

Indirect effects of marine reserve protection on New Zealand's rocky coastal marine communities

DOC SCIENCE INTERNAL SERIES 192

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Published by
Department of Conservation
PO Box 10-420
Wellington, New Zealand

DOC Science Internal Series is a published record of scientific research carried out, or advice given, by Department of Conservation staff or external contractors funded by DOC. It comprises reports and short communications that are peer-reviewed.

Individual contributions to the series are first released on the departmental website in pdf form. Hardcopy is printed, bound, and distributed at regular intervals. Titles are also listed in the DOC Science Publishing catalogue on the website, refer <http://www.doc.govt.nz> under Publications, then Science and Research.

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ISSN 1175-6519

ISBN 0-478-22633-0

In the interest of forest conservation, DOC Science Publishing supports paperless electronic publishing. When printing, recycled paper is used wherever possible.

This report was prepared for publication by DOC Science Publishing, Science & Research Unit; editing by Helen O'Leary and Geoff Gregory and layout by Geoff Gregory. Publication was approved by the Manager, Science & Research Unit, Science Technology and Information Services, Department of Conservation, Wellington.

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ABSTRACT

The density and population structure of sea urchins (*Evechinus chloroticus*), the extent of urchin barrens habitat, and algal community structure were compared between reserve and non-reserve locations throughout New Zealand to investigate the role of predators in controlling benthic community structure. In addition, the potential effect of environmental variables in explaining differences between reserve and non-reserve sites was investigated. At Leigh and Tawharanui, which had been protected for 24 and 17 years, respectively, results supported previous work, with the extent of urchin barrens habitat and the overall density of *E. chloroticus* being significantly lower in these reserves than on the adjacent coasts. Algal communities were more than twice as productive at reserve sites in the 4–6 m depth stratum at Leigh and Tawharanui, but no differences were found at other depths. In addition, differences in herbivorous gastropods (*Cellana stellifera* and *Cookia sulcata*) were found between reserve and non-reserve sites. These differences may be a direct effect of higher predation in the reserve but also an indirect effect associated with decreased sea urchin abundance and changes in algal assemblages. These patterns, however, were not consistent for the other marine reserves examined, which generally had been protected for shorter periods. Instead, algal communities were strongly related to a number of environmental variables, and the importance of *E. chloroticus* changed across environmental gradients, both within and among locations. As a result, there were no universal differences among locations between reserve and non-reserve sites. In many locations, such as Long Bay, Kapiti Island, and Gisborne, grazers do not appear to play an important role in structuring algal communities. Under such conditions, the indirect effects of predators on algal assemblages resulting from marine reserve protection are likely to be subtle. Furthermore, spatial comparisons between reserve and non-reserve sites need to take the environmental variability within locations into account when investigating such indirect effects.

Keywords: marine reserves, environmental variables, biotic interactions, subtidal communities, sea urchin, *Evechinus chloroticus*, algal communities, New Zealand

© November 2004, New Zealand Department of Conservation. This paper may be cited as:

Shears, N.T.; Babcock, R.C. 2004: Indirect effects of marine reserve protection on New Zealand's rocky coastal marine communities. *DOC Science Internal Series 192*. Department of Conservation, Wellington. 48 p.

1. Introduction

Most of the world's fish stocks are being over-exploited (Botsford et al. 1997; Pauly et al. 1998). No-take marine reserves are an important conservation management tool, as they protect natural populations from fishing, and they are increasingly used as a means of determining the potential impact of fishing on marine ecosystems (Sala et al. 1998; Tegner & Dayton 2000). It has been widely shown that fished species recover following marine reserve protection (Bennett & Attwood 1991; Russ & Alcala 1996; Edgar & Barrett 1999; Kelly et al. 2000; McClanahan 2000; Willis et al. 2003), although the indirect effects on lower trophic levels are poorly understood. In some reef systems, the re-establishment of previously fished predator populations in marine reserves has been shown to have cascading effects at the ecosystem level (McClanahan & Shafir 1990; Sala et al. 1998; Babcock et al. 1999; McClanahan et al. 1999; Shears & Babcock 2002). This not only highlights the impact humans have had on marine systems at multi-trophic levels, but also provides important ecological information on the role of predators in controlling some marine systems.

The role of predators in structuring temperate reef kelp communities has been a focal point of subtidal ecology and has received much debate (Chapman & Johnson 1990; Elnor & Vadas 1990; Foster 1990). The removal of top-level predators through harvesting by humans has been linked to increases in sea urchin numbers and an expansion of sea urchin-grazed habitats in many systems (Wharton & Mann 1981; Estes & Duggins 1995; Vadas & Steneck 1995; Sala et al. 1998; Babcock et al. 1999). Both the quality of empirical evidence and the generality of this trophic cascade have, however, been sources of contention (Foster & Schiel 1988; Scheibling 1996). Whereas the top-down role of otters in Alaska is the most unequivocal example (Estes & Duggins 1995), Foster & Schiel (1988) found that, within the historical range of otters in California, such otter-kelp interactions were only present at a small number of sites. Instead, kelp communities exhibited a dynamic range of composition that appeared to be driven by a complex of interacting physical and biological factors. Furthermore, Laur et al. (1988) found that the indirect effect of otter foraging varied depending on the physical setting of particular sites, as some reefs were more vulnerable to overgrazing by sea urchins than others. It has been suggested that the importance of biotic interactions varies across environmental gradients (Menge & Sutherland 1987), and therefore trophic cascade effects are also likely to vary. Few studies have examined the generality of such cascades across regions, and in particular how they are likely to change across environmental gradients, e.g. from sheltered to exposed locations.

Marine reserves provide a valuable tool in examining the occurrence of trophic cascades and their generality across regions (Grace 1983; Cole 1993; Walker 1999; Shears & Babcock 2004). To date, most marine reserve studies have investigated the indirect effects of fishing and trophic cascades through comparisons of benthic communities between protected and unprotected areas (McClanahan & Shafir 1990; McClanahan 1994; Sala & Zabala 1996; Edgar & Barrett 1997, 1999; Cole & Keuskamp 1998; Babcock et al. 1999; McClanahan et al. 1999; McClanahan & Arthur 2001). This methodology relies on the

assumption that the only systematic difference between the reserve and non-reserve areas is fishing intensity, and that sufficient replication of sites will reduce the likelihood of concluding that chance environmental effects are actually a result of protection from fishing. However, because reserve and 'control/reference' sites are never in practice drawn randomly from the same pool, it is possible that putative 'reserve effects' could be due to a tendency to place reserves in unrepresentative areas, rather than to the effects of protection from fishing (Stewart-Oaten & Bence 2001). One way to get around this problem is to measure potentially confounding environmental variables and factor them out of statistical comparisons between reserve and control sites. On only a few occasions has the effect of physical variables been measured in explaining the variation between reserve and non-reserve sites (McClanahan 1994; McClanahan & Arthur 2001). In most cases, studies have instead selected comparable non-reserve or 'control' sites based on visual or subjective estimates. Consequently, differences in environmental variables or other causal processes not directly related to protection are likely to confound the ability to detect potential effects of fishing or trophic cascades between reserve and non-reserve sites.

Marine reserves are a fairly new tool for investigating trophic cascades in temperate reef kelp communities. In most cases there is little evidence for indirect effects of fishing on kelp communities (e.g. Edgar & Barrett 1999). However, research carried out in two northeastern New Zealand marine reserves, the Leigh Marine Reserve (Cape Rodney to Okakari Point) and Tawharanui Marine Park, has provided strong evidence for a trophic cascade (Babcock et al. 1999; Shears & Babcock 2002). Both of these reserves support high abundances of previously fished species (Cole et al. 1990; MacDiarmid & Breen 1993; Kelly et al. 2000; Willis et al. 2003). Current densities of legal-size snapper, *Pagrus auratus*, are between nine and 16 times higher within both of these reserves than outside them (Willis et al. 2003). Spiny lobster, *Jasus edwardsii*, are also larger and more abundant (Kelly et al. 2000). Both snapper and spiny lobster are important predators of the common sea urchin *E. chloroticus*, and the chance of predation is seven times higher in these reserves than outside them (Shears & Babcock 2002). As a result, sea urchin densities are much lower within both of these reserves and the extent of this sea urchin-grazed zone (termed 'urchin barrens') is less than outside (Shears & Babcock 2002, 2003). This is supported by long-term data in the Leigh Reserve, which shows a decline in urchin barrens and increase in kelp habitats (Babcock et al. 1999; Shears & Babcock 2003). These indirect effects of fishing would not have been detected, and may in fact have been undetectable, without the presence of these reserves. However, the generality of this trophic cascade and its relevance to other areas in New Zealand, or even to other areas in northeastern New Zealand, is unknown.

The organisation of subtidal reef communities in northeastern New Zealand changes across environmental gradients (Grace 1983; Cole 1993; Walker 1999; Shears & Babcock 2004). The communities of moderately exposed reefs such as Leigh and Tawharanui are characterised by a shallow fucal zone (0-3 m) and deeper kelp forests (> 8 m) dominated by *Ecklonia radiata* (Choat & Schiel 1982). Intermediate depths are maintained relatively devoid of large macroalgae by the grazing activities of *E. chloroticus*, resulting in a bimodal depth

distribution in macroalgal biomass. With increasing exposure the vertical extent of urchin barrens increases, whereas at sheltered locations (e.g. Long Bay) urchin barrens do not occur (Shears & Babcock 2004). This variation in benthic communities across wave exposure gradients also occurs over smaller spatial scales (within locations, e.g. Hahei, Cape Karikari) (Shears & Babcock 2004). Therefore, the occurrence of trophic cascades is likely to vary among reefs in northeastern New Zealand depending on the environmental conditions. Furthermore, this environmental variability has the potential to confound the detection of trophic cascades when comparing reserve and non-reserve sites. In many other parts of New Zealand, sea urchins do not appear to have an important role in structuring algal communities (Schiel 1990; Schiel & Hickford 2001), and therefore the predator-sea urchin-kelp trophic cascades are likely to be manifested differently among regions.

The generality of these trophic cascade effects were investigated by comparing a number of no-take marine reserves throughout New Zealand, all of which included extensive areas of subtidal reef (Table 1). Although these reserves have been protected for varying lengths of time (Table 1), it has generally been shown that previously harvested predator species such as snapper, blue cod, and spiny lobster are larger and/or more abundant than in adjacent unprotected areas (Cole et al. 2000; Kelly et al. 2000; Davidson 2001; Davidson et al. unpubl. 2002; Ward unpubl. 2002; Babcock 2003; Denny et al. 2003, 2004; Willis et al. 2003). Therefore, there is the potential for reserve protection to have flow-on effects on benthic communities at other locations, similar to those seen at Leigh and Tawharanui.

1.1 OBJECTIVES

The main objectives of this study were to:

- Determine whether trophic cascade effects are apparent at existing marine reserves in New Zealand, by comparing subtidal reef communities between sites inside and outside each reserve.
- Investigate how these effects change along environmental gradients and assess the importance of environmental factors in explaining differences between reserve and non-reserve sites.
- Identify other potential impacts of reserve protection on benthic communities.
- Develop hypotheses as to the generality of the kelp-urchin-predator trophic cascade to New Zealand's shallow subtidal reef communities.

These objectives were examined by conducting spatial comparisons of benthic communities between thirteen marine reserves throughout New Zealand and their associated unprotected areas (Table 1). In particular, comparisons of the extent of sea urchin-grazed habitat, the density and population structure of sea urchins and other grazers, algal communities, and environmental variables were made between reserve and non-reserve sites. In most cases, pre-reserve data on the benthic communities within New Zealand's reserves are lacking and it is not possible to document long-term changes. Descriptions of the reef communities for each location are given in Shears & Babcock (2004).

TABLE 1. SAMPLING LOCATIONS, MARINE RESERVES, AND SAMPLING INFORMATION. SEE APPENDIX 1 FOR SITE POSITIONS AND DETAILS.

LOCATION	MARINE RESERVE	SITES (reserve, non-reserve)	SAMPLING DATES
Leigh	Cape Rodney to Okakari Point (1975, 518 ha)	15 (7, 8)	12 Mar - 1 Apr 1999
Tawharanui	Tawharanui Marine Park (1982, 350 ha) ^a	10 (5, 5)	19 Apr - 3 May 1999
Long Bay	Long Bay-Okura (1995, 980 ha)	10 (5, 5)	12-15 Apr 1999
Hahei	Te Whanganui A Hei (Hahei) (1993, 840 ha)	10(5, 5)	10-14 May 1999
Poor Knights -Mokohinau Is	Poor Knights Is (1998 ^b , 2410 ha)	18 (9, 9)	1-11 June 1999
Tuhua	Mayor I. (Tuhua) (1993, 1060 ha)	8 (4, 4)	15-18 Mar 2000
Gisborne	Te Tapuwae o Rongokako (1999, 2450 ha)	4 (2, 2)	16-17 Jan 2002
New Plymouth	Sugarloaf I. (1986) ^a	6 (2, 4)	18-20 Dec 2000
Kapiti I.	Kapiti I. (1992, 2167 ha)	6 (3, 3)	6-10 Dec 2000
Queen Charlotte Sound	Long I. (1993, 619 ha)	12 (6, 6)	16-22 Nov 1999
Abel Tasman	Tonga I. (1993, 1835 ha)	10 (5, 5)	30 Nov - 4 Dec 1999
Banks Peninsula	Flea Bay (Pohatu) (1999, 218 ha)	5 (5, 0)	23-25 Feb 2000
Doubtful Sound	Te Awaatu Channel (The Gut) (1993, 93 ha)	7 (1, 6)	21-22 Jan 2000

^a Tawharanui Marine Park and Sugarloaf Is Marine Park are administered by Ministry of Fisheries, all other marine reserves are administered by The Department of Conservation under the Marine Reserves Act 1971.

^b The Poor Knights Is have been completely no-take since 1998; prior to this the islands had been partially no-take (restricted line fishing was allowed), with two small completely no-take areas, since 1981.

2. Methods

Shallow subtidal reef communities were quantified at 121 sites within 13 locations throughout New Zealand where marine reserves occurred (Fig. 1). Replicate sites were sampled in both reserve and non-reserve areas within each location (Table 1), except at Flea Bay, where adverse weather conditions meant no non-reserve sites could be sampled, and also in Doubtful Sound, where only one site was sampled in the small Te Awaatu Channel marine reserve. Subsequently, these two locations were excluded from formal analyses. The Poor Knights Islands are completely surrounded by a no-take reserve, so the Mokohinau Islands, being the closest offshore island group, were designated as the paired unprotected reference location (MKI/PKI hereafter). Both of these island groups are situated in clear oceanic water and are influenced by the East Auckland Current (Heath 1985). Sites with moderately sloping reefs and similar topographic complexity were preferentially selected for the purpose of standardising comparisons. A photograph of the intertidal rock formations was taken at each site to enable exact relocation for future sampling. Reef communities at each site were sampled to a maximum depth of 12 m, using a line-transect and a series of depth-stratified quadrats (1 m²) within four given depth ranges. A number of physical variables were also measured in order to characterise the environmental conditions at each site.

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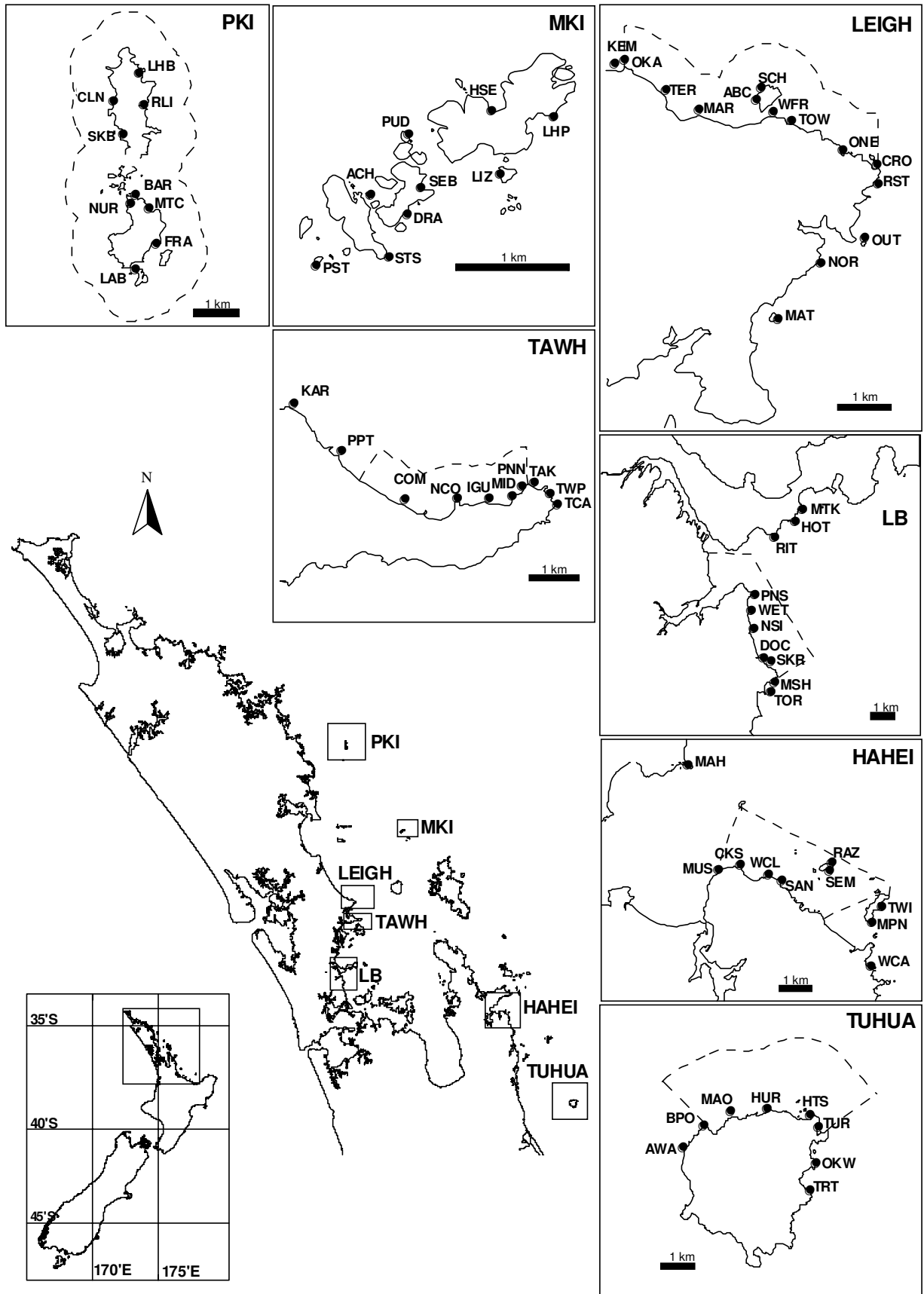


Figure 1A. Northeastern New Zealand marine sampling locations (PKI, Poor Knights Islands; MKI, Mokohinau Islands; TAWH, Tawharanui; LB, Long Bay). Note: PKI and MKI are treated as a paired reserve-non-reserve location.

See Appendix 1 for site names and details.

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 abundance and size structure of macroalgae and large mobile macro-invertebrates were quantified at each site by sampling five 1 m² quadrats in each of four depth ranges (< 2 m, 4–6 m, 7–9 m, and > 10 m). Depths were corrected to MLWS; when available depths were less than 10 m, the deepest strata were omitted. Quadrats were positioned haphazardly, adjacent to the transect line in the desired depth range. The distance along the transect was recorded to ensure that future sampling could be carried out in the same general area. Within each quadrat, all mobile macro-invertebrates and macroalgae were measured and counted. For *E. chloroticus*, the test diameter of each sea urchin was measured in 5 mm increments and its behaviour (cryptic or exposed) was recorded. The largest shell dimension (width or length) of gastropods was measured, the actual measurement depending on species shell morphology (i.e. shell height for *Cantharidus purpureus*, shell width for *Turbo smaragdus*, *Trochus viridis*, and *Cookia sulcata*). The total lengths of *Haliotis* species, limpets (*Cellana stellifera*), and chitons were also measured. The total lengths of large macroalgae were measured to the nearest 5 cm. The primary (substratum) percentage cover of foliose algae, turfing algae, encrusting algal species, encrusting invertebrates, and sediment were also recorded in each quadrat (1 m²) using a visual technique. Quadrats were divided into quarters to assist in estimating covers of dominant forms, and the covers of minor forms were estimated on the basis that a 10 × 10 cm area equates to 1% cover. This technique was considered to be the most suitable, as it is efficient and ensures that the covers of all forms are recorded, unlike point-intercept methods (Benedetti-Cecchi et al. 1996). Furthermore, the same two experienced divers carried out 89% of the quadrat sampling in order to minimise inter-observer variability.

Estimates of the following environmental variables were also made at each site: wave exposure, turbidity (secchi depth), sedimentation, overall reef slope, and maximum depth. Wave exposure was estimated using an index of potential fetch consistent with Thomas (1986). The index was calculated by summing the potential fetch for each 10 degree sector of the compass rose. For open sectors of water, the radial distance was arbitrarily set to be 300 km. Turbidity was measured using a standard 25 cm diameter black and white secchi disc (Larson & Buktenica 1998). The reading was taken as the depth (m) of descending disappearance and ascending reappearance. Sedimentation at each site was estimated using the percentage cover of sediment on the substratum as recorded during depth-stratified quadrat sampling. The overall reef slope for each site was calculated as the total transect distance divided by the maximum depth.

2.2 STATISTICAL ANALYSIS

2.2.1 Extent of urchin barrens

The proportion of urchin barrens habitat at each site was analysed using a generalised linear mixed model with fixed factors Location and Status (Reserve and Non-reserve). As only one transect was sampled at each site, within-site

variability was not factored into the analysis. 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).

2.2.2 Sea urchin density

Patterns in the density of exposed sea urchins among locations, and among reserve and non-reserve sites were investigated. Only exposed sea urchins were analysed, as these individuals typically represent the adult population that are responsible for maintaining the urchin barrens habitat (Andrew & Choat 1982; Shears & Babcock 2002). The count data were modelled using a Poisson distribution employing the GLMMIX macro in SAS. The log-linear model was back-fitted using maximum likelihood with fixed effects Status (Reserve and non-reserve) and Depth, and the random factor Site(Status). Depth strata in which *E. chloroticus* were rare, or absent, were excluded from analyses. Separate analyses were carried out for each location. Ratios of density between reserve and non-reserve sites were calculated from the model along with 95% confidence limits (confidence limits are asymmetrical as they are calculated on the log-scale). The same procedure was used to test for differences in the abundance of herbivorous gastropod species between reserve and non-reserve sites for each location.

2.2.3 Algal community structure

Densities and lengths of algae were converted to biomasses using species-specific relationships of length-weight or percentage cover-weight (see Appendix 2). Algal species were grouped into 19 groups (listed in Appendix 2) for analysis of patterns in algal community structure. These groups include the dominant macroalgal species, and also groups of species, that were considered to be structurally dominant at the locations examined.

Patterns in algal community structure among all 121 sites and their relationships with environmental variables were investigated using principal coordinates analysis and multivariate multiple regression. The computer program, DISTLM (Anderson 2002), was used to test the multivariate null hypothesis that there is no relationship between algal communities and the matrix of environmental variables. The algal groups, environmental variables, and reserve status, were also correlated with principal coordinate axes 1 and 2 to give an indication of their overall relationship with algal communities among sites and locations. Analysis was carried out on fourth-root-transformed algal biomass data for each site, with the following environmental variables: wind fetch, turbidity, sediment cover, reef slope, maximum depth, and exposed *E. chloroticus* density. Sea urchins were treated as an environmental variable in this analysis as they are an important component in structuring algal communities.

Differences in algal communities between reserve and non-reserve sites, for each depth within each location, were tested using non-parametric multivariate analysis of variance (NP-MANOVA) (Anderson 2001). In all cases data were transformed to the fourth-root, analysis was based on Bray-Curtis dissimilarities, and the effects of Status and Site(Status) were tested. For depths within

locations, where the number of sites between reserve and non-reserve sites were uneven, the computer program DISTLM was used. This program calculates a non-parametric test for multivariate multiple regression for any linear model, in this case, codes for the unbalanced ANOVA design with factors Status and Site(Status).

To test the importance of environmental variables in explaining the observed patterns in algal communities, between sites within locations, multiple regression (DISTLM) was used. Analyses were carried out separately for each depth within each location on the algal data at the quadrat level. The data were transformed to the fourth-root and a Bray-Curtis similarity measure was used. Where a significant difference between reserve and non-reserve sites was found for depths within locations (from NP-MANOVA), the effect of status was then tested by setting the environmental variables as co-variables.

2.2.4 Macrolgal productivity

Reserve-related differences in total macroalgal biomass and primary productivity were tested for locations where differences were found between algal communities at reserve and non-reserve sites, despite the environmental variability. Maximum photosynthetic rates ($\mu\text{mol O}_2 \text{ h}^{-1} \text{ m}^{-2}$) were used as a proxy for productivity based on the standing stock (dry-weight) of macroalgal communities. The maximum photosynthetic rates ($\mu\text{mol O}_2 \text{ h}^{-1} \text{ gDW}^{-1}$, Appendix 3) were calculated in the laboratory for species within each of the algal groups used in the above analyses, following the procedure of Taylor (1998). The biomass (dry-weight) of algal species or groups was then converted to estimates of maximum photosynthesis for each quadrat. Differences in both biomass and productivity were tested between reserve and non-reserve sites, and with depth, using GLMMIX (as for *E. chloroticus* density).

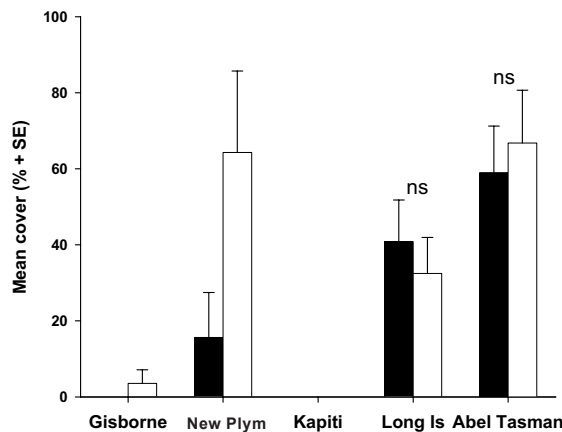
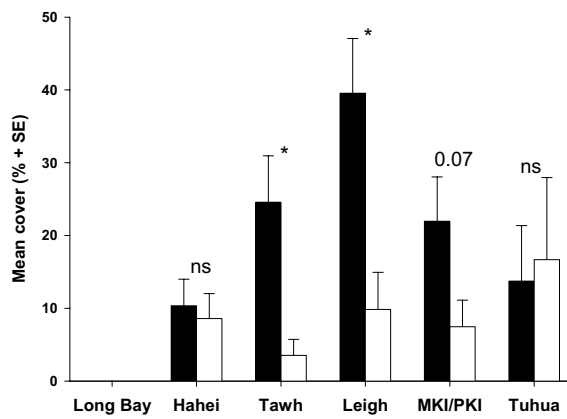
3. Results

3.1 EXTENT OF URCHIN BARRENS HABITAT

The urchin barrens habitat occurred at all northeastern New Zealand locations sampled except for the sheltered reefs at Long Bay (Fig. 2(a)). Consequently, reserve and non-reserve sites at Long Bay were removed from further analysis. Overall, there was no difference in the extent of urchin barrens among the other northeastern locations ($F_{4,55} = 1.71$, $p = 0.161$), but the proportion of urchin barrens did vary with reserve status ($F_{1,55} = 12.69$, $p < 0.001$). Paired comparisons indicated that the cover of urchin barrens was significantly higher at non-reserve sites for Leigh ($F_{1,13} = 7.65$, $p = 0.016$) and Tawharanui ($F_{1,8} = 7.61$, $p = 0.025$), where it covered between 20% and 40% of the reef sampled. At reserve sites in these locations, urchin barrens only covered between 5% and 10% of the reef (Fig. 2), and macroalgal habitats dominated. There was no difference in the extent of urchin barrens between reserve and non-reserve sites at Hahei ($F_{1,8} = 0.12$, $p = 0.735$) and Tuhua ($F_{1,6} = 0.05$,

Figure 2. The percentage cover of urchin barrens habitat between reserve (open bars) and non-reserve (shaded bars) sites for northeastern and other locations. * $P < 0.05$.

Tawh = Tawharanui,
MKI/PKI = Mokohinau/
Poor Knights Is.



$p = 0.835$). Sites at the Mokohinau Islands tended to have a higher cover of urchin barrens than those at the Poor Knights (mean cover c. 2.5 times higher), but this was not significant ($F_{1,16} = 3.75$, $p = 0.071$), possibly due to lack of replication of transects at the site-level.

At other locations around New Zealand, such differences between reserve and non-reserve sites were not apparent (Fig. 2). At New Plymouth, however, urchin barrens appeared more extensive inside the small no-take area relative to the other sites examined. However, this could not be statistically tested as only two sites were sampled in the reserve. At Gisborne and Kapiti I., the barrens habitat was rare at both reserve and non-reserve

sites. In contrast, at both Long I. and Abel Tasman sites, urchin barrens were extensive inside and outside the reserves. The urchin barrens habitat was not recorded at Banks Peninsula, but occurred in a narrow band (3–5 m) at the site in the Te Awaatu marine reserve in Doubtful Sound and also at some of the non-reserve sites in Doubtful Sound.

3.2 SEA URCHIN DENSITY

Evechinus chloroticus was the dominant sea urchin, and in most cases the only sea urchin species, recorded at the locations studied. Among the northeastern New Zealand locations sampled, densities of exposed *E. chloroticus* were highly variable with depth, and between reserve and non-reserve sites (Table 2, Fig. 3). On the shallow sheltered reefs of Long Bay, sea urchins only occurred at very low numbers. For the other locations, clear depth-related patterns in sea urchin abundance were apparent. At coastal locations, sea urchins were generally concentrated in the 4–6 m depth range, while at offshore islands, urchins were abundant at all depth ranges sampled. In general, densities of exposed sea urchins were lower at marine reserve sites (Table 2), but the effect of marine reserve status appeared to differ among locations (interaction between Location and Status, $p = 0.06$). Analysis of sea urchin densities for individual locations found a significant effect of reserve status for Leigh,

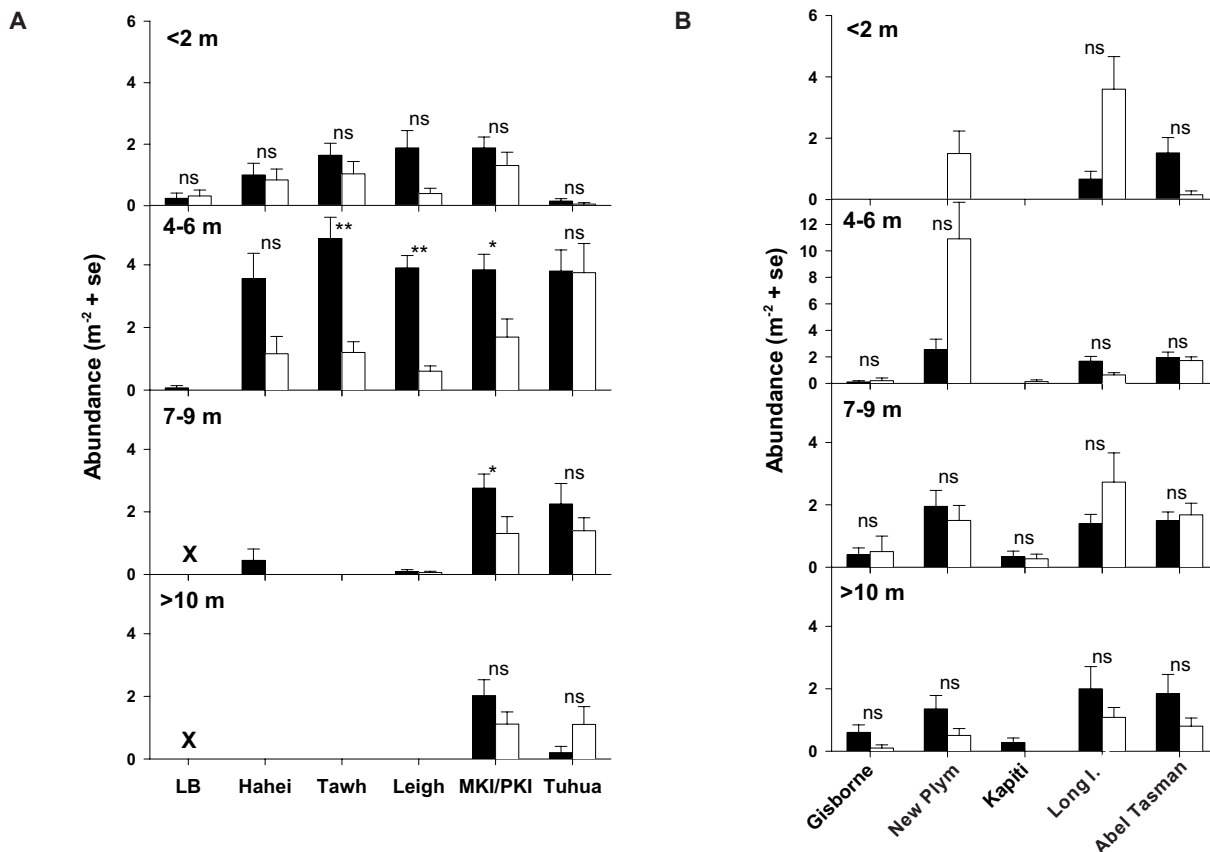


Figure 3. Mean density of exposed *Evechinus chloroticus*, for non-reserve sites (shaded bars) and reserve sites (open bars), at (A) northeastern and (B) other New Zealand locations. * $P < 0.05$, ** $P < 0.01$. LB = Long Bay, Tawh = Tawharanui, MKI/PKI = Mokohinau/Poor Knights Is.

Tawharanui and Mokohinau/Poor Knights Is (MKI/PKI) (Table 2). At Leigh and Tawharanui, exposed sea urchins were 6.2 times (upper and lower confidence limits, $CL_{95} = 2.7, 14.3$) and 2.9 times ($CL_{95} = 1.6, 5.1$) more abundant at non-reserve sites at shallow depths (< 2 m and 4–6 m), while at MKI/PKI, exposed sea urchins were 2.1 times ($CL_{95} = 1.2, 3.5$) times more abundant at non-reserve sites across all depths. There was no difference in exposed sea urchin abundance between reserve and non-reserve sites at Long Bay, Hahei, or Tuhua (Table 2). While reserve sites at Hahei tended to have a higher density of exposed *E. chloroticus* in the 4–6 m depth stratum, compared to non-reserve sites, this was not significant ($F_{1,8} = 3.47, p = 0.100$). However, this non-significant result was strongly influenced by one quadrat in the Hahei reserve, in which 12 exposed sea urchins were recorded.

At the other locations sampled throughout New Zealand, there were no overall differences in the abundance of exposed sea urchins associated with reserve status (Fig. 3, Table 2). *E. chloroticus* was generally rare at Gisborne and Kapiti I. and there were no clear patterns with depth or between reserve and non-reserve sites. At New Plymouth, exposed sea urchin density varied significantly with depth, and this effect differed with reserve status. Although not significant, the reserve sites tended to have higher densities in shallow water. For the two South Island locations, Abel Tasman and Long I., there was also a significant status \times depth interaction, but no clear differences between reserve and non-reserve sites (Fig. 2).

TABLE 2. MIXED MODEL ANALYSIS ON EXPOSED *EVECHINUS CHLOROTICUS* FROM QUADRAT SAMPLING AT RESERVE AND NON-RESERVE SITES.

Model back-fitted by removing non-significant interaction terms. Analysis excludes depth strata where urchins were absent or very rare. * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

FIXED EFFECTS						COVARIANCE PARAMETER ESTIMATE
(a) Northeastern locations	Location	Status	Depth	Location•Status	Location•Depth	Site (Status)
All locations (all depths)	$F_{5,60} = 2.51^*$	$F_{1,60} = 8.89^{**}$	$F_{3,834} = 22.17^{***}$	$F_{5,60} = 2.25^{0.06}$	$F_{6,834} = 2.62^*$	0.19**
		Status	Depth	Status•Depth		Site (Status)
Leigh (excl. 7-9, > 10 m)		$F_{1,13} = 18.13^{***}$	$F_{1,134} = 12.02^{***}$	ns		0.36
Tawharanui (excl. 7-9, > 10 m)		$F_{1,8} = 13.48^{**}$	$F_{1,89} = 10.26^{**}$	ns		0.03
Long Bay (all depths < 2, 4-6 m)		$F_{1,9} = 0.02$	$F_{1,63} = 2.19$	ns		1.17
Hahei (excl. 7-9, > 10 m)		$F_{1,8} = 3.23$	$F_{1,89} = 7.64^{**}$	ns		0.23
MKI/PKI (all depths)		$F_{1,16} = 7.52^*$	$F_{3,334} = 2.83^*$	ns		0.18
Tuhua (all depths)		$F_{1,6} = 0.01$	$F_{3,149} = 13.27^{***}$	ns		0.17
(b) Other locations						
Gisborne (excl. <2 m)		$F_{1,2} = 0.14$	$F_{2,49} = 1.18$	ns		1.77
New Plymouth (excl. <2 m)		$F_{1,4} = 0.10$	$F_{2,80} = 18.90^{***}$	$F_{2,80} = 9.41^{***}$		1.14
Long I. (all depths)		$F_{1,10} = 0.10$	$F_{3,217} = 1.40$	$F_{3,217} = 6.43^{***}$		0.3911 ^{0.05}
Abel Tasman (all depths)		$F_{1,8} = 4.50$	$F_{3,184} = 3.84^*$	$F_{3,184} = 3.24^*$		0.19

3.3 SEA URCHIN POPULATION SIZE-STRUCTURE

For northeastern New Zealand locations, the population size structures of *E. chloroticus* (Fig. 4) varied significantly between reserve and non-reserve sites at Leigh, Tawharanui and MKI/PKI (Pair-wise Kolmogorov-Smirnov tests (K-S), $(d_{\max})_{0.05,20,100} > 12$, $p < 0.05$). The modal size-class of adult exposed sea urchins was generally larger at reserve sites, and at Leigh and Tawharanui the populations were more bimodal with a higher proportion of cryptic individuals, compared to non-reserve sites. In contrast, non-reserve sites at MKI/PKI tended to have higher numbers of larger individuals. However, a larger proportion of the adult population at the reserve sites (Poor Knights Is) were cryptic. There was no difference in total sea urchin numbers between Poor Knights and Mokohinau Is ($F_{1,16} = 1.94$, $p = 0.183$). This demonstrated that the difference found in the density of exposed sea urchins (Table 2(a)) is due to differing levels of sea urchin crevice-occupancy between these two island groups. For both Leigh and Tawharanui the effect of status remained significant when total sea urchin numbers were analysed ($F_{1,13} = 12.29$, $p = 0.004$ and $F_{1,8} = 7.96$, $p = 0.023$).

At Hahei and Tuhua there was no difference in sea urchin population structures between reserve and non-reserve sites (K-S $(d_{\max})_{0.05,20,100} < 12$). However, sites at Tuhua had strongly bimodal population structures, with a high proportion of juveniles, compared with Hahei, which had a low proportion of juveniles. The numbers of sea urchins recorded at Long Bay were too low to statistically assess

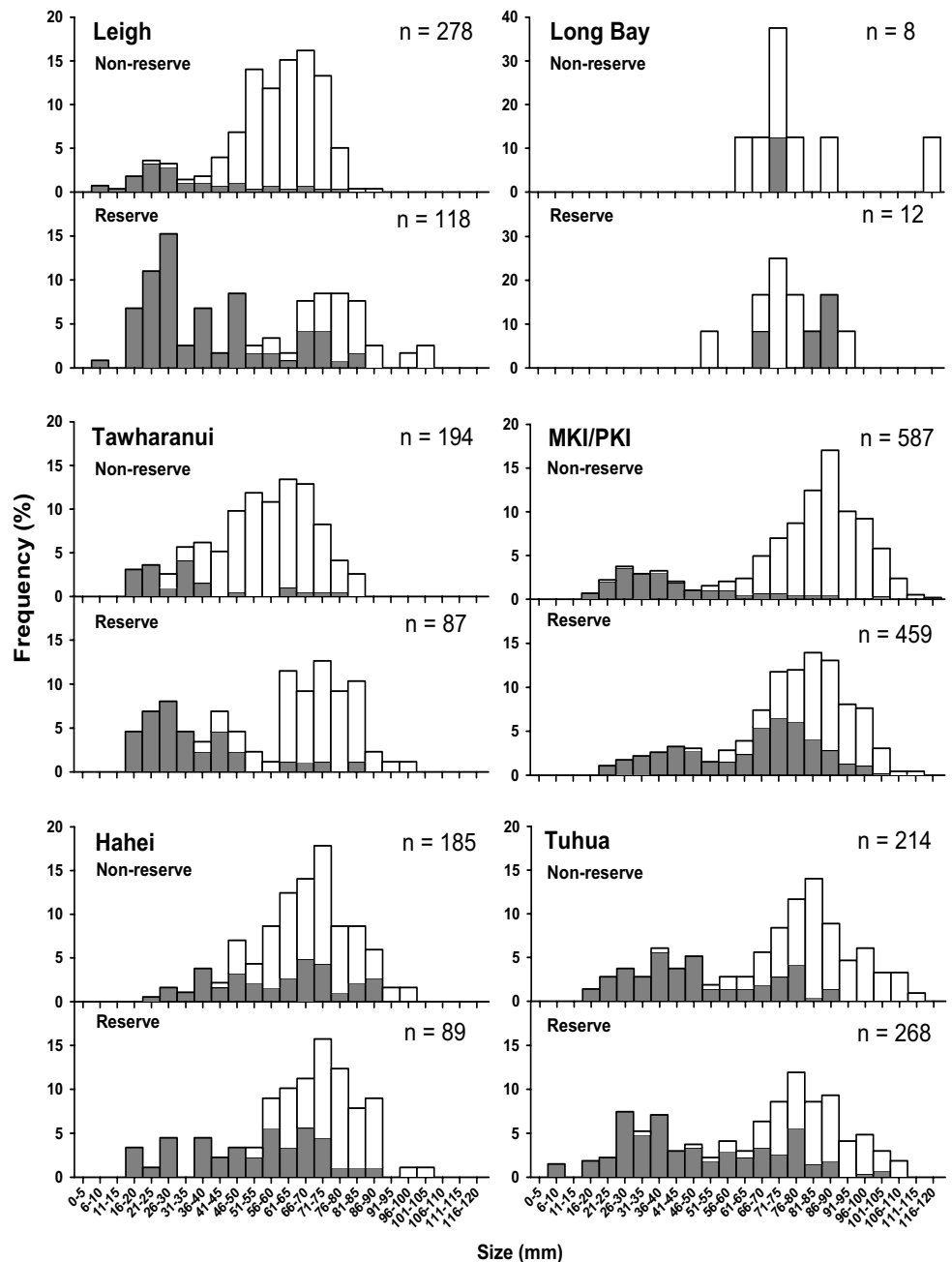


Figure 4. Size frequency distribution of *E. chloroticus* populations for non-reserve sites (left) and reserve sites (right) at northeastern New Zealand locations. Shaded bars indicate the proportion of cryptic individuals, while open bars indicate the proportion of exposed individuals.

possible differences between reserve and non-reserve sites, although they did appear similar (Fig. 4).

Differences in sea urchin population structure between reserve and non-reserve sites were not as apparent at the other locations examined throughout New Zealand (Fig. 4). At Gisborne and Kapiti I., large sea urchins dominated the populations (mean size \pm standard error: 126.9 ± 5.2 mm and 122.7 ± 6.1 mm, respectively) and the densities were too low to test for differences between reserve and non-reserve sites. For New Plymouth, Long I., and Abel Tasman