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Responses to additional questions from committee members

1. Individual research papers report on biomass or density changes for a wide range of both target and non-target species depending on the aims of the research or the hypothesis being tested.

2. I would suggest that biodiversity, by definition, can neither increase nor decrease, but simply change. The idea with sanctuary zones is that biodiversity will change to more closely represent what is natural, or what we assume to be natural as this can be hard to assess because we have exploited almost everywhere.

Biomass, however, can increase and generally what is seen is large resident fish increase in numbers and median age. This may alter all sorts of current patterns, such as abundance of kelp. As a consequence ecological processes will differ from less protected areas, as will the structure and function of marine communities.

So, while biomass may increase for some species, and generally does, there is value in sanctuary zones whatever the final outcome as they represent more natural areas in the marine environment.

Enclosed is a paper describing how changes are still occurring in a sanctuary zone that had been protected for 25 years at the time of the paper's publication (Shears & Babcock, 2003).

3. There is already significant linkage between some government departments, notably the Marine Parks Authority and Industry and Investment (Fisheries). It is important that departments liaise with each other, provide input and expert advice where appropriate, and look outside of their particular area of management to improve environmental and resource use outcomes.

However, in terms of amalgamating operations, it is clearly inappropriate for the Marine Parks Authority to manage fisheries and it is equally inappropriate for fisheries to manage marine parks. This would be the same as agriculture or forestry managing terrestrial national parks. It would create an immediate conflict of interests and demonstrate a clear lack of understanding of what marine parks were established to do.

The Marine Parks Authority is best managed by DECCW, with input from I&I as an important stakeholder, while fisheries management should be the responsibility of I&I, with DECCW consulted as a stakeholder.

4. There are already a number of recreational fishing organizations claiming to be peak bodies and voices for the recreational fishing sector in NSW. It is for the recreational fishing sector to determine which of those should be viewed as the peak body, how they should be structured and who was asked to be involved and from which sectors. The conservation sector already makes a certain contribution to the management of recreational fishing through the NCC rep on ACORF and RFSTEC and, despite the challenges, I suggest the current rep is seen as constructive and approachable by the rest of the committee members. There is much value in this arrangement and there is clearly a lot of common ground between the rec fishing and conservation sectors.

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Biological responses in marine no-take reserves versus partially protected areas

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ABSTRACT: Marine Protected Areas (MPAs) are a common tool for conserving and managing marine and coastal ecosystems. MPAs encompass a range of protection levels, from fully protected no-take reserves to restriction of only particular activities, gear types, user groups, target species, or extraction periods. There is a growing body of scientific evidence supporting the ecological benefits of full reserve protection, but it is more difficult to generalize about the effects of other types of MPAs, in part because they include a range of actual protection levels. However, it is critical to determine whether partial protection and no-take reserves provide similar ecological benefits given potential economic costs of lost fishing grounds in no-take areas, common sociopolitical opposition to full protection, and promotion of partially protected areas as a compromise solution in ocean zoning disputes. Here we synthesize all empirical studies comparing biological measures (biomass, density, species richness, and size of organisms) in no-take marine reserves and adjacent partially protected and unprotected areas across a range of geographic locations worldwide. We demonstrate that while partially protected areas may confer some benefits over open access areas, no-take reserves generally show greater benefits and yield significantly higher densities of organisms within their boundaries relative to partially protected sites nearby.

KEY WORDS: Marine reserves · Marine protected areas · Protection level · Conservation · Ocean zoning

INTRODUCTION

Human activities have broad effects on coastal and oceanic marine systems (Halpern et al. 2008b), often degrading ecosystem services (UNEP 2006), including many fisheries worldwide (Gewin 2004, Worm et al. 2006). These changes have led to calls for more ecosystem-based approaches to marine management, including ocean zoning and the implementation of marine protected areas (Palumbi 2002, Lubchenco et al. 2003, Browman & Stergiou 2004, Crowder et al. 2006, Halpern et al. 2008a). In particular, ocean zoning provides a means to spatially separate incompatible human activities and reduce conflict among user groups (Crowder et al. 2006). However, when attempting to implement a zoning approach or establish a network of MPAs, it is critical to understand the potential ecological consequences of different types of restrictions. There is often a tension between conservationists and extractive user groups regarding the level of protection established, and it is important to evaluate whether this friction is necessary.

No-take marine reserves are often promoted for their ability to offer simple and full protection for marine resources and ecosystems. Numerous syntheses of monitoring studies have documented beneficial effects of reserve protection (Palumbi 2002, Halpern 2003, S. E. Lester unpubl. data), particularly for biomass and density of exploited species within reserve boundaries (Gell & Roberts 2003, Micheli et al. 2004). In addition to

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these demonstrated conservation benefits, there is some theoretical work and more limited empirical evidence that reserves can produce fisheries benefits, either through export of larvae or spillover of adults into unprotected waters (Roberts et al. 2001, Halpern et al. 2004, Hilborn et al. 2004, Goni et al. 2006). Marine reserves are also promoted over partially protected areas for political reasons, such as less complicated regulations and more straightforward enforcement (Bohnsack 2004).

Despite the benefits of marine reserves, prohibiting all extractive activities in certain areas can have socioeconomic costs. Marine reserves often face strong opposition by extractive users, making the process of reserve implementation politically difficult and polarizing. Indeed, even if reserves benefit fisheries, local fishers may be negatively affected by the loss of fishing grounds, at least in the short-term. As a result, MPAs with less restrictive regulations are typically seen as a politically more feasible management strategy and are often advanced as compromise solutions (NRC 2001, Shears et al. 2006). For example, MPAs often allow recreational fishing, subsistence fishing, or fishing with less destructive gear types, depending on the stated management goals.

Partially protected areas have also been shown to produce ecological responses (e.g. Murawski et al. 2000, Blyth-Skyrme et al. 2006, Floeter et al. 2006), although it is difficult to generalize about these effects because empirical results remain scattered throughout the literature. A further challenge is that the intensity and frequency of permitted extractive or destructive activities is a source of variation that is difficult to quantify and thus control for in analyses. We address these challenges here by synthesizing available peer-reviewed data on MPA performance in those locations where there is an adjacent marine reserve. In doing so, we exclude those studies that have looked only at MPA performance, but we gain power by having a controlled, direct comparison to no-take marine reserves. These results can inform decisions on appropriate or necessary level of protection when establishing MPAs in order to meet specified management or conservation goals.

METHODS

We conducted a comprehensive survey of peer-reviewed scientific literature to compile a database of studies documenting and comparing biological effects of fully-protected no-take marine reserves, partially protected marine protected areas (MPAs) and open access areas, all within the same vicinity. Studies must have measured at least 1 of 4 key biological variables (density, biomass/area of organisms, individual organism size, or species richness/area) and must have quantified the variable(s) either (1) inside the reserve, inside the partial protection area and outside the protected areas (open access) after protection was implemented, or (2) in all three areas before and after protection was implemented. The areas referred to in this paper as 'open access' may be subject to some fishing restrictions (e.g. no dynamite fishing), but are less protected than the no-take reserves and partial protection areas. Furthermore, in many of the studies, recreational or subsistence fishing is allowed in the 'partial protection' area (Table 1), while recreational, subsistence and some commercial fishing are allowed in the 'open access' area.

The resulting database contains 20 peer-reviewed scientific publications published between 1977 and 2007 examining 21 protected areas in 11 countries (Table 1). For each study, we extracted quantitative data from text, tables, and figures for the 4 biological variables. Data were extracted at the most aggregated taxonomic level available, even if the level of taxonomic resolution differed within or among studies. If a study reported data for categories of other variables (e.g., by depth, habitat type, or organism size classes), we calculated an un-weighted average of the values reported for these categories to extract a single value for each protection level. If data were collected over time, we used the most recent because they represent the longest duration of protection (for before/after comparisons, this holds for the after data).

To quantify the effects of different levels of protection using comparable metrics across studies, we calculated response ratios for the biological variables as (1) the ratio of inside the no-take reserve to the open access area, (2) the ratio of the partially protected area to the open access area, and (3) the ratio of the no-take reserve to the partially protected area. If the study included before and after protection data, the above three ratios were calculated using the ratios of after versus before for each of the protection levels.

When data were extracted for multiple taxa in a given study, we averaged these response ratios to determine the overall study ratio for all taxa examined, such that study-level ratios can represent from 1 to >100 species depending on the study (Table 1). Two studies (McClanahan & Muthiga 1988, McClanahan et al. 2006) reported data separately for more than 1 of the 3 broad taxonomic groups (fish, invertebrates, algae), and thus we calculated an average for each group first and then averaged these group values to determine the overall ratio. For all analyses, we used log ratios to meet statistical criteria (Hedges et al. 1999) and conducted all statistical tests using JMP 7.0 (SAS Institute).

Table 1. Studies reporting data for adjacent no-take reserves, partially protected areas, and open access areas, including the names of these areas, metrics reported, taxa studied, and the regulations in the partially protected area. Metrics: B, biomass; D, density; R, richness; S, size

No-take reserve	Partially protected area	Open access area	Metrics reported	Taxa studied	Regulations in partially protected area	Source
Tortugas Bank No-take Marine Reserve, USA	Dry Tortugas National Park	Tortugas Bank Fished	D	21 fish species	No commercial fishing; only recreational hook-and-line fishing allowed	Ault et al. (2006)
Tortugas/Fort Jefferson, USA	Sport harvest area between reserve and open access area	Commercial harvest area outside reserve and sport harvest area	D	1 lobster species	No commercial fishing; recreational fishing by skin or SCUBA diving allowed	Davis (1977)
Poor Knights Island Marine Reserve, NZ	Mimiwhangata Marine Park	Cape Brett and Mokohinau Islands	D, S	1 fish species	No commercial fishing; recreational fishing allowed using the following methods: unweighted, single-hook lines, trolling and spearing	Denny & Babcock (2004)
Arquipelago, Brazil	Timbebas/Escalvada/ Pedra Vermelha	Guarapari/ Saco do Anequim	D	135 fish species	Partially protected by distance or park regulations allowing only some fishing gears (e.g. spear, nets, hook-and-line)	Floeter et al. (2006)
Scandola, France	Elbu	Galeria	B, D	17 fish species	Partially protected by distance or park regulations allowing small boats, low-power engines, and traditional fishing methods	Francour (1991)
Scandola, France	Non-integral reserve	Outside reserve	D	3 fish families	Some fishing allowed by permit	Francour (2000)
No-take areas throughout the main Hawaiian islands, USA	Partial protection areas throughout the main Hawaiian islands	Open access areas throughout the main Hawaiian islands	B, D, R	Reef fish assemblage	Allow some fishing methods, varying by area (e.g. hook and line fishing allowed)	Friedlander et al. (2003)
No-take areas throughout the main Hawaiian islands, USA	Partial protection areas throughout the main Hawaiian islands	Open access areas throughout the main Hawaiian islands	B	Reef fish assemblage	Allow some fishing methods, varying by area (e.g. hook and line fishing allowed)	Friedlander et al. (2007)
Invertebrate no-take reserve, Catalina Island, USA	Recreational fishing area, Catalina Island	Commercial and recreational fishing area, Catalina Island	B, D, S	1 lobster species	No commercial fishing; recreational fishing allowed by hand or with hoop nets and with daily bag limit	Iacchei et al. (2005)
Cousin Island, Seychelles	Sainte Anne	Baie Ternay and Curieuse	B	115 fish species	No commercial fishing; subsistence fishing by park residents allowed (~10 fish traps and occasional hand-lines)	Jennings et al. (1996)
Cerbère-Banyuls Marine Reserve, France	Partially protected area (PPA)	Unprotected area (UPA)	D, S	1 urchin species	Commercial fishing only with fixed nets; recreational fishing allowed	Lecchini et al. (2002)

Table 1 (continued)

No-take reserve	Partially protected area	Open access area	Metrics reported	Taxa studied	Regulations in partially protected area	Source
Las Cruces, Chile	Adjacent semi-protected area	Adjacent open-access area	D, S	1 gastropod species	Open to fishing but access restricted by private property	Manriquez & Castilla (2001)
Malindi Marine National Park, Kenya	Kanamai	Diani	D	1 urchin and the fish community	Partial protection determined by fishing pressure, influenced by proximity to large tourist settlements	McClanahan & Muthiga (1988)
Kisite, Kenya/Tanzania	Tanga, Tanzania	Open access area	B, D, R	Algae, hard and soft coral, urchins, sponges, reef fishes	No dynamite fishing or beach seines and some temporary closures	McClanahan et al. (2006)
Ustica Island Integral Reserve, Italy	Ustica Island General Reserve	Ustica Island Partial Reserve	D, R	161 species (molluscan assemblage)	No commercial fishing; recreational (angling) and subsistence fishing allowed	Milazzo et al. (2000)
Ras Mohammed, Egypt	Sharm-el-Sheikh	Dahab	B, D, S, R	45 fish species	Partial protection determined by accessibility and human population density	Roberts & Polunin (1992)
Platform Gail de facto reserve, USA	Santa Monica Bay	Footprint	D	1 fish family	Closed to commercial fishing activities that use trawls, drag nets, gill nets, and traps, except for a small live-bait fishery that uses lampara nets; also closed to handlines with more than 2 hooks	Schroeder & Love (2002)
Tawharanui Marine Reserve, NZ	Mimiwhangata Marine Park	Tawharanui fished	D	1 lobster species	No commercial fishing; recreational fishing using the following methods allowed: unweighted, single-hook lines, trolling and spearing	Shears et al. (2006)
University of Washington marine research preserves (Shady Cove, Point George, Yellow Island), USA	Marine Protected Areas (Bell Island, Lime Kiln)	Unprotected areas (Cliff Island, Bell Island outside, Lime Kiln outside)	D	1 urchin species	Collection of finfish (not including salmon) prohibited	Tuya et al. (2000)
Punta La Restinga-Mar de Las Calmas, Spain	Buffer zone (ZA)	Neighboring fishing area (AV)	B, D	4 fish species	No commercial fishing; fishing with traditional gears allowed	Tuya et al. (2006)
Isla La Graciosa e islotes del norte de Lanzarote, Spain	Buffer zone (ZA)	Neighboring fishing area (AV)	B, D	4 fish species	No commercial fishing, traps, or underwater gear; fishing with traditional gears (e.g. hook-and-line) and shrimp pots allowed	Tuya et al. (2006)

RESULTS

Partially protected areas (MPAs) may confer some ecological benefits relative to unprotected areas, producing positive but non-significant responses for biomass, density, richness and individual size relative to unprotected areas (Fig. 1) (Partial:open response ratios; *t*-tests, means not significantly different from zero: $p > 0.1$ for all metrics). No-take reserves had larger increases on average relative to unprotected areas than those for partially protected areas (Fig. 1: No-take:open response ratios); these responses were statistically significant for density (*t*-test, means significantly different from zero: $p = 0.015$) and suggestive (though non-significant) for organism size ($p = 0.09$), but not significant for biomass or species richness ($p > 0.1$). Additionally, the reserve effects documented in this dataset are comparable to values in previous more comprehensive analyses of no-take reserves (Halpern 2003; Fig. 1: Halpern ratios).

To control for potential differences among study locations and species sampled, we conducted pairwise comparisons of full versus partial protection areas. We found that no-take areas had higher biomass, density, species richness and individual organism size on average relative to partially protected areas (Fig. 2). This difference was statistically significant only for density ($p = 0.02$ for density, $0.1 < p < 0.9$ for biomass, species richness and organism size), although it should be noted that organism size and species richness had very low sample sizes ($n = 5$, $n = 4$, respectively).

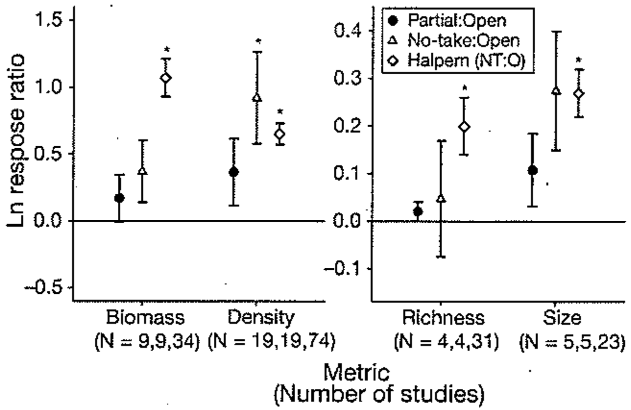

Fig. 1. Response ratios of overall study means (± SE) for partially protected areas compared to open access areas (●), for no-take reserves compared to open access areas from this synthesis (△), and for no-take reserves compared to open access areas from the comprehensive synthesis of Halpern (2003) (◇). *: mean significantly different from zero (*t*-test, $p < 0.05$). Sample size for each ratio is shown in parentheses following the sequence in the plot. Response ratios (RR) from Halpern (2003) were converted from logRR to lnRR to match the transformation used in this synthesis

DISCUSSION

While partially protected areas may result in higher values of ecological metrics than open access areas, no-take reserves generally produced greater increases and yielded significantly higher densities of organisms within their boundaries relative to partially protected sites nearby. These results suggest that no-take reserves have advantages over less protected areas and may therefore represent a preferable management strategy, depending on management goals and social, economic and political constraints. Although the effect of no-take protection relative to partial protection was only significant for density, this is also the biological measure for which we had the most data. The no-take:open ratios from our synthesis are within the same range as those of Halpern's (2003) more comprehensive analysis of no-take reserves, and there is a remarkable similarity between studies for density, organism size and species richness. This suggests that the reserves in our dataset are a representative sample and we should be able to detect an effect of partial protection, at least for density, if such an effect exists.

It is important to note that there is considerable variability in the documented effects of no-take versus partial protection, likely resulting from various factors that could not be accounted for in our analyses due to lack of information or insufficient data, including duration of protection, MPA/reserve size, habitat type and qual-

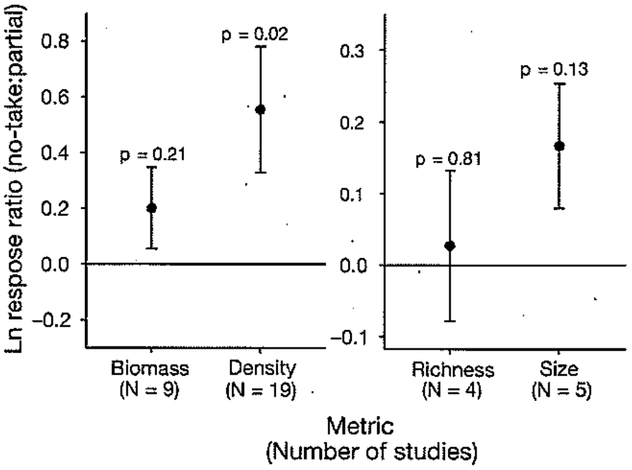

Fig. 2. Response ratios of overall study means (± SE) for no-take reserves and partially protected areas. p-values indicate the results of *t*-tests (testing for means significantly different from zero)

ity, and enforcement and compliance. Additionally, given the limited amount of data available, we aggregated across all taxa and thus were not able to control for specific taxon traits, such as trophic level or whether or not taxa are exploited. Thus, there is a critical need for more empirical studies documenting biological effects in adjacent open access, partially protected, and no-take areas; these studies should be conducted in a variety of locations and habitat types worldwide and focus on a range of taxa. Ideally such studies would also collect data prior to protection to avoid confounding effects of protection when MPAs are sited in 'better' areas.

We did not find significant ecological effects of partially protected areas relative to open access areas. A more complete synthesis of the studies that have examined only effects of partially protected MPAs relative to open access areas could help refine our understanding of the potential for MPAs to provide management and conservation benefits; a key challenge would be accounting for and controlling likely drivers of differences in MPA performance (e.g. the range and intensity of activities permitted within the MPA as well as differences in habitat, geography and species composition). Almost certainly, the amount of protection provided to species of interest within MPAs (e.g. fishery species) will greatly influence MPA performance relative to no-take marine reserves. Indeed, it is not surprising that we failed to document significant ecological effects of partially protected MPAs given that most of the studies we reviewed reported results for species targeted (although often by different fishing methods) in both open access and partially protected areas. Some species, particularly those heavily targeted by both commercial and recreational fishers, may be protected only by no-take reserves. Our focus here on studies that examined both MPAs and no-take reserves does not eliminate these challenges, but allowed us to directly compare these management options and helped minimize the potential for factors such as habitat type, species composition, or geography to influence the results.

Many partially protected areas, including those in this study, frequently exclude commercial fishing but allow recreational and/or subsistence fishing (Table 1). There is a widely held perception that recreational fishing does not have a substantial impact on marine ecosystems. For example, a recent poll prepared for the American Sportfishing Association reported that 64% of Californians think that recreational fishing is a 'not serious' threat to marine ecosystems (FRC 2007). However, there is a growing body of evidence indicating that recreational fishing can constitute a significant portion of the regional catch for some species (Schroeder & Love 2002, Coleman et al. 2004, Cooke & Cowx 2004), and the lack of an MPA effect in our analyses on species that remain targeted by recreational fisheries further supports this evidence. Schroeder & Love (2002) examined 20 yr of landings data for nearshore fisheries species in California and found that for 16 of 17 species, recreational angling was the primary source of fishing mortality. Even catch-and-release fisheries can have dramatic effects on longer-lived species due to relatively small increases in mortality incurred post-hooking (Schroeder & Love 2002). Additionally, recreational fishing can have ecosystem-level effects similar to those from commercial fishing (Cooke & Cowx 2004, 2006); in some cases, recreational fishing can have even larger impacts because of a greater focus on higher trophic levels (Coleman et al. 2004) and shallower nearshore environments (Cooke & Cowx 2004).

One potential reason for smaller ecological effects in MPAs is that in some cases fishing effort becomes concentrated in partially protected areas relative to open access areas because of a perception among fishers that MPAs are likely to have more or larger fish due to the exclusion of commercial fishing (Denny & Babcock 2004, Shears et al. 2006). Likewise, rotational closures also often experience high levels of fishing that counteract the benefits of temporary protection (Murawski et al. 2005). For example, a study investigating rotational management in Hawaii found that fish biomass increased during closed periods, but not enough to compensate for the reduction in biomass during open periods (Williams et al. 2006).

MPA and reserve designation requires a balance of ecological, political, economic and social goals. Thus, regardless of the larger ecological responses in no-take reserves relative to partially protected areas, human needs will require MPA networks to allow a mix of protection levels and restrictions to accommodate multiple objectives, human activities and stakeholder groups. Additionally, partial protection can be used to exclude activities that are deemed too destructive (such as benthic trawl commercial fishing) despite potentially increasing fishing pressure for some species. It is important, however, for policy makers and managers to be aware of the ecological cost of conferring lower levels of protection in MPAs so that management decisions can be fairly evaluated by their ability to meet stated goals. Furthermore, there are numerous other advantages of no-take protection over partial protection not tested here (Schroeder & Love 2002, Bohnsack 2004). For example, reserves may provide control areas for fisheries-independent stock assessments and for teasing apart natural versus anthropogenic changes to marine ecosystems. Additionally, reserves can enhance various non-extractive uses such as recreation and tourism, many of which can provide economic benefits (Bhat 2003, Brander et al. 2007). Determining the appropriate level of protection for different areas of the ocean requires a careful balancing of conservation and management priorities, and analyses like those presented here can help inform this decision-making process.

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Continuing trophic cascade effects after 25 years of no-take marine reserve protection

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ABSTRACT: Between 1978 and 1996 benthic communities in the Leigh Marine Reserve shifted from being dominated by sea urchins to being dominated by macroalgae. This was a result of a trophic cascade thought to be an indirect effect of increased predator abundance. We assessed further changes in communities from 1996 to 2000, differences in benthic communities between reserve and adjacent unprotected sites, and the stability of these patterns from 1999 to 2001. Since 1996, densities of sea urchins *Evechinus chloroticus* have continued to decline in shallow areas of the reserve (<8 m), and all sites classified as urchin barrens in 1978 are now dominated by large brown algae. Comparisons between reserve and non-reserve sites revealed differences consistent with a trophic cascade at reserve sites. The greatest differences in algal communities between reserve and non-reserve sites occurred at depths where *E. chloroticus* was most abundant (4 to 6 m). Reserve sites had lower urchin densities and reduced extent of urchin barrens habitat with higher biomass of the 2 dominant algal species (*Ecklonia radiata* and *Carpophyllum maschalocarpum*). At reserve sites densities of exposed *E. chloroticus* (openly grazing the substratum) declined so that urchin barrens were completely absent by 2001. Lower density of the limpet *Cellana stellifera* and higher densities of the turbinid gastropod *Cookia sulcata* at reserve sites are thought to be responses to changes in habitat structure, representing additional indirect effects of increased predators. The overall difference in community types between reserve and non-reserve sites remained stable between 1999 and 2001. Localised urchin mortality events due to an unknown agent were recorded at some sites adjacent to the marine reserve. Only at 1 of these sites did exposed urchins decline below the critical density of 1 m^{-2}, which resulted in the total replacement of urchin barrens with macroalgae-dominated habitats. At other sites urchin barrens have remained stable. Declines in the limpet *C. stellifera* occurred across all sites between 1999 and 2001 and may be indirectly associated with urchin declines. Long-term changes in benthic communities in the Leigh reserve and the stability of differences between reserve and non-reserve sites over time are consistent with gradual declines in urchin densities due to increased predation on urchins, thus providing further evidence for a trophic cascade in this system. The rapid declines in urchin numbers at some unprotected sites, however, demonstrate how short-term disturbances, such as disease, may result in shifts in community types over much shorter time frames.

KEY WORDS: Benthic community structure · Macroalgae · Macro-invertebrate herbivores · Marine protected areas · Northeastern New Zealand · Sea urchins · Temporal change

INTRODUCTION

Trophic cascades represent a series of interactions whereby plant community structure or 'biomass of primary producers' is indirectly controlled by the presence of top predators (Hairston et al. 1960, Menge 1995). When predators do not suppress herbivores, grazing reduces plant biomass. The occurrence of both trophic cascades and the potential for human-induced alterations to trophic cascades are becoming more apparent (Pace et al. 1999, Polis et al. 2000). Trophic cascades are characterised by 3 features: (1) top-down control of assemblage structure by predators; (2) conspicuous indirect effects, with 2 or more links distant from the primary one; and (3) persistence of alternative community states. While trophic cascades in the marine environ-

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ment have received much attention, and their potential is indicated by theoretical studies, there are few empirical studies, with one of the main limitations being the lack of long-term data (Pinnegar et al. 2000).

Fishing is the most widespread human impact on the marine environment (Pauly et al. 1998, Jackson et al. 2001). Fishing not only has direct effects on target populations but also results in indirect effects throughout the ecosystem when top-level predators are removed (see reviews by Jennings & Kaiser 1998, Pinnegar et al. 2000, Tegner & Dayton 2000). On many temperate reefs shifts from macroalgae-dominated habitats to habitats grazed by sea urchins, termed 'urchin barrens', have been linked to the over-harvesting of top predators, e.g. Alaska (Estes & Duggins 1995), Northwest Atlantic (Wharton & Mann 1981, Vadas & Steneck 1995), New Zealand (Babcock et al. 1999, Shears & Babcock 2002) and the Mediterranean (Sala et al. 1998). Despite the widespread occurrence of apparent trophic cascades, evidence for a key role of predators is mostly circumstantial (Scheibling 1996), and little is known about the stability of the alternate stable states and the processes leading to their establishment.

Grazing by high densities of sea urchins results in the transition from kelp forests to urchin barrens (Lawrence 1975). Therefore, understanding the factors regulating sea urchin abundance is pivotal to understanding the mechanisms responsible for this shift in community type. Reversals of this shift (from urchin barrens back to kelp) have been linked to not only the recovery of predators (e.g. sea otters, Estes & Duggins 1995), but also to high algal recruitment (Harrold & Reed 1985) and mass mortality of urchins due to storms (Ebeling et al. 1985) and disease (Scheibling & Hennigar 1997). Similarly, harvesting of sea urchins results in the reestablishment of macroalgal forests (Steneck 1997). In systems where harvesting occurs at many trophic levels, e.g. Californian kelp forests (Dayton et al. 1998), many trophic interactions have been lost, and consequently our ability to understand the processes responsible for the establishment and stability of algal assemblages is severely compromised.

Marine reserves, or other areas where fishing is completely prohibited, are therefore a valuable tool in understanding the persistence and stability of communities. Such areas provide an ecosystem-level experimental framework to detect both the direct and indirect effects of fishing, which may not be detectable using small-scale manipulations (Shears & Babcock 2002, cf. Andrew & Choat 1982). Furthermore, monitoring marine reserves and adjacent unprotected areas over long periods allows the differentiation of fishing effects from long-term changes associated with other factors such as natural disturbance and climate change. If predators have an important regulatory effect on sea urchins, we would expect a transition from urchin barrens back to kelp after a period of predator recovery. Not all studies on temperate reefs that have utilised marine reserves to address such questions have found strong evidence for trophic cascades (Edgar & Barrett 1997, 1999, Cole & Keuskamp 1998, Sala et al. 1998). This may be due to a number of reasons, including inherent aspects of the particular system examined, studies being carried out over insufficient periods of time and also a lack of long-term data.

Long-term studies at permanent sites in New Zealand's oldest marine reserve, the Cape Rodney to Okakari Point Marine Reserve (hereafter 'Leigh Reserve'; established in 1976), have revealed a transition from urchin barrens to kelp after 20 yr of marine reserve protection (Babcock et al. 1999). On moderately exposed reefs in this part of northeastern New Zealand the urchin barrens habitat typically occurs at depths between 3 and 8 m (Choat & Schiel 1982, Shears & Babcock 2000) and is maintained by the grazing activity of the sea urchin *Evechinus chloroticus* (Andrew & Choat 1982, Shears & Babcock 2002) along with a group of herbivorous gastropod species (Ayling 1981, Choat & Andrew 1986). Urchin numbers in the Leigh Reserve have declined, and there has been a subsequent 10-fold decline in the extent of urchin barrens habitat from 31.4% of available reef in 1978 to 3.2% in 1996 (Babcock et al. 1999). In addition, both the density of *E. chloroticus* and the extent of the urchin barrens habitat is significantly lower in the Leigh Reserve, and also in the nearby Tawharanui Marine Park, compared with adjacent unprotected areas (Shears & Babcock 2002). Both reserves have considerably higher abundances of predators, predominantly the snapper *Pagrus auratus* (Willis et al. 2000, in press) and the spiny lobster *Jasus edwardsii* (Kelly et al. 2000) compared with unprotected areas where these species are heavily targeted by both recreational and commercial fishermen. Both snapper and spiny lobsters are the dominant predators of adult *E. chloroticus*, and the chance of predation on tethered urchins is approximately 7 times higher in these reserves than on the adjacent coast (Shears & Babcock 2002). Consequently, the long-term declines in urchin barrens in the Leigh Reserve and the spatially consistent contrasts between these fished and un-fished areas have been attributed to a top-down role of predators (Babcock et al. 1999, Shears & Babcock 2002).

While these patterns provide strong evidence for a trophic cascade in this system, no temporal data exist for non-reserve sites, and many inferences concerning the effects of reserves are based on one-off comparisons of reserve and non-reserve sites. Furthermore, little is known about the stability of the observed changes and the processes that lead to transitions from one habitat state to the next. If such a trophic cascade exists in this system, we make the following predictions based on the 3 characteristics of trophic cascades described above: (1) Habitat change in the reserve will continue towards kelp domination given the persistence of top-down control on assemblage structure. (2) Indirect effects 2 or more steps away from the primary one will be apparent, e.g. potential effects on algae and also other grazers associated with declines in *Evechinus chloroticus*. (3) Alternative stable states will persist through time between reserve and non-reserve sites. These hypotheses were tested by extending time-series data from permanent sites within the reserve first measured between 1976 and 1978 (Ayling 1978), from 1996 (Babcock et al. 1999) to 2000. In addition, benthic communities at a number of reserve and non-reserve sites were monitored from 1999 to 2001. Since the abundance of the dominant urchin predators has remained considerably higher at reserve sites compared to unprotected areas, the habitat change should remain stable or continue its trend towards a kelp-dominated state. Alternatively, if the spatial contrasts in habitat structure since 1978 were related to some chance temporal variation, we should expect to see considerable variation in habitat structure between 1994 and 2000, in which time the reserve has been more intensively monitored. If spatial differences in habitat structure between reserve and non-reserve sites are a result of trophic interactions, they are predicted to be stable over time. However, if habitat structure changes towards a kelp-dominated system outside the reserve, other processes may be responsible for such transitions.

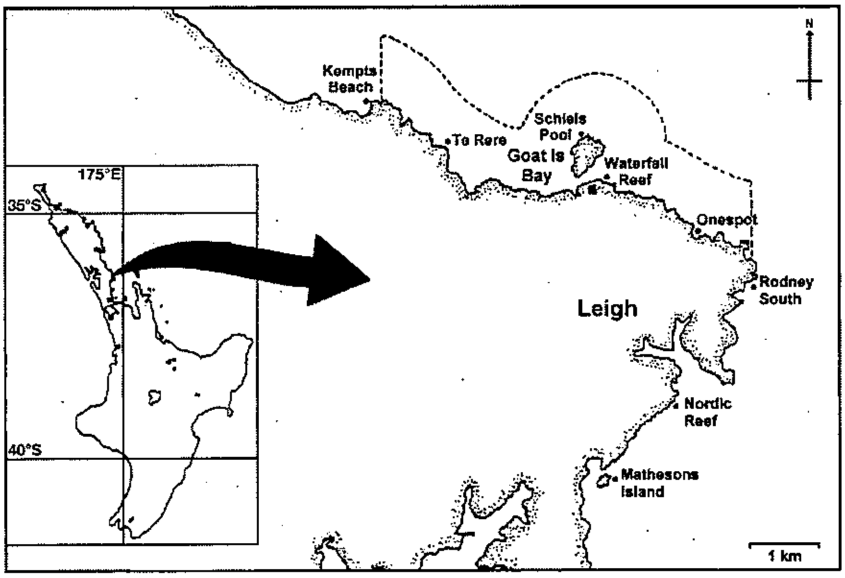

Fig. 1. Location of Cape Rodney to Okakari Point Marine reserve in northeastern New Zealand. Names indicate study sites where subtidal communities were monitored from 1999 to 2001. Dashed line indicates reserve boundary

METHODS

Study area. The Leigh Reserve is located approximately 90 km north of Auckland on the east coast of New Zealand's North Island (Fig. 1). The nearshore areas within the reserve and along the adjacent coasts contain areas of contiguous reef extending from mean low water spring (MLWS) to depths generally greater than 10 m. Reef communities in the Leigh area have previously been described (Bergquist 1960, Choat & Schiel 1982, Taylor 1998, Shears & Babcock 2000). See Table 1 for a description of habitats.

Temporal change at permanent sites. Thirteen 100 m^2 'permanent sites', established by Ayling (1978), were re-sampled during 20–24 September 1999 and 3–9 August 2000. These were grouped among 3 depth strata: shallow (<5 m; n = 4), mid-depth (6 to 8 m; n = 5) and deep (10 to 13 m; n = 4). Most of the permanent sites were located in Goat Island Bay (Fig. 1), although a shallow and a mid-depth site were located at Waterfall Reef in the eastern part of the reserve. In 1978, shallow sites were classified as 'shallow broken rock/rockflats', mid-depth sites as 'rock flats' and deep sites as 'kelp forest' (Table 1; Ayling 1978).

The positions of Ayling's sites were located using compass bearings and distances from prominent landmarks as in Babcock et al. (1999). Each site was sampled using 10 haphazardly placed 1 m^2 quadrats. All large brown macroalgae and invertebrate herbivores were counted and measured. The density and size structure of dominant species were compared with data from 1994, 1996 (Babcock et al. 1999), and the original 1976–78 data (Ayling 1978).

Spatial contrasts and temporal change at reserve and non-reserve sites. ***Site selection and locations:*** Eight sites were sampled throughout the Leigh Reserve and along the adjacent coastline (Fig. 1). All sites had moderately sloping reefs and similar topographic complexity. GPS co-ordinates were recorded at each site, along with a photograph of the intertidal rock formations, allowing exact relocation of the sites. Sampling was carried out during late summer 1999 (12 to 29 March), 2000 (5 to 15 April) and 2001 (27 March to 10 April). It is unlikely that the seasonal variation in sampling time (both among these samples and relative to the 'permanent' sites of Ayling 1978) will introduce a significant source of variation in algal communities. Previous

Table 1. Description of benthic habitats encountered in this study

Habitat	Depth range (m)	Description
Shallow *Carpophyllum*[a]	<3	Dominated by high abundances (≥20 m^{-2}) of *Carpophyllum maschalocarpum*, *C. plumosum* and *C. angustifolium*. *Ecklonia radiata*, *Xiphophora chondrophylla* and *Pterocladia lucida* are also common. Urchins rare and generally cryptic
Mixed algae[a]	2–10	Mixture of short *Ecklonia radiata* plants and fucalean algae[b] (mainly *C. maschalocarpum*), usually only partial canopy (≥4 adult plants m^{-2}) and urchins may also be common
Urchin barrens ('rockflats' in Ayling 1978)	2–9	Areas where the grazing activity of *Evechinus chloroticus* (>2 adults m^{-2}) leaves the substratum relatively devoid of macroalgae and dominated by crustose coralline algae. Large brown algae, particularly *C. flexuosum*, may occur at low densities (<4 adult plants m^{-2})
Turfing algae	3–9	Substratum predominantly covered by turfing algae (e.g. articulated corallines [Coralline turf] and short foliose red algae) (>30% cover). Low numbers of large brown algae (<4 adult plants m^{-2}) and urchins may occur
Kelp forest	5–20	Generally monospecific stands of mature *Ecklonia radiata* forming a complete canopy (≥4 adult plants m^{-2}), occasional *C. flexuosum* plants. Urchins rare, usually cryptic

[a] Ayling's (1978) 'shallow broken rock' habitat is a combination of both shallow *Carpophyllum* and mixed algae
[b] Fucalean algae refer to members of the Order Fucales

studies have described little if any seasonal variation and the persistence of habitats year round (Novaczek 1980, Ayling 1981, Schiel 1985). Reef communities at each site were sampled to a maximum depth of 12 m using a combination of line transects and depth-stratified quadrats. This provided information on the distribution of habitats along the depth gradient as well as a quantitative measure of abundance of benthic communities within 4 given depth ranges.

Line transects: Three line transects were haphazardly placed at each site to identify the depth distribution of habitats and to obtain information on the reef profile at each site. Transects were run perpendicular to the shore on a fixed compass bearing from MLWS (or the top of *Carpophyllum maschalocarpum* band) to the edge of the reef, or a maximum of 12 m depth, whichever was encountered first. The habitat type (Table 1), depth, rock type, slope and distance from shore were recorded at 5 m intervals along these transects. The habitat classification used was similar to that used by Ayling (1978) but with an additional 'mixed algal' habitat, typically characterised by a mixture of *Ecklonia radiata* and *C. maschalocarpum* (see Shears & Babcock 2000).

Transect data were analysed as the proportion of major habitat types at each site. Proportions were calculated as the distance covered by each habitat type from the start of the transect (MLWS) to a depth of 10 m, divided by the transect length. The cut-off depth of 10 m was chosen because urchin barrens rarely occur below this depth around Leigh, and the reefs are completely dominated by kelp forest (Shears & Babcock 2002). The proportions of each of the major habitat types were analysed using a generalised linear mixed model with fixed factors Year (1999, 2000 and 2001) and Status (Reserve and Non-reserve). Covariance parameter estimates were calculated for the random factor Site (Year × Status) and also for the auto-regressive error structure (AR(1)) to account for repeated measures. The proportion data were modelled using a binomial distribution, and the model was back-fitted using residual (restricted) maximum likelihood employing the GLMMIX macro in SAS (Littell et al. 1996). The parameter estimates from the model were used to calculate the relative odds ratio, or chances of habitats occurring at reserve versus non-reserve sites, along with 95% confidence limits (see Willis & Millar [2001] for explanation of interpreting relative odds). Note that confidence limits are asymmetrical as they are calculated on the log-scale.

Depth-stratified quadrats: At each site, 5 haphazardly placed 1 m^{-2} quadrats were sampled in each of 4 depth ranges (<2, 4 to 6, 7 to 9 and >10 m below MLWS) to provide information on abundance and size structure of dominant organisms. Depths were corrected according to the state of the tide to ensure accurate positioning of quadrats within the desired depth range. It was important that specific narrow depth ranges were selected to ensure comparable repeated sampling. The depth ranges chosen also ensured that sampling was carried out within specific zones previously described at Leigh, shallow *Carpophyllum maschalocarpum* (<2 m), urchin barrens (4 to 6 m) and kelp forest (7 to 9 and >10 m) (Choat & Schiel 1982, Shears & Babcock 2000). Quadrats were positioned haphazardly adjacent to the transect line in the desired depth range, and the distance along the transect recorded to ensure that subsequent sampling could be carried out in the same general area.

Within each quadrat all macroalgae and macroinvertebrate herbivores were counted. The test diameter of all urchins (>5 mm) was measured to the nearest 5 mm as well as whether each urchin occupied a crevice (cryptic) or openly grazed the substratum (exposed). The total lengths of individual thalli of large brown macroalgae were measured (±5 cm), as it is difficult to differentiate individual plants for many species. Additional measures of stipe length were made for *Ecklonia radiata*. The percent cover of encrusting, turfing and foliose forms of algae was estimated (turfing algae were defined as mat forming species generally less than 5 cm height). Algal measurements were converted to biomass for statistical analysis, using length-weight and percent cover-weight relationships (Table 2). To obtain length-weight relationships a number of plants covering a range of sizes were measured to the nearest cm, dried at 80°C and weighed to the nearest 0.1 g. For functional groups, which generally only made a small contribution to overall algal biomass, percent cover estimates were converted to dry weight. These were calculated from three 10 × 10 cm ($0.01\ m^2 = 1\%$) samples that were collected, dried and weighed.

Overall differences in algal communities between years and between reserve and non-reserve sites were tested using non-parametric multivariate analysis of variance (NP-MANOVA) (Anderson 2001). Ecological data very rarely conform to the strict normality assumptions of traditional parametric MANOVA, so non-parametric techniques based on permutation tests are preferred. Analysis was carried out on biomass data for the 12 most-dominant species, while the remaining species were grouped into 11 functional groups (Table 2). The analysis was based on Bray-Curtis similarities, and data were fourth-root transformed to ensure that all species or groups, abundant or rare, contributed to the triangular matrix (Clarke & Warwick 1994). NP-MANOVA currently does not allow 3-way tests, so separate analyses on the effect of Year and Status, with Site as a nested term, were carried out for each of the 4 depth ranges. No corrections were made to adjust for multiple testing; however, permutation tests calculate exact p-values. Non-metric multidimensional scaling (MDS) was used to display similarities in overall algal communities between sites and years and similarity percentages analysis (SIMPER) was used to identify the species responsible for differences between reserve and non-reserve sites (Clarke & Warwick 1994).

Differences in the abundance of urchins, herbivorous gastropods and the biomass of the 2 dominant macroalgal species (*Ecklonia radiata* and *Carpophyllum maschalocarpum*) were compared between reserve and non-reserve sites and between years using a generalised linear mixed model. The factors Year, Status and Depth range were treated as fixed factors and Site (Year × Status) as a random effect. The model was fit-

Table 2. Algal species and functional groups used in analysis along with length-weight and/or percent cover-weight relationships for biomass estimates. y = dry weight (g), x = total length (cm), SL = stipe length (cm) and LL = laminae length (cm)

Species	Equation	R^2	n
Brown algae			
Carpophyllum angustifolium[a]	$y = 0.068x - 0.27$	0.92	23
C. maschalocarpum	$\ln(y) = 1.764\ln(x) - 4.311$	0.72	46
C. plumosum	$\ln(y) = 1.472\ln(x) - 3.850$	0.66	62
C. flexuosum	$\ln(y) = 2.049\ln(x) - 5.251$	0.90	52
Xiphophora chondrophylla	$y = 1.786x - 4.171$	0.62	18
Ecklonia radiata[a] – Stipe	$\ln(y) = 1.671\ln(SL) - 3.787$	0.97	46
– Laminae	$\ln(y) = 1.177\ln(SL \times LL) - 3.879$	0.94	55
Sargassum sinclairii	$y = 0.075x + 0.124$	0.58	25
Landsburgia quercifolia	$\ln(y) = 1.971\ln(x) - 5.058$	0.83	19
Small brown algae,	$\ln(y) = 2.587\ln(x) - 6.443$		
e.g. *Zonaria turneriana*	$1\% = 2.5$ g	0.83	27
Brown turf, e.g. *Distromium*, *Dictyota* spp.	$1\% = 1.5$ g		
Brown encrusting, e.g. *Ralfsia*	$1\% = 0.1$ g		
Red algae			
Osmundaria colensoi	$\ln(y) = 1.720 \ln(x) - 3.379$	0.70	14
	$1\% = 22.9$ g		
Pterocladia lucida	$\ln(y) = 1.963 \ln(x) - 5.076$	0.73	47
	$1\% = 10.0$ g		
Melanthalia abscissa	$\ln(y) = 1.775 \ln(x) - 4.247$	0.64	22
Red foliose, e.g. *Plocamium* spp.	$\ln(y) = 2.649 \ln(x) - 8.812$	0.80	34
Red turfing (<5 cm), e.g. *Champia* spp.	$1\% = 1.7$ g		
Coralline turf[b], e.g. *Corallina officinalis*	$1\% = 4.5$ g		
Crustose corallines	$1\% = 0.1$ g		
Red encrusting	$1\% = 0.1$ g		
Green algae			
Codium convolutum	$1\% = 4.7$ g		
Others, e.g. *Ulva* sp.	$1\% = 1.7$ g		
Filamentous algae	$1\% = 0.2$ g		

[a] From Choat & Schiel (1982)

[b] The proportion of $CaCO_3$ in *Corallina officinalis* has been estimated as 45% of the dry weight (M. Taylor unpubl. data). The value given is the total dry-weight of samples less 45%

ted using the same procedure as for the habitat data (previous section) but to a Poisson distribution. Ratios of density or biomass between levels of significant fixed factors were calculated to provide an estimate of the size of main effects.

RESULTS

1978 to 2000: Long-term changes at permanent sites

The greatest changes since 1978 have occurred at permanent sites located in the mid-depths (Fig. 2). These sites, originally classified as urchin barrens (Ayling 1978), are now dominated by *Ecklonia radiata*, and urchins are rare. At shallow sites, urchin densities have generally been variable since 1978 (Fig. 2), although the density of *E. radiata* and fucalean algae have increased in recent years. The deeper sites (Fig. 2), which are dominated by mono-specific stands of *E. radiata*, have remained relatively stable over time. Low densities of *E. radiata* in 1994 resulted from a large-scale dieback which occurred in 1993 (Cole & Babcock 1996). The relatively high densities in 1978 are attributable to a large number of recruits (Ayling 1978), and the densities of adults are comparable to those today.

In general, trends in habitat change between 1978 and 1994 have continued since 1996 at all permanent sites, but this change has not been simultaneous at all sites. Prior to this study the mid-depth site at Waterfall Reef remained as urchin barrens, but in 2000 there was a considerable increase in both *Ecklonia radiata* and fucaleans (Fig. 3). Urchin populations at this site were dominated by adults (>50 mm TD) in 1978, 1994 and 1996 (Fig. 3), and both *Carpophyllum maschalocarpum* and *E. radiata* were rare. In 1999 and 2000 the number of adult urchins were declining and cryptic juveniles dominated the populations, allowing successful recruitment of *C. maschalocarpum* and *E. radiata* (Fig. 3).

1999 to 2001: Spatial contrasts and temporal change at reserve and non-reserve sites

Habitat distributions

Large differences were found in the extent of major habitat types between reserve and non-reserve sites in the shallow subtidal (<10 m depth) (Fig. 4). Most notable was the dominance of urchin barrens at non-reserve sites and the decline of urchin barrens from 4.9 ± 2.5% to complete loss of this habitat at all reserve sites between 1999 and 2001. Prior to 2001 urchin barrens occurred at low levels at sites in the western part of the reserve (Waterfall and Onespot). The complete absence of urchin barrens in reserve sites in 2001 rendered statistical analysis pointless. At non-reserve sites there was no overall difference among years in the extent of urchin barrens ($F_{2,21}$ = 1.52, p = 0.24). However, at Rodney South urchin barrens declined from 42.1 ± 0.4 and 49.7 ± 6.2% in 1999 and 2000, respectively, to being completely absent in 2001. This corresponded to an increase in turfing algae, mixed algae and kelp forest at this site.

The reefs at reserve sites had significantly higher cover of mixed algae ($F_{1,20}$ = 11.71, p < 0.01) and kelp forest ($F_{1,20}$ = 42.68, p < 0.01) than those at non-reserve sites (Fig. 4). The likelihood of mixed algae occurring at reserve sites was 3.6 (CL_{95} = 1.1, 6.1—upper and lower confidence limits) times higher than at non-reserve sites, while kelp forest was 2.7 (CL_{95} = 2.0, 3.7) times more likely to occur in the reserve. These

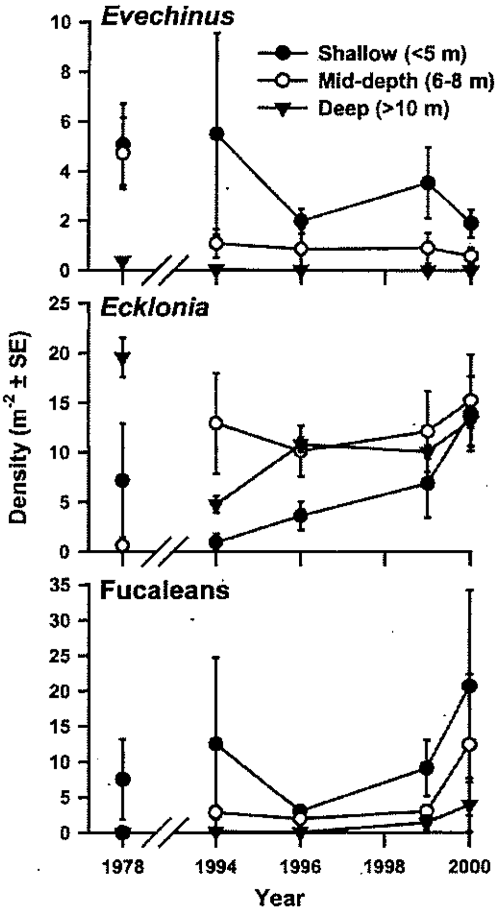

Fig. 2. Changes in *Evechinus chloroticus*, *Ecklonia radiata* and fucalean density at permanent sites located in the Leigh Reserve between 1978 and 2001

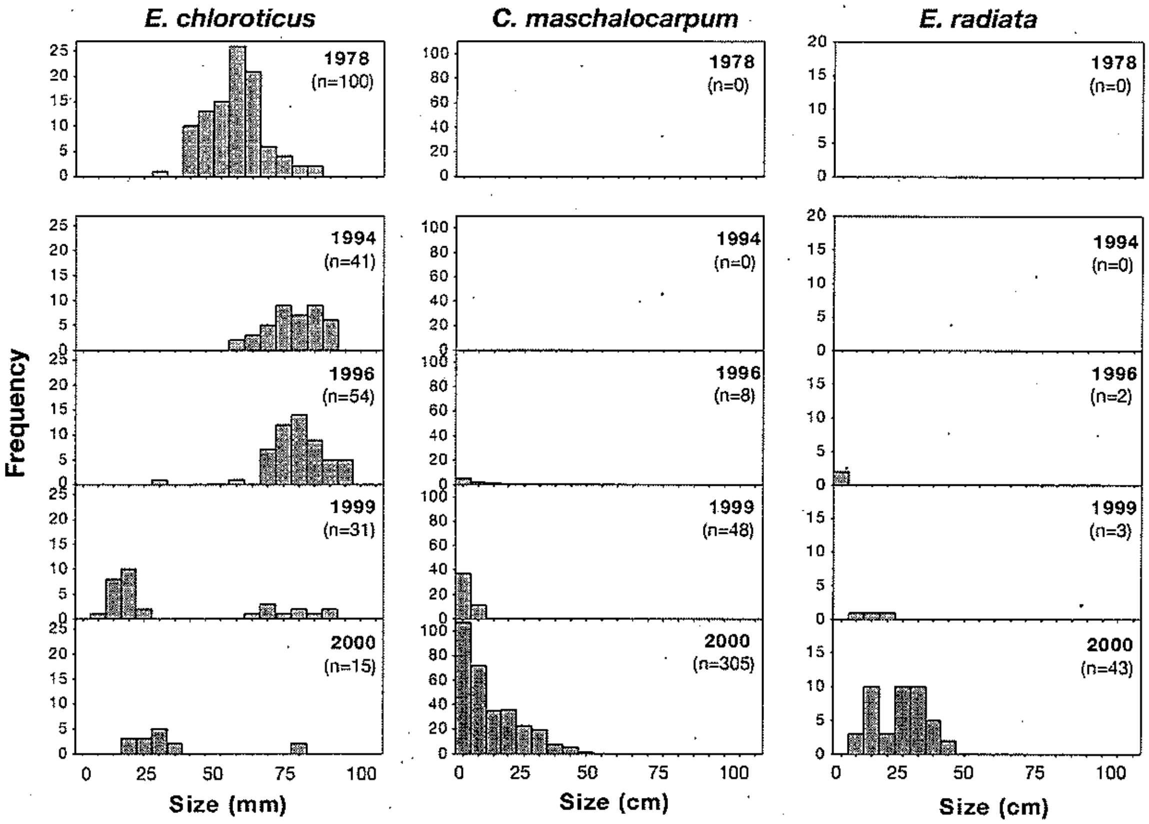

Fig. 3. Changes in *Evechinus chloroticus*, *Carpophyllum maschalocarpum* and *Ecklonia radiata* size-frequency distributions at the Waterfall Reef (mid-depth) permanent site between 1978 and 2001

reserve-related patterns were consistent among years, and there was no overall difference among years in the extent of either mixed algae ($F_{2,20}$ = 0.16, p = 0.85) or kelp ($F_{2,20}$ = 1.94, p = 0.17).

The cover of shallow *Carpophyllum maschalocarpum* habitat and turfing algae (Fig. 4) did not differ between reserve and non-reserve sites ($F_{1,20}$ = 1.3, p = 0.27 and $F_{1,20}$ = 0.46, p = 0.50) or between years ($F_{2,20}$ = 0.77, p = 0.48 and $F_{2,20}$ = 2.07, p = 0.15, respectively). However, there was an apparent increase in turfing algae at non-reserve sites between 2000 and 2001 (Fig. 4).

Invertebrate herbivores

The density of urchins varied significantly with depth (Fig. 5, Table 3) with most urchins being concentrated in the 4 to 6 m depth stratum. Densities were 1.7 (CL_{95} = 1.0, 2.9) and 2.9 (CL_{95} = 1.7, 4.8) times higher in the 2 shallow depth ranges (0 to 2 and 4 to 6 m) compared to the 7 to 9 m depth range. Urchins occurred in very low numbers in the deepest depth stratum (>10 m), so this depth was not included in analyses. Non-reserve sites had 1.84 (CL_{95} = 1.18, 2.87) times higher densities than reserve sites. There was no difference in overall urchin densities between years.

Urchins exhibiting cryptic behaviour also varied significantly with depth and reserve status but not between years (Fig. 5, Table 3). The density of cryptic urchins, predominantly juveniles (Fig. 6), was actually 2.21 (CL_{95} = 1.32, 3.71) times higher at reserve sites. The density of exposed urchins at reserve sites was low in 1999, and by 2001 they were absent at all depths except the 7 to 9 m depth stratum (Fig. 5). Exposed *Evechinus chloroticus* also declined at all non-reserve sites except Kempts Beach over the 3 yr. The greatest decline occurred at Rodney South, where the densities of exposed urchins dropped from 4.8 ± 1.0 m^{-2} in 1999 to 2.4 ± 0.8 m^{-2} in 2000, becoming completely absent in 2001. There were clear differences in urchin population size structures with reserve status (Fig. 6). While the contrast in reserve and non-reserve populations was relatively stable between years, a general decline in exposed urchins at reserve and non-reserve sites was apparent.

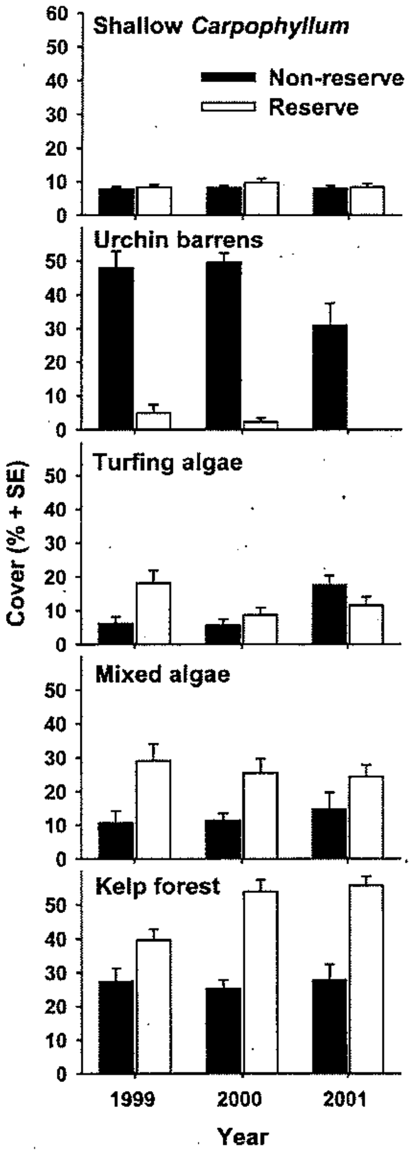

Fig. 4. Extent of major habitat types from line transects (n = 3) at reserve and non-reserve sites for 1999 to 2001

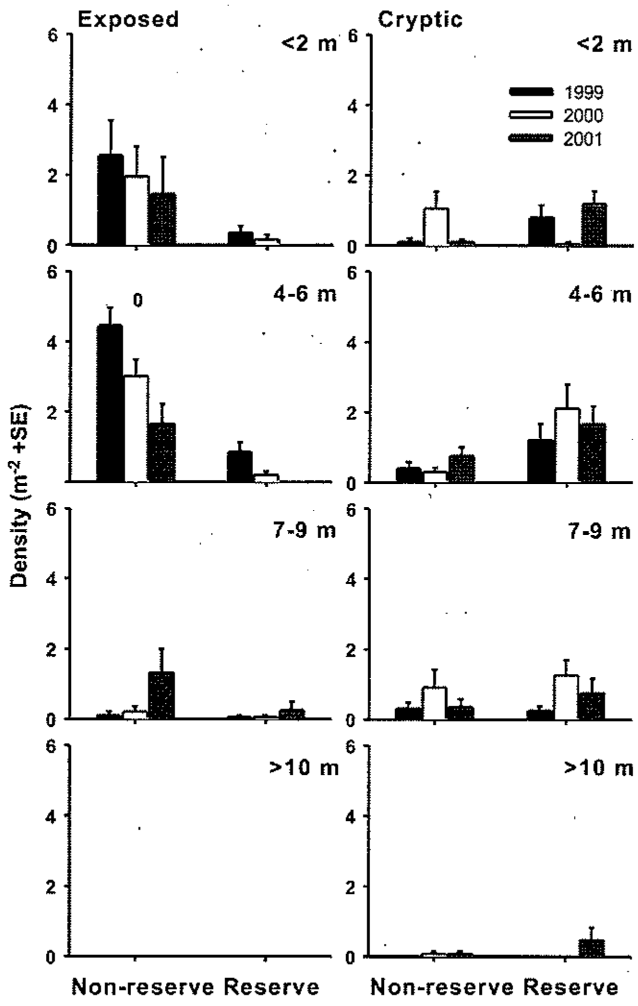

Fig. 5. Density of exposed and cryptic *Evechinus chloroticus* at reserve and non-reserve sites between 1999 and 2001

The densities of herbivorous gastropod species were generally variable, particularly among depths (Fig. 7, Table 3). *Cookia sulcata* and *Cellana stellifera* tended to be more abundant in the 2 shallow depth strata, while *Trochus viridis* and *Cantharidus purpureus* occurred at very low densities in the shallow strata and at high densities in the deeper strata. There were widespread declines in both *C. sulcata* and *C. stellifera* across all sites between 1999 and 2001. *C. sulcata* was 2.6 (CL_{95} = 1.4, 4.8) times more abundant in 1999 than 2001, and *C. stellifera* 16.9 (CL_{95} = 4.9, 58.3) times more abundant in 1999. There was also a significant effect of reserve status, with *C. sulcata* being 3.0 (CL_{95} = 1.2, 7.2) times more abundant at reserve sites, whereas *C. stellifera* was 2.5 (CL_{95} = 0.9, 7.2) times more abundant at non-reserve sites (Table 3).

Macroalgae

Macroalgal assemblages. There were large differences in algal assemblages between reserve and non-reserve sites (Table 4). These effects differed with depth (Table 5A), and were only significant for the 4 to 6 m depth range (Fig. 8), where algal biomass was low at non-reserve sites, consistent with high densities of exposed *Evechinus chloroticus* (Fig. 5). In the 4 to 6 m depth strata the biomass of *Ecklonia radiata*, *Carpophyllum maschalocarpum*, crustose corallines and

Table 3. Results from mixed model analysis on dominant invertebrate herbivores and algal species from quadrat sampling at reserve and non-reserve sites from 1999 to 2001. Model back-fitted by removing non-significant interaction terms. Analysis excludes depth strata where taxon was absent or very rare. Significance: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

	Fixed effects				Covariance parameter estimates	
	Year	Status	Depth range	Status × Depth range	Site (Status × Year)	AR (1)
Evechinus chloroticus						
All (excl. >10 m)	$F_{2,20} = 0.26$	$F_{1,20} = 7.11^{*}$	$F_{2,334} = 8.95^{***}$	–	0.04	0.16^{*}
Cryptic (excl. >10 m)	$F_{2,20} = 1.82$	$F_{1,20} = 9.00^{**}$	$F_{2,334} = 3.27^{*}$	–	0.01	0.10
Herbivorous gastropods						
Cookia sulcata (all depths)	$F_{2,20} = 7.34^{**}$	$F_{1,20} = 25.12^{***}$	$F_{3,420} = 3.43^{*}$	$F_{3,420} = 4.07^{**}$	0.28^{*}	0.18^{***}
Cellana stellifera (excl. 7–9 and >10 m)	$F_{2,20} = 15.39^{***}$	$F_{1,20} = 7.26^{*}$	$F_{1,214} = 13.12^{***}$	$F_{1,214} = 5.40^{*}$	0.82^{*}	–0.06
Trochus viridis (excl. <2 m)[a]	$F_{2,20} = 0.80$	$F_{1,20} = 1.54$	$F_{2,298} = 8.13^{***}$	$F_{2,298} = 3.27^{*}$	0.56^{**}	0.20^{**}
Cantharidus purpureus (excl. <2 m)	$F_{2,20} = 0.56$	$F_{1,20} = 0.29$	$F_{2,302} = 30.67^{***}$	$F_{2,302} = 6.54^{**}$	0.82^{**}	0.11
Algae[b]						
Ecklonia radiata (all depths)	$F_{2,20} = 5.16^{*}$	$F_{1,20} = 3.02$	$F_{3,420} = 50.20^{***}$	$F_{3,420} = 8.32^{***}$	0.22^{**}	0.12^{*}
C. maschalocarpum (excl. 7–9 and >10 m)	$F_{2,20} = 3.23^{0.06}$	$F_{1,20} = 1.62$	$F_{1,215} = 46.30^{***}$	–	0.29^{*}	0.33^{***}

[a] *Trochus viridis* also had a significant Year × Depth interaction ($F_{4,298} = 2.42$, $p = 0.0489$)

[b] Mixed model for algal species carried out on algal dry-weight estimates (g)

coralline turf was higher at reserve sites, while at non-reserve sites there was more filamentous algae and also *C. flexuosum* (Table 4). Within the other depth ranges, there were some clear differences for particular species. For example, in the shallow depth range (<2 m) reserve sites had a much higher biomass of *C. angustifolium* and *Pterocladia lucida*. Nevertheless, there was no significant difference in overall algal

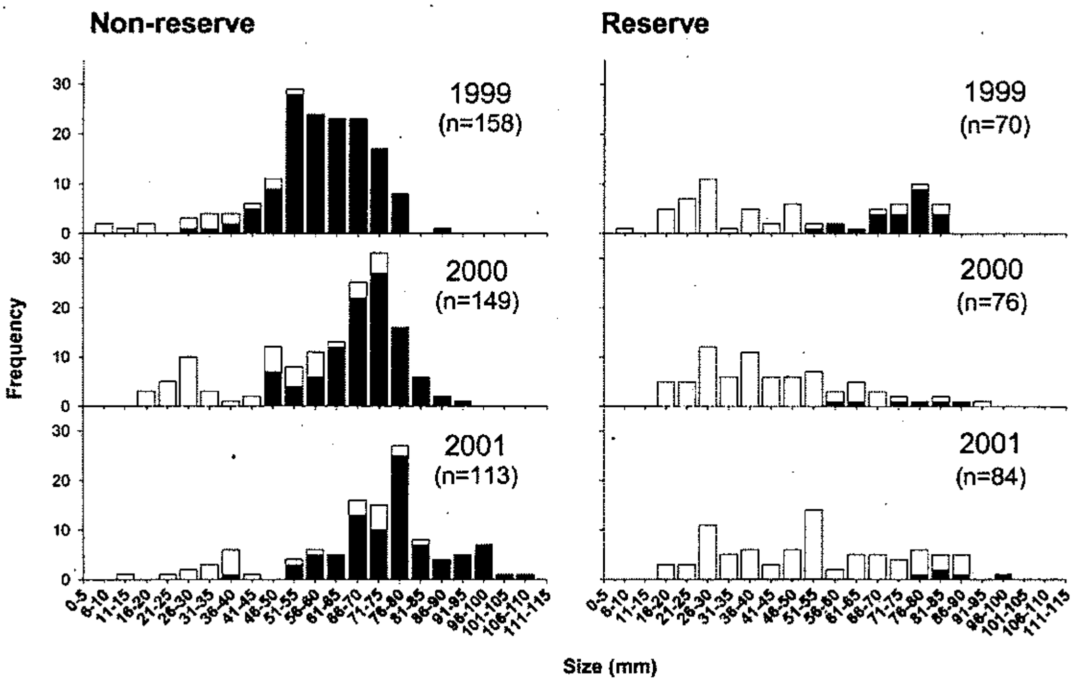

Fig. 6. *Evechinus chloroticus* size frequency distribution for reserve (4 sites) and non-reserve (4 sites) populations between 1999 and 2001. Samples pooled across all depths. Filled bars indicate exposed individuals; open bars indicate cryptic urchins

Table 4. The main algal species separating reserve and non-reserve sites in the 4 to 6 m depth stratum from 2001 sampling. The top 10 species are ranked according to their contribution to the difference between reserve and non-reserve sites. Note that in some cases species refers to an algal group, e.g. Filamentous. For each species the average biomass (g m^{-2} ± SE) for reserve and non-reserve sites, the average dissimilarity (*Dis*), the ratio of average dissimilarity and standard deviation (*Dis*/SD), the percent contribution to overall dissimilarity (%*Dis*), the cumulative percentage (Σ %*Dis*) and the percent contribution to total algal biomass (%B) at that depth are presented

Species	Reserve	Non-reserve	*Dis*	*Dis*/SD	%*Dis*	Σ %*Dis*	%B
Average dissimilarity 61.31%							
Ecklonia radiata	205.1 ± 42.1	29.4 ± 16.4	15.4	1.74	25.2	25.2	45.5
Carpophyllum maschalocarpum	120.3 ± 30.6	5.9 ± 2.6	13.0	1.72	21.2	46.4	24.4
Filamentous	0.3 ± 0.1	7.0 ± 1.2	7.0	1.59	11.5	57.8	1.4
Coralline turf	72.0 ± 13.7	43.2 ± 11.3	4.9	1.27	8.1	65.9	22.3
Crustose corallines	7.3 ± 0.4	3.3 ± 0.5	3.6	1.42	5.9	71.8	2.1
Red turf	1.0 ± 0.2	1.1 ± 0.6	2.9	1.33	4.8	76.6	0.4
Pterocladia lucida	1.3 ± 1.0	3.3 ± 1.8	2.4	0.53	3.9	80.5	0.9
C. flexuosum	0	3.9 ± 2.5	2.2	0.5	3.6	84.1	0.8
Codium convolutum	0.5 ± 1.2	0.9 ± 0.2	2.8	0.86	3.4	87.5	0.3
Sargassum sinclairii	0.7 ± 0.4	0.9 ± 0.5	2.3	0.91	3.3	90.8	0.3
Others (6 spp.)	6.2	2.3			9.1		1.6

assemblages between reserve and non-reserve sites at these depths.

Overall algal assemblages were stable over time (1999 to 2001) at all depths (Table 5B). However, in the 4 to 6 m depth range the effect of year was marginally insignificant (NP-MANOVA, p = 0.06, Table 5B) and changes were apparent in the similarity of algal communities at reserve and non-reserve sites (Fig. 8).

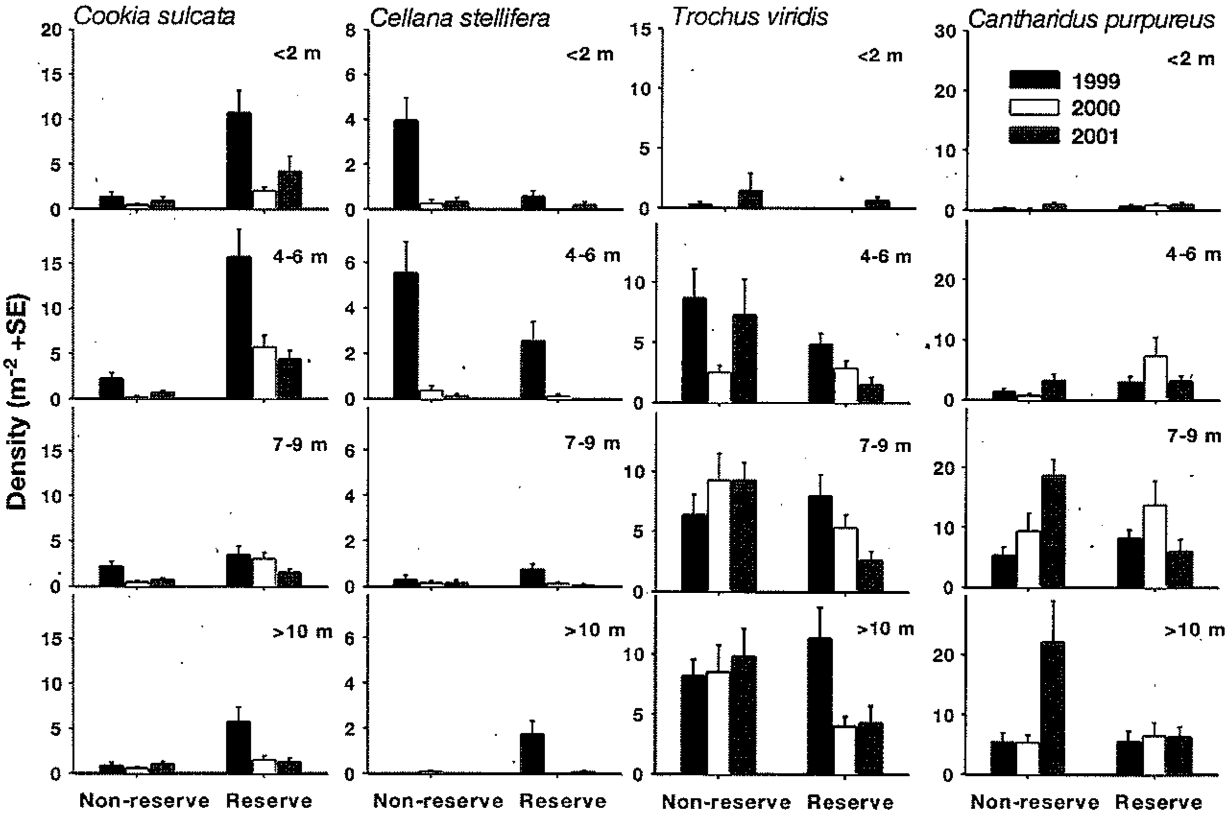

Fig. 7. Density of the 4 most common gastropod species at reserve and non-reserve sites between 1999 and 2001. Note differing *y*-axis scales

Reserve sites grew more similar (similarity increased from 56.2 to 73.8%), as all sites became dominated by the large brown algae *Ecklonia radiata* and *C. maschalocarpum*, while sites outside the reserve became more different (similarity decreased from 65.2 to 45.2%), due to the increase in large brown algae at Rodney South. At Kempts Beach there was high variation among samples each year (Fig. 8) due to the position of the urchin barren-kelp forest border. While the overall difference in algal communities between reserve and non-reserve sites was consistent from 1999 to 2001 (Fig. 8), changes were apparent in the dominant species.

Dominant species. Ecklonia radiata and *Carpophyllum maschalocarpum* (Fig. 9) were the greatest contributors to total algal biomass each year (67.6 ± 1.2 and 22.4 ± 1.4%, respectively) and were largely responsible for the differences at 4 to 6 m between reserve and non-reserve sites (Table 4). *E. radiata* biomass varied significantly with year (Table 3). A large increase in *E. radiata* biomass across all depths was apparent between 1999 and 2000. There was no overall difference between reserve and non-reserve sites, but the effect of status changed with depth (Table 3). Significant differences with status occurred between 4 and 6 m ($F_{1,20} = 21.99$, $p < 0.01$), where *E. radiata* biomass was 12.5 ($CL_{95} = 4.4$, 35.9) times higher at reserve sites, and deeper than 10 m ($F_{1,14} = 6.03$, $p = 0.03$), where the biomass was actually 2.0 (1.2, 3.4) times higher at the non-reserve sites. This effect was largely due to the high biomass of *E. radiata* at 2 non-reserve sites, Mathesons Island and Nordic Reef, where the plants were larger than those at other sites.

Carpophyllum maschalocarpum dominated the shallowest depth stratum, was common at 4 to 6 m depth and rare in the deeper strata (Fig. 9). While biomass varied significantly between depths there was no overall difference among years or with reserve status (Table 3). These patterns were consistent at depths <2 m, but at 4 to 6 m *C. maschalocarpum* biomass increased significantly between years ($F_{2,20} = 4.12$, $p = 0.03$) and was 28.5 ($CL_{95} = 7.4$, 109.9) times higher at reserve sites ($F_{1,20} = 23.6$, $p < 0.01$).

Table 5. Differences in algal communities (A) between reserve and non-reserve sites and (B) between 1999 and 2001. Results from NP-MANOVA; data were transformed to $\ln(x+1)$; analysis based on Bray-Curtis dissimilarities; restricted permutation of raw data with 4999 permutations. The tests for the effect of Status are presented for the 2001 data

	df	MS	*F*	p
(A) Reserve status				
0–2 m				
Status	1	6655.4	1.96	0.06
Site(Status)	6	3390.5	3.89	**<0.01**
4–6 m				
Status	1	22219.7	8.07	**0.03**
Site(Status)	6	2754.9	4.03	**<0.01**
7–9 m				
Status	1	3446.8	1.60	0.09
Site(Status)	6	2150.9	5.33	**<0.01**
>10 m				
Status	1	2576.6	1.30	0.29[a]
Site(Status)	6	1988.8	8.49	**<0.01**
(B) Time 1999–2001				
0–2 m				
Time	2	5522.9	1.43	0.12
Site(Time)	21	3857.9	4.92	**<0.01**
4–6 m				
Time	2	11868.6	2.27	0.06
Site(Time)	21	5233.4	8.13	**<0.01**
7–9 m				
Time	2	1597.6	0.96	0.48
Site(Time)	21	1667.6	4.78	**<0.01**
>10 m				
Time	2	2210.6	0.83	0.58
Site(Time)	15	2668.7	9.93	**<0.01**

[a] Only 10 possible permutations

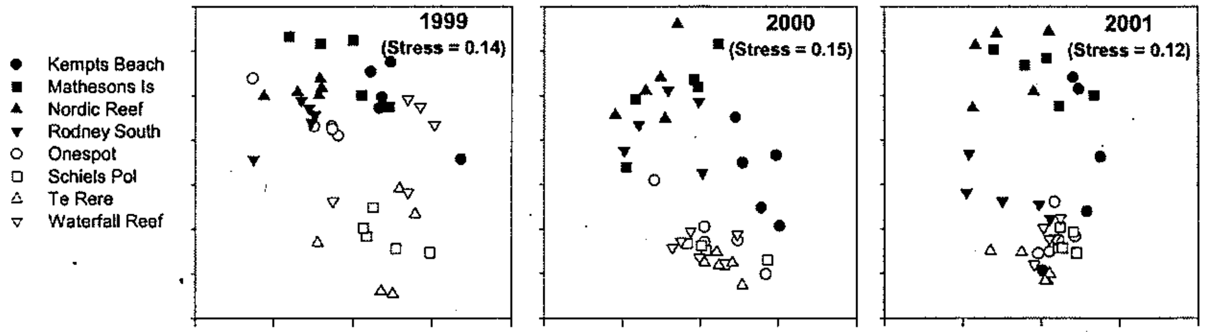

Fig. 8. Temporal changes in algal communities for the 4 to 6 m depth range between 1999 and 2001. MDS ordination based on Bray-Curtis similarities of quadrat data from each year. Data were fourth-root transformed. Open symbols indicate reserve sites, and closed symbols non-reserve sites

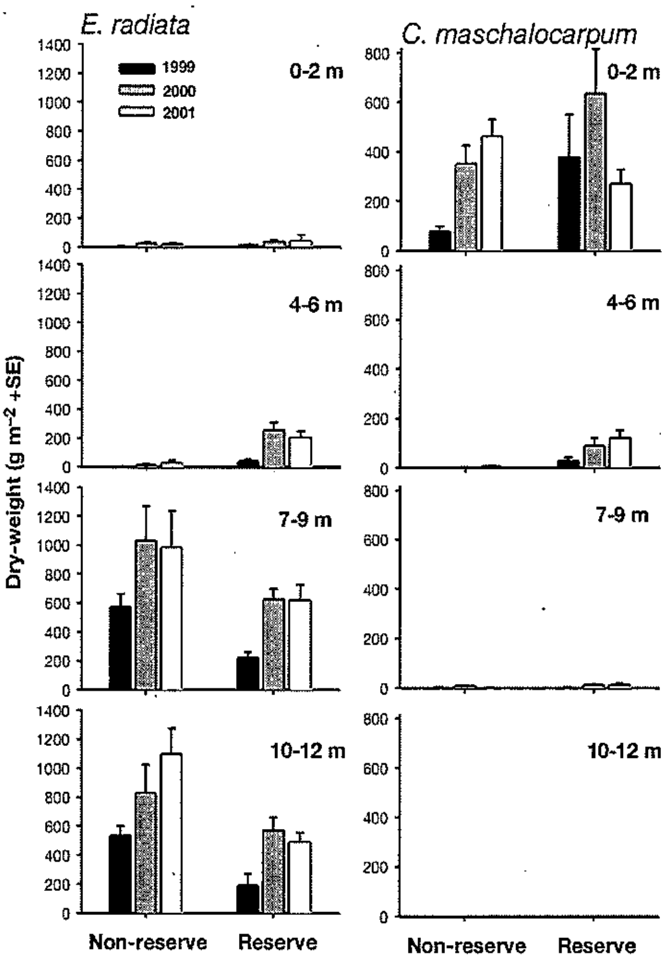

Fig. 9. Biomass of *Ecklonia radiata* and *Carpophyllum maschalocarpum* at reserve and non-reserve sites between 1999 and 2001

DISCUSSION

Long-term habitat change in the Leigh Reserve

The transition from urchin barrens to kelp has continued in the Leigh Reserve since 1996, consistent with the top-down control of urchins by predators in this system (Babcock et al. 1999, Shears & Babcock 2002). In 1978 the urchin barrens habitat dominated between depths of 5 and 9 m (Ayling 1978). Now, all of Ayling's (1978) permanent sites originally classified as 'rockflats' (= 'urchin barrens'; Table 1) are dominated by large brown algae. In 1996 the permanent site located on Waterfall Reef persisted as urchin barrens (Babcock et al. 1999), as it had done for over 25 yr (Ayling 1981). Cole & Keuskamp (1998) recorded a 10 yr decline in density of the sea urchin *Evechinus chloroticus* at this site prior to 1998. This decline has continued in 1999 and 2000, and this area is now dominated by large brown algae (Fig. 3).

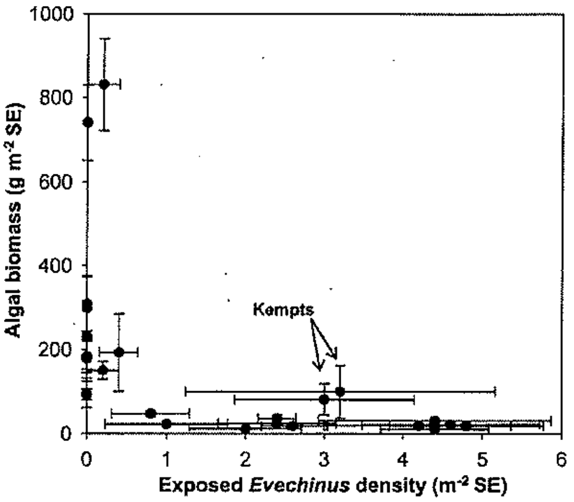

Fig. 10. Relationship between total algal biomass and exposed urchin density in the 4 to 6 m depth range. Data are site averages (n = 5 quadrats) at each sampling time (1999–2001). The 2 outliers are from Kempts Beach, where sampling was carried out on the kelp forest border, where urchins are in close proximity to *Ecklonia radiata*

Permanent sites located in shallower (<5 m) and deeper (>10 m) water have historically been dominated by large brown algae, and these areas have remained relatively stable since 1978. At shallow depths sea urchins are typically cryptic, due to higher water motion and also a more abundant supply of drift algae (Lissner 1980, Rogers-Bennett et al. 1995), and have limited grazing effects on algae. Cryptic behaviour also reduces susceptibility to predation, and subsequently in the shallow permanent sites *Evechinus chloroticus* remains at moderate but variable densities. Deeper permanent sites are dominated by monospecific stands of *Ecklonia radiata*, and *E. chloroticus* occurs at very low densities; consequently, these areas have remained stable since 1978. Low numbers of sea urchins in kelp forests have been attributed to low recruitment (Duggins et al. 1990), low juvenile survivorship (Andrew & Choat 1985), physical abrasion of algae on adult urchins (Konar 2000) and predators associated with kelp (Breen & Mann 1976). At the permanent sites sampled there were no apparent long-term effects on *E. radiata* populations resulting from the widespread dieback event recorded in 1992–93 (Cole & Babcock 1996).

While data are lacking for the permanent sites between 1978 and 1994, trends in habitat change have continued along the same trajectory since 1994. In other systems these habitats show long-term persistence, and transitions between barrens and kelp are thought to occur irregularly without any detectable periodicity (reviews by Harrold & Pearse 1987, Chapman & Johnson 1990, but see Hagen 1995). The dominant algae in this system (*Ecklonia radiata* and *Carpophyllum maschalocarpum*) are both relatively resilient long-lived species (Novaczek 1980, Schiel 1985, T. Haggitt unpubl. data), and algal habitats appear stable once established. It is therefore unlikely that the depth-specific changes seen are a result of short-term or cyclical patterns in abundance of major structural species. This long-term data on urchin and kelp abundances at specific sites have proved highly valuable in identifying the trophic cascades responsible for shifts between these alternate states.

Contrasts between reserve and non-reserve sites

Differences in both grazer and algal communities between reserve and non-reserve sites are consistent with the direct and indirect effects associated with higher abundances of urchin predators (Kelly et al. 2000, Willis et al. 2000, in press) at reserve sites, thus providing evidence for a trophic cascade. The greater cover of urchin barrens habitat and higher urchin densities at unprotected sites seen in this study have previously been attributed to lower levels of predation on urchins compared to reserve sites (Babcock et al. 1999, Shears & Babcock 2002). As seen in changes at permanent sites, these effects are depth-specific, and in this case reserve-related differences were only apparent in the 4 to 6 m depth stratum. In this depth range exposed *Evechinus chloroticus*, which are responsible for maintaining the urchin barrens habitat (Shears & Babcock 2002), were rare in the reserve, and the biomass of *Ecklonia radiata* and *C. maschalocarpum* was 12.5 and 28.5 times higher at reserve than non-reserve sites.

The size structure of urchins also differed between reserve and non-reserve sites. Previous studies suggested that bimodal population structures in the Leigh reserve and Tawharanui Marine Park resulted from high levels of size-specific predation (Cole & Keuskamp 1998, Shears & Babcock 2002). In our study reserve populations were weakly bimodal in 1999, but in subsequent years this bimodality was lost due to the continual decline in abundance of large exposed urchins. Within the reserve, proportionally more urchins exhibited cryptic behaviour than at non-reserve sites, and crypsis was also maintained by larger individuals. Cryptic behaviour of urchins at reserve sites is likely to be due to a combination of factors, including a more abundant supply of drift algae that reduces the need for active foraging (Harrold & Reed 1985), abrasion by macroalgae (Konar 2000), and greater levels of predation (Shears & Babcock 2002).

In addition to trophic cascades, evidence for further, indirect effects (Menge 1995) is provided by differences in the abundance of the limpet *Cellana stellifera* and the turbinid gastropod *Cookia sulcata* between reserve and non-reserve sites. The density of *C. sulcata* was 3 times higher at reserve sites. This may be related to the higher cover of coralline turf seen at reserve sites associated with reduced urchin densities (Shears & Babcock 2002). Coralline turf is a major component of the diet of *C. sulcata* (Keestra 1987), and the abundance of *C. sulcata* is generally positively correlated with the cover of coralline turf (N. T. Shears unpubl. data). Such indirect effects may provide an example of habitat facilitation (Menge 1995), whereby predators indirectly improve the habitat for *C. sulcata* through the removal of *Evechinus chloroticus*.

Conversely, densities of *Cellana stellifera* were 2.5 times lower in the reserve than at non-reserve sites. This is consistent with patterns recorded in the Aleutian Islands, where limpets occur at higher densities where sea otters are absent (Simenstad et al. 1978). While the lower abundance of *C. stellifera* in the reserve may be related to the higher abundance of predators, the grazing activity of *Evechinus chloroticus* maintains a suitable substratum (crustose coralline algae) for the attachment and movement of *C. stellifera* (Andrew & Choat 1982). Experimental removals of urchins typically result in increased biomass of turfing algae and a decline in limpet densities (Andrew & Choat 1982, Fletcher 1987, Andrew & Underwood 1993, N. T. Shears unpubl. data). Therefore, the indirect effect of increased predator density is a lower density of limpets in the reserve, which could be interpreted as an example of habitat inhibition (cf. Menge 1995).

Temporal consistency of reserve-related differences

Differences in community structure between reserve and non-reserve sites were stable from 1999 to 2001, consistent with a trophic cascade. While this spatial contrast indicates stability of long-term changes, there were some short-term changes in urchin density and algal communities at both reserve and non-reserve sites. In 1999 exposed urchins and urchin barrens habitat occurred in the 4 to 6 m depth range at the sites in the eastern part of the reserve (Waterfall and Onespot). However, in subsequent years *Evechinus chloroticus* declined below an apparent threshold density, allowing macroalgae to dominate, consistent with patterns seen at the permanent site at Waterfall Reef. By 2001 the urchin barrens habitat was absent, and exposed urchins were rare at reserve sites. Comparisons of exposed urchin density and algal biomass at sites in this study (Fig. 10) revealed that the threshold density of exposed urchins required to maintain the barrens habitat appears to be around 1 m^{-2}, below which macroalgae quickly colonize. Breen & Mann (1976) estimated that kelp could not recolonize barren areas in Nova Scotia when urchin biomass exceeds 150 g m^{-2} (wet weight). This is consistent with our study, in which the average test diameter (D) of exposed urchins was 69.0 ± 0.7 mm, equating to a wet weight of 134.2 g (weight = $0.000843D^{2.8288}$; R. Taylor unpubl. data). It is not clear what the threshold urchin density would be for the reversal of kelp to urchin barrens and also not clear is the time-scale of such transitions. Ayling (1981) suggested that only when urchin densities increased above ~6 m^{-2} was grazing intensity sufficient to allow the formation of urchin barrens. Similarly, in Nova Scotia a threshold urchin biomass of 2 kg m^{-2} (wet weight) is necessary to initiate destructive grazing of kelp forests (Breen & Mann 1976, Scheibling et al. 1999). In our study this would equate to a density of exposed *E. chloroticus* of 14.9 m^{-2}. Such densities are currently rare on reefs in the Leigh area (N. T. Shears pers. obs.).

Rapid declines in urchin densities were recorded at 3 of the non-reserve sites associated with a local-scale urchin mortality event observed around Leigh in summer 1999-2000 (J. Walker & R. Babcock unpubl. data). However, only at 1 of these sites (Rodney South) did urchin density drop below 1 m^{-2}, allowing macroalgae to establish. The urchin barrens habitat remained stable at the other sites among years despite reduced urchin densities. Mass mortality of *Evechinus chloroticus* has not been previously documented in northeastern New Zealand, but the rapid declines and the symptoms of 'sick' and dying urchins are consistent with disease in stronglyocentrotid species (Shimizu et al. 1995). Urchins exhibiting these symptoms were only observed at sites outside the reserve. Large declines in *Cellana stellifera* also occurred between 1999 and 2001, which is consistent with a reduction in urchin density (Andrew & Choat 1982). Recovery of urchins from such die-offs is likely given the small-scale of mortalities. In Jamaica recovery of *Diadema antillarum* has been reported (Edmunds & Carpenter 2001) even after the large-scale mass mortalities there (Lessios 1988).

Over the duration of our study (1999 to 2001) climatic conditions were in a weak La Niña phase, with consistently warmer than average summer water temperatures (J. Evans unpubl. data). This may have been related to the occurrence of the urchin die-off seen at some non-reserve sites. Urchin mortalities in other parts of the world have also been associated with higher than normal water temperatures (Scheibling & Hennigar 1997). The long-term trends seen in the reserve at Leigh, however, do not appear to be correlated with any changes in oceanographic conditions. Since 1978 there have been no clear trends in sea temperature, with both warmer and colder than average years (J. Evans, Leigh Marine Laboratory, unpubl. data). Furthermore, the contrasting states between reserve and non-reserve sites discount oceanographic changes as a mechanism for explaining long-term changes at reserve sites.

CONCLUSIONS

The findings from this study provide further evidence for a trophic cascade on subtidal reefs in northeastern New Zealand:

- The continued, long-term decline in urchin-dominated habitats and increase in algal habitats at reserve sites is consistent with top-down control of predators on assemblage structure.
- Conspicuous indirect effects on algae are apparent between reserve (high predators) and non-reserve (low predators) sites. Other indirect interactions such as habitat facilitation and inhibition at 2 trophic levels below top predators have also been observed.
- The contrasts in assemblage structure between reserve and non-reserve sites have generally remained stable over the last 3 yr.

In northeastern New Zealand the urchin barrens habitat can persist for long periods while urchin numbers decline, due to the low threshold density of urchins required to maintain the habitat. Predation is highest on juvenile urchins, while only low rates of predation occur on the large urchins, which are responsible for maintaining the habitat (Shears & Babcock 2002). Therefore the indirect effects of increases in predator abundance associated with marine reserve protection on benthic community structure have occurred over a long period in the Leigh reserve. The trophic effects of other disturbances that directly affect adult urchins (e.g. disease, harvesting) can operate over much shorter time scales, which result in rapid changes in assemblage structure such as those observed outside the reserve. Trajectories of habitat change at non-reserve sites will be of continued interest along with the degree of persistence of kelp communities in the reserve.

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

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

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

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

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

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

This review synthesizes available information, including extensive previously unpublished results and gray literature, on the effects of zoning and spatial management on the GBR, with an emphasis on the 2004 Zoning Plan and in the context of adaptive management of the GBR Marine Park. The paper examines direct effects of the zoning on target fish and sharks on no-take and no-entry coral reefs, indirect effects on corals, crown-of-thorns starfish, and reef food webs, and effects for nonreef habitats and species of conservation concern. These ecological insights are complemented by an examination of

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

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

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

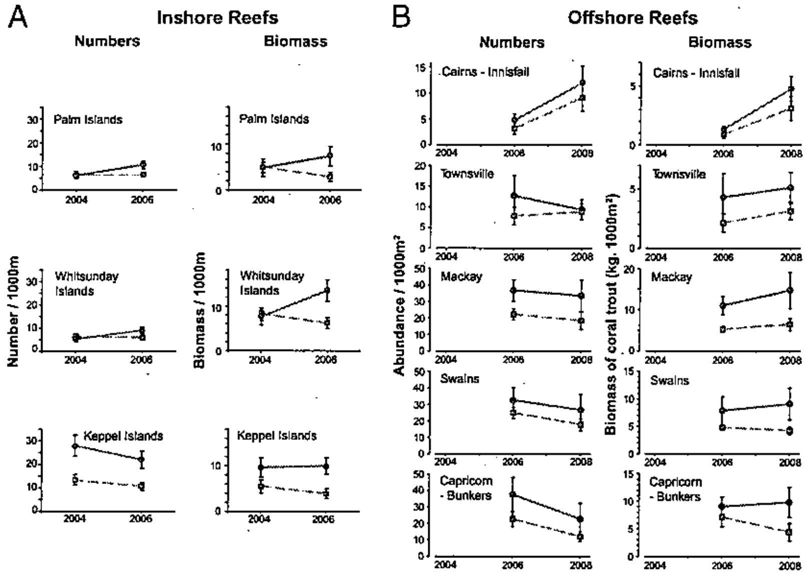

Fig. 1. Abundance and biomass of coral trout on fished and no-take reefs spread across ≈1,000 km of the Great Barrier Reef (see map in Fig. S1). Solid lines are no-take zones; dashed lines are fished reefs. Data are means ±SEM from scuba-based, visual transects of reefs zoned in 2004, updated from ref. 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 redthroat emperor (*L. miniatus*), and lutjanids (tropical snappers) were markedly more abundant and coral trout were larger in no-entry zones than in no-take zones (Fig. S3) (20). Although the data for no-entry zones have some limitations, this is a critical result because it raises the possibility that lower abundance in no-take zones is due to incomplete compliance (no-entry zones are much simpler to enforce, and hence have more effective compliance; further explanation, *SI Section 2*). It also suggests that baseline populations of target fish may have been significantly more abundant than previously recognized, with stocks in most areas significantly depleted in comparison with that baseline.

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

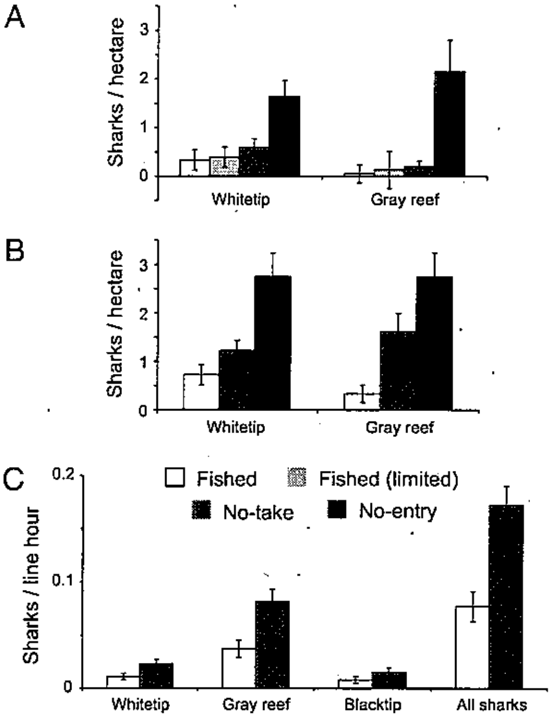

Fig. 2. Abundance of reef sharks in different zones in the northern and central GBR. Abundance of sharks based on scuba-based, visual transects for *A* (from ref. 20) and for *B* (from ref. 21). (*C*) Catch rates of sharks using commercial line fishing, disaggregated from ref. 20. All data are means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

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.

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).

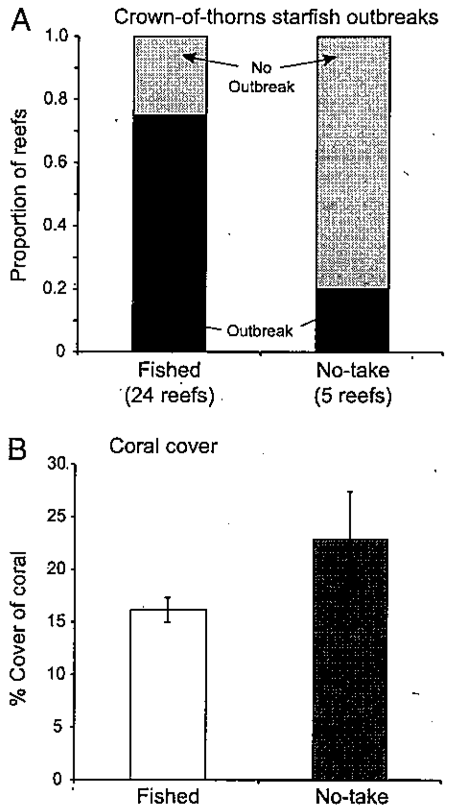

Fig. 3. Effects of zoning on coral-eating starfish and hence on coral populations. (*A*) Frequency of outbreaks of crown-of-thorns starfish on no-take and fished midshelf reefs in regions with active outbreaks present. Data are for 1994–2004, redrawn from ref. 31; note low numbers of no-take reefs were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

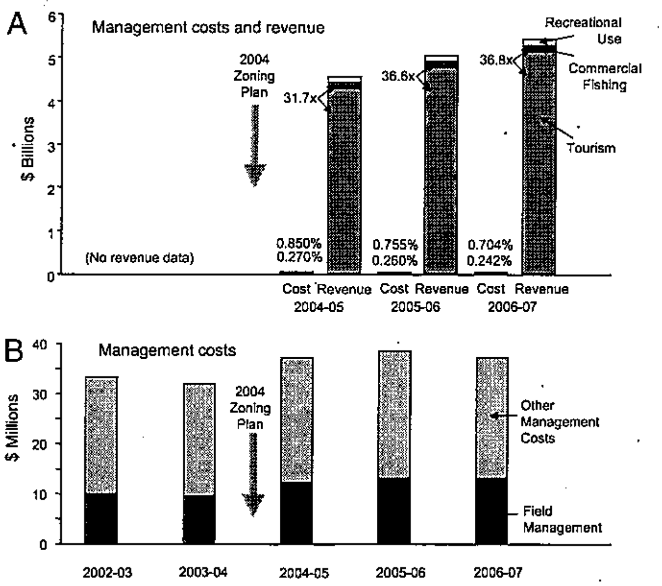

Fig. 4. Economic costs and benefits for the Great Barrier Reef. (*A*) Economic value of the GBR to the Australian economy (50–52), compared to expenditure on management of the Great Barrier Reef Marine Park (65–67). Tourism provides the vast majority of economic benefits (numbers indicate ratio of tourism 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.

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).

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.

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Rapid recolonisation of snapper *Pagrus auratus*: Sparidae within an offshore island marine reserve after implementation of no-take status

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ABSTRACT: This study reports the response of snapper *Pagrus auratus* to the establishment of no-take status in a marine reserve around the Poor Knights Islands in northeastern New Zealand. The Poor Knights and 2 reference locations, Cape Brett and the Mokohinau Islands, were sampled biannually for 4 yr using baited underwater video (BUV). Following the implementation of full marine reserve status at the Poor Knights in October 1998, snapper showed significant increases in abundance and biomass relative to fished control locations. This was particularly apparent for large snapper (>270 mm), whose numbers increased rapidly to levels 7.4 times higher in the final survey compared to the initial pre-reserve survey, and total snapper biomass increased by 818%. There was no significant increase in the abundance, biomass or size of snapper at the reference locations over this time. There was a strong seasonal trend in snapper abundance, with higher numbers in autumn (March/April) compared to spring (September/October). The daily batch fecundity was 11 to 18 times higher at the Poor Knights compared to the reference locations. Once fishing ceased in previously partially protected areas, a rapid recovery of snapper ensued, suggesting that partial fishing regulations are ineffective for protecting targeted species. The speed of increase in snapper density resulted from the immigration of adult fish into the reserve, rather than from within-reserve recruitment.

KEY WORDS: Baited underwater video · Poor Knights · Fishing · Partial protection · Temperate reefs · Temporal variation

INTRODUCTION

Marine reserves are becoming an increasingly popular concept for protecting fish species susceptible to exploitation from fishing, and the evidence that marine reserves increase the density, biomass and size of target species on reefs appears considerable (see reviews in Roberts & Polunin 1991, Dugan & Davis 1993, Rowley 1994, Attwood et al. 1997, Mosquera et al. 2000, Palumbi 2001, Halpern 2003). However, in a recent review, Russ (2002) concluded that the empirical evidence for positive marine reserve effects is more equivocal than other reviews have suggested, with a lack of any well designed, definitive experiments carried out at appropriate scales of time and space (also see Guidetti 2002, Willis et al. 2003b).

The lack of suitable data prior to the establishment of a marine reserve makes it difficult to quantify the rate of response to protection. However, where pre-reserve data are available, rapid rates of increase have been reported (White 1988, Russ & Alcala 1996, Edgar & Barrett 1999). For example, McClanahan & Kaunda-Arara (1996) found that lethrinids showed a 13.5-fold increase in biomass in the Mombasa National Park over 3 yr following reserve establishment. In a recent meta-analysis, Halpern & Warner (2002) noted that significant increases in density and biomass are

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attained in the first 1 to 3 yr after protection. However, the strength of their meta-analysis is reduced by the heterogeneity of the sample, mixing well managed with poorly managed reserves, and partial with full protection (Gell & Roberts 2003).

The Poor Knights Islands Marine Reserve, located in northeastern New Zealand, was established in 1981 with special fisheries regulations. Prior to 1 October 1998, when the Poor Knights was given no-take marine reserve status, it was effectively a partial marine reserve. Allowing certain forms of fishing in marine reserves or marine protected areas (MPAs) is a common scenario, and is often advocated by groups with direct fishing interests as a 'compromise' solution, allowing both protection and fishing. For example, Francour et al. (2001) found that amateur and commercial fishing was allowed in half the MPAs in the Mediterranean, and of the 100 MPAs in California, less than a quarter of 1 % of their combined area is completely protected from fishing (McArdle 1997). Studies of the effects of fishing have indicated that relatively little fishing pressure is needed to cause significant reductions in the density of targeted species (Russ & Alcala 1989, Jennings & Polunin 1996). Despite this, the effectiveness of partial closures for either conservation or enhanced fishing has not been well evaluated (but see Francour 1994, Vacchi et al. 1998, Westera et al. 2003, Denny & Babcock 2004).

This study examines the effects of full marine reserve protection on snapper *Pagrus auratus* (Bloch and Schneider 1801) populations at the Poor Knights, and compares temporal trends in snapper density with 2 reference locations, Cape Brett and the Mokohinau Islands. Snapper are the most abundant demersal predatory fish species in northeast New Zealand, and they support one of New Zealand's most valuable commercial and recreational fisheries. This species is a dominant predator, and is thought to have an impact on the structure and dynamics of coastal marine ecosystems in New Zealand (Babcock et al. 1999, Shears & Babcock 2002, 2003). In this study, baited underwater video (BUV) was used to provide quantitative estimates of snapper abundance, biomass, size and egg production. This study provides a record of the rate of recolonisation of a key fish species, providing valuable insights into the mechanisms of fish recovery in marine reserves.

MATERIALS AND METHODS

Study sites. Three locations were surveyed in northeastern New Zealand: the Poor Knights Islands, Cape Brett and the Mokohinau Islands (Fig. 1). The Poor Knights Islands Marine Reserve was established in 1981 with special fisheries regulations. From 1981 to October 1998, all commercial fishing was prohibited. However, recreational fishers were able to use unweighted, single-hook lines, trolling and spearing to catch a permitted number of species within 95% of the reserve area (see Fig. 1 for protected areas). The 2 unprotected reference locations were selected to be as similar to the Poor Knights as possible in terms of hydrology and topography to minimise differences that may exist between the locations. However, as Underwood (1994) noted, it is impractical and unnecessary to choose locations with identical characteristics or abundances of the targeted species, provided sampling bias is avoided.

The initial survey at the Poor Knights was conducted in September 1998, prior to full marine reserve establishment in October. Surveys continued biannually in spring (September/October), and autumn (March/

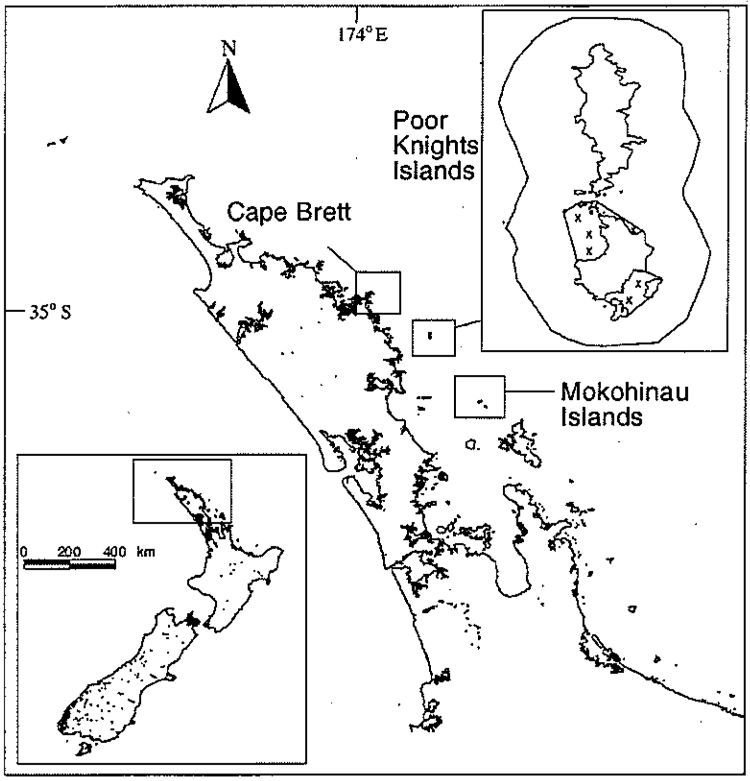

Fig. 1. Northern New Zealand, showing location of Cape Brett, the Poor Knights and Mokohinau Islands. Inset, upper right, of the Poor Knights shows reserve boundary (outer line) and areas closed to fishing prior to 1 October 1998 (marked with X)

April) until September 2002. The 2 reference locations were surveyed biannually from September 1999 until September 2002. It would have been desirable to include the reference sites in the study from the beginning; however, this was not possible. Even so, the study still addresses whether trends in fish abundance differ between the Poor Knights from those at reference locations (Underwood 2000).

Baited underwater video (BUV). Use of the BUV technique (Willis & Babcock 2000) allows sampling of carnivorous species that are not amenable to underwater visual census methods and can sample at depths greater than scuba divers can operate. The BUV system consists of a triangular stainless steel stand, with a Sony XC-777P high-resolution colour camera in a waterproof housing, positioned 1.25 m above a bait container with ca. 300 g of pilchard *Sardinops neopilchardus*. The BUV was deployed from the research vessel to depths of up to 50 m. Each sequence was recorded for 30 min from the time the video assembly reached bottom. A 100 m-long coaxial cable connected the underwater camera to a Sony GV-S50E video monitor and 8 mm recorder on the research vessel, enabling the operator to ensure the stand was upright and positioned over suitable substratum. Thirty replicate deployments were made at each location.

At the laboratory, 8 mm videotapes were copied to 16 mm VHS tapes for analysis and archiving. Videotapes were played back with a real-time counter, and the maximum number of snapper observed during each minute was recorded to determine the maximum number of snapper in each replicate. Recording the maximum number has been previously shown to provide the best estimates of relative snapper density (Willis & Babcock 2000). The lengths of snapper were obtained by digitising video images using the Sigmascan, image analysis system. Measurements were taken only of those fish present when the count of the maximum number of fish of a given species in a sequence was made. This means that some fish moving in and out of the field of view may not have been measured, and the method avoids repeated measurements of the same individuals. This approach is likely to result in more conservative abundance estimates in high-density areas than low-density areas; differences between sites are therefore likely to be conservative.

To calculate the biomass (weight: *W*) of snapper, lengths (standard length: SL, mm) were converted to mass (g) using the formula:

$$W = 0.00007194 \times \mathrm{SL}^{2.793} \qquad \text{(Taylor \& Willis 1998)}$$

To determine the difference in potential reproductive output between the reserve and reference locations, snapper fecundity (expressed as daily batch fecundity: *F*) was estimated using the formula:

$$F = 73 \times 9 \times W - 7793 \qquad \text{(Zeldis \& Francis 1998)}$$

These authors found the significance of the relationship between fish weight and batch fecundity was $r^2 = 0.72$. (See Willis et al. 2003a for a detailed description of this methodology.)

Data analysis. BUV data are counts and therefore do not satisfy the assumptions of normality and homogeneity of variance that are required by ANOVA. Accordingly, the data were analysed using a log-linear model (assuming a Poisson distribution) to obtain unbiased estimates of the relative abundance of snapper and determine the ratio of snapper change. The minimum legal size (MLS) of 270 mm SL is the smallest size at which this species can be legally retained if caught by recreational fishers. Therefore, changes in the density of sublegal (<270 mm SL) and legal (>270 mm) snapper present between spring surveys were also determined. 'Survey', 'Location' and 'Season' were the factors used in the model. Changes in the biomass and the daily batch fecundity of snapper were examined using the model described above.

The initial survey at the Poor Knights was conducted when areas had either full or partial protection (see Fig. 1). This allowed an assessment of the effectiveness of different protection regimes. The number of snapper per BUV from both fully protected areas and areas with partial protection, using only the spring 1998 survey, were analysed using a log-linear model, with 'Status' as the factor in the main model.

To test whether the regression slope of legal snapper density versus time (spring data only) was significantly different between locations, the Graphpad Prism® (V4) computer program was used. This program compares regression lines (Zar 1984) and is equivalent to ANCOVA.

Changes in the size of snapper were analysed using pairwise Kolmogorov-Smirnov tests and ANOVA. Data were tested for normality using the Shapiro-Wilks test and examination of residual plots. The observed differences between the mean sizes were tested for statistical significance using Tukey's studentized range test.

RESULTS

Total snapper density at the Poor Knights Islands increased significantly after complete protection, so that after 4 yr snapper were 6.9 times more abundant (lower 95% confidence limit, CL, of 3.6; upper 95% CL of 13.2) ($\chi^2_{4,147} = 59.5$, $p < 0.01$). When legal snapper (>270 mm) were examined at the Poor Knights (fish over this size are vulnerable to fishing), overall densities had increased by 7.4 times (95% CL 3.8, 14.5) since the initial survey ($\chi^2_{4,147} = 71.1$, $p < 0.01$) (Fig. 2a). Changes in the density of legal snapper between

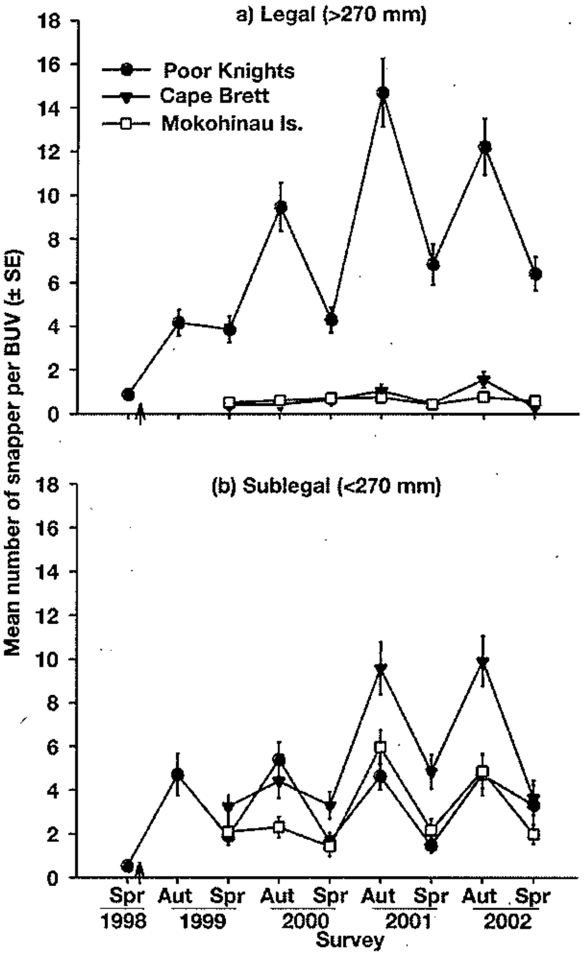

Fig. 2. *Pagrus auratus.* Mean number of (a) legal size snapper (>270 mm), (b) sublegal snapper (<270 mm) per baited underwater video (BUV) (±SE) at the Poor Knights from spring 1998 to autumn 2002 and at Cape Brett and Mokohinau Islands from spring 1999 to spring 2002. Spr and Aut: spring and autumn, respectively. Arrow on *x*-axis indicates establishment of no-take reserve status

spring surveys were examined, as fish present during spring are likely to be residents (Willis et al. 2001). Numbers increased significantly by 4.5 times (95% CL 2.3, 8.5) in the spring surveys between 1998 and 1999 ($\chi^2_{1,57}$ = 26.21, p < 0.01) and by 1.59 times between 2000 and 2001 ($\chi^2_{1,60}$ = 5.92, p = 0.015). There was no significant change in the density of legal snapper at the reference locations (Fig. 2a). The density of legal snapper at the Poor Knights was 22.1 and 10.8 times higher than at Cape Brett and the Mokohinau Islands (95% CL 8.8, 55.6 and 5.1, 23.1, respectively). The regression slope of legal snapper density versus time (using spring data) was significantly different between the Poor Knights and both the Mokohinau Islands (ANCOVA, *F* = 10.96, p = 0.02) and Cape Brett (*F* = 11.64, p = 0.019). There was no statistically significant difference in the regression slope between reference locations.

The density of sublegal snapper increased significantly at the Poor Knights by 6.2 times (95% CL 2.5, 15.8) since the initial survey ($\chi^2_{4,147}$ = 22.9, p < 0.01) (Fig. 2b). The overall density of sublegal fish did not differ significantly between locations but did tend to be higher at Cape Brett than at either island location. Moreover, the density of sublegal snapper appears to be variable, with Cape Brett varying more than the island locations (Fig. 2b).

There was a significant difference in snapper density between autumn and spring at all 3 locations ($\chi^2_{1,701}$ = 129.36, p < 0.01), a trend apparent for both legal and sublegal fish (Fig. 2). The mean number of snapper was 2.3 times (95% CL 1.9, 2.6) higher in autumn compared to spring.

The relative density of legal snapper was compared between areas with full and partial protection in Spring 1998 (prior to full no-take status). There was no statistically significant difference in the density of snapper between the fully and partially protected areas. In fact, the starting densities were virtually identical and both increased only after full reserve protection was given to the entire area.

There was an increase in the number of larger snapper at the Poor Knights, with the vast majority of fish in the later surveys being over the minimum legal size (Fig. 3). In contrast, there was no change in the size of snapper at the Mokohinau Islands (mean range between 215 and 258 mm) or Cape Brett, where the highest numbers of small fish were consistently recorded (mean range between 200 and 221 mm). Tukey's test found that the mean size of snapper was always significantly larger at the Poor Knights compared to the reference locations, and snapper at the Mokohinau Islands were usually significantly larger than at Cape Brett (Table 1). Large snapper (>400 mm) have become increasingly common at the Poor Knights, whereas at the reference locations, these large fish are almost never recorded (Fig. 3). There was no significant difference in the size of snapper between seasons at the Poor Knights and Cape Brett. However, snapper were significantly larger in spring at the Mokohinau Islands compared to the autumn surveys (ANOVA, $F_{1,731}$ = 35.87, p < 0.01), due to low numbers of sublegal fish in spring (Fig. 3).

The mean snapper biomass per BUV deployment increased significantly by 818% at the Poor Knights ($\chi^2_{8,2548}$ = 66.8, p < 0.01) from 771 g (±305 SD) in the initial survey to 6310 g (±552) in the final survey. There was no significant increase in biomass at the reference locations. In fact, snapper biomass for the final surveys at the reference locations were very similar to the

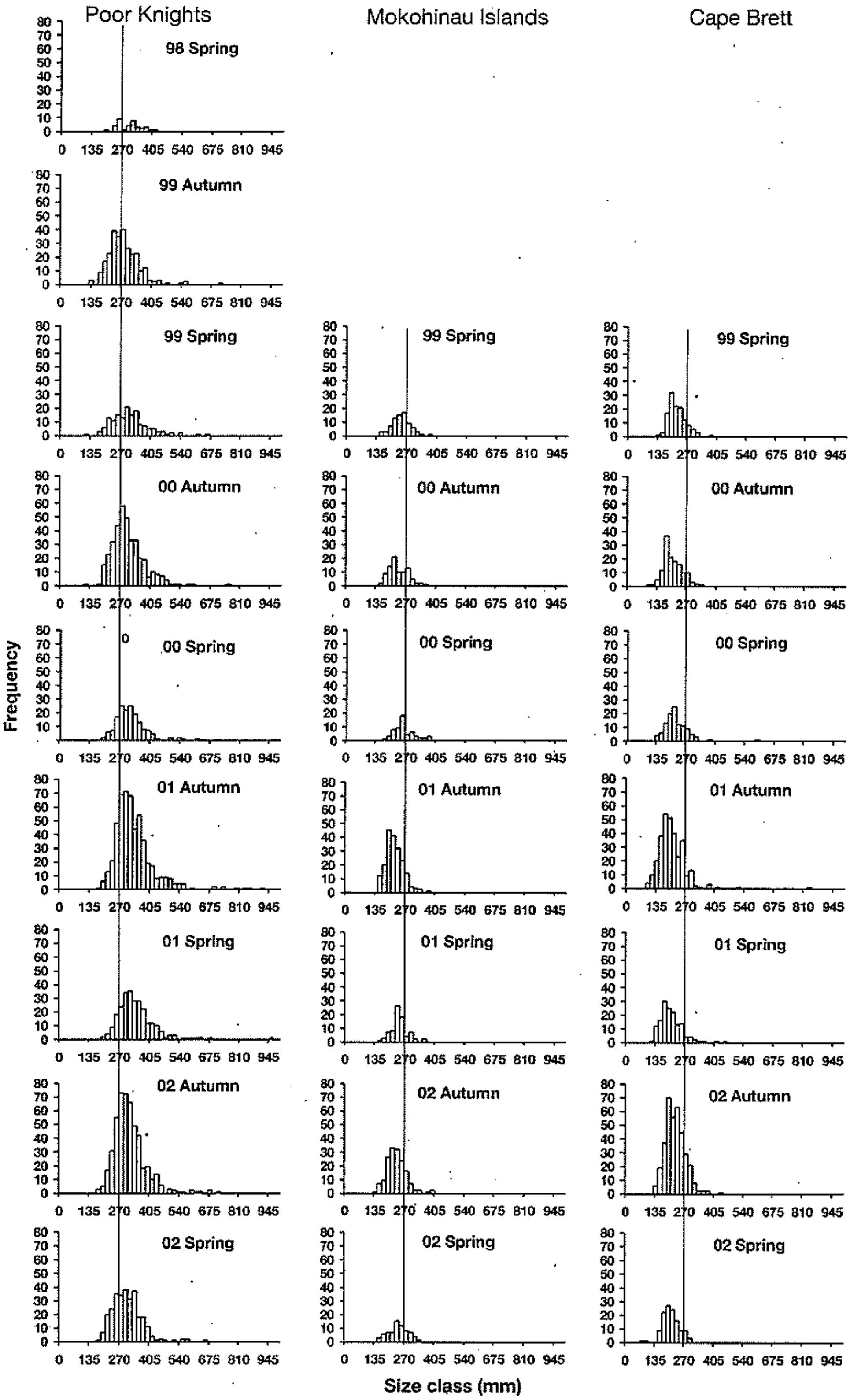

Fig. 3. *Pagrus auratus*. Size frequency (mm) of snapper at the Poor Knights from spring 1998 to spring 2002 and at Cape Brett and Mokohinau Islands from spring 1999 to spring 2002. Vertical line indicates the minimum legal size (270 mm)

Table 1. *Pagrus auratus.* Tukey's studentized range (HSD) test for snapper size differences (mm) between locations with 95% confidence limits (CL). *p < 0.05. PKIMR: Poor Knights Islands Marine Reserve

Survey	**PKIMR–Mokohinau Island** Difference between means	95% CL	**PKIMR–Cape Brett** Difference between means	95% CL	**Mokohinau Island–Cape Brett** Difference between means	95% CL
1999 spring	67.2*	46.6–87.8	88.1*	70.3–106.0	20.9	−0.5–42.3
2000 autumn	69.5*	51.8–87.1	97.0*	82.0–111.9	27.5*	7.1–47.9
2000 spring	52.1*	30.3–73.9	91.4*	73.7–109.1	39.3*	16.2–62.5
2001 autumn	112.4*	97.5–127.3	127.8*	115.0–140.7	15.4*	−0.9–31.7
2001 spring	99.1*	77.7–120.5	135.6*	118.5–152.7	36.5*	13.4–59.7
2002 autumn	83.2*	70.6–95.8	88.7*	79.0–98.3	5.4	−7.7–18.6
2002 spring	63.4*	45.0–81.9	94.4*	79.4–109.4	31.0*	10.2–51.8

initial Poor Knights survey; 747 g (±158) at the Mokohinau Islands and 878 (±114) at Cape Brett.

The daily batch fecundity of snapper was similar between the Poor Knights and the reference locations in the initial surveys. However, when the final surveys were compared, daily egg production at the Poor Knights was 18.7 (±2.3 SE) and 11.6 (±1.8) times higher than at Cape Brett and the Mokohinau Islands, respectively ($\chi^2_{2,3042}$ = 138.78, $p < 0.01$). In addition, daily egg production significantly increased 8.5 (±0.7) times at the Poor Knights between the initial and final survey ($p < 0.01$).

DISCUSSION

Following the implementation of full marine reserve status at the Poor Knights in 1998, snapper showed significant increases relative to reference locations in abundance and biomass over time. The magnitude of increase in snapper in the Poor Knights Reserve is consistent with many other studies that found a significant increase in the density and/or biomass of large predatory fish following no-take status (White 1988, McClanahan & Kaunda-Arara 1996, Russ & Alcala 1996, Edgar & Barrett 1999). The increase in snapper abundance following protection was surprisingly rapid: some time-lag period might be expected when fish populations are recovering from previous heavy fishing pressure (Polunin & Roberts 1993). For example, Russ & Alcala (1996) found a slow increase in fish biomass in the first 3 to 5 yr of protection, followed by a more rapid increase in the next 4 yr. This time lag might be particularly noticeable where recovery is dependent on recruitment. Recovery rates are likely to be variable, and can depend on other factors such as species, location and level of exploitation.

The rapid recovery of snapper at the Poor Knights, particularly in the first year, is due to the immigration of large fish, rather than juvenile recruitment. These large fish arrive at the Poor Knights because of regular seasonal onshore and offshore movements (Willis et al. 2003a). A proportion of these fish take up residence on the reefs, where they may remain in home range areas of less than 300 m diameter (Parsons et al. 2003) for more than 4 yr (Willis et al. 2001). This idea has been visited by Willis et al. (2003a), and is well supported by data at the Poor Knights where fish present had a modal size of 410 mm SL by autumn 2000. These fish would have be approximately 14 yr old (Millar et al. 1999) so could not have grown to this size in the 2 yr after full protection. The variable densities of sublegal snapper, related to sea surface temperature and seasonal deviations in the EAC (Francis 1993), probably accounts for the initial increase in sublegal snapper at the Poor Knights, rather than an effect of the marine reserve itself.

Seasonal variation in snapper abundance is consistent with other studies on snapper in New Zealand (Willis et al. 2003a). This seasonal trend is a well-known phenomenon among reef fish, with many species undertaking relatively extensive seasonal migrations that can range from a few metres up to several kilometres (Hobson 1973, Hyndes et al. 1999). The most likely reason for the seasonal variation in snapper is an onshore migration to shallower waters in summer to spawn (Crossland 1977, Robertson 1983) and a return to deeper offshore areas in winter. Alternatively, the observed temporal variation may be explained by feeding migrations (Ogden & Buckman 1973). Despite the commercial importance of snapper, their behaviour and ecology at small spatial scales is still poorly known. The investigation of snapper movements, home range sizes and spatial patterns of resource use using radio telemetry is currently underway (Egli & Babcock 2002).

Large snapper are capable of producing more eggs per unit body mass than smaller fish (Zeldis & Francis 1998). Therefore, the number of large snapper and their high potential egg production means that the Poor Knights could act as a source of eggs and/or larvae, which may eventually settle outside the reserve as well as within it (Jones et al. 1999, Swearer et al. 1999). Potential egg production at the Poor Knights, 18.7 times higher than the coast, is very similar to the values found by Willis et al. (2003a). If we assume that potential egg production is 18 times higher in the Poor Knights compared to the adjacent coast, then the Poor Knights with a coastline of 20.1 km represents egg production equal to 362 km of 'fished' coastline. Thus, relatively small no-take reserves have the potential to sustain recruitment in much larger portions of the coast.

This study provides evidence that partial fishing regulations are ineffective at protecting targeted species, at least where recreational and commercial fishers both target the same species. This presents a powerful argument against the widely held view that recreational fishing cannot affect fish populations. There was no build-up of snapper populations at the Poor Knights following the creation of the 'marine reserve' in 1981 that allowed partial harvest within 95% of the reserve. This was most likely due to recreational fishing pressure, as even limited fishing effort would maintain fish biomass at low levels (Jennings & Polunin 1996). Similar results were found at the Mimiwhangata Marine Park (identical fishing restrictions as were present at the Poor Knights prior to full reserve status) where no difference was found in snapper numbers between protected and adjacent unprotected areas (Denny & Babcock 2004). Paradoxically, fishing pressure may have been higher in the 1980s and 1990s at the Poor Knights than at the Mokohinau Islands or the adjacent coast. In the absence of commercial fishing, there may have been a perception that fish were larger and more plentiful in the reserve area. Thus, 'marine reserve' status and fishing gear restrictions at the Poor Knights may have had exactly the opposite effect to that intended.

There was no difference in relative snapper density between the small, fully protected areas and partially protected areas, prior to the islands receiving no-take status. The exclusion zones may have been too small to effectively protect snapper from fishing pressure: tagging studies suggest that some snapper move over moderate distances (>100 km) (Paul 1967), although Parsons et al. (2003) found some snapper to have considerable site fidelity (home ranges not exceeding 650 m). This finding is important because recent meta-analyses (e.g. Mosquera et al. 2000, Halpern 2003) have made general statements about the uniformity of response to protection from fishing, regardless of reserve size. Their conclusions are not universal, and will not apply to all species or all locations. There may also have been considerable edge effects because of the small size and configuration of the closed areas, resulting in fish being caught outside the areas. Edge effects have been demonstrated at the Leigh Marine Reserve (Willis et al. 2000), where recreational fishers commonly anchor and fish on the reserve boundary.

This study has clearly demonstrated the effectiveness of no-take status at the Poor Knights Islands Marine Reserve for increasing the density of a targeted fish species. The increase in density of snapper to the complete cessation of fishing suggests that partial protection is ineffective as a conservation tool for heavily targeted species. It is clear that the rate of recolonisation of fishes to protected areas is likely to be at least partially dependent on the natural abundance of fish found in the locality, as well as local habitat quality. This can be seen in the varying reserve:non-reserve ratios of legal snapper at no-take reserves on the nearby mainland coast, which range from 8.8:1 to 16.5:1 (Willis et al. 2003a). There has been no observed recovery of snapper in reserves in southern New Zealand, e.g. Tonga Island (R. Davidson pers. comm.). That such large location-specific differences in the rate and magnitude of response to reserve protection can occur within a heavily exploited species complicates efforts to make general predictions about reserve effects, even for single species. It follows that assemblage-level predictions are even more difficult to make with accuracy. Small-scale habitat characteristics may be effective predictors in some cases, but reserves should not be regarded as independent of processes occurring in the surrounding, exploited waters.

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Do partial marine reserves protect reef fish assemblages?

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Abstract

Fish assemblages in the Mimiwhangata Marine Park, an area closed to commercial fishing but open to most forms of recreational fishing, were compared with adjacent fished areas. Two survey methodologies were used; baited underwater video and underwater visual census. Snapper (*Pagrus auratus*), the most heavily targeted fish species in the region, showed no difference in abundance or size between the Marine Park and adjacent control areas. When compared to the fully no-take Poor Knights Island Marine Reserve and two other reference areas open to all kinds of fishing (Cape Brett and the Mokohinau Islands), the abundance and size of snapper at the Marine Park were most similar to fished reference areas. In fact, the Marine Park had the lowest mean numbers and sizes of snapper of all areas, no-take or open to fishing. Baited underwater video found that pigfish (*Bodianus unimaculatus*), leatherjackets (*Parika scaber*) and trevally (*Pseudocaranx dentex*) were significantly more common in the Marine Park, than in the adjacent control areas. However, none of these species are heavily targeted by fishers. Underwater visual census found similar results with five species significantly more abundant in the Marine Park and five species more abundant outside the Marine Park. The lack of any recovery by snapper within the Marine Park, despite the exclusion of commercial fishers and restrictions on recreational fishing, indicates that partial closures are ineffective as conservation tools. The data suggest fishing pressure within the Marine Park is at least as high as at other 'fished' sites.

Keywords: Marine protected area; Mimiwhangata Marine Park; *Pagrus auratus*; Snapper; New Zealand; Gear restrictions

1. Introduction

Marine protected areas (MPAs) have recently become a major focus in marine conservation. While much of the literature on MPAs has dealt with no-take areas, MPAs can offer many levels of protection and many afford only partial protection, allowing certain types of fishing. For example, Francour et al. (2001) found that amateur and commercial fishing was allowed in half the MPAs in the Meditteranean and Bohnsack (1997) pointed out that 99.5% of the Florida Keys Marine Sanctuary provided no protection for any species. The world's largest MPA, the Great Barrier Reef Marine Park, has many levels of zoning, most of which allow fishing of some kind and less than 5% of the area is no-take (Anon., 2002). With growing worldwide pressure to increase the level of protection afforded to marine habitats, partial fishing closures are often advocated by groups with direct fishing interests. Such partial closures are promoted as a 'compromise' solution allowing both protection and fishing (Willis and Denny, 2000).

Partial closures may reduce the impacts on by-catch. This is particularly so in areas affected by destructive fishing practices, and in such circumstances they can be quite effective (Thrush et al., 1998). Depending on the behaviour of fish and fishers, partial closures may result in reduction of incidental mortality even in hook and line fisheries. Furthermore, partial closures may benefit some species. Allowing fishing for the dominant predators on a reef may actually increase the abundance of prey species. This may be a useful technique to increase the abundance of an endangered prey species. However, the effectiveness of partial closures for either conservation or enhanced fishing for a subset of fishers has not been well evaluated. In spite of the number of MPAs worldwide, only a few studies have assessed the effects of partial protection on reef fish populations (Francour, 1994; Vacchi et al., 1998; Francour et al., 2001).

The Mimiwhangata Marine Park was established in 1984 with the aim of protecting long lived reef fish that are vulnerable to overfishing or have low reproductive

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rates. Special fisheries regulations exist at Mimiwhangata prohibiting all commercial fishing, nets and long-lines. However, recreational fishers may use the following methods: unweighted, single-hook lines, trolling and spearing. A number of species are permitted to be caught within the Marine Park, all thought to be nomadic or pelagic at the time of the park's creation (see Table 3 for takeable species). That is, they were not considered part of the resident demersal reef fish assemblage. However, the inclusion of these species was based on very limited knowledge of their biology and behaviour. Three of these species, trevally (*Pseudocaranx dentex*), snapper (*Pagrus auratus*), and kingfish (*Seriola lalandi*) are now known to be wholly or partially resident of reefs. Trevally are reef-associated as juveniles, whereas adults can be found near reefs or in open water (Kingsford, 1989; Francis, 2001), snapper can become permanent residents on particular areas of reefs (Willis et al., 2001), and kingfish are largely reef associated rather than ocean pelagics (Saul and Holdsworth, 1991). All three species are targeted by both recreational and commercial fishers, but snapper are the most abundant demersal predatory fish species in northeast New Zealand and support New Zealand's most valuable commercial and inshore recreational fisheries.

The main objective of this survey was to evaluate the effectiveness of partial protection on the reef fish assemblages within and around the Mimiwhangata Marine Park. Furthermore, snapper abundance at Mimiwhangata was compared with data from three nearby areas in northern New Zealand, the no-take Poor Knights Islands Marine Reserve, the Mokohinau Islands and Cape Brett which are both fully open to fishing (Fig. 1). In this survey, two different methods were used to provide quantitative estimates of fish abundance and size; underwater visual census and baited underwater video.

2. Methods

2.1. Study areas

The Mimiwhangata Marine Park, established in 1984, is located on New Zealand's northeast coast (35°25′S, 174°26′E), extending 1 km offshore, and covering about 20 km² (Fig. 1). Within the Marine Park boundaries, there are a variety of habitats such as shallow and deep rocky reefs, boulder fields, sandy areas, urchin barrens, and algal turf flats. For the current survey, the Marine Park was divided into four areas, and these were compared with four control areas outside the Marine Park (two at either end of the Marine Park) to assess differences inside and outside the Marine Park (Fig. 2). This sampling design has been used in numerous other studies of fish in New Zealand marine reserves (Willis and Babcock, 2000; Willis et al., 2000, 2003). This design has the dual advantages of ensuring reference areas are similar to reserve areas, as well as enabling the detection

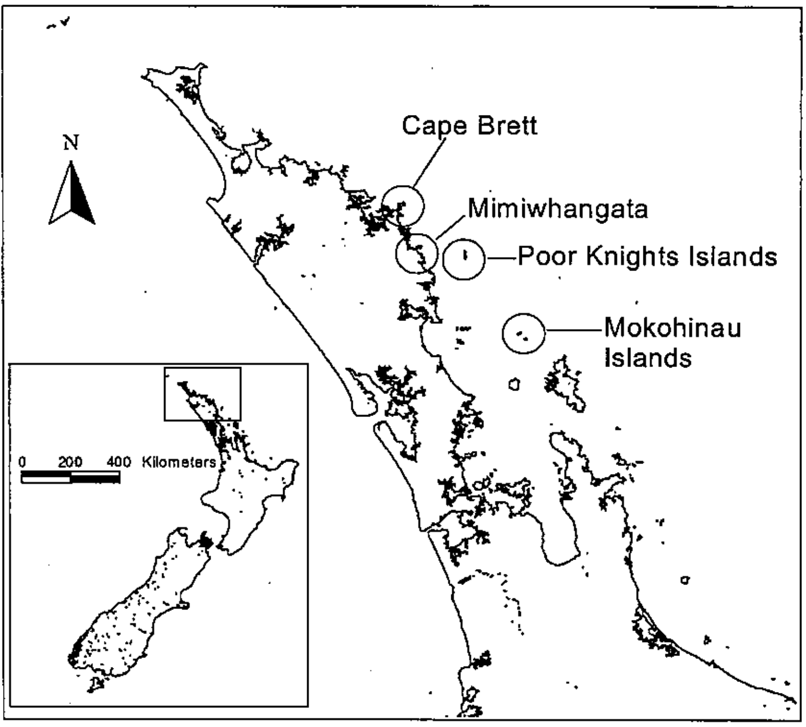

Fig. 1. Map of northern New Zealand showing the location of Mimiwhangata, Cape Brett, the Poor Knights and Mokohinau Islands.

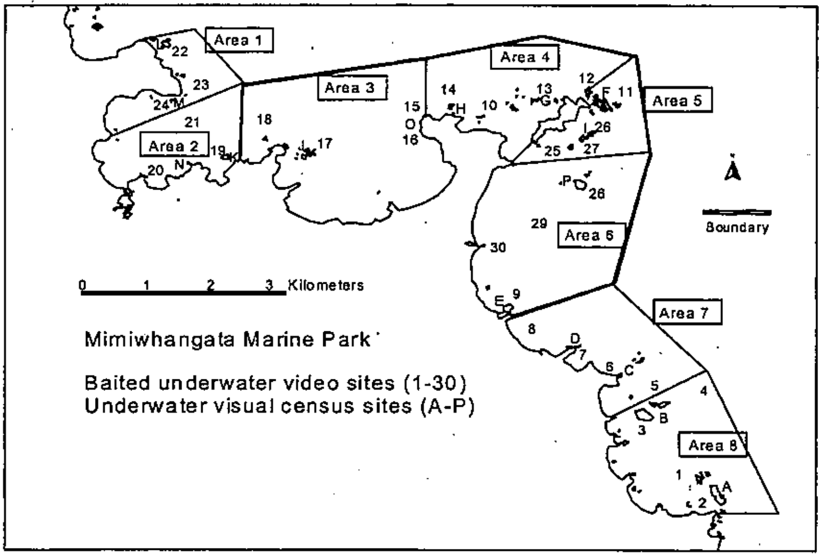

Fig. 2. Map of Mimiwhangata showing the location of the baited underwater video sites (1–30) and the underwater visual census sites (A–P) in April 2002.

of any edge effects that might be related to the encroachment of fishing effects into the reserve, (or alternatively spillover). Sampling was conducted between 08:00 and 17:00 h from 2 to 5 April 2002. Data were collected concurrently at three additional locations in northeastern New Zealand as part of a related study; two island locations (the Poor Knights Islands and Mokohinau Islands) and another mainland location (Cape Brett) (Fig. 1). Their inclusion in this study provided an example of how snapper numbers in other fished and unfished areas of northern New Zealand compare with Mimiwhangata. Biogeographic differences between these sites and Mimiwhangata limit their usefulness in the context of comparing whole fish assemblages (Choat and Ayling, 1987; Brook, 2002).

2.2. Baited underwater video

The use of the baited underwater video technique is relatively new and allows sampling of carnivorous species that are not amenable to visual methods as well as enabling sampling at depths greater than those at which divers are able to operate (Willis and Babcock, 2000). The video system consists of a triangular stainless steel stand, with a high-resolution colour camera, positioned 1.25 m above a bait container holding approximately 300 g of pilchards (*Sardinops neopilchardus*). The baited underwater video was deployed from the research vessel to depths of up to 40 m at sites at least 1 km from diving activities (so the presence of divers would not interfere with fish responses to the bait). Each sequence was recorded for 30 min from the time the video assembly reached bottom. A 100 m long coaxial cable connected the underwater camera to a Sony GV-S50E video monitor and 8 mm video recorder on the research vessel, which enabled the person recording to ensure the stand was upright and over suitable substratum. Four replicate video deployments were done in each of the eight survey areas (Fig. 2), except areas one and two where three replicate drops were done (due to logistical constraints). Thirty replicate drops were also conducted at the Poor Knights, Cape Brett, and the Mokohinau Islands (for locations see Willis and Denny, 2000). A total of 60 h of videotape was collected for later analysis.

Videotapes were later copied to VHS tapes for analysis and archiving. Videotapes were played back with a real-time counter, and the maximum numbers of each species of fish observed during each minute were recorded (30 counts made during each 30-min sequence). The lengths of snapper were obtained by digitising video images using the Sigmascan® image analysis system. Measurements were only made of those fish present when the count of the maximum number of fish of a given species in a sequence was made. While this meant that some fish moving in and out of the field of view may not have been measured, it avoided repeated measurements of the same individuals. It is likely that the use of maximum number present results in more conservative abundance estimates in high density areas than low density areas, and therefore observed relative differences between sites are also likely to be conservative.

2.3. Underwater visual census

Underwater visual census techniques are regularly used by researchers to quantify reef fishes, study their distribution, and to estimate their sizes (e.g. Kingsford and Battershill, 1998). The advantages of underwater visual census include the high levels of replication possible, few logistical requirements (apart from SCUBA gear), and the flexibility of being able to record other types of data in situ. The disadvantages include constraints of depth (<30 m), high levels of inter-observer variability, diving limitations due to currents and poor underwater visibility, and bias associated with diver positive/negative species. Despite these flaws, acknowledged by most workers, underwater visual census is the best method for non-destructive surveys of a broad spectrum of fish species. In this survey, two sites within each of the eight areas at Mimiwhangata were surveyed by underwater visual census (16 sites in total; Fig. 2). At least 16 sites were surveyed by underwater visual census at each of the three other locations. Three divers recorded the numbers of all fish and the size of several selected species vulnerable to fishing using 5 m×25 m strip transects (each transect covers 125 m^2). Three replicate transects were completed at each site by each diver therefore each site covered 1125 m^2 (9×125 m^2). To avoid overlap divers decided which direction to swim prior to each dive. Each diver tied a fibreglass tape measure to a kelp holdfast with wire, swam out 5 m to avoid counting species attracted to the initial activity, and preceded to swim 25 m, counting all fish within a strip 2.5 m either side of the diver (Denny et al., 2003). All divers had previous experience using this methodology.

2.4. Statistical analysis

The baited underwater video data are counts and therefore do not satisfy the assumptions of normality and homogeneity of variance that are required by ANOVA. Therefore, the video data were analysed using the Poisson distribution using the GENMOD procedure in SAS to obtain unbiased estimates of relative abundance for dominant carnivorous species. See Willis et al. (2000) for a more detailed description of this analysis.

To determine whether there were any differences in overall fish community structure between fished and unfished areas, underwater visual census data were analysed using metric multidimensional scaling in the CAP statistical package (Anderson, 2002). Site transect data were pooled, square root transformed, and a Bray–Curtis similarity matrix was generated. The purpose of multidimensional scaling is to construct a 'map' of configuration of the samples in a specified number of dimensions, which attempts to satisfy all the conditions imposed by the rank similarity matrix. For example, if site 1 has a higher similarity to site 2 than it does to site 3 then site 1 will be placed closer on the map to site 2 than it is to site 3. For single species, comparisons were made using the GENMOD procedure in SAS, as described for the video analysis.

3. Results

3.1. Baited underwater video

Similar numbers of sandy and rocky habitats were surveyed in both areas and slightly more gravel/sand habitats were surveyed in the Marine Park. Sites surveyed in the Marine Park were slightly deeper on average (6–30 m depth range) than in the adjacent control areas (7–24 m depth range). These deeper sites were mainly in area four where the steeply sloping *Ecklonia radiata* covered reefs made it difficult to conduct shallower video drops.

There was no significant difference between the mean maximum number of snapper per baited underwater video inside (4.44±1.15 S.E.) and outside the Marine Park (4.5±1.59). Numbers of sublegal snapper (fish too small to be legally taken, <270 mm SL) mirrored the pattern of all snapper (Fig. 3a), as these smaller fish made up the bulk of snapper recorded (Fig. 3b). There were very low numbers of legal snapper (those fish that can be legally retained, >270 mm SL) in any area (Fig. 3c). Comparisons with the other locations showed that Mimiwhangata had the lowest mean snapper numbers, particularly legal size snapper (Table 1). Interestingly, the mean number of sublegal (<270 mm) snapper at Mimiwhangata was similar to sublegal snapper numbers at the Poor Knights and the Mokohinau Islands (Table 1).

Out of the 126 snapper measured at Mimiwhangata, 117 were under the legal minimum size of 270 mm. The average snapper size inside the Marine Park was 209 mm (±4.6), slightly larger than in the control area at 199 mm (±5.8), however, this difference was not sig-

Table 1
Mean number of all, legal (>270 mm) and sublegal (<270 mm) snapper per baited underwater video (±S.E. in parentheses) at the Poor Knights, Cape Brett, Mokohinau Islands, and Mimiwhangata in autumn 2002

Snapper	Autumn 2002 (April/May)			
	Poor Knights	Cape Brett	Mokohinau Is.	Mimiwhangata
All	16.9 (2)	11.5 (1.2)	5.6 (0.8)	4.13 (0.9)
Legal (>270 mm)	11.5 (1.2)	1.5 (0.4)	0.9 (0.3)	0.3 (0.1)
Sublegal (<270 mm)	4.4 (0.9)	9.75 (1.2)	4.8 (0.8)	3.83 (0.9)

nificant ($P=0.7$). Overall, the average snapper size at Mimiwhangata was 204 mm (±3.6), significantly lower ($P<0.01$) than at Cape Brett (221 mm±2.3) and the Mokohinau Islands 227 mm (±3.4; Fig. 4). The average size at the no-take Poor Knights Islands Marine Reserve was 310 mm (±3.2; Fig. 4). Large fish (>350 mm), recorded at other areas, were not seen at Mimiwhangata where the largest snapper was only 320 mm (Fig. 4).

Analysis of the baited underwater video data found that of the seven most commonly recorded species, pigfish (*Bodianus unimaculatus*), leatherjackets (*Parika scaber*) demoiselles (*Chromis dispilus*) and trevally were significantly more common in the Marine Park than in adjacent areas (Table 2). Only sweep (*Scorpis lineolatus*) were significantly more common in the control areas (Table 2).

3.2. Underwater visual census

Species richness at Mimiwhangata (31 species) was much lower than at the other three survey areas, where 40 species were recorded at Cape Brett, 49 at the Poor Knights, and 43 at the Mokohinau Islands. Species at Mimiwhangata were characteristic of the mainland species observed at Cape Brett and only a few of the subtropical species found at the Poor Knights and Mokohinau Islands were recorded there.

Densities of the 12 most common fish species recorded at Mimiwhangata were highly variable both within and between sites (Figs. 5 and 6). There was little differentiation in fish communities between Marine Park sites and control sites (Fig. 7). The majority of species

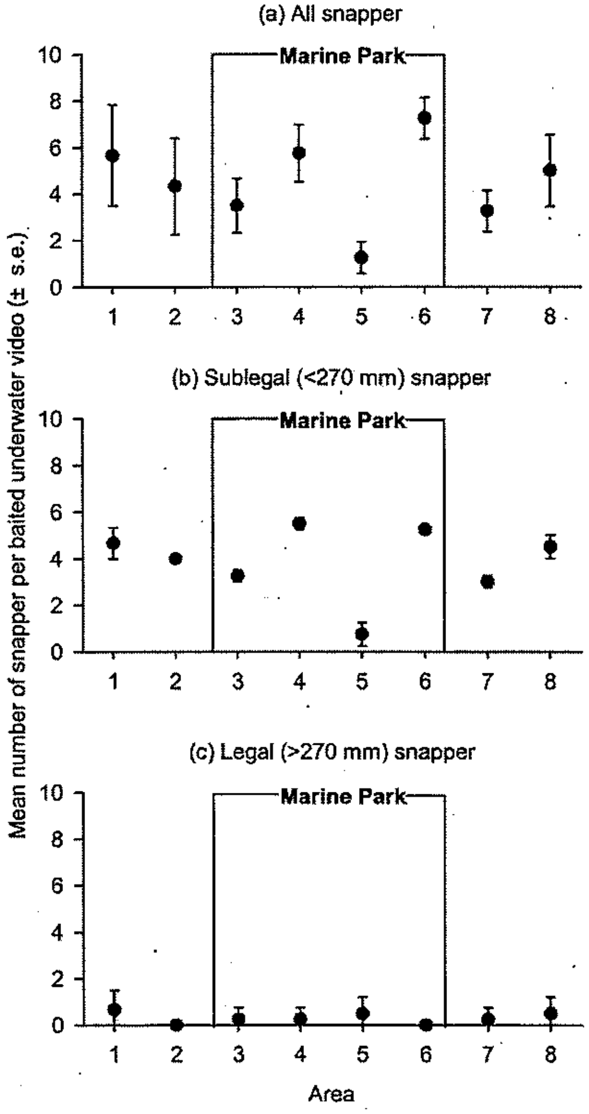

Fig. 3. Mean maximum number of (a) all snapper, (b) sublegal (<270 mm) snapper and (c) legal (>270 mm) snapper per baited underwater video (±S.E.) at eight areas at Mimiwhangata.

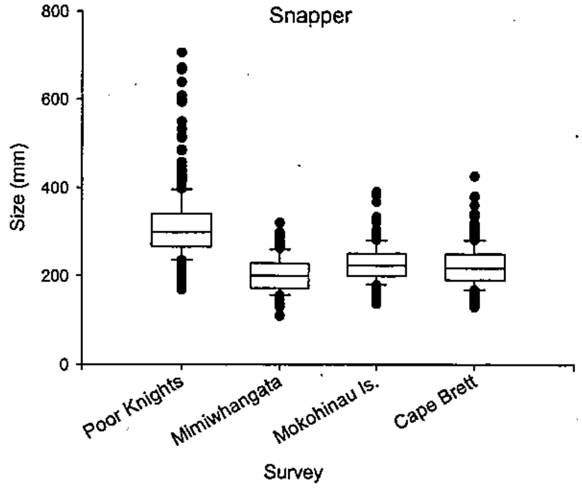

Fig. 4. Box and whisker plot of snapper at Mimiwhangata, Mokohinau Islands, Cape Brett, and the Poor Knights Islands, autumn 2002. The boundary of the box closest to zero indicated the 25th percentile, the line in the box represents the median, and the boundary of the box farthest from zero indicates the 75th percentile. The whiskers above and below the box indicate the 90th and 10th percentiles and the black circles represent outliers.

Table 2
Differences in fish density of seven species inside and outside the Mimiwhangata Marine Park, estimated by baited underwater video in April 2002 with 95% lower and upper confidence limits (CL)

Species	Abundance ratio	95% Lower CL	95% Upper CL	χ^2	*P*-value
Snapper	1.01	0.72	1.42	0.01	0.94
Pigfish	3.06	1.0	9.3	3.9	0.048*
Leatherjacket	4.96	2.08	11.8	13.07	<0.01*
Demoiselles	10.5	1.37	80.8	5.1	0.024*
Trevally	10.9	2.59	46.2	10.6	0.01*
Sweep	0.55	1.3	2.7	12.33	0.01*
Yellow moray	1.31	0.22	7.9	0.09	0.77

* Indicates species whose abundance ratio is significantly different at the $P<0.01$ value.

censused (21/31) showed no significant difference in density between the Marine Park and adjacent control sites. However, in spite of there being no significant difference in overall fish assemblages, some species were significantly more common in the Marine Park. These were black angelfish (*Parma alboscapularis*), leatherjackets, sandagers wrasse (*Coris sandageri*), goatfish (*Upeneichthys lineatus*) and blue maomao (*Scorpis violaceus*; Table 3). Conversely, other species were significantly more common outside the Marine Park. These were spotties (*Notolabrus celidotus*), demoiselles, sweep, jack mackerel (*Trachurus novaezelandiae*) and koheru (*Decapterus koheru*; Table 3). Interestingly, in areas where pigfish were absent (areas 1–3), spotties occurred in high numbers (Fig. 5D and E). Other species such as orange wrasse (*Pseudolabrus luculentus*) and scarlet wrasse (*P. miles*) common at the Poor Knights and Cape Brett were rare at Mimiwhangata.

4. Discussion

Snapper is the most heavily targeted recreational and commercial fish species throughout northeastern New Zealand. Where no-take marine reserves are in place, and enforced, the recovery of this species has been

Table 3
Scientific name, species, family, abundance ratio, 95% lower and upper confidence limits, χ^2 and *P*-values of 31 fish species observed in underwater visual census at the Mimiwhangata Marine Park in April 2002

Scientific name	Species	Family	Abundance ratio	95% Lower CL	95% Upper CL	χ^2	*P*-value
Allomycterus jaculiferus	Porcupinefish	Diodontidae	No fit				
Aplodactylus arctidens	Marblefish	Aplodactylidae	0.5	0.09	2.7	0.64	0.42
Arripis trutta	Kahawai[a]	Arripadae	1.36	0.79	2.36	1.22	0.29
Bodianus unimaculatus	Pigfish[b]	Labridae	1.4	0.44	4.41	37.83	0.56
Cheilodactylus spectabilis	Red moki	Cheilodactylidae	0.98	0.66	1.45	0.01	0.92
Chironemus marmoratus	Hiwihiwi[b]	Chironemidae	1.09	0.47	2.59	0.05	0.83
Chromis dispilus	Demoiselle	Pomacentridae	0.76	0.70	0.83	36.8	<0.01*
Coris sandageri	Sandagers wrasse[b]	Labridae	10.1	4.67	22.1	34.2	<0.01*
Decapterus koheru	Koheru[a]	Carangidae	0.47	0.38	0.58	47.32	<0.01*
Epinephelus daemelii	Spotted black grouper[b]	Serranidae	No fit				
Girella tricuspidate	Parore	Girellidae	1.18	0.88	1.57	1.21	0.27
Gymnothorax prasinus	Yellow moray[b]	Muraenidae	No fit				
Kyphosus sydneyanus	Silver drummer	Kyphosidae	No fit				
Myliobatus tenuicaudatus	Eagle ray	Myliobatidae	No fit				
Nemadactylus douglasii	Porae[b]	Cheilodactylidae	No fit				
Notolabrus celidotus	Spotty[b]	Labridae	0.47	0.37	0.47	37.83	<0.01*
Notolabrus fucicola	Banded wrasse[b]	Labridae	0.71	0.23	2.25	0.33	0.57
Obliquichthys maryannae	Oblique swimming triplefins	Tripterygiidae	No fit				
Odax pullus	Butterfish	Odacidae	0.2	0.02	1.71	2.16	0.14
Pagrus auratus	Snapper[a]	Sparidae	0.5	0.05	5.5	0.32	0.57
Parika scaber	Leatherjacket	Monacanthidae	2.99	1.81	4.98	18.1	<0.01*
Parma alboscapularis	Black angelfish	Pomacentridae	4.5	1.52	13.3	7.4	<0.01*
Pempheris adspersus	Bigeye	Pempheridae	No fit				
Pseudolabrus luculentus	Orange wrasse	Labridae	No fit				
Pseudolabrus miles	Scarlet wrasse[b]	Labridae	1	0.14	7.1	0	1
Scorpaena cardinalis	Northern scorpionfish[b]	Scorpaenidae	No fit				
Scorpis lineolatus	Sweep[b]	Scorpidae	0.59	0.53	0.66	88.63	<0.01*
Scorpis violaceus	Blue maomao[b]	Scorpidae	47.9	31.2	73.9	308.3	<0.01*
Seriola lalandi	Kingfish[a]	Carangidae	No fit				
Trachurus novaezelandiae	Jack mackerel[a]	Carangidae	0.33	0.29	0.37	384.6	<0.01*
Upeneichthys lineatus	Goatfish	Mullidae	4.5	2.84	7.14	40.72	<0.01*
Takeable species not observed in this study							
Thyrsites atun	Barracouta[a]	Gempylidae					
Pseudocaranx dentex	Trevally[a]	Carangidae					
	Tuna—6 species[a]	Scombridae					
	Billfishes—6 species[a]	Istiophoridae					
	Mackerel—5 species[a]	Carangidae					
	Sharks—27 species[a]	Many families					

[a] Signifies species permitted to be caught.

[b] Signifies species known to be caught as by-catch.

* Indicates species whose abundance ratio is significantly different at the $P<0.01$ value.

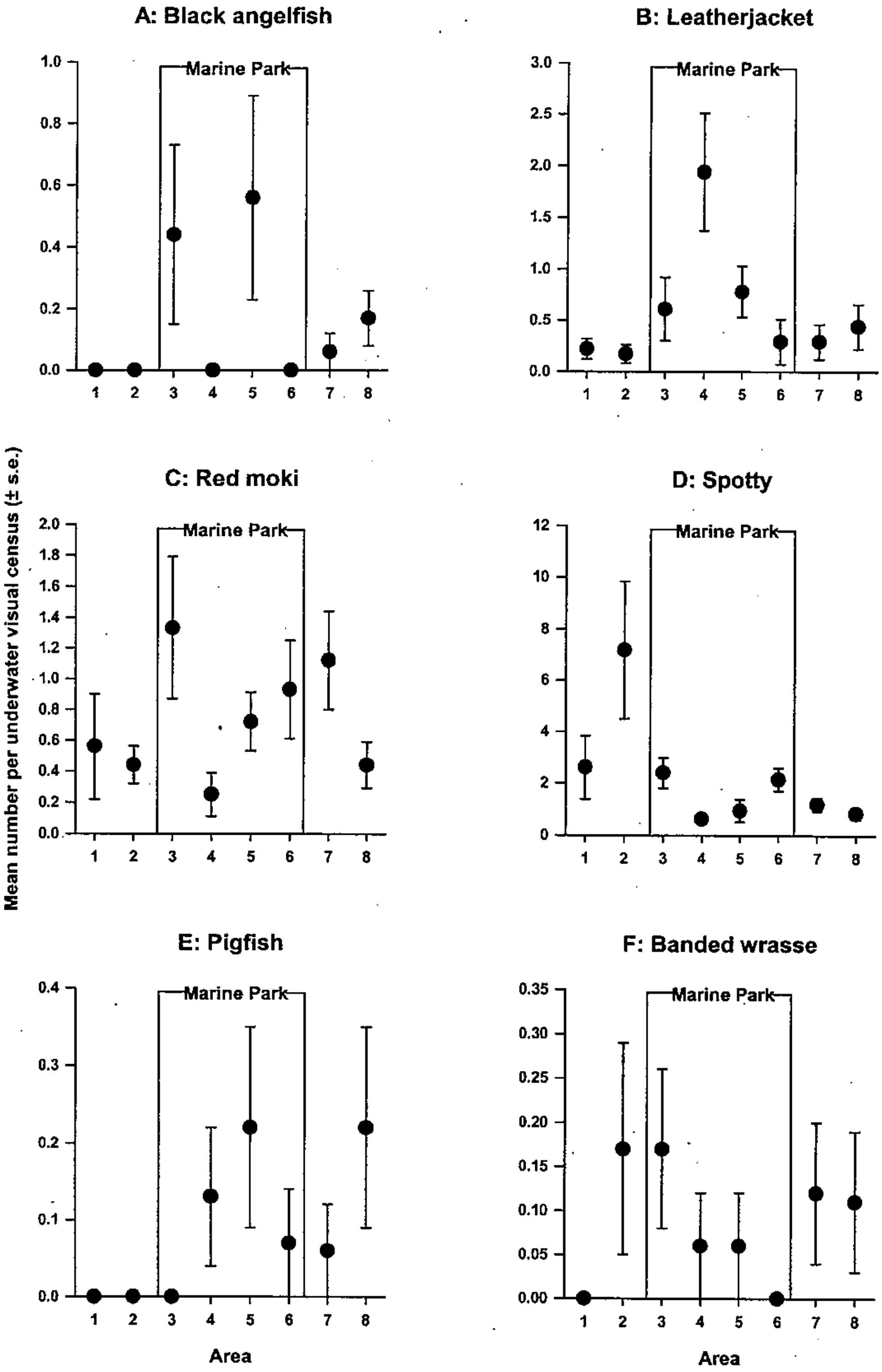

Fig. 5. Mean number of fish per underwater visual census (125 m^2) (±S.E.) in eight areas around Mimiwhangata: (A) *Parma alboscapularis*, black angelfish, (B) *Parika scaber*, leatherjacket, (C) *Cheilodactylus spectabilis*, red moki, (D) *Notolabrus celidotus*, spotty, (E) *Bodianus unimaculatus*, pigfish, and (F) *Notolabrus fucicola*, banded wrasse.

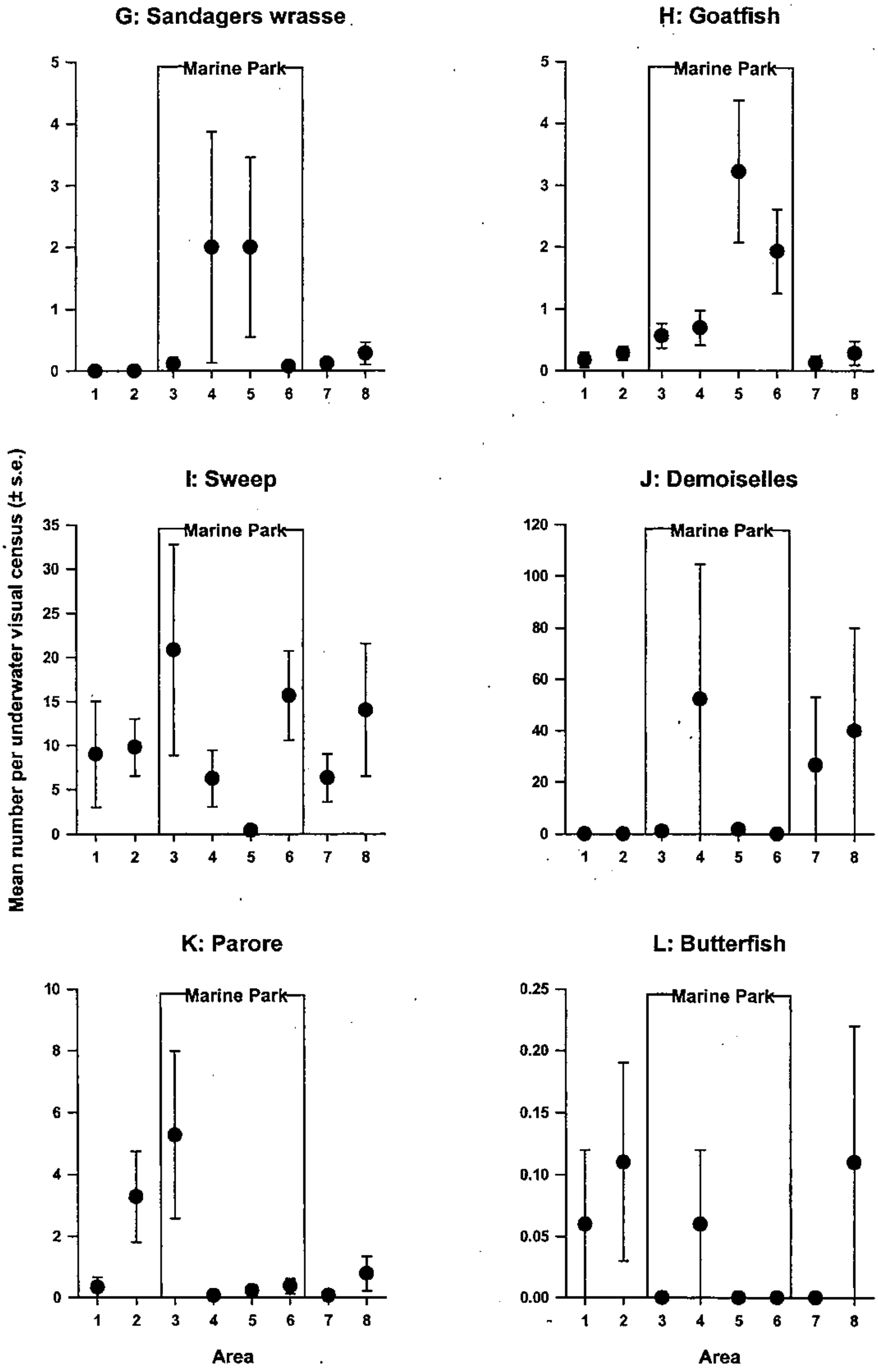

Fig. 6. Mean number of fish per underwater visual census (125 m^2) (±S.E.) in eight areas around Mimiwhangata; (G) *Coris sandageri*, sandagers wrasse, (H) *Upeneichthys lineatus*, goatfish, (I) *Scorpis lineolatus*, sweep, (J) *Chromis dispilus*, demoisielles, (K) *Girella tricuspidata*, parore, and (L) *Odax pullus*, butterfish.

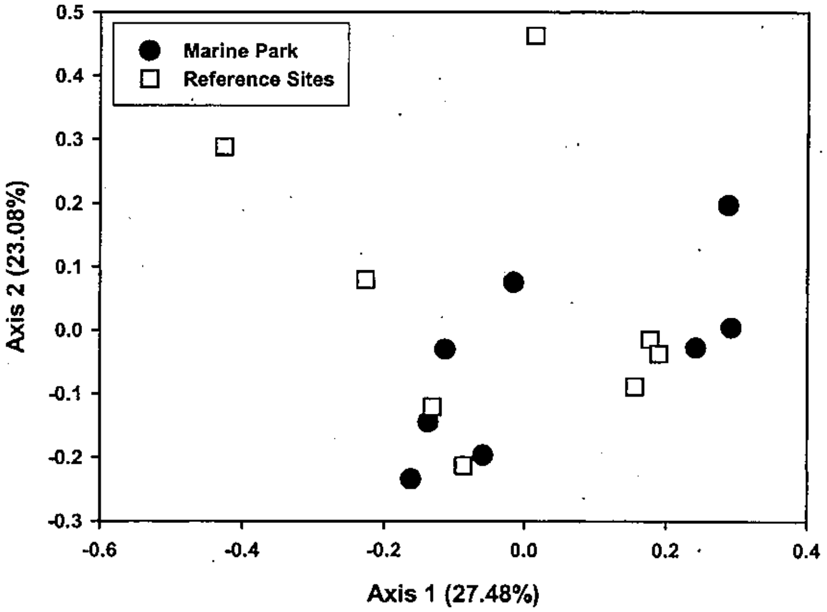

Fig. 7. Metric multidimensional scaling ordination plot of the 16 sites (pooled replicates) based on underwater visual census surveys of 28 species of reef fish at Mimiwhangata in April 2002.

dramatic, both in size and number (Table 4). Thus we should expect that if the gear and species restrictions at Mimiwhangata were in any way effective at protecting snapper, there would be more numerous and larger snapper inside the Marine Park. However, when areas inside and outside the Marine Park were compared, there were almost identical numbers of snapper numbers per baited underwater video and no significant difference in snapper size. Therefore, it appears that partial restrictions on gear and species are ineffective for this species. Restricting the use of weighted lines in the Marine Park is unlikely to protect snapper as, although taken on weighted lines, snapper can be caught effectively on unweighted lines, a practice permitted in the Marine Park.

Mimiwhangata had fewer and smaller snapper than either of the unprotected areas, Cape Brett or the Mokohinau Islands, probably due to high fishing pressure. This area is easily accessible to fishers from Tutukaka and from launching sites in Whangaruru/Oakura, and it is heavily fished during holiday periods (P. Bendle, personal communication).

Paradoxically, fishing pressure may even be higher within the Marine Park than outside it as there may be a perception that, in the absence of commercial fishing, fish are larger and more plentiful in Marine Parks. In addition, Marine Parks are often placed in areas that are pleasant to fish in, and consequently heavily utilised. Thus, Marine Park status and fishing gear restrictions at Mimiwhangata may, in fact, result in exactly the opposite pattern to the one intended. This possibility is supported by comparisons of snapper size and density at non-reserve sites in the region. In France, Francour (1994) found that the density and biomass of fish on rocky reefs was lower in partially protected areas than unprotected areas. For example, the density of reef fish in a partially protected zone was 0.15 per 10 m^2 compared with 0.31 per 10 m^2 in an area with no protection.

Table 4
Northeastern New Zealand sites surveyed with baited underwater video to assess relative legal sized (>270 mm) snapper abundance and the reserve: non-reserve snapper ratio

Location	Year	Reserve mean	Non-reserve mean	Reserve:non-reserve ratio	Source
Leigh MR	1975	7.18	0.45	16	Willis et al. (2003)
Hahei MR	1992	3.15	0.19	16.5	Willis et al. (2003)
Long Bay MR	1995	3.48	0.37	9.4	Ward and Babcock (unpublished data)
Poor Knights MR	1998	12.2	0.76(MK)	16	Denny et al. (2003)
Tawharanui MR	1981	3.5	0.4	8.8	Willis et al. (2003)
Mimiwhangata MP	1982	0.25	0.35	0.71	

Note that MR is no-take marine reserve, MP is marine park, and MK is the Mokohinau Islands, a non-reserve island reference for the Poor Knights.

Species that are targeted by spearfishers were seldom observed in visual transects transects. For example, no blue cod (*Parapercis colias*), three undersize snapper and two porae (*Nemadactylus douglasii*) were observed. This is in contrast to a pre-protection survey in 1973, in which it was noted that large snapper ('15–20 lbs') were relatively common at Mimiwhangata (Ballantine et al., 1973). Spearfishing, a common activity at Mimiwhangata (P. Bendle, personal communication) that tends to reinforce avoidance behaviour in fishes, may account for the low numbers of these species. Furthermore, the ability of spearfishers to selectively target large kingfish and snapper can lead to overall declines in the mean size and numbers of such species.

No significant difference was found in the overall fish assemblages within and outside the Marine Park using underwater visual census. There were five species significantly more common inside and outside the Marine Park, however, these differences were probably site related, rather than reserve effects, as fishers do not target the majority of these species. Species more common outside the Marine Park were typically schooling fish such as jack mackerel, koheru and sweep. The baited underwater video found that pigfish, leatherjackets and trevally were significantly more common in the Marine Park than in the adjacent control areas. Although Marine Park fishing regulations may protect these species, the Wide Berths in the centre of the Marine Park may simply represent a better habitat for these species than adjacent shallower, and more sheltered coastal waters. The Wide Berths project further out to sea that the rest of the Park and are likely to be influenced by a different current regime and a higher level of wave exposure that the rest of the Park. As expected, plankton feeders, such as demoiselles and trevally were more common in this area. This finding was consistent with the fact that these species are more common at offshore islands like the Poor Knights and Mokohinau, or on the mainland sites with 'offshore' physical characteristics (e.g. Cape Brett) (Kingsford, 1989). Unsurprisingly, both methods found that the deeper reefs in Areas 4 and 5 had significantly more leatherjackets, as deep reefs are their preferred habitat (Ayling, 1981).

As expected, the reef fish assemblage at the Mimiwhangata Marine Park most closely resembled that of the other 'mainland' site Cape Brett. The lower number of species recorded at Mimiwhangata, compared to the other three surveyed areas, was mainly accounted for by low numbers of subtropical wrasse species, common on offshore islands (Denny et al., 2003). This may be because the East Auckland Current, although not having such a heavy influence, does occasionally impinge on the Mimiwhangata coast bringing with it low numbers of subtropical species.

Studies of snapper populations in other coastal marine reserves in northeastern New Zealand have shown a sharp gradient in snapper abundance between no-take areas and adjacent fished areas (Willis et al., 2000, 2003). Gradients of snapper abundance in other coastal marine reserves in northeastern New Zealand suggest fishing effects that extend inside the reserve, rather than spillover effects. At the Cape Rodney to Okakari Point Marine Reserve the peak abundance is in the centre of the reserve, well inside the reserve boundaries (Willis et al., 2000, 2003). It is thus highly unlikely that the lack of contrast between the Mimiwhangata Marine Park and adjacent fished areas is due to the possibility than any effect of protection is being obscured by spillover.

This study demonstrates that the partial closures at Mimiwhangata are ineffective as conservation tools either for heavily targeted species, or for fish communities in general (i.e. through reduction in by-catch). The fact that snapper numbers may actually be lower in the partially protected Marine Park than in the unprotected control areas begs the question; is no protection at all better than partial protection? This may be so for two reasons: firstly, partial reserves may give a false impression that a conservation outcome has been achieved. Secondly, this impression may focus fishing effort, locally resulting in even greater fishing effects. The findings of this study have important implications for conservation managers, many of whom have had to accept the provision of fishing within a marine reserve as a 'solution' to political issues surrounding the declaration of marine reserves. This was because there was a lack of evidence either for or against the effects of limited fishing within a marine reserve. In light of the results in this study, we conclude that only no-take marine reserves should be created, as partial protection is an ineffective conservation strategy.

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