age structure of *Plectropomus leopardus* (Serranidae) between reefs open and closed to fishing on the Great Barrier Reef. *Can J Fish Aquat Sci* 57:1448–1458.
42. Almany GR, et al. (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs* 28:339–351.
43. ESRI (2002) ArcView Version 3.3 (Environmental Systems Research Institute, Redlands, CA).
44. ESRI (2006) ArcMap Version 9.2 (Environmental Systems Research Institute, Redlands, CA).
45. Jenness J (2004) Nearest Features (nearfeat.avx) extension for ArcView 3.x, v. 3.8a (Jenness Enterprises). Available at http://www.jennessent.com/arcview/nearest_features.htm.

46. Sweatman H (2008) No-take reserves protect coral reefs from predatory starfish. *Curr Biol* 18:R598–R599.
47. Miller IR (2003) *Crown-of-Thorns Starfish and Coral Surveys Using the Manta Tow and Scuba Search Techniques.* (Australian Institute of Marine Science, Townsville), Standard operational procedure, No 8.
48. Brown M, Forsythe AB (1974) Robust tests for equality of variances. *J Am Stat Assoc* 69:364–367.
49. Underwood AJ (1997) *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance* (Cambridge University Press, Cambridge).
50. Evans RD (2009) No-take marine protected areas: Abundance, biomass, batch fecundity and genetic connectivity of target species on the Great Barrier Reef. PhD thesis (James Cook University, Townsville, Australia).
51. Pitcher CR, et al. (2007) *Seabed Biodiversity on the Continental Shelf of the Great Barrier Reef World Heritage Area: CRC Reef Research Task Final Report.* (CSIRO Marine Marine and Atmospheric Research and CRC Reef Research Centre, Cleveland, QLD).
52. Pitcher R, Venables B, Browne M, Doherty P, De'ath G (2007) *Indicators of Protection Levels for Seabed Habitats, Species and Assemblages on the Continental Shelf of the Great Barrier Reef World Heritage Area. Report to the Marine and Tropical Sciences Research Facility* (Reef and Rainforest Research Centre, Cairns).
53. Poiner IR, et al. (1998) The environmental effects of prawn trawling in the far northern section of the Great Barrier Reef Marine Park: 1991-1996 (CSIRO and Queensland Department of Primary Industries, Cleveland, QLD), Final Report to GBRMPA and FRDC.
54. Pitcher CR, et al. (2008) Recovery of seabed habitat from the impact of prawn trawling in the Far Northern Section of the Great Barrier Reef Marine Park. (CSIRO, Cleveland, Qld, Australia).
55. Coles R, Grech A, Dew K, Zeller B, McKenzie L (2008) *A Preliminary Report on the Adequacy of Protection Provided to Species and Benthic Habitats in the East Coast Otter Trawl Fishery by the Current System of Closures.* (Department of Primary Industries and Fisheries, Brisbane).
56. Limpus CJ (2007) *A Biological Review of Australian Marine Turtle Species. 1. Loggerhead Turtle, Caretta caretta (Linnaeus)* (Queensland Environmental Protection Agency, Brisbane).
57. Courtney AJ, et al. (2007) *Bycatch Weight, Composition and Preliminary Estimates of the Impact of Bycatch Reduction Devices (BRDs)* (Queensland Department of Primary Industries and Fisheries, Brisbane, Australia), Report to the Fisheries Research and Development Corporation No. 2000/170.
58. Marsh H, De'ath G, Gribble N, Lane B (2005) Historical marine population estimates: Triggers or targets for conservation? The dugong case study. *Ecol Appl* 15:481–492.
59. International Union for Conservation of Nature (2009) IUCN Red List of Threatened Species. Version 2009.1. (IUCN, Gland, Switzerland and Cambridge, UK).
60. Great Barrier Reef Marine Park Authority (1981) *Nomination of the Great Barrier Reef by the Commonwealth of Austalia for Inclusion in the World Heritage List* (Great Barrier Reef Marine Park Authority, Townsville, Australia).
61. Havemann P, Thiriet D, Marsh H, Jones C (2005) Decolonising conservation? Traditional use of marine resources agreements and dugong hunting in the Great Barrier Reef World Heritage Area. *Environmental and Planning Law Journal* 22:258–280.
62. Grech A, Marsh H (2008) Rapid assessment of risks to a mobile marine mammal in an ecosystem-scale marine protected area. *Conserv Biol* 22:711–720.
63. Davis KLF, Russ GR, Williamson DH, Evans RD (2004) Surveillance and poaching on inshore reefs of the Great Barrier Reef Marine Park. *Coast Manage* 32:373–387.
64. Young J, Temperton J (2007) *Measuring Community Attitudes and Awareness Towards the Great Barrier Reef 2007* (Great Barrier Reef Marine Park Authority, Townsville), Research Publication No. 90.
65. Sutton S, Tobin R (2009) Recreational fishers' attitudes towards the 2004 rezoning of the Great Barrier Reef Marine Park. *Environ Conserv* Published online December 14, 2009 doi:10.1017/S0376892909990270.
66. Close CH, Hall GB (2006) A GIS-based protocol for the collection and use of local knowledge in fisheries management planning. *J Environ Manage* 78:341–352.
67. Hall GB, Close CH (2007) Local knowledge assessment for a small-scale fishery using geographic information systems. *Fish Res* 83:11–22.
68. De Freitas DM, Tagliani PRA (2009) The use of GIS for the integration of traditional and scientific knowledge in supporting artisanal fisheries management in southern Brazil. *J Environ Manage* 90:2071–2080.
69. Russ GR, et al. (2008) Rapid increase in fish numbers follows creation of world's largest marine reserve network. *Curr Biol* 18:R514–R515.
70. Stowar M, et al. (2008) *Influence of Zoning on Midself Shoals from the Southern Great Barrier Reef. Report to the Marine and Tropical Sciences Research Facility* (Reef and Rainforest Research Centre Limited, Cairns).

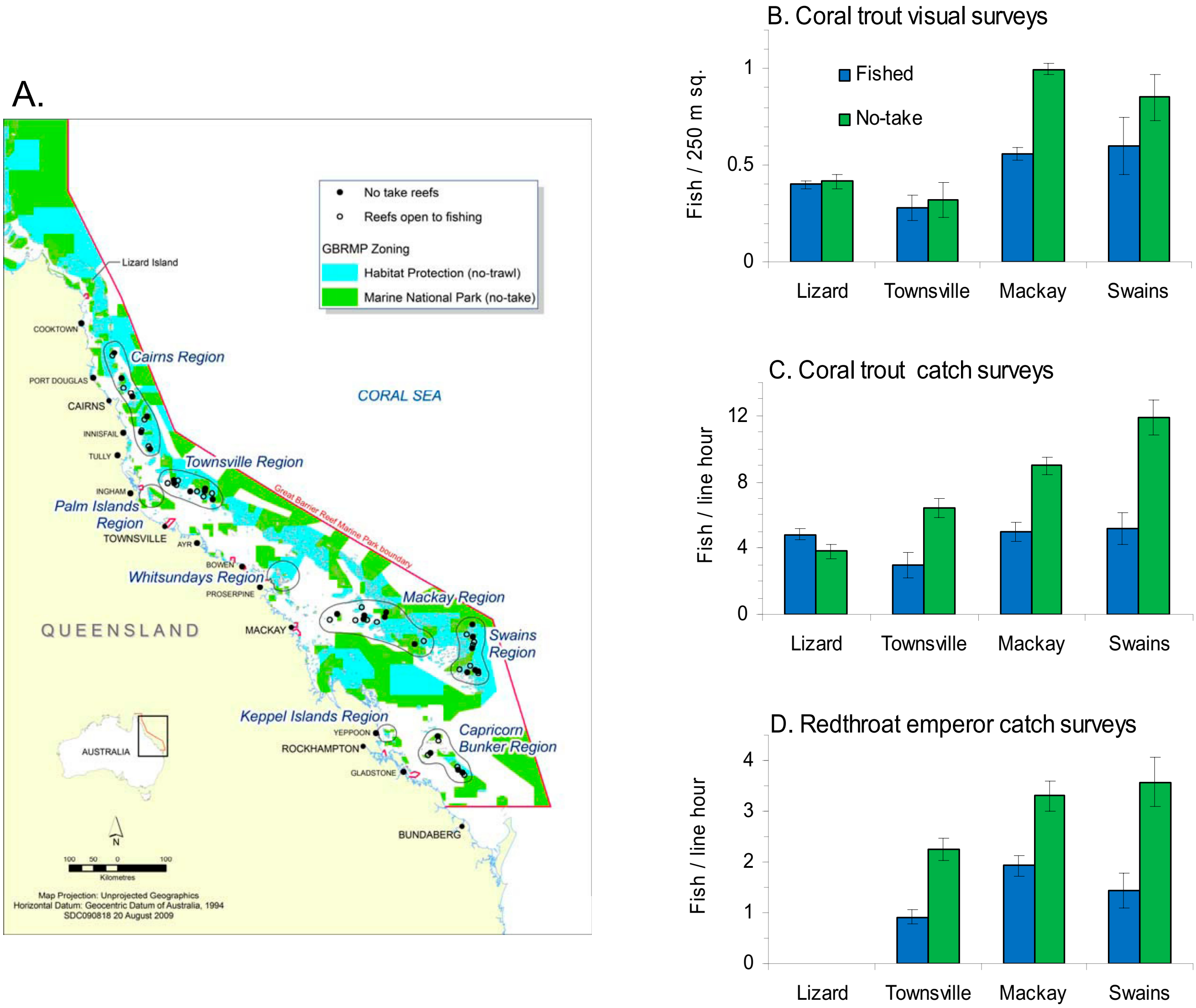


Fig. S1. (*A*) Map of the Great Barrier Reef Marine Park showing the location of study regions and study reefs for *B–D*. Abundance of target fish on fished and no-take reefs before the new zoning plan, showing variations between species, regions, and survey methods. Data, not previously published in 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*.

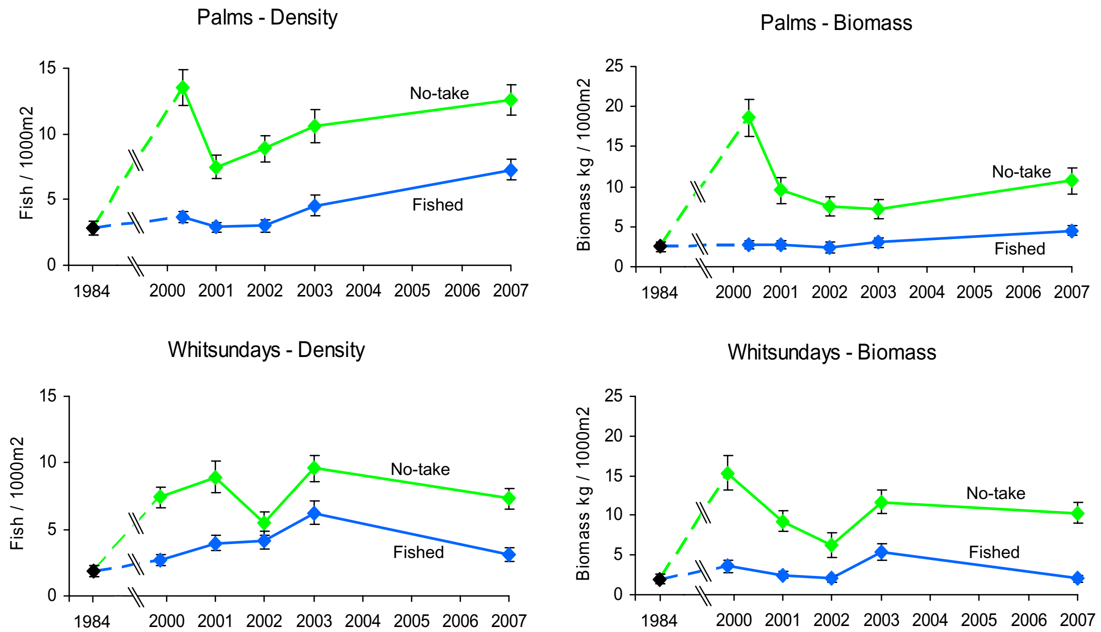


Fig. S2. Temporal dynamics in coral trout (*Plectropomus* spp.) in no-take and fished zones of the inshore Palm and Whitsunday Island groups, for zones implemented before 2004. Baseline data from 1984 were collected before the establishment of no-take zones in 1988. Data are mean (±SEM). Data previously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

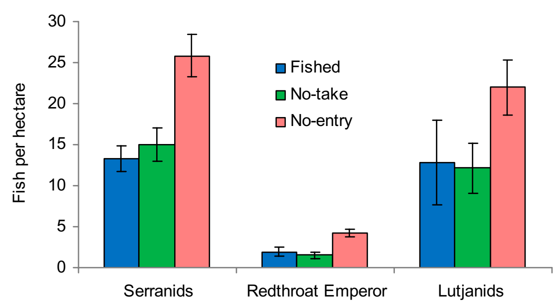


Fig. S3. Abundance of target fish in no-entry, no-take, and fished reefs in the central GBR. Serranids are predominantly coral trout; data, expanded from ref. 12, are means ±SEM, based on scuba-based, visual transects.

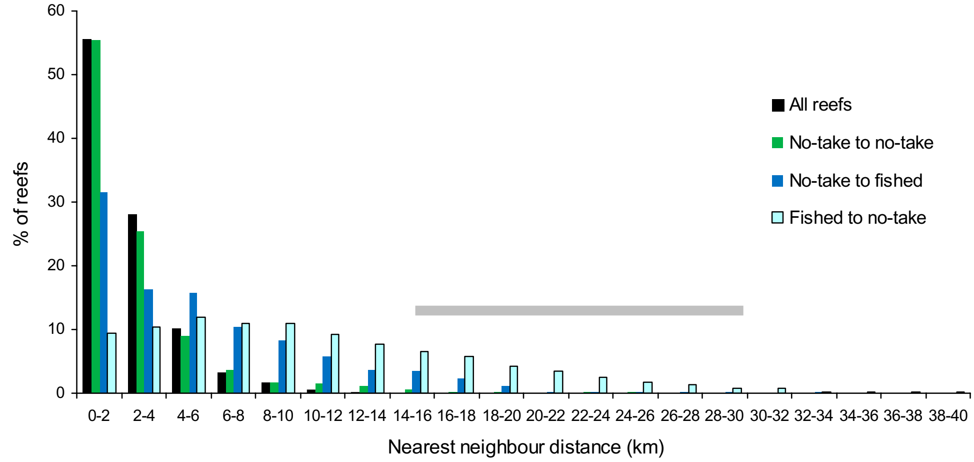


Fig. S4. Distance between neighboring reefs within the Great Barrier Reef Marine Park. Distances indicate, for each reef, the distance to the nearest reef that could contribute larvae to maintain populations on the first reef (graph truncated at 40 km). Recent studies recommend maximizing proportions 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.)

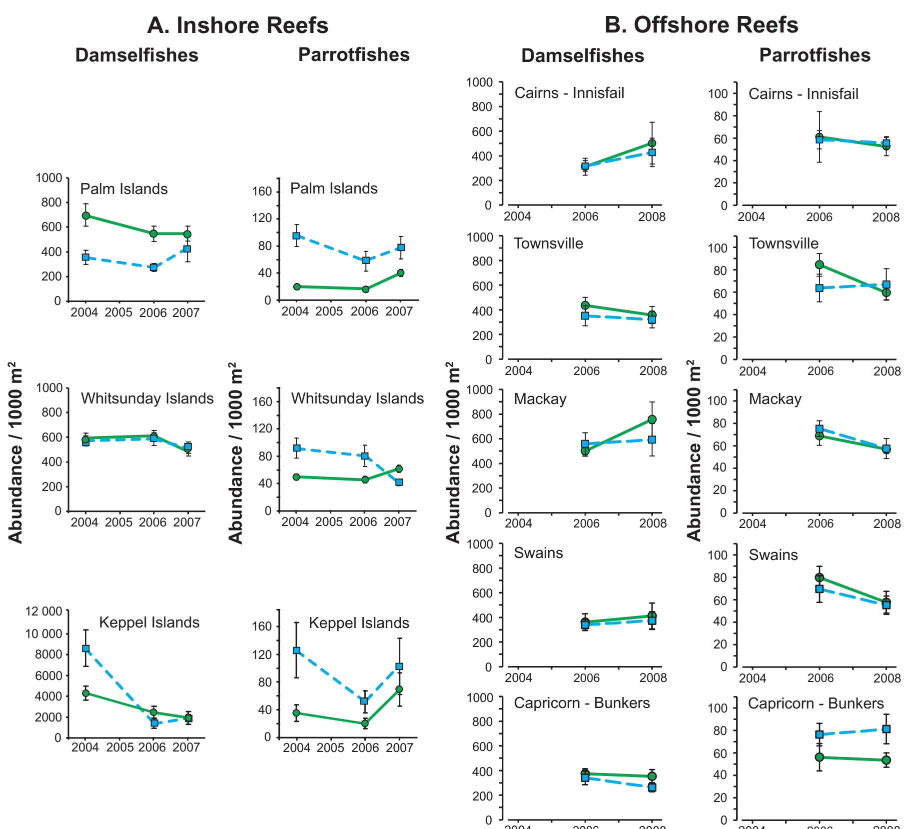


Fig. S5. Abundance of damelfishes and small parrotfishes on (A) inshore reefs and (B) offshore reefs of the GBR. Green lines are no-take zones; blue are fished reefs. Data, not previously published, are means ±SEM from scuba-based, visual transects of reefs zoned in 2004. Data for inshore reefs (A) include 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.

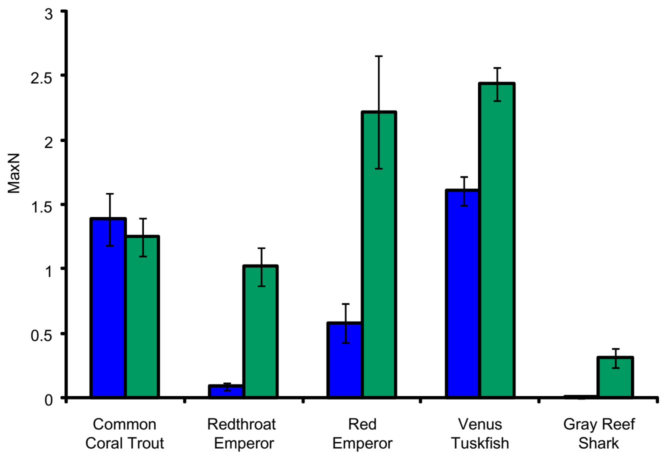


Fig. S6. Mean abundance of targeted fish and sharks on deepwater shoals in the southern GBR based on baited, remote, underwater video surveys. Data are mean ±SEM of MaxN, the maximum number of individuals observed at any moment (n = 89 and 97 surveys for fished and no-take reefs respectively; detailed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

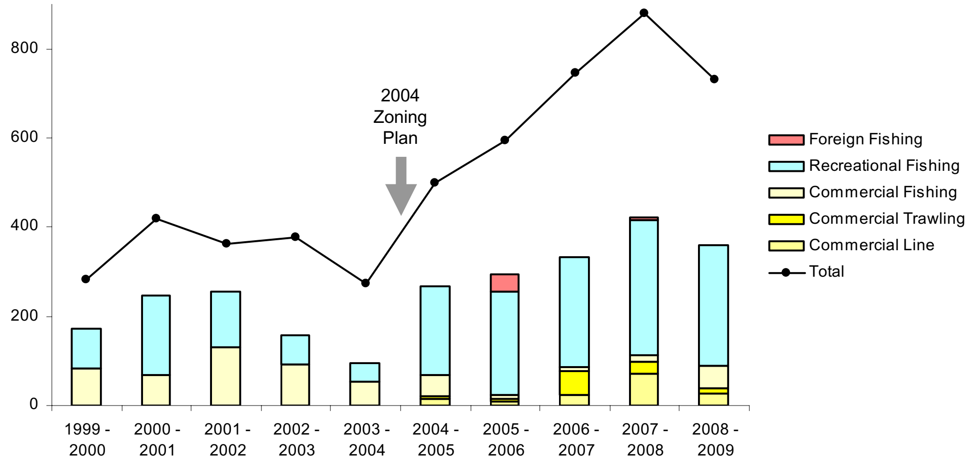


Fig. S7. Recorded compliance offenses related to zoning in the Great Barrier Reef World Heritage Area 2004–2008 (Data courtesy GBRMPA). Total figure includes nonzoning offenses. Separate data for commercial trawling and line fishing offenses are only available after 2004.

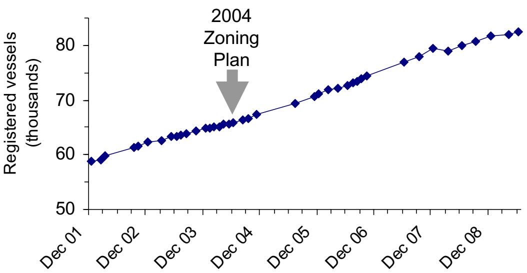


Fig. S8. Recreation vessel registrations in GBR coastal communities. Data courtesy GBRMPA and Queensland Transport.

Other Supporting Information

Table S1 (PDF)
Table S2 (PDF)