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COMMUNITY ECOLOGY

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Marine reserves demonstrate top-down control of community structure on temperate reefs

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Abstract Replicated ecological studies in marine reserves and associated unprotected areas are valuable in examining top-down impacts on communities and the ecosystem-level effects of fishing. We carried out experimental studies in two temperate marine reserves to examine these top-down influences on shallow subtidal reef communities in northeastern New Zealand. Both reserves examined are known to support high densities of predators and tethering experiments showed that the chance of predation on the dominant sea urchin, *Evechinus chloroticus*, within both reserves was approximately 7 times higher relative to outside. Predation was most intense on the smallest size class (30–40 mm) of tethered urchins, the size at which urchins cease to exhibit cryptic behaviour. A high proportion of predation on large urchins could be attributed to the spiny lobster, *Jasus edwardsii*. Predation on the smaller classes was probably by both lobsters and predatory fish, predominantly the sparid *Pagrus auratus*. The density of adult *Evechinus* actively grazing the substratum in the urchin barrens habitat was found to be significantly lower at marine reserve sites (2.2±0.3 m^{-2}) relative to non-reserve sites (5.5±0.4 m^{-2}). There was no difference in the density of cryptic juveniles between reserve and non-reserve sites. Reserve populations were more bimodal, with urchins between 40 and 55 mm occurring at very low numbers. Experimental removal of *Evechinus* from the urchin barrens habitat over 12 months lead to a change from a crustose coralline algal habitat to a macroalgal dominated habitat. Such macroalgal habitats were found to be more extensive in both reserves, where urchin densities were lower, relative to the adjacent unprotected areas that were dominated by urchin barrens. The patterns observed provide evidence for a top-down role of predators in structuring shallow reef communities in northeastern New Zealand and demonstrate how marine reserves can reverse the indirect effects of fishing and re-establish community-level trophic cascades.

Keywords Kelp communities · Marine protected areas · Northeastern New Zealand · Trophic cascades · Urchin predation

Introduction

Top-down regulation of biological communities has been a focal point in ecological theory (Hairston et al. 1960). This is ironic, given the efficiency with which humans have themselves harvested the large-bodied animals which may be responsible for the top-down control of ecosystems, in many cases to extinction (MacPhee 1999). Examples of top-down regulation or “trophic cascades” (see Polis et al. 2000) are increasingly being identified in a range of terrestrial (Schmitz et al. 2000), freshwater (Brett and Goldman 1996) and marine (Sala et al. 1998; Pinnegar et al. 2000; Tegner and Dayton 2000) ecosystems. In the marine environment where many fisheries have had to resort to harvesting at lower levels of the food chain (Botsford et al. 1997; Pauly et al. 1998), the impacts of fishing on trophic organisation and function are substantial [reviewed in Jennings and Kaiser (1998)]. Removal of top predators has resulted in the loss of lower-level interactions and consequently many trophic cascades have been lost (Pace et al. 1999). Our ability to understand, manage or restore natural systems is therefore compromised by our inability to differentiate anthropogenic impacts from the “natural” dynamics of systems (Dayton et al. 1998).

Trophic cascades are defined as predatory interactions involving three or more trophic levels, whereby primary carnivores indirectly increase plant abundance by suppressing herbivores (Menge 1995). In many subtidal reef systems throughout the world, a reduction in algal forests and an increase in urchin barrens (areas dominated by crustose corallines where the grazing activity of sea urchins has removed all large macroalgae), have been

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linked to fisheries-related declines in urchin predators (Wharton and Mann 1981; Estes and Duggins 1995; Vadas and Steneck 1995; Sala et al. 1998). However, good empirical examples supporting the existence of such trophic effects are generally lacking (Scheibling 1996). The best known example is that of the role of sea otters in structuring kelp communities in the northeastern Pacific [reviewed by Pinnegar et al. (2000) and Tegner and Dayton (2000)]. Where sea otters are abundant, herbivorous sea urchins are rare and kelp dominates, whereas where otters are absent urchins are abundant and kelp rare (Estes and Duggins 1995). Recent declines in otter numbers in Alaska have been related to an observed increase in killer whale attacks on otters (Estes et al. 1998) adding another level to this trophic cascade. In some areas where sea otters do not occur, fish and lobsters have been implicated as important predators of urchins [e.g. southern Califonia (Cowen 1983; Tegner and Levin 1983) and the northwestern Atlantic (Bernstein et al. 1981; Breen and Mann 1976; Wharton and Mann 1981)]. While the destruction of kelp beds by sea urchins in these areas has been linked to overfishing of both lobsters and fish, the existence of a direct causal linkage has received much debate (Scheibling 1996). For kelp communities in the southern hemisphere it has been widely accepted that the absence of a sea otter analogue results in a simpler two-tiered system with no top-down control of urchins (Estes and Steinberg 1988; Steinberg et al. 1995).

Marine reserves provide a new opportunity for testing the top-down impact of predators and demonstrating indirectly the ecosystem-level effects of fishing. They function as an experimental tool where large-scale ecosystem manipulations are carried out by preventing fishing and subsequently elevating predator densities. The treatments can be viewed as either with or without humans as the top predator, or as without or with “natural” predators. This enables comparisons of trophic structure and further experimental manipulations to be made between reserve and non-protected areas. On coral reefs in East Africa, marine reserves have been used in this way. Predatory fish densities have been found to be higher, urchin densities lower and predation on urchins higher, in Kenyan marine reserves relative to unprotected areas (McClanahan and Shafir 1990). Subsequently protected reefs had a higher species diversity and topographic complexity, with higher cover of hard coral and calcareous algae than unprotected areas. In the Mediterranean Sea an expansion of urchin barrens into areas previously occupied by erect algae has been linked to overfishing of urchin predators (Sala and Zabala 1996. Studies utilising marine reserves in the Mediterranean have shown that predatory fish are an important determinant in controlling urchin populations [reviewed by Sala et al. (1998)]. However, there has not yet been any decline in the extent of urchin barrens in these protected areas. Other factors such as recruitment, pollution, disease, large-scale oceanographic events, urchin harvesting, food subsidies and availability of shelters may also be important in controlling algal assemblage structure (Sala et al. 1998).

For temperate systems there are few examples of the use of marine reserves to examine the trophic effects of fishing in subtidal kelp communities. In Australia, Edgar and Barrett (1999) found an increase in the density of large fish and lobsters and an increased mean size of abalone in a Tasmanian marine reserve after 7 years of protection, relative to an associated unprotected area. They also found some changes in algal assemblages; however, the cause of these changes was unknown and trophic cascade effects were not inferred to be present. The strongest evidence for a key role of predators in controlling subtidal reef communities in the southern hemisphere is from two New Zealand marine reserves (Leigh Marine Reserve and Tawharanui Marine Park) where there has been a decline in urchin densities and an associated change from urchin barrens to kelp over a 20-year period (Babcock et al. 1999). The density and size of the dominant urchin predators, the snapper *Pagrus auratus* (Sparidae), blue cod *Parapercis colias* (Pinguipedidae) and the spiny lobster *Jasus edwardsii* (Palinuridae), are considerably higher in these reserves than in adjacent fished areas (Kelly et al. 2000; Willis et al. 2000; Willis 2001). Both snapper and spiny lobster are heavily targeted by commercial and recreational fisherman around New Zealand, and Babcock et al. (1999) suggest that this has ecosystem-level effects, indirectly resulting in large-scale reduction of macroalgal habitats and subsequently benthic primary productivity. While there is strong circumstantial evidence for a topdown effect, experimental evidence supporting a key predatory role is generally lacking (reviewed in Schiel 1990). Differences in urchin demography, behaviour and morphology, and also a higher loss of transplanted urchins in the Leigh marine reserve compared to outside have been inferred to be due to higher levels of predation by Cole and Keuskamp (1998). The subtidal reef communities in northeastern New Zealand are suited to the occurrence of community-level cascades (Polis et al. 2000) with a simple trophic structure, discrete habitats and low species diversity. The sea urchin, *Evechinus chloroticus* is the dominant grazer (Andrew 1988), and through its grazing activity can form urchin barrens habitat at depths between approximately 3 and 10 m (Ayling 1981; Choat and Schiel 1982).

The aim of this study was to demonstrate the indirect effects of fishing on lower trophic levels by experimentally examining the top-down role of predators in explaining the habitat change documented in marine reserves in northeastern New Zealand. This was done by:

1. An urchin-tethering experiment to test whether relative predation levels on urchins were higher at marine reserve sites and to determine the sources of predation.
2. Comparing the density and demography of urchins in the urchin barrens habitat at multiple sites in two reserve and two non-reserve areas.
3. Experimental removal of urchins to test whether the observed habitat changes in the Leigh reserve were consistent with a reduction in urchin populations.

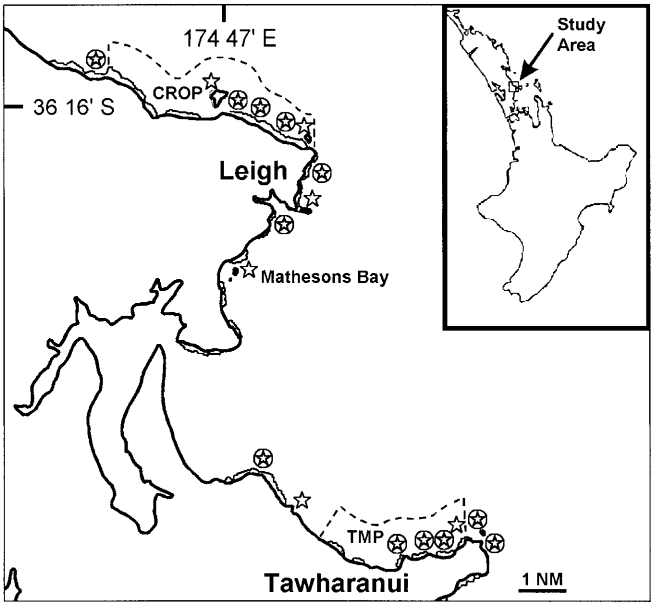

Fig. 1 Location of study sites in the Cape Rodney to Okakari Point Marine reserve (*CROP*) at Leigh and Tawharanui Marine Park (*TMP*). *Circles* indicate sites where the predation experiment was carried out. *Inset* shows general location of study area on New Zealand's North Island

4. Comparing the distribution of macroalgal communities among reef habitats between reserve and non-reserve areas.

Materials and methods

Study area

This study was carried out at sites located in two marine reserves and at adjacent unprotected sites in northeastern New Zealand (Fig. 1). The two reserves examined are completely no-take and include New Zealand's oldest marine reserve, the Cape Rodney to Okakari Point (Leigh) Marine Reserve (549 ha, established in 1976), and Tawharanui Marine Park (350 ha, established in 1982), 8 km to the south. Both marine reserves are subject to similar environmental conditions and have extensive subtidal reef communities typical of moderately exposed coasts in northeastern New Zealand (Choat and Schiel 1982).

Predation

Relative predation levels on *Evechinus* were compared between marine reserves and adjacent fished areas using tethering experiments. Tethering is a simple technique, suited to sedentary benthic organisms (Aronson et al. 2001), that has been used extensively on coral reefs (McClanahan and Muthiga 1989; McClanahan et al. 1999) and in the Mediterranean (Sala and Zabala 1996) to test predation potential on sea urchins between protected and unprotected reefs.

The tethering technique involved inserting a hypodermic needle (1.2 mm×38 mm) through the dorsal and ventral surface of the urchins test, as far away from the oral-aboral axis as possible (McClanahan and Muthiga 1989). Nylon monofilament was then threaded through the needle and tied-off. Laboratory trials found 100% survival of 80 tethered urchins [ranging in size from 25 to 75 mm test diameter (TD)] after 10 days. Trials in the field found that tether-related mortality could be reduced by holding the urchins in the laboratory for a week prior to experimentation. This procedure also allowed the urchins to heal, minimising the potential effects of coelomic fluid leakage on predation (McClanahan and Muthiga 1989).

Tethering also provided information on the source of predation through direct observation or from examination of urchin-test remains. Slow-moving predators such as the starfish, *Coscinasterias muricata*, and the gastropod, *Charonia lampax* were often seen feeding on the urchin or remained nearby. From trial experiments we were able to classify the source of predation into the following categories: (1) unknown (urchin missing with nylon loop still intact demonstrating urchin had been broken off), (2) lobster (test had characteristic pattern of lobster predation which involves a large opening around the Aristotle's lantern), (3) *Coscinasterias* (test intact with patches of freshly stripped spines) and (4) *Charonia* (test intact and mucous covered).

The tethering experiments were carried out at three reserve and three non-reserve sites (Fig. 1); first at Leigh (4 August 1999) and then repeated at Tawharanui (19 August 1999). Thirty urchins, of three different size classes (n=10), were tethered at each site and their survival monitored for 10 days. The three size classes used for the experiments were: 35–40 mm, representing the size where urchins move from a sheltered to an exposed habit (Andrew and Choat 1982; Cole and Keuskamp 1998), 55–60 mm and 75–80 mm, representing the dominant adult size class outside and inside the Leigh reserve, respectively (Cole and Keuskamp 1998). Experimental urchins were collected from non-reserve sites at Leigh where all size classes can be found openly grazing the substratum. Urchins were positioned in a 10×10-m^2 plot located in the urchin barrens habitat adjacent to the kelp forest border. Urchins were tethered on 25-cm monofilament traces, attached to masonry nails that had previously been embedded in the substratum at random coordinates. It was important that urchins were attached without drawing the attention of diver-positive predatory fish at marine reserve sites (Cole 1994; Cole and Keuskamp 1998). This was done by keeping the urchins concealed while one diver created a disturbance nearby. There were no instances of fish predation on recently tethered urchins. Daily monitoring enabled detection and replacement of urchins that appeared to be dying as a result of tethering. In each experiment only four out of a total of 180 tethered urchins died as a result of tethering.

Differences in the survival of urchins after 10 days were analysed using a generalised linear mixed model (GLMMIX). The model was back-fitted to a binomial distribution using residual (restricted) maximum likelihood with the GLMMIX macro in SAS (Littell et al. 1996). This technique was used in preference to ANOVA as survival data follow a binomial distribution. The factors Area (Leigh and Tawharanui), Status (reserve and non-reserve) and Size (the three size classes) were treated as fixed effects and Site(Area×Status) as a random effect.

Urchin density and size structure

Comparisons of urchin populations were made between reserve and non-reserve sites at both Leigh and Tawharanui (Fig. 1). Five sites were sampled within the Leigh reserve and five outside during March and April 1998, while at Tawharanui four sites were sampled within the reserve and four outside in June 1998. Sites were selected in areas where urchin barrens habitat was present. At each site ten 1-m^2 quadrats were placed haphazardly within the urchin barrens at 4–6 m depth (below MLWS). Within each quadrat we measured the TD of each urchin using vernier callipers (±1 mm) and noted whether urchins were located in a crevice (cryptic) or were openly grazing the substratum (exposed). In addition, the percent cover of dominant encrusting algal forms was visually estimated to determine if any differences occurred between reserve and non-reserve sites.

Urchin counts were analysed using GLMMIX. A Poisson distribution was used as count data seldom fit the assumptions of normality and homogeneity of variance. The factors Area and Status were treated as fixed effects and Site(Area×Status) as a random effect.

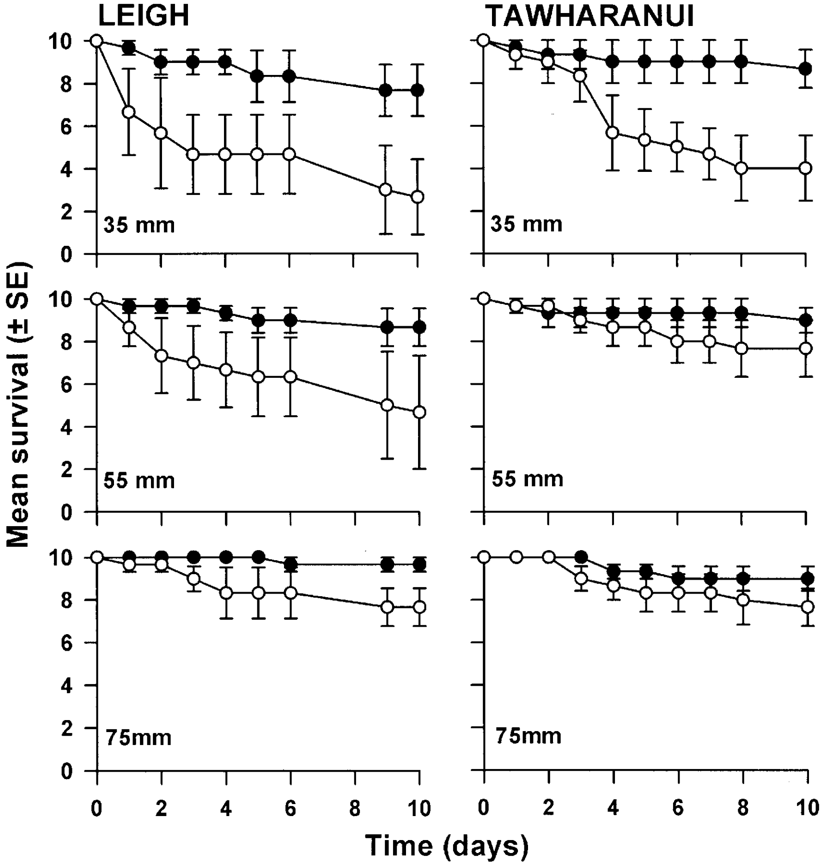

Fig. 2 Survival of tethered urchins at reserve (○) and non-reserve (●) areas. The mean number of tethered urchins surviving in each of the three size classes is given for Leigh and Tawharanui

Differences in size of exposed urchins between reserve and non-reserve areas were tested using mixed-model ANOVA with fixed factors Area and Status. Site was treated as a random factor and nested within Area and Status. Size data were tested for normality using Shapiro-Wilk's test. Significant interaction terms were investigated using a multiple comparison (Tukey-Kramer) of all possible combinations of the main effects.

Urchin removal

A sea urchin-removal experiment was undertaken to investigate the role *Evechinus* plays in maintaining the urchin barrens habitat and the response of algal communities to a reduction in urchin density. The experiment was carried out at Mathesons Bay (Fig. 1) near the Leigh marine reserve on an area of reef with extensive urchin barrens habitat. The reef was dissected by sand-filled crevices, which form semi-isolated blocks of reef, allowing the establishment of discrete experimental plots within a 500-m^2 area of reef in the urchin barrens habitat. Six blocks of reef were selected, ranging in size from 10 to 20 m^2, at a depth of 4–5 m. All urchins were removed from three randomly selected blocks, the remaining three were left as controls. The urchins were removed in January 1998, with weekly re-clearances until January 1999.

The initial density of grazers and macroalgae in the experimental areas was estimated in five haphazardly placed 0.25-m^2 quadrats. The percent cover of encrusting algae (crustose coralline algae, articulated coralline turf, filamentous algae and other encrusting algae) was also measured by estimating the number of 10×10-cm cells within the 0.25-m^2 quadrats each algal type "filled" (Benedetti-Cecchi et al. 1996). Sampling was repeated monthly to determine the response of the communities to manipulation. To test for differences in the dominant species between treatments and between plots within treatments at the start of the experiment and over time GLMMIX was used. Treatment and Time were set as fixed effects. Covariance parameter estimates were calculated for the random effect Plot(Treatment) and also for the auto-regressive error structure [AR(1)] to account for repeated measures. A binomial distribution with logit-link was used for percent cover data and a Poisson distribution with log-link for count data.

Distribution of urchin barrens habitat

To investigate whether urchin barrens were more abundant in reserves, the proportions of habitats were measured at 22 sites located in and around both reserves using 1-m-wide strip transects (three at each site). Transects were run perpendicular to the shore from MLWS to the reef edge or a maximum depth of 12 m. Both depth and habitat type were recorded every metre. Habitat type was recorded as one of the following categories, based on the density of plants within each 1-m^2 area along the transect: (1) macroalgal habitat, >3 adult phaeophytes m^{-2} e.g. *Ecklonia radiata* or *Carpophyllum flexuosum*; (2) urchin barrens, >50% cover of crustose coralline algae; (3) shallow fucoid zone, >20% cover or 3 adult phaeophytes m^{-2} at depths <4 m; (4) turf habitat, >50% cover of turf forming red or green algae with large phaeophytes <3 m^{-2}.

The proportional cover of urchin barrens habitat within three depth ranges (0–3, 4–6 and 7–9 m) was examined using GLMMIX with a binomial distribution. Area, Status and Depth were treated as fixed factors, and Site(Area×Status) was treated as a random factor.

Results

Predation

Predation on urchins was significantly higher at reserve sites than at non-reserve sites (F=9.44, P=0.0133), with the relative odds of predation being 6.9 times higher at reserve sites (Fig. 2, Table 1). This was consistent

Table 1 Summary statistics for reserve/non-reserve comparisons with size of effect expressed as a ratio with 95% confidence limits (*CL*). Likelihood ratios calculated by the SAS procedure generalised linear mixed model for mortality of tethered *Evechinus* (binomial distribution), *Evechinus* density (Poisson distribution), the cover of urchin barrens and coralline turf (both binomial distribution). For count data the ratio indicates the effect size whereas for mortality and percent data the ratio indicates the relative odds [see Willis and Millar (2001) for explanation of interpreting relative odds ratio]

	Reserve mean SE	Non-reserve mean SE	Reserve:non-reserve ratio	Upper 95% CL	Lower 95% CL
Predation on *Evechinus* (% mortality)	42.8 (9.0)	12.2 (3.4)	6.88	2.01	23.57
Exposed *Evechinus* density (m^{-2})	2.2 (0.3)	5.5 (0.4)	0.60	0.45	0.79
Exposed *Evechinus* mean size (mm)	69.8 (2.5)	57.3 (1.3)	–	–	–
Cover of coralline turf (%)	29.3 (2.9)	12.6 (1.5)	1.80	0.90	3.60
Extent of urchin barrens (%)	14.8 (4.8)	41.4 (4.2)	0.17	0.07	0.41

Table 2 Source of predation on tethered urchins

	Reserve			Non-reserve		
Size class	35 mm	55 mm	75 mm	35 mm	55 mm	75 mm
Number preyed	40	23	13	11	7	4
Proportion						
Unknown	100.0	56.5	46.2	54.5	42.9	0.0
Lobster	0.0	43.3	46.2	0.0	0.0	0.0
Coscinasterias	0.0	0.0	7.7	45.5	42.9	50.0
Charonia	0.0	0.0	0.0	0.0	14.3	50.0

between both areas (F=0.41, P=0.5357). There was a significant effect of size on predation (F=12.60, P<0.0001), which was also consistent between areas and between reserve and non-reserve sites. Predation occurred on all size classes of tethered urchins, at both reserve and non-reserve sites, but was highest on the smallest size class (Fig. 2). The likelihood of predation on the small and middle size-class urchins was 6.3 [95% confidence limits (CL) 3.0–13.3] and 2.2 (CL 1.1–4.7) times greater, respectively, than predation on the largest size class. The odds of predation did not vary significantly between reserve and non-reserve sites for each area (Z=1.52, P=0.0639).

The fate of all small urchins (35 mm) preyed upon at reserve sites was unknown as the tests were completely removed from the tethers (Table 2). This could have been due either to predation by fish, which completely engulf the urchin, or by lobsters breaking up or removing small urchins. At reserve sites approximately 45% of preyed individuals in the larger size classes (55 and 75 mm) showed patterns of damage characteristic of spiny lobster predation. No urchins showed signs of spiny lobster predation at non-reserve sites. In most cases mortality at non-reserve sites could be attributed to starfish (*Coscinasterias muricata*) or the gastropod, *Charonia lampax*, both of which are slow-moving predators.

Urchin density and size structure

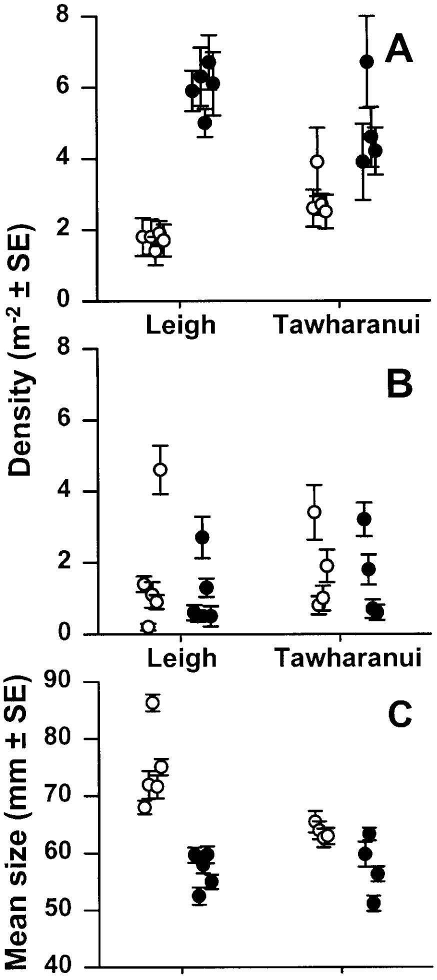

Fig. 3 Mean density of **A** exposed and **B** cryptic urchins, and **C** mean size of exposed urchins from quadrat sampling (n=10) at all reserve (○) and non-reserve sites (●)

Densities of *Evechinus* in the urchin-grazed habitat varied widely between sites but were generally lower at reserve sites for both areas (Fig. 3). The density of exposed urchins (Fig. 3A) was significantly lower at marine reserve sites (Tables 1, 3). Exposed urchins were 1.7 times more abundant overall at non-reserve sites (Table 1). There was no difference in urchin density between areas (Leigh and Tawharanui) but there was a significant interaction between Area and Status. This can

Table 3 Exposed urchin density statistics. Type 3 tests for counts of exposed urchins for fixed effects Area (Leigh and Tawharanui) and Status (reserve and non-reserve). Parameter estimates for the random effect Site(Area×Status)

Fixed effects		*df*	*F*-value	*Pr>F*
Status		1, 14	73.65	<0.0001
Area		1, 14	2,21	0.1597
Area×Status		1, 14	13.06	0.0028
Covariance parameter	Estimate	SE	*Z*-value	*Pr Z*
Site(Area×Status)	0.0023	0.0135	0.17	0.4312

Table 4 Cryptic urchin density statistics. Type 3 tests for count of exposed urchins for fixed effects Area (Leigh and Tawharanui) and Status (reserve and non-reserve). Parameter estimates for the random effect (Area×Status)

Fixed effects		*df*	$\chi2$	*P*
Status		1, 14	0.37	0.5529
Area		1, 14	0.62	0.445
Area×Status		1, 14	0.01	0.9274
Covariance parameter	Estimate	SE	*Z*-value	*Pr Z*
Site (Area×Status)	0.5194	0.2465	2.11	0.0175

Table 5 Urchin size statistics. Mixed-model ANOVA results for exposed urchin size at Leigh and Tawharanui (Area), reserve and non-reserve site (Status)

	df	Mean square	*F*-value	*Pr>F*
Area	1	3,343.2	5.58	0.0321
Area×Status	1	4,552.8	7.60	0.0147
Status	1	19,374.0	32.48	<0.0001
Site(Area×Status)	14	726.0	7.33	<0.0001

be explained by examining the size of the effect of Status between both areas; for Leigh densities were 3.5 (95% CL 2.8–4.4) times higher at non-reserve sites while at Tawharanui densities were 1.7 (1.2–2.4) times higher. Separate analysis for each area found a significant difference in density between reserve and non-reserve sites for both Leigh (P<0.0001) and Tawharanui (P=0.0342).

The abundance of cryptic urchins (Fig. 3B) did not differ significantly between reserve and non-reserve locations or between Leigh and Tawharanui (Table 4), although there was significant site-level variability.

There was significant variation in the size of exposed urchins between sites (Fig. 3C, Table 5). The mean size of exposed urchins was significantly larger at marine reserve sites (Table 1) although the Area effect was significant and there was a significant Area and Status interaction. This can be explained by the larger effect of Status at Leigh which results in a significant interaction between Area and Status. There was no difference in size between the non-reserve sites for each area [Tukey's honestly significant difference (HSD) P=0.8112], but for both areas there were significant differences between reserve and non-reserve sites (Tukey's HSD P<0.0001). There was also significant difference between reserve populations at Leigh and Tawharanui (Tukey's HSD P<0.0001).

The population structure of *Evechinus* varied between reserve and non-reserve sites (Fig. 4). Populations were

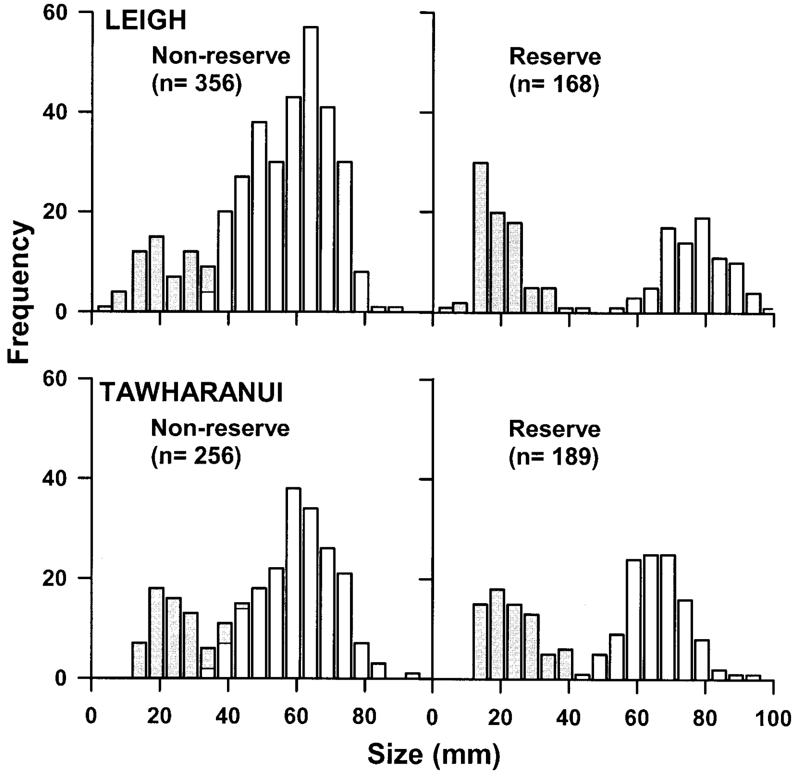

Fig. 4 Size frequency distributions of all *Evechinus* measured during quadrat sampling at each area. *Shaded bars* indicate proportion of cryptic urchins

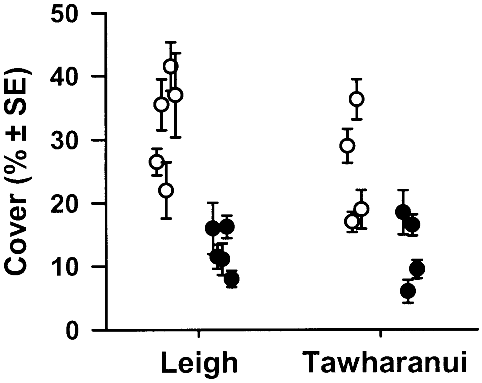

Fig. 5 The percent cover of Coralline turf from quadrat sampling (n=10) at all reserve (○) and non-reserve sites (●). Means are given for each site

more bimodal at reserve sites, with very low numbers of urchins between 30 and 50 mm, and they generally remained cryptic to a greater size. This pattern was stronger in the Leigh marine reserve.

Quadrat sampling also revealed that, overall, the percent cover of coralline turf (*Corallina officinalis*) was significantly higher at reserve sites ($F_{1,9}$=14.18, P=0.0044) (Table 1, Fig. 5). The relative odds ratio was 1.8 times higher at marine reserve sites (Table 1). This was consistent between areas ($F_{1,9}$=0.50, P=0.4960) and while the pattern was clearest at Leigh (Fig. 5) the effect of reserve status was consistent between areas ($F_{1,9}$=1.79, P=0.2140).

Urchin removal

At the commencement of the experiment in January 1998 *Evechinus* densities did not vary between treatments ($F_{1,4}$=0.06, P=0.8135). Densities of urchins ranged from 1.2 to 2.4 per 0.25 m^2. Crustose coralline algae (*Lithothamnion* and *Lithophyllum* spp.) were dominant, covering 63–99% of the substratum. Articulated coralline turf was the other dominant encrusting form with cover ranging between 0 and 35%. There was no significant difference in either crustose coralline algae ($F_{1,4}$=0.36, P=0.5789) or coralline turf ($F_{1,4}$=0.63, P=0.4730) between treatments or between plots within treatments (Z=1.1, P=0.1367, Z=1.08, P=0.1411). Macroalgae were rare at the start of the experiment, with *Carpophyllum flexuosum*, which is relatively resilient to urchin grazing (Cole and Haggitt 2001), being the only conspicuous large brown seaweed (<1 per 0.25 m^2). There was no significant difference in the number of *C. flexuosum* between treatments ($F_{1,4}$=0.52, P=0.5123) or between plots within treatments (Z=0.53, P=0.2966). *Ecklonia radiata* was absent from all plots.

After 1 year the control plots remained as urchin barrens dominated by crustose coralline algae, while the urchin-removal plots had become dominated by coralline turf, with a mixture of large and small brown algae (a “mixed algal habitat”). A temporary decrease in the cover of crustose coralline algae across all plots was due to a large settlement of filamentous algae at the start of the experiment (Fig. 6). The change from crustose coralline to articulated coralline algae occurred rapidly for the first 4 months then remained stable throughout the winter. The cover of crustose corallines and coralline turf varied significantly over time (Table 6). While the overall effect of treatment was not clear, the effect of urchin removal on coralline algae and coralline turf over time was significant (Table 6).

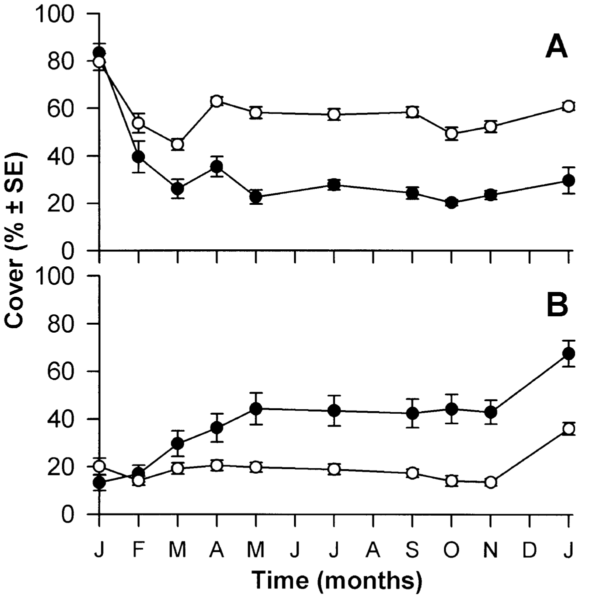

Fig. 6A, B Response of encrusting and turfing algae to urchin removal. The mean proportional cover of **A** crustose coralline algae and **B** coralline turf in both control (○) and urchin removal (●) plots following commencement of the experiment in January 1998. *J* January, *F* February, *M* March, *A* April, *M* May, *J* June, *J* July, *A* August, *S* September, *O* October, *N* November, *D* December

A number of brown algal species became established in the urchin-removal plots (Fig. 7). In most cases these species remained absent from control plots so differences between treatments could not be statistically tested. Only *Carpophyllum flexuosum* occurred at sufficient densities in both control and removal plots throughout the experiment for statistical analysis (Fig. 7A). There was no effect of urchin removal on the density of *C. flexuosum* (Table 6), the numbers remaining stable over time. Several large *Ecklonia radiata* sporophytes became established (Fig. 7B) within the urchin removal plots while remaining absent in control areas. Survival of *Ecklonia* recruits was observed to be low as they appeared to be prime targets for any urchins which did immigrate into treatment plots. Total exclusion of urchins would probably have resulted in a more rapid response of *Ecklonia.* Low numbers of two other species of large brown algae, *Carpophyllum maschalocarpum* and *Sargassum sinclairii* also became established in the urchin-removal areas. Small brown algae showed a marked response to urchin removal. These included *Halopteris*

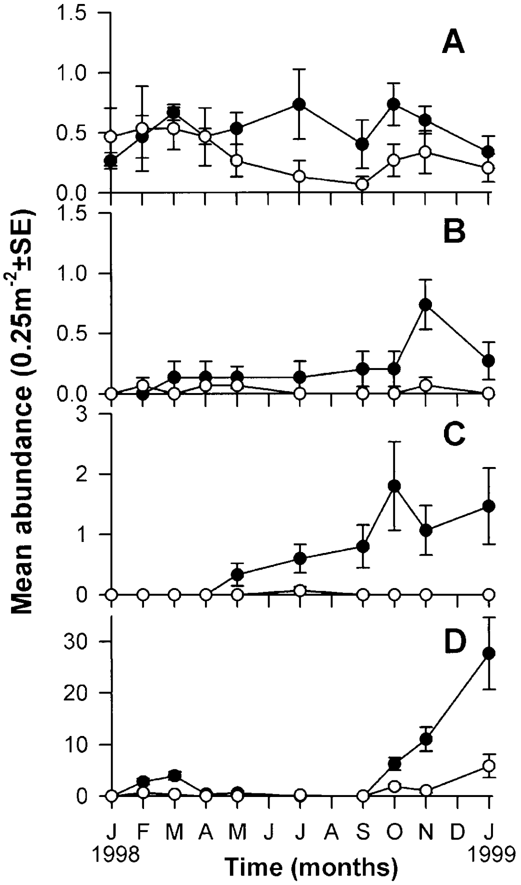

Fig. 7A–D Response of macroalgae to urchin removal. The mean abundance of **A** *Carpophyllum flexuosum*, **B** *Ecklonia radiata*, **C** *Halopteris virgata* and **D** small brown seasonal algae in both control (○) and urchin-removal (●) plots following commencement of the experiment in January 1998

virgata (Fig. 7C) and a number of short-lived seasonal species (Fig. 7D), including *Dictyota* sp. and *Colpomenia sinuosa*. A few red algal species such as *Asparagopsis armata* and *Champia novaezelandicae* also recruited into urchin-removal plots.

Within 6 months of completion of the experiment the urchin-removal plots had been heavily grazed and reverted to urchin barrens habitat, dominated by crustose coralline algae. The only brown algae present were stunted *Carpophyllum flexuosum* plants (personal observation).

Distribution of urchin barrens habitat

The general distribution of habitats (Fig. 8) at non-reserve sites is typical of northeastern New Zealand with shallow fucoid assemblages, deep kelp forests (*Ecklonia radiata*) and intermediate depths dominated by urchin barrens (Choat and Schiel 1982). However, at marine reserve sites all depth ranges were dominated by macroalgal habitats. The proportion of urchin barrens habitat was significantly lower than at non-reserve sites (Tables 1, 7). The relative odds ratio for the proportion of urchin barrens at reserve vs. non-reserve sites was 0.2:1 (Table 1), or inversely, 5.9 times higher at non-reserve sites. This pattern was consistent between both areas but varied significantly with depth (Table 7). Differences between reserve and non-reserve sites were greatest in the shallow depth strata (0–3 m and 4–6 m) where urchin barrens covered approximately 54% of available reef at non-reserve sites and only about 20% of the reef at reserve sites. The deeper strata (7–9 m and 10–12 m) at both reserve and non-reserve sites were dominated by macroalgal habitat, predominantly *Ecklonia* forest.

Table 6 Response of crustose coralline algae, coralline turf and *Carpophyllum flexuosum* following urchin removal. Type 3 analysis for the percent cover of crustose coralline algae and coralline turf, and the number of *C. flexuosum* plants following urchin removal for fixed effects Treatment and Time. Parameter estimates for the random effect Plot(Treatment) and the repeated measures effect [*AR(1)*]

Crustose coralline				
Fixed effects		*df*	*F*-value	*Pr>F*
Treatment		1, 4	7.43	0.0527
Time		9, 276	21.76	<0.0001
Treatment×Time		9, 276	4.57	<0.0001
Covariance parameter	Estimate	SE	*Z*-value	*Pr Z*
Plot(Treatment)	0.2247	0.1678	1.34	0.0903
AR(1)	0.3961	0.0650	6.10	<0.0001
Coralline turf				
Fixed effects		*df*	*F*-value	*Pr>F*
Treatment		1, 4	1.24	0.3278
Time		9, 276	24.74	<0.0001
Treatment×Time		9, 276	9.48	<0.0001
Covariance parameter	Estimate	SE	*Z*-value	*Pr Z*
Plot(Treatment)	0.8042	0.5754	1.40	0.0811
AR(1)	0.1938	0.0640	3.03	0.0024
Carpophyllum flexuosum				
Fixed effects		*df*	*F*-value	*Pr>F*
Treatment		1, 4	1.32	0.3141
Time		9, 276	1.20	0.2947
Treatment×Time		9, 276	1.36	0.2077
Covariance parameter	Estimate	SE	*Z*-value	*Pr Z*
Plot(Treatment)	1.0384	0.9185	1.13	0.1291
AR(1)	–0.0660	0.0630	–1.05	0.2948

Table 7 Statistics for the proportion of urchin barrens. Type 3 analysis for fixed factors Status (reserve/non-reserve), Area (Leigh/Tawharanui) and Depth (0–3, 4–6 and 7–9 m). Non-significant interaction terms were removed from the model. Parameter estimates given for the random effect Site(Area×Status)

Fixed effects		*df*	*F*-value	*Pr>F*
Status		1, 19	15.24	0.0010
Area		1, 19	0.00	0.9740
Depth		2, 174	32.73	<0.001
Covariance parameter	Estimate	SE	*Z*-value	*Pr Z*
Site(Area×Status)	0.8844	0.3715	2.38	0.0087

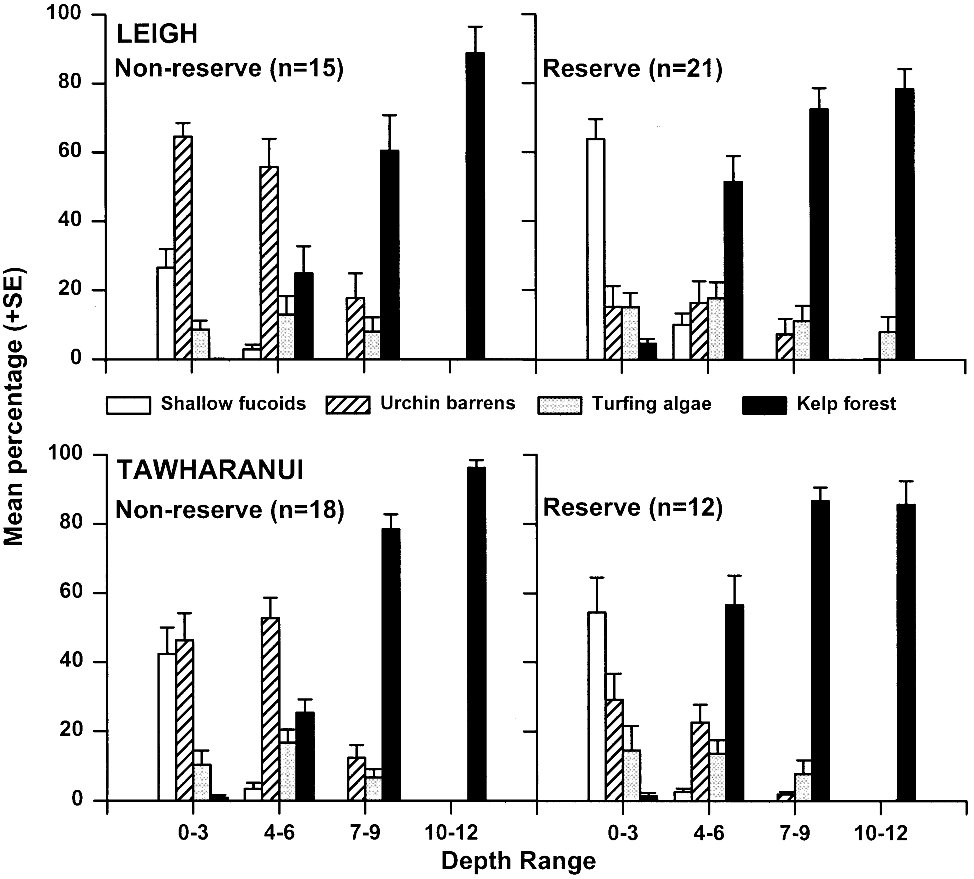

Fig. 8 Mean percent cover of major habitat types (shallow fucoids, urchin barrens, turfing algae and kelp forest), within each depth range for reserve and non-reserve sites at Leigh and Tawharanui

Discussion

New Zealand's two oldest marine reserves at Leigh and Tawharanui support higher predator densities than similar unprotected areas of coastline (Babcock et al. 1999; Kelly et al. 2000; Willis et al. 2000; Willis 2001). Snapper are at least 5.8–8.7 times more abundant inside these reserves and spiny lobster 1.6–3.7 times more abundant, than in adjacent unprotected areas (Babcock et al. 1999). Relative rates of predation on sea urchins were found to be higher in the reserves, the densities of actively grazing urchins lower, and the cover of macroalgal forests higher relative to adjacent unprotected areas. These patterns confirmed and extended previous results (Cole and Keuskamp 1998; Babcock et al. 1999) and provide experimental evidence for a top-down impact of predators on subtidal reef communities. The fact that these patterns were found through comparisons of multiple sites inside and outside more than one marine reserve mean that it is highly unlikely that the effects were due to spatial variations in other factors such as nutrients or larval supply.

The spiny lobster, *Jasus edwardsii*, was found to be an important predator of sea urchins at marine reserve sites. At least 45% of predation on the larger size classes of tethered urchins at reserve sites could be attributed to lobsters. This is noteworthy, considering that spiny lobsters were not previously thought to forage in the urchin barrens habitat (Andrew and Choat 1982; Andrew and MacDiarmid 1991). The actual proportion of predation attributable to lobsters is likely to be higher than estimated, as a spiny lobster may completely consume a tethered urchin or take it back to shelter, in both cases leaving no remains from which the source of predation could be ascertained. In addition, lobster-predated tests of untethered urchins were found regularly at reserve sites during the study, demonstrating that spiny lobster were also feeding on natural urchin populations. The highest levels of predation occurred on the 30- to 40-mm size class, which are normally sheltered at reserve sites but exposed at non-reserve sites. While the specific predators responsible for attacks on this size class could not be identified they were likely to have been both lobsters, which preferentially take smaller urchins (Andrew and MacDiarmid 1991), and predatory fish. Gut content analysis (Babcock et al. 1999) and visual observations (personal observation) indicate that snapper and blue cod only feed on small urchins (<50 mm). Cole and Keuskamp (1998) suggested that the higher loss of transplanted urchins of this size in the Leigh reserve sites was due to predation by fish.

Predation of tethered urchins at non-reserve sites was attributed to a different suite of predators, mainly *Coscinasterias* and *Charonia*. These species are natural predators of urchins (personal observation) but tethering reduced the chance of urchins escaping from these slow-moving predators. At reserve sites both of these predatory species tend to occur at much lower densities than at non-reserve sites (N. Shears, unpublished data), subsequently there was only one instance of predation by *Coscinasterias* recorded at reserve sites. Similar patterns have been shown in other studies where different predators are important at fished sites where the primary predators have been removed. In the Gulf of Maine, Vadas and Steneck (1995) found high levels of fish predation on urchins at an offshore reef subject to low fishing pressure, while at heavily fished coastal sites predation on urchins was attributed to crabs. This was also suggested to be at least in part an artefact of tethering. Likewise, in the Mediterranean a predatory gastropod was an important predator at fished sites while at protected sites fish were the dominant predators (Sala and Zabala 1996). Our urchin-tethering experiment provided strong evidence that the lower densities of urchins in both reserves are due to relatively higher levels of predation within marine reserves.

Previous experimental studies carried out in the Leigh reserve acknowledged that both snapper (Andrew and Choat 1982) and spiny lobsters (Andrew and MacDiarmid 1991) were important predators of *Evechinus* in northeastern New Zealand, but concluded that predation by these species was not of sufficient magnitude to substantially alter urchin populations and cause community-level effects. Andrew and Choat (1982) found that the survival of juvenile urchins was enhanced in caged areas where predatory fish were excluded. Despite potential caging artefacts they concluded that sufficient numbers of juveniles escaped predation by predatory fishes to sustain the adult population and maintain the urchin barrens habitat. Their study was carried out after only 4 years of marine reserve protection. If it were to be repeated now after 25 years of protection and recovery of predator populations a larger effect might be expected. Spiny lobsters were also discounted as playing a key regulatory role in controlling urchin populations principally because they were not thought to occur, or forage, in the urchin barrens habitat (Andrew and Choat 1982; Andrew and MacDiarmid 1991). In addition, Andrew and MacDiarmid (1991) investigated the relationship between lobsters and urchins in the shallow broken rock habitat and found that, at the scale of 9 m^2, urchins and lobsters were spatially segregated. However, *Jasus edwardsii* are known to forage over large areas (up to 100 m from their dens) (MacDiarmid et al. 1991). Our study has shown that lobsters do forage in the urchin barrens habitat at marine reserve sites and predation does occur on adult urchins which are responsible for maintaining the habitat.

The density of the dominant sea urchin, *Evechinus chloroticus*, in the urchin barrens habitat was between 1.6 and 3.5 times lower at marine reserve sites compared to equivalent habitats in adjacent areas. Cole and Keuskamp (1998) carried out sampling in 1996 at Leigh and Tawharanui and though they found lower densities in the Leigh reserve they reported no difference between Tawharanui Marine Park and Kawau Is, a nearby unprotected area. This may be explained by changes in urchin densities over the 2 years prior to our study, or due to the fact that their sampling was carried out over a larger depth range (5–10 m) and did not sample sites adjacent to the marine reserve. The smaller effect of reserve status seen at Tawharanui compared to Leigh may be due to several factors; higher levels of poaching (personal observation), younger reserve age and smaller reserve size. The size structures of *Evechinus* populations we found were consistent with those found by Cole and Keuskamp (1998). At reserve sites the exposed urchins were larger and populations were more bimodal than at non-reserve sites. Our tethering experiment provides support for the hypothesis that bimodality in *Evechinus* populations is related to higher size-specific predation on juveniles moving from a cryptic to exposed lifestyle (Andrew and Choat 1982; Cole and Keuskamp 1998).

Lower densities of urchins at protected sites compared to fished sites has been linked to higher predator densities in other marine systems (Sala and Zabala 1996; McClanahan and Shafir 1990; McClanahan et al. 1999). Reduced densities of urchins in marine reserves have implications for the maintenance of the urchin barrens habitat and the mechanisms underlying differences between fished and protected areas. While some areas of reef at reserve sites were classified as “urchin barrens” these areas had a higher cover of articulated coralline turf compared to non-reserve sites. Our urchin-removal experiment demonstrated that the initial response to a reduction in grazing pressure was an increase in the cover of coralline turf. With continued removal of urchins from the urchin barrens habitat, there was a change from a crustose coralline-dominated habitat to one dominated by macroalgae. These findings are comparable to those of previous urchin-removal experiments carried out in the Leigh reserve. Ayling (1981) recorded an increase in coralline turf when urchins were removed from small caged areas (0.0625 m^2) but no response of large brown algae. Larger scale urchin clearances (1,000 m^2) carried out by Andrew and Choat (1982) resulted in a rapid increase in large brown algae (*Ecklonia radiata* and *Sargassum sinclairii*) as well as coralline turf while the control area remained dominated by crustose coralline algae. The rate of change from urchin barrens to macroalgal forests therefore depends on the spatial scales at which urchins are removed. The decrease in the extent of urchin barrens habitat in the Leigh reserve (Babcock et al. 1999) and the greater abundance of macroalgal habitats in both reserves is consistent with a large-scale urchin removal.

This study demonstrates the value of marine reserves as experimental tools to test ecosystem-level hypotheses at ecologically relevant scales, previously unfeasible using traditional caging and manipulation experiments (Andrew and MacDiarmid 1991). Marine reserves have enabled us to measure the top-down role of predators in structuring subtidal reef communities in northeastern New Zealand, as well as the indirect effects of fishing on the trophic structure of reef communities. It is unclear whether, or to what extent, these findings can be extrapolated to other regions where urchin barrens are less common and interactions between trophic levels are weaker (unpublished data; Choat and Schiel 1982; Schiel and Foster 1986). Manipulations of the scale provided by marine reserves are likely to be of equal if not greater importance in understanding these systems.

Dayton et al (1998) stated that current programs aimed at understanding the functioning of kelp communities will fail to distinguish the “ghosts of missing animals” resulting in reduced expectations of what is “natural”. Our study has demonstrated that the existence of reserves increases our expectations of what is natural, and demonstrates that in some systems conservation of large predators can lead to the re-establishment of lost trophic interactions.

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