

CONTEXT-DEPENDENT EFFECTS OF FISHING: VARIATION IN TROPHIC CASCADES ACROSS ENVIRONMENTAL GRADIENTS

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Abstract. Marine reserves provide a large-scale experimental framework to investigate the effects of fishing on food web dynamics and how they vary with environmental context. Because marine reserves promote the recovery of previously fished predators, spatial comparisons between reserve and fished sites are often made to infer such effects; however, alternative explanations for differences between reserve and fished sites are seldom tested (e.g., environmental variation among sites). We investigated the context dependency of the predator–urchin–kelp trophic cascade reported in northeastern New Zealand by comparing the abundance of herbivorous sea urchins (*Evechinus chloroticus*), the extent of urchin barrens habitat, and macroalgal biomass between reserve and fished sites within six locations that span an environmental gradient in wave exposure, sedimentation, and water clarity. At depths where differences in urchin abundance or macroalgal biomass were found between reserve and fished sites we used a model selection approach to identify which variables (fishing or environmental factors) best explained the variation among sites. Differences between reserve and fished sites were not ubiquitous across the locations examined and were highly depth specific. At sheltered locations, urchins were rare and barrens absent at both reserve and fished sites. At moderately exposed coastal locations, actively grazing urchins were most abundant at 4–6 m depth, and significant differences in macroalgal biomass between reserve and fished sites were observed. In contrast, at offshore island locations, urchins extended into deeper water, and differences between reserve and fished sites were found at 4–9 m depth. These differences could only be attributed to trophic cascades associated with protection from fishing in two of the six locations examined. In other cases, variation between reserve and fished sites was equally well explained by differences in sediment or wave exposure among sites. These results suggest that trophic cascades are not ubiquitous to northeastern New Zealand’s subtidal reefs and the importance of sea urchins, and indirectly predators, in controlling macroalgal biomass will vary at local and regional scales in relation to abiotic factors. A better mechanistic understanding of how environmental variation affects the strength of species interactions across multiple spatial scales is needed to predict the ecosystem-level effects of fishing.

Key words: community structure; context dependency; environmental gradients; fishing; kelp forests; macroalgae; marine protected areas; marine reserves; sea urchins; temperate reefs; trophic cascades; wave exposure.

INTRODUCTION

Increasing evidence from marine and terrestrial systems suggests that the depletion of predators can initiate trophic cascades (indirect effects of predators on plants via herbivores) (Paine 1980, Estes and Duggins 1995, Croll et al. 2005, Ripple and Beschta 2006) and alter ecosystem processes (Duggins et al. 1989, Daskalov et al. 2007, Salomon et al. 2008). The magnitude of predator impacts however is well known to vary as a function of biotic and abiotic factors (Hunter and Price 1992, Power 1992) and the strength of species interac-

tions can change dramatically across gradients of environmental stress (Menge and Sutherland 1987). Nevertheless, few studies have investigated how trophic cascades vary as a function of environmental context (Frank et al. 2006, Elmhagen and Rushton 2007, Korpinen et al. 2007). In New Zealand, there is strong evidence that the overfishing of predators can have cascading effects on reef communities (Babcock et al. 1999, Shears and Babcock 2002). Reconciling where and when these effects are likely to occur is a critical issue for ecosystem-based management and marine protection initiatives. We investigated the context-dependent nature of trophic cascades on reefs throughout northeastern New Zealand using an experimental framework provided by six no-take marine reserves located across a large-scale environmental gradient.

Humans have exploited ocean predators for centuries (Jackson et al. 2001) and in kelp forest ecosystems

Manuscript received 25 October 2007; revised 17 March 2008; accepted 26 March 2008; final version received 21 April 2008. Corresponding Editor: P. K. Dayton.

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worldwide the deforestation of macroalgal habitats by sea urchins has been attributed to the depletion of sea urchin predators (Wharton and Mann 1981, Estes and Duggins 1995, Vadas and Steneck 1995, Sala et al. 1998, Babcock et al. 1999). The generality of this assertion has been a source of contention (Foster 1990, Paine 1991), and much of this debate can be boiled down to two factors; lack of controlled experimental manipulations (Elner and Vadas 1990) and high spatial variability observed in system responses (Foster 1990). The occurrence of the predator–urchin–kelp trophic cascade on temperate reefs relies on strong top-down interactions between (1) predators and urchins and (2) urchins and macroalgae. Therefore, in systems where urchins are rare or do not exert strong control on macroalgae, one would expect top-down effects to be weak, and changes in macroalgal biomass would not result from changing predator abundance.

Many environmental factors can potentially decouple the top-down influence of urchins (and indirectly predators) on macroalgae. Environmental stress associated with wave action, sedimentation, and low salinity have been shown to restrict the abundance of sea urchins and/or their grazing efficiency (Witman and Grange 1998, Siddon and Witman 2003, Walker 2007). Furthermore, these environmental factors can vary at many spatial scales, e.g., among regions, sites within regions, and across depths within sites. Oceanographic variability can also influence the delivery of propagules and nutrients to nearshore environments (Menge et al. 2003) and potentially affect the relative importance of urchins in controlling kelp in space and time. For example, recruitment variability can strongly influence the abundance of urchins and therefore their effects on kelp (Watanabe and Harrold 1991, Estes and Duggins 1995), while oceanographic conditions that promote high kelp production can overwhelm the grazing effects of urchins (Harrold and Reed 1985). Therefore, in temperate reef systems, understanding how the abundance of urchins, and their potential effects on macroalgae, varies across environmental gradients at multiple scales is essential in predicting the magnitude of predator impacts.

No-take marine reserves provide large scale experimental manipulations to examine the indirect effects of fishing and the existence of trophic cascades. Previously fished predatory species have been widely shown to recover following no-take marine reserve protection (Edgar and Barrett 1999, Kelly et al. 2000, Willis et al. 2003). Thus, spatial comparisons of benthic communities between protected and fished sites are often used to investigate the indirect effects of predators or fishing (Babcock et al. 1999, Lafferty 2004, Micheli et al. 2005, Guidetti 2006). This methodology relies on the assumption that the most likely systematic difference between reserve and fished areas is fishing intensity and that sufficient numbers of sampling sites will reduce the likelihood that observed differences are a result of environmental variation, rather than the effects of protection from fishing. However, due to a tendency to

place reserves in unrepresentative areas, inherent differences in environmental variables or other causal processes may confound such comparisons.

In northeastern New Zealand, there is a well-described depth-related variation in the trophic effects of urchins on moderately exposed coasts: the shallow reef (0–3 m) is characterized by stands of fucal algae, intermediate depths are maintained relatively devoid of large macroalgae by the grazing activities of the sea urchin *Evechinus chloroticus* (hereafter *Evechinus*), and deeper reef (>8 m) is dominated by *Ecklonia radiata* kelp forests (Choat and Schiel 1982, Shears and Babcock 2004). Experimental removal of urchins from intermediate depths results in a recovery of macroalgal habitats (Andrew and Choat 1982, Shears and Babcock 2002). Within marine reserves, it has been shown that a recovery of previously fished predators (primarily snapper, *Pagrus auratus* and spiny lobster, *Jasus edwardsii*) results in a decline in urchins and recovery of macroalgal habitats at intermediate depths (Babcock et al. 1999, Shears and Babcock 2002). The depth and extent of these zones vary across a large environmental gradient from sheltered inshore coastal reefs where zones are compressed, to exposed offshore island where zones are broader and extend to greater depths (Grace 1983). These patterns suggest that the interaction between urchins and kelp, and therefore the occurrence of trophic cascades, is likely to vary both within and among reefs depending on environmental context.

Studies across multiple marine reserves over a large geographic range provide an opportunity to examine the circumstances which promote or inhibit fishery-induced trophic cascades. In this study, we investigated the context dependency of top-down effects of predators (and indirectly fishing) on subtidal reefs by comparing the extent of urchin barrens, the density of sea urchins and the biomass of macroalgae, in various depth ranges at reserve and fished sites within six locations throughout northeastern New Zealand. These locations span a strong environmental gradient from sheltered reefs with high levels of sedimentation and turbidity, to more exposed open coast and offshore island locations that have lower sedimentation and greater water clarity. Predatory snapper and lobster are heavily targeted by recreational and commercial fishers throughout this region (Annala et al. 2004) and all but one of the reserves examined have higher abundances of snapper and/or spiny lobster relative to adjacent unprotected areas (Table 1, Fig. 1). Our objective was to investigate how fishery-induced trophic cascades vary across environmental gradients at three spatial scales: fine (depth within sites, meters), local (among sites, 1–5 km), and regional (among locations, 10–100 km) scales. To provide a more robust assessment of the effects of fishing in each location, we used a model-selection approach to evaluate the strength of evidence that observed differences were an indirect effect of fishing rather than an effect of environmental variation among sites.

TABLE 1. Sampling locations, no-take marine reserves, and sampling information (see Appendix A for site locations).

Location	Marine reserve	No. sites (reserve, fished)	Sampling dates (this study)
Coastal			
Leigh	Cape Rodney to Okakari Point (established 1975, 518 ha)	15 (7, 8)	12 Mar–1 Apr 1999
Tawharanui	Tawharanui Marine Park (established 1981, 350 ha)†	10 (5, 5)	19 Apr–3 May 1999
Long Bay	Long Bay-Okura (established 1995, 980 ha)	10 (5, 5)	12–15 Apr 1999
Hahei	Whanganui A Hei (Hahei) (established 1993, 840 ha)	10 (5, 5)	10–14 May 1999
Offshore islands			
Poor Knights/ Mokohinau Islands	Poor Knights Islands (established 1998, 2410 ha)‡	18 (9, 9)	1–11 Jun 1999
Tuhua	Mayor (Tuhua) Island (established 1993, 1060 ha)	8 (4, 4)	15–18 Mar 2000

Notes: The survey year and source for spiny lobster (*Jasus edwardsii*) and snapper (*Pagrus auratus*) data presented in Fig. 1 are also given. All lobster and snapper surveys employed the same sampling techniques that are described in Kelly et al. (2000) for lobster and Willis et al. (2003) for snapper.

† Tawharanui Marine Park is administered by the Auckland Regional Council; all other marine reserves are administered by the New Zealand Department of Conservation under the Marine Reserves Act of 1971.

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

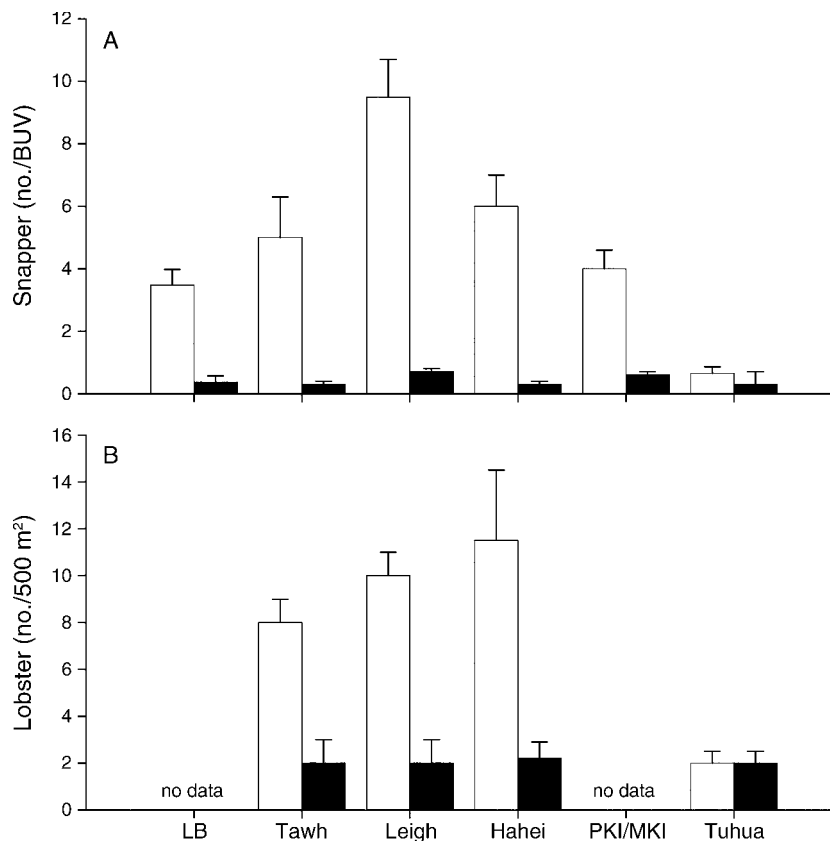


FIG. 1. Predator abundance (mean + SE) at reserve (open bars) and fished (solid bars) sites at each location. (A) Maximum number of legal-sized snapper, *Pagrus auratus*, per 30-min baited underwater video (BUV) deployment (see Willis et al. [2003] for methodological details). (B) Density of legal-sized lobster, *Jasus edwardsii*, from visual transects (see Kelly et al. [2000] for methodological details). Snapper and lobster data are presented for the survey year that most closely corresponds to the sampling dates of the present study (see Table 1 for data source and survey year). Location abbreviations are: LB, Long Bay; Tawh, Tawharanui; PKI/MKI, Poor Knights Islands/Mokohinau Islands.

TABLE 1. Extended.

Lobster surveys	Snapper surveys
2000 (T. Haggitt and S. Kelly, <i>unpublished data</i>)	1999 (Willis et al. 2003)
1996 (Kelly et al. 2000)	1999 (Willis et al. 2003)
No data	2002 (R. Babcock and N. Ward, <i>unpublished data</i>)
1999 (T. Haggitt and S. Kelly, <i>unpublished data</i>)	1999 (Willis et al. 2003)
No data	1999 (Denny et al. 2004)
1996 (Kelly et al. 2000)	2004 (Shears and Usmar 2006)

METHODS

Shallow subtidal reef communities were surveyed at 71 sites within six locations in northeastern New Zealand between March 1999 and March 2000 (Table 1, Appendix A). Four to eight replicate sites were sampled in both reserve and fished areas within each location, and replicate samples were taken within four depth strata at each site. The marine reserves examined all include extensive areas of subtidal reef and the benthic communities at the sites surveyed are described in Shears and Babcock (2004). The inner Hauraki Gulf location (Long Bay) is located near the city of Auckland, experiences high levels of anthropogenic nutrient loading and sedimentation, and supports persistent phytoplankton populations (Zeldis et al. 2004, Salomon et al. 2008). Three locations (Leigh, Tawharanui, and Hahei) were sampled on the moderately exposed open coast, where reefs extend into deeper water, phytoplankton concentrations and sedimentation are generally lower, and water clarity is greater than Long Bay. Two offshore island marine reserves (Poor Knights Islands and Tuhua) were also examined, which are situated in clear oceanic water and are influenced by the oligotrophic East Auckland Current (Zeldis et al. 2004). The Poor Knights Islands are completely surrounded by a no-take reserve, so the nearby Mokohinau Islands were designated as the fished reference location (PKI/MKI hereafter). At all locations, sites with moderately sloping reefs and similar topographic complexity were preferentially selected to standardize comparisons.

Sampling provided a snapshot of the status of benthic communities at each site; however we are confident that the spatial patterns revealed were representative of regional processes rather than short term variability. Seasonal and interannual stability in New Zealand kelp forests is relatively high with the canopy kelp species (*Ecklonia radiata*) persisting year round (Haggitt 2004). In addition, depth-related patterns at key locations are known to have persisted at least since the 1980s (Choat and Schiel 1982). Kelp forest assemblages in northeast New Zealand are relatively simple and facilitate the

occurrence of community-level cascades (Polis et al. 2000), with clear trophic linkages between two key urchin predators (lobsters and snapper), one dominant urchin species, and one dominant canopy-forming kelp species (Shears and Babcock 2002, 2004). Other smaller predators and herbivores are present in the system but were not considered to play a key role in the predator–kelp trophic cascade. Furthermore, there is only a small mainly recreational urchin fishery in this region. These features simplify the interpretation of trends among locations and between fished and reserve sites.

Sampling procedure

The extent of urchin barrens habitat at each site was measured along a line transect. Transects ran perpendicular to the shore on a fixed compass bearing from mean low water spring (MLWS) out to the edge of the reef, or a maximum of 12 m depth, whichever was encountered first. The distance from shore, depth, rock type, slope, and habitat type (Shears and Babcock 2003) were recorded at 5-m intervals along these transects. The proportional cover of urchin barrens habitat was compared between reserve and fished sites. Proportions were calculated as the distance covered by each habitat type from the start of the transect (MLWS) to a depth of 12 m, divided by the transect length.

The abundance and size structure of macroalgal species and sea urchins were quantified at each site by sampling five 1-m² quadrats in each of four depth ranges (<2, 4–6, 7–9, and 10–12 m, corrected to MLWS). The deepest strata were omitted at some sites where reefs were truncated by sand at shallower depths. Quadrats were positioned haphazardly in the desired depth range. Within each quadrat, all *Evechinus* and macroalgae were measured and counted. For *Evechinus*, the test diameter of each urchin was measured to the nearest 5 mm and its behavior (cryptic or exposed) recorded. The length of large brown macroalgal species were measured to the nearest 5 cm, while the percent cover of turfing, encrusting, and foliose algal species was visually estimated (Shears and Babcock 2004).

Environmental variables

Estimates of wave exposure, water clarity, and sediment cover were made at each site to quantify the environmental gradient within and among locations. These particular variables were considered to reflect important factors that may explain variation in urchin and/or algal biomass among sites. To estimate wave exposure at each site we calculated a topographical index of fetch for each site (e.g., Burrows et al 2008) by summing the distance to land for each 10-degree sector of the compass rose. For open sectors of water, the radial distance was arbitrarily set to be 300 km. Average wind speeds were not factored into wave exposure estimates as the prevailing winds in this region are generally offshore (southwesterly) while the open sea direction and dominant swells are from the northeast

(Gorman et al. 2003). There was high concordance between fetch and estimates of wave exposure derived from the New Zealand regional wave hindcast model (Gorman et al. 2003). However, fetch was found to be a greater predictor of biological variation (N. Shears, *unpublished data*) than the modeled estimates, most likely because the model predictions are not as accurate in shallow depths or along highly complex coastlines such as the offshore islands (Gorman et al. 2003). Therefore, we considered fetch to be the best available estimate of local exposure to ambient swell conditions for the shallow coastal sites examined in this study.

Water clarity was measured using a standard 25 cm diameter black and white secchi disc. The reading was taken as the depth (m) of descending disappearance and ascending reappearance. Based on a strong positive relationship between secchi depth (m) and chl *a* (mg/m^3) estimated from satellite data (Salomon et al. 2008; $R^2 = 0.96$, $\ln(\text{secchi depth}) = -0.51 \ln(\text{chl } a) + 2.22$, $n = 31$), this measurement was considered to reflect relative ambient summer time conditions. Sedimentation at each site was estimated using the percent cover of sediment on the substratum from the depth stratified quadrat sampling.

Statistical analysis

All univariate analyses of variance were carried out using generalized linear mixed models (GLZs) fit by residual restricted maximum likelihood (REML) with the GLIMMIX macro in SAS (Littell et al. 1996). Location and status (reserve vs. fished) were treated as fixed factors, while site was treated as a random factor. Differences in environmental variables between locations, and between reserve and fished sites, were first tested to identify any obvious confounding factors. Environmental variables were modeled assuming a normal distribution, although sediment cover (%) data was first arcsine transformed. Only a single measurement of wave exposure and secchi depth were made at each site, so we were unable to test for site-level variation for these variables. The proportion of urchin barrens habitat at each site was also arcsine transformed and analysed using a normal distribution, although within-site variability was not factored into the analysis as only one transect was sampled at each site.

Exposed sea urchin densities were analyzed assuming a Poisson error distribution. Patterns in the density of exposed urchins among locations and among reserve and fished sites were investigated as these individuals typically represent the adult population that are responsible for maintaining the urchin barrens habitat (Shears and Babcock 2002). Depth strata where *Evechinus* were rare or absent were excluded from analyses; otherwise models would not converge. Because the age of reserves varies among locations separate analyses of the effects of status were also carried out for each location and each depth within locations. Ratios of density between reserve and fished sites were calculated

from the model along with 95% confidence limits (confidence limits are asymmetrical as they are calculated on the log-scale).

Macroalgal data were converted to biomasses using length-dry mass or percent-cover-dry mass relationships (Shears and Babcock 2004) to account for the different units used for measuring different growth forms and functional groups (e.g., percent cover or length measurements). Total macroalgal biomass was used instead of biomass or abundance of individual taxa or groups of taxa as it was considered to be the most ecologically relevant metric in terms of investigating community-level trophic cascades (Polis et al. 2000). The same statistical methods used above for urchins were used to test for differences in macroalgal biomass among locations and between reserve and fished sites, although all depths were included in the analysis as macroalgae were recorded across all depth strata at all sites.

Where significant differences were found in the abundance of exposed urchins between reserve and fished sites, a model selection approach was used to determine which combination of environmental factors (wave exposure, water clarity, sediment cover) and/or fishing (status) best predicted the variation among sites. This analysis was carried out separately for each location and only at depths where differences were found, as environmental variables may have differing effects with depth and among locations. We compared model fits for all possible linear combinations of factors and selected the best approximating model with small-sample-bias-corrected Akaike's Information Criterion (AIC_c) standardized to the best fit model to produce ΔAIC_c values (Burnham and Anderson 1998). This allowed us to evaluate the relative strength of evidence for alternative regression models. For example, if a model of urchin density based on fishing status alone outperformed all other models, this would indicate that the observed differences are best predicted by fishing status. In contrast, if models based on environmental variables performed well or better, this provides an alternative explanation for observed differences between fished and reserve sites. The level of empirical support for a model is substantial when $\Delta\text{AIC}_c \leq 2$. We normalized the model likelihoods to a set of positive Akaike weights (w_i) representing the strength of evidence in favor of a given model. The importance of each variable was then determined with variable weights which were calculated by summing the Akaike weights across all models in which that variable was found. The response variable (exposed urchin density) was log transformed and the models were fit assuming normally distributed errors. We report the top five models of each model set (Appendices D and E).

The same procedure was used for each location to quantify the extent to which significant differences in macroalgal biomass among protected and unprotected sites could be attributed to exposed urchin density and the environmental variables listed above. In this case, we

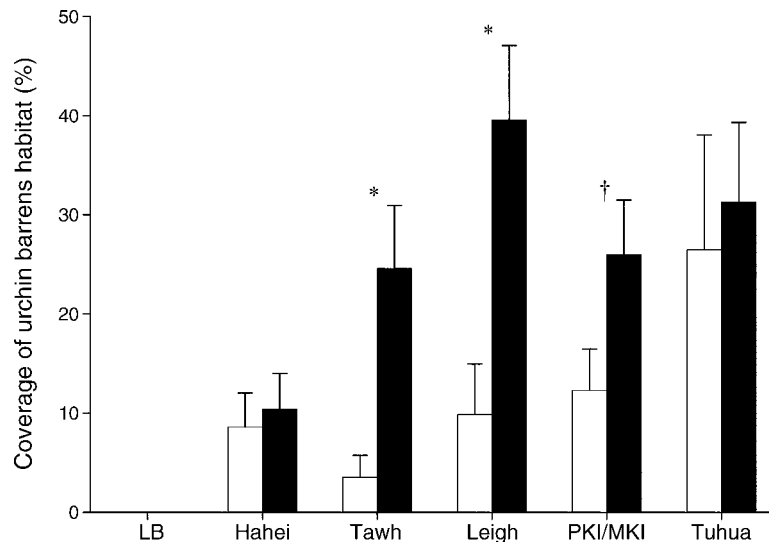


FIG. 2. Coverage (mean + SE) of urchin barrens habitat at reserve (open bars) and fished (solid bars) sites at each location. † $P = 0.07$; * $P < 0.05$.

did not include fishing (status) as a variable, given that the effects of fishing on kelp are manifested through the effects of predators on urchin density, such that fishing status and urchin density would covary.

RESULTS

Environmental variation among sites and locations

There was substantial variation in environmental variables among locations; however, we did not detect an overall difference in environmental variables between reserve and fished sites (status; Appendix B). Wave exposure (wind fetch) was lowest at the inshore location (Long Bay), highest at Tuhua and similar among the remaining locations. Wave exposure did not clearly correlate with the inshore-offshore gradient as the sites at PKI/MKI were spaced around both island groups and subjected to a wide range of wave exposure conditions (Appendix A). However, at Tuhua all sites were located on the exposed northern and eastern sides of the island, which explains the higher wave exposure estimates for this location. Water clarity (Secchi depth) varied consistently across the inshore-offshore gradient and was lowest at Long Bay, high at the offshore island locations, and the remaining coastal locations were intermediate. The cover of sediment was more variable among sites within locations but on average was highest at Long Bay and lowest at the offshore islands. The cover of sediment also increased with depth at all locations (Appendix B). Tests for differences among reserve and fished sites for individual locations revealed no significant differences in environmental variables, although there was some evidence at Hahei that the cover of sediment was higher at reserve sites ($P = 0.073$, Appendix B). Wave exposure also appeared to be

marginally higher at fished sites at Hahei although this was not significant.

Extent of urchin barrens habitat

Urchin barrens habitat was recorded at all locations except Long Bay (Fig. 2). Subsequently, Long Bay sites were not included in further analyses of the extent of barrens. Overall, there was no difference in the extent of urchin barrens among the other 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 higher at fished sites for Leigh ($F_{1,13} = 7.65$, $P = 0.016$) and Tawharanui ($F_{1,8} = 7.61$, $P = 0.025$) where they covered 10–60% of the reef (<10 m depth). At reserve sites in these locations, urchin barrens covered 0–15% of the reef (Fig. 2), and macroalgal habitats dominated (data not presented). Mokohinau Islands sites tended to have a higher cover of urchin barrens than those at the protected Poor Knights (mean cover ~2.5 times higher), although the pattern was less clear ($F_{1,16} = 3.75$, $P = 0.071$). There was no difference in the extent of urchin barrens between reserve and fished sites at Hahei ($F_{1,8} = 0.12$, $P = 0.735$) or Tuhua ($F_{1,6} = 0.05$, $P = 0.835$).

Urchin density

Evechinus chloroticus was the dominant sea urchin, and in most cases the only sea urchin species recorded at the locations studied (Shears and Babcock 2004). Densities of exposed *Evechinus* were highly variable among locations, depth, and varied with reserve status (Table 2, Fig. 3). The effect of depth varied across locations. At Long Bay, urchins only occurred at very low numbers and at shallow depths; however the reefs did not extend beyond 6 m in this location. At the more

TABLE 2. Results from mixed-model analysis on exposed sea urchins, *Evechinus chloroticus*, from quadrat sampling at reserve and fished sites for each location.

Sea urchin location	Fixed effects			
	Location	Status	Depth	Location \times status
All locations (all depths)	$F_{5,60} = 2.51^*$	$F_{1,60} = 8.89^{**}$	$F_{3,834} = 22.17^{***}$	$F_{5,60} = 2.25^\dagger$
Coastal locations (<2 and 4–6 m depth)				
Leigh		$F_{1,13} = 18.13^{***}$	$F_{1,134} = 12.02^{***}$	
Tawharanui		$F_{1,8} = 13.48^{**}$	$F_{1,89} = 10.26^{**}$	
Long Bay		$F_{1,9} = 0.02$	$F_{1,63} = 2.19$	
Hahei		$F_{1,8} = 3.23^{0.10}$	$F_{1,89} = 7.64^{**}$	
Offshore islands (all depths)				
PKI/MKI		$F_{1,16} = 7.52^*$	$F_{3,334} = 2.83^*$	
Tuhua		$F_{1,6} = 0.01$	$F_{3,149} = 13.27^{***}$	

Notes: The model was back-fitted by removing nonsignificant interaction terms. Analysis of coastal locations excludes depth strata where urchins were absent or very rare (7–9 and 10–12 m).

$^\dagger P = 0.06$; $* P < 0.05$; $** P < 0.01$; $*** P < 0.001$; ns, not significant.

exposed coastal locations, urchins were most abundant in the 4–6 m depth range and rare in deeper strata, while at offshore island locations, urchins were abundant across all depths.

Overall, densities of exposed urchins were lower at reserve sites (Table 2), but there was evidence that this affect varied among locations (location \times status, $P = 0.06$). We detected a significant status effect in Leigh, Tawharanui, and PKI/MKI (Table 2). At Leigh and Tawharanui, exposed urchins were 6.2 (95% CL = 2.7, 14.3 [upper and lower confidence limits]) and 2.9 (95% CL = 1.6, 5.1) times more abundant at fished sites at shallow depths (<2 m and 4–6 m), while at PKI/MKI exposed urchins were 2.1 (95% CL = 1.2, 3.5) times more abundant at fished sites across all depths. There was no difference in exposed urchin abundance between reserve and fished sites at Long Bay, Hahei, or Tuhua (Table 2). While reserve sites at Hahei tended to have a higher density of exposed *Evechinus* at 4–6 m, compared to fished sites, this was not significant ($F_{1,8} = 3.47$, $P = 0.08$).

The population size structures of *Evechinus* (Appendix C) varied significantly between reserve and fished sites at Leigh, Tawharanui, and PKI/MKI (pairwise Kolmogorov-Smirnov [K-S] tests, $(d_{\max})_{0.05,20,100} > 12$, $P < 0.05$). The modal size class of adult exposed 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 fished sites. In contrast, fished sites at PKI/MKI tended to have higher numbers of larger individuals. However, a larger proportion of the adult population at the reserve sites (Poor Knights), were cryptic. Interestingly, there was no difference in total urchin numbers between the Poor Knights and the Mokohinau Island's ($F_{1,16} = 1.94$, $P = 0.183$), demonstrating that the difference in density of exposed urchins (Table 2) is due to differing levels of urchin crevice occupancy between these two island groups. At Hahei and Tuhua, there was no difference

in urchin population structures between reserve and fished sites (K-S $(d_{\max})_{0.05,20,100} < 12$).

Macroalgal biomass

Differences in macroalgal biomass between reserve and fished sites (Table 3, Fig. 4) were almost always found at locations and depths where differences in exposed *Evechinus* abundance were identified (Fig. 3). Total macroalgal biomass varied significantly between locations and with depth, and there was a significant interaction between these factors (Fig. 4, Table 3). While there was no overall effect of status, there was a significant interaction between status and location as well as status and depth. There was no effect of status on algal biomass at Long Bay or Tuhua, but there was either a significant status effect or status \times depth interaction, at all of the other locations (Table 3). However, at Leigh and PKI/MKI, differences were also found in the shallowest stratum, and in the 4–6 m stratum at Hahei. At Leigh, Tawharanui, and Hahei, total macroalgal biomass at 4–6 m depth was 2.9 (95% CL = 1.4, 6.1), 3.8 (95% CL = 2.5, 5.7) and 3.3 (95% CL = 1.4, 7.5) times higher at reserve sites compared to fished sites. For PKI/MKI, there was an overall effect of reserve status that was consistent across all depths (Table 3). Overall, algal biomass was 2.0 (CL₉₅ = 1.4, 2.8) times higher at the Poor Knights than at the Mokohinau Islands, although there was no significant difference at 10–12 m depth (Fig. 4).

Environmental drivers of variation between reserve and fished sites

Exposed sea urchins.—At depths of 4–6 m at Leigh and Tawharanui reserve, status alone explained 57% and 69%, respectively, of the variation in exposed urchin density. Models based solely on this factor outperformed all other models. However, at Tawharanui, there was strong evidence ($\Delta AIC_c = 0.21$, $R^2 = 0.83$) that both status and sediment cover governed spatial variation in exposed urchin density (Appendix D). Nonetheless, the

TABLE 2. Extended.

Fixed effects		Covariance parameter estimate
Location × Depth	Status × Depth	Site(Status × Depth)
$F_{6,834} = 2.62^*$		0.19**
	ns	0.36
	ns	0.03
	ns	1.17
	ns	0.23
	ns	0.18
	ns	0.17

importance of reserve status in driving urchin density in Leigh and Tawharanui is also reflected by the large variable weights of this factor (Table 4a). At Hahei, the model best describing the pattern of exposed urchin density at 4–6 m was reserve status, however, this model explained only a small proportion of the variation ($R^2 = 0.35$), its variable weight was low (0.391) and the model based on sediment alone performed nearly as well ($\Delta AIC_c = 1.76$; Appendix D). At 4–6 m in the offshore islands location PKI/MKI, the most parsimonious model explaining urchin density among sites was based on status alone yet there was strong evidence for the model which accounted for both status and wave exposure ($\Delta AIC_c = 0.80$), which also yielded the best overall fit ($R^2 = 0.32$). At greater depths (7–9 m), strong evidence suggests that wave exposure (fetch) was a major determinant of urchin density across sites (variable weight = 0.866; Table 4a). Wave exposure was negatively associated with urchin density at 4–6 m and positively associated at 7–9 m.

Macroalgae.—Exposed urchin density explained 62% of the variation in macroalgal biomass at 4–6 m at sites in Leigh and 71% of the variation at sites in Tawharanui (Appendix E). Accounting for sediment cover only slightly improved fits of the macroalgal biomass model for both locations. Only 41% of the variation in macroalgal biomass at 4–6 m at Hahei was accounted for by exposed urchin density (Appendix E), while sediment cover and wave exposure appeared to have measurable positive and negative associations (Table 4b). At the same depths for PKI/MKI, the model based on exposed urchins ($\Delta AIC_c = 0.00$, $R^2 = 0.54$) was essentially indistinguishable from the model based on both exposed urchins and wave exposure ($\Delta AIC_c = 0.30$, $R^2 = 0.61$) suggesting that adding wave exposure at this depth only slightly improved our predictive power. This was not the case at greater depths (7–9 m) where a model considering both wave exposure and exposed urchins was best supported by the data (Appendix E). At shallow depths (<2 m) macroalgal biomass was best explained by wave exposure, and although exposed

urchins were almost as important (Table 4b), in both cases the model fit was low ($R^2 = 0.22$ and 0.19). At Leigh, the best model of macroalgal biomass at depths >2 m included a combination of secchi, sediment, and exposed urchin densities ($R^2 = 0.67$).

DISCUSSION

Strong mechanistic evidence from fished and reserve sites at two moderately exposed coastal locations in northeastern New Zealand (Leigh and Tawharanui) indicate that the removal of predators through fishing has triggered a cascade of indirect effects on shallow reef communities (Babcock et al. 1999, Shears and Babcock 2002, 2003). Here, we show that these trophic cascades are highly context dependent and vary as a function of regional and local-scale environmental gradients. We demonstrate that urchin abundance varies in relation to abiotic factors at multiple spatial scales, and this appears to have clear consequences for benthic macroalgal communities. While spatial comparisons between reserve and fished sites provide a useful means for

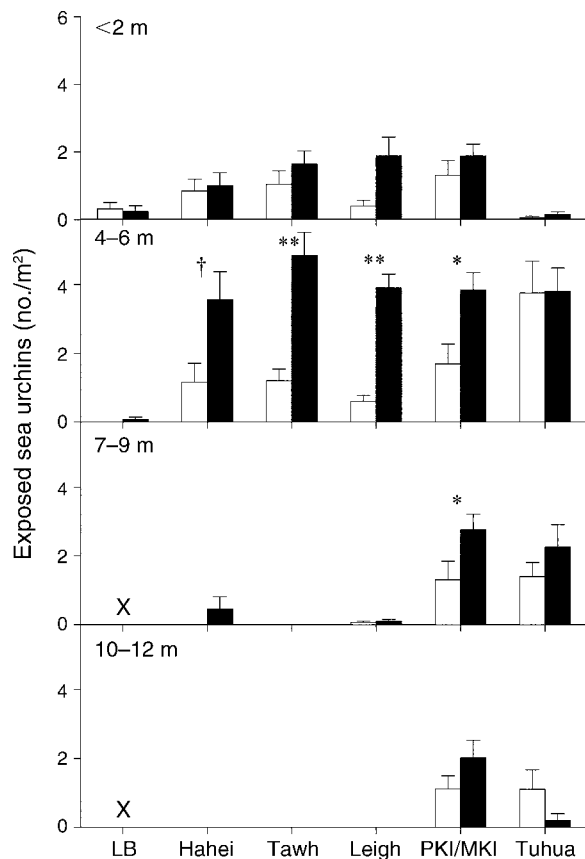


FIG. 3. Density (mean + SE) of exposed sea urchins *Evechinus chloroticus* for reserve (open bars) and fished (solid bars) sites at each location. An “X” indicates that these depths were not sampled, as the reefs are inundated by sand at ~5 m depth at this location.

† $P = 0.08$; * $P < 0.05$; ** $P < 0.01$.

TABLE 3. Results from mixed-model analysis on macroalgal biomass from quadrat sampling at reserve and fished sites.

Sea urchin location	Fixed effects				
	Location	Status	Depth	Location × Status	Location × Depth
All locations	$F_{3,967} = 9.63^{***}$	$F_{1,212} = 2.19$	$F_{3,212} = 24.86^{***}$	$F_{5,967} = 2.99^*$	$F_{13,967} = 3.87^{***}$
Long Bay		$F_{1,13} = 1.17$	$F_{1,13} = 0.42$		
Leigh		$F_{1,47} = 1.92$	$F_{3,47} = 10.76^{***}$		
Tawharanui		$F_{1,28} = 1.78$	$F_{3,28} = 29.55^{***}$		
Hahei		$F_{1,25} = 3.43^{0.07}$	$F_{3,25} = 2.43^{0.09}$		
PKI/MKI		$F_{1,66} = 14.25^{***}$	$F_{3,66} = 3.40^*$		
Tuhua		$F_{1,27} = 0.34$	$F_{3,27} = 9.90^{***}$		

Note: The model was back-fitted by removing nonsignificant interaction terms.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

evaluating the effects of fishing, local-scale environmental factors that potentially modify consumer abundance and efficiency, recruitment rates, and macroalgal productivity must be taken into account if we are to accurately predict the occurrence and magnitude of fishery-induced trophic cascades.

Regional-scale context dependence: variation in trophic cascades among locations

The abundance and depth distribution of exposed sea urchins (Fig. 3), and extent of urchin barrens habitat (Fig. 2), varied predictably among locations across the regional environmental gradient examined. At the sheltered inner Hauraki Gulf location of Long Bay, urchins occurred in low numbers at all sites and urchin barrens were absent. This location experiences high levels of sedimentation which is known to have adverse effects on larval and post-settlement survival of *Evechinus* (Phillips and Shima 2006, Walker 2007). At the more wave-exposed coastal and offshore island locations, exposed urchins were abundant and urchin barrens habitat more extensive (Fig. 2). There were, however, clear regional differences in the depth distribution of urchins among these locations (Fig. 3) that also reflected variation in environmental conditions. At Leigh, Tawharanui, and Hahei, exposed urchins were most abundant in the 4–6 m depth range. This may be in part explained by high water motion at shallow depths (<2 m) that likely restricts the movement and grazing activity of urchins (e.g., Siddon and Witman 2003), while at greater depths (7–9 m and 10–12 m), higher sedimentation associated with reduced water motion may prevent *Evechinus* from both settling and moving into deeper water (Andrew and Choat 1985, Walker 2007). At the offshore island locations, the cover of sediment was reduced in the deeper strata and urchins were found to extend to greater depths compared to coastal locations. While the underlying causal mechanisms are not fully understood and are yet to be tested experimentally, these general patterns provide insights into the nature of areas where urchins can influence macroalgal communities when predator abundances have been reduced by fishing.

Our comparisons of macroalgal biomass between reserve and fished sites among locations across this

environmental gradient were consistent with that expected based on the regional pattern in urchin abundance. We found no difference in macroalgal biomass between reserve and fished sites at Long Bay, where urchins were rare. In contrast, at more exposed coastal locations (Leigh, Tawharanui, and Hahei), reduced exposed urchin density and greater macroalgal biomass at reserve sites were detected, but only in 4–6 m depth. Similar differences were also found between the Poor Knights Islands Marine Reserve and the Mokohi-

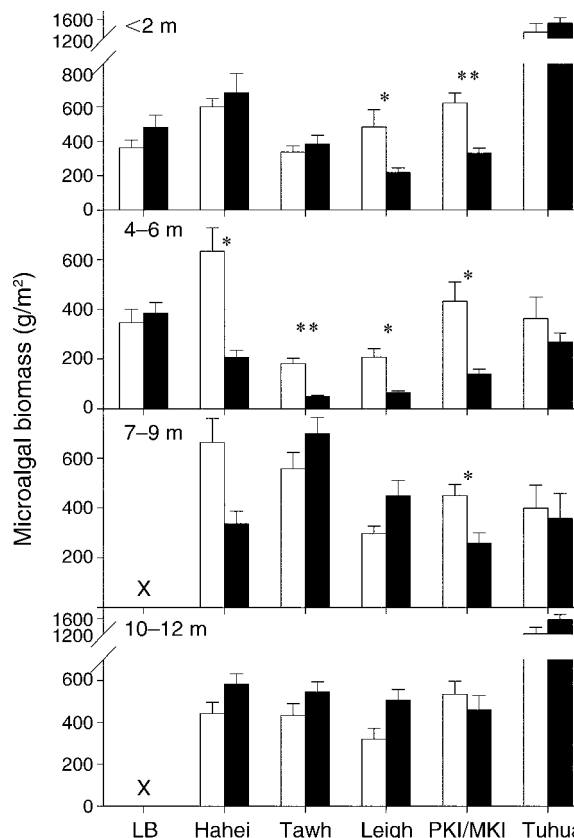


FIG. 4. Macroalgal biomass (mean + SE) at reserve (open bars) and fished (solid bars) sites at each location. An “X” indicates that these depths were not sampled, as the reefs are inundated by sand at ~5 m depth at this location.

* $P < 0.05$; ** $P < 0.01$.

TABLE 3. Extended.

Fixed effects	Covariance parameter estimate
Status × Depth	Site(Status × Depth)
$F_{3,212} = 6.87^{***}$	0.31 ^{***}
ns	0.08 ^{0.07}
$F_{3,47} = 5.20^{**}$	0.27 ^{***}
$F_{3,28} = 5.46^{**}$	0.08*
$F_{3,25} = 3.35^*$	0.18 ^{**}
ns	0.50 ^{***}
ns	0.42 ^{**}

nau Islands (PKI/MKI) but at 4–6 m and 7–9 m. No differences were found between reserve and fished sites at Tuhua, which is not surprising given the low numbers of predators (Fig. 1) and high levels of poaching in this reserve (Shears and Usmar 2006). However, following a recovery of predators at offshore island reserves such as Tuhua we would expect declines in urchins and an increase in macroalgal biomass between 4 and 9 m depth.

Local-scale context dependence: site-level variation in trophic cascades

The physical factors potentially driving variation at regional scales may also vary among sites at smaller spatial scales (e.g., <1 km; Siddon and Witman 2003). To address the importance of local-scale variation in environmental factors in explaining differences between reserve and fished sites, we compared alternative models of the factors (environmental or fishing) driving variation in urchin density and macroalgal biomass. At Leigh and Tawharanui, comparisons among models provided further confidence that the differences between reserve and fished sites were an indirect effect of fishing and not attributable to variation in environmental factors among sites (Table 4, Appendices D and E). At Hahei, there was some evidence that exposed urchin abundance was lower and macroalgal biomass higher at reserve sites at depths of 4–6 m, which is consistent with

the greater abundance of snapper and spiny lobster compared to adjacent fished waters (Fig. 1). However, there was only weak evidence that these differences in urchins and macroalgae were due to fishing alone (Table 4) and there was similar support that sediment governed the variation across sites (Appendices D and E). Sites at Hahei span a local gradient in both wave exposure and sedimentation, and reserve sites tend to have higher sediment cover and be more sheltered from waves. Exposed urchin density was positively related to wave exposure and negatively related to sediment cover (Table 4), providing an alternative explanation for potential differences in urchin numbers between reserve and fished sites. This demonstrates how urchins, and therefore their effects on macroalgae, may vary among sites in relation to environmental factors over relatively small spatial scales (e.g., 1–10 km). These results further demonstrate the importance of addressing environmental variation to more accurately assess the mechanisms responsible for differences between reserve and fished sites.

Differences in the extent of barrens, exposed urchin abundance, and macroalgal biomass at PKI/MKI were broadly consistent with the higher abundance of snapper in the reserve (Denny et al. 2004) and suggestive of a trophic cascade effect. However, the Poor Knights had only been completely protected (no-take) for one year at the time of sampling. Given that it took more than 15 years for kelp forests to recover in the Leigh reserve (Babcock et al. 1999, Shears and Babcock 2003), these differences are more likely to be explained by inherent environmental differences than by the rapid recovery of predators. While fishing explained 17–22% of the variation in urchin density among the PKI/MKI sites, there was also a strong association with wave exposure. Given that there was no overall difference in wave exposure between the two island groups (Appendix B), variation in this variable is not likely to explain the overall differences in urchins and macroalgae. Numerous other environmental factors not examined in this

TABLE 4. Variable weights from the model-selection procedure for (a) the analysis of variation in exposed *Evechinus* among sites and (b) the analysis of variation of macroalgal biomass among sites.

Variable	Leigh		Tawharanui	Hahei	PKI/MKI		
	<2 m	4–6 m	4–6 m	4–6 m	<2 m	4–6 m	7–9 m
a) Exposed <i>Evechinus</i>							
Status	—	(–) 0.990	(–) 0.983	(–) 0.391	—	(–) 0.703	(–) 0.473
Wave exposure	—	(–) 0.137	(–) 0.040	(+) 0.128	—	(–) 0.316	(+) 0.866
Water clarity	—	(+) 0.168	(+) 0.098	(–) 0.083	—	NA	NA
Sediment	—	(–) 0.123	(–) 0.417	(–) 0.181	—	(+) 0.272	(+) 0.178
b) Macroalgal biomass							
Exposed urchin	(–) 0.703	(–) 0.996	(–) 0.976	(–) 0.438	(–) 0.392	(–) 0.997	(–) 0.614
Wave exposure	(+) 0.120	(+) 0.135	(–) 0.045	(–) 0.166	(+) 0.504	(–) 0.491	(–) 0.801
Water clarity	(+) 0.788	(–) 0.139	(+) 0.066	(+) 0.088	NA	NA	NA
Sediment	(+) 0.621	(+) 0.292	(–) 0.172	(+) 0.232	(+) 0.163	(–) 0.203	(–) 0.168

Notes: The sign of each factor coefficient is indicated in parentheses. A dash indicates that the location was not tested as there was no significant difference between reserve and fished sites. NA indicates that weights are not available; these were not tested as there was no difference in measurements among all sites from PKI/MKI.

study may also vary between the Poor Knights and Mokohinau Island's, which are separated by approximately 60 km, underscoring the difficulty in attributing differences observed between two island groups to the effects of fishing (e.g., Vadas and Steneck 1995, Lafferty 2004). On average, macroalgal biomass was higher at the Poor Knights compared to the Mokohinau's, but the overall abundance of sea urchins did not differ between the two island groups. The observed differences in exposed urchin densities were due to a higher proportion of large urchins occupying crevices at the Poor Knights (Appendix C). The differences between the two island groups appear analogous to patterns observed by Harrold and Reed (1985) in Southern California where variation in kelp abundance was not associated with changes in urchin abundance, but with changes in the behavior and grazing activity of urchins. Under oceanographic conditions that promoted kelp growth and recruitment, urchins occupied protected microhabitats and fed largely on drift kelp, while under less favorable conditions for kelps (e.g., low nutrients and storms) urchins abandoned microhabitats and actively grazed kelps. It is possible that inherent spatial variation in oceanographic conditions may have similar consequences to kelp production and urchin behavior. For example, the Poor Knights are more closely situated to both the mainland coast and the shelf break than the Mokohinau Islands, and numerous oceanographic features such as upwelling (Zeldis et al. 2004) and internal waves (Sharples et al. 2001) may be important mechanisms that enhance nutrient supply to shallow waters. These factors combined with the typically clear water surrounding the Poor Knights may promote higher macroalgal productivity compared to the Mokohinau's. While the mechanisms underlying higher algal biomass at the Poor Knights are largely speculative, the indirect effects of predators will be less evident under conditions that promote high kelp productivity and thereby reduce the effects of urchin grazing.

The importance of context-dependent effects

In our study, variation in urchin populations and macroalgal biomass between reserve and fished sites could only be attributed to trophic cascades resulting from fishing in the two oldest reserves where both snapper and lobster are abundant. We could not attribute differences between the younger reserves (<7 years) and their associated fished areas to the effects of fishing, despite the fact that in most cases a recovery of predators had already occurred (Fig. 1). While it is possible that predators have not reached sufficient densities to control urchin populations (e.g., Guidetti and Sala 2007) and subsequent indirect effects are likely to take longer than 7 years in this system, our results suggest that environmental variation at fine (depth within sites), local (within locations), and regional scales (among locations) will influence where urchins can affect

macroalgal assemblages, regardless of predator density and fishing intensity.

This conclusion is broadly consistent with suggestions that the importance of biotic interactions changes across environmental gradients and that predation (in this case herbivory) decreases with increasing environmental stress (Menge and Sutherland 1987). At the regional scale, in locations like Long Bay where there is high environmental stress associated with sedimentation, urchins consistently occur at low numbers and are not likely to have an important role in structuring algal communities. Other examples from temperate reefs where urchins do not appear to play an important role in controlling algal assemblages potentially as a result of environmental stress include a number of sheltered (Dayton 1985, Miller 1985) and highly exposed areas (Miller 1985, Sivertsen 1997, Vanderklift and Kendrick 2004). At smaller scales, within and between sites, environmental stress associated with abiotic processes also appears to restrict the depth distribution of urchins. For example, in very shallow water high water motion appears to limit the movement and grazing efficiency of urchins. Similarly, the absence of urchins in deeper water at many sites may be a result of environmental stress associated with reduced water motion and increased sedimentation. Therefore, at regions, sites and depths where abiotic factors limit urchin abundance or grazing activity, barrens do not develop in the absence of predators and habitat-level changes following a recovery of predators are not likely.

The relative effects of herbivores have also been shown to be depressed under environmental regimes that promote high primary productivity in a variety of systems (Elser and Goldman 1991, Steneck and Dethier 1994, van de Koppel et al. 1996). In the present study, the sites at the Poor Knights and Tuhua supported relatively high algal biomasses despite exposed urchin densities greater than 2 urchins/m², more than twice the density required to maintain barrens at coastal sites (Shears and Babcock 2003). This suggests that the oceanographic conditions at these offshore islands promote high macroalgal productivity and urchins are less effective at controlling or reducing macroalgal biomass. Subsequently, the indirect effects of predators are expected to be more subtle in highly productive environments. While these patterns suggest that regional scale oceanographic conditions can influence the likelihood of trophic cascades, oceanographic conditions can also vary considerably over much smaller spatial scales and influence the dynamics of kelp forests (Parnell et al. 2006).

In northeastern New Zealand, the strength of abiotic and bottom-up processes appear important in determining where predators can have strong top-down effects on benthic reef ecosystems. Efforts to understand the specific conditions under which trophic cascades will occur and the mechanisms driving them is likely to be much more constructive than a focus on the generality

of trophic cascades (Paine 1991). It is probable that some systems may be inherently more dynamic or variable than others and pulse disturbances such as storms or El Niño Southern Oscillation (ENSO) events may dominate and override the top-down role of predators (e.g., Southern California [Dayton et al. 1999]). Furthermore, in systems where multiple anthropogenic stressors are acting on kelp forests and their inhabitants, the importance of top-down effects, and our ability to detect them, may be diminished. This may be the case when fishing occurs at multiple trophic levels such that reef predators, urchins and kelp are harvested (Dayton et al. 1998), or where land-based activities influence the persistence of key components of the trophic cascade (e.g., Walker 2007). Nevertheless, as highlighted by gaps in our understanding of northeastern New Zealand's kelp forest ecosystem, we contend that the way forward is to measure important processes (e.g., productivity, recruitment, grazing, and predation rates) and how these vary with environmental context at multiple spatial scales.

Implications for conservation and management

Our work in northeastern New Zealand suggests that, in some cases, urchin barrens can provide an ecological indicator for ecosystem-based fisheries management signifying where the exploitation of reef predators has led to community-wide trophic cascades. However, the present study suggests that the occurrence of such effects is highly context dependent and that the indirect repercussions of fishing will vary among regions, sites and even depths. With increasing networks of marine reserves being established worldwide in a variety of environmental contexts, there are increasing opportunities to improve our understanding of these dependencies.

Our comparisons between reserves and adjacent fished sites across a large environmental gradient provided insights into where fishing may have important impacts on kelp forest ecosystems. While time series data from before and after protection across multiple reserves provides a more robust assessment of such effects, our study demonstrates the importance of addressing regional- and local-scale environmental variation when interpreting and predicting both spatial and temporal patterns between reserve and fished sites. Application of methods similar to those used in this study that test for alternate explanations for differences between reserve and fished sites at multiple spatial scales provides a more critical approach to developing realistic predictions about how fishing and/or marine reserves alter marine communities. Furthermore, given the highly context-dependent nature of both the direct (Edgar et al. 2004, Russ et al. 2005, Barrett et al. 2007) and indirect (Micheli et al. 2005, this study) effects of protection from fishing, broad conclusions drawn from meta-analyses must be treated cautiously. With increasing efforts globally to protect and restore terrestrial, aquatic and marine ecosystems both conservation and resource

managers are increasingly being tasked to predict and forecast the response of communities to protection. Understanding context dependencies, such as those described here, and the mechanisms responsible is key to developing realistic predictions as to where and when the reduction or recovery of key ecosystem components will have detectable community-level impacts and poses a major challenge to the fields of ecology and conservation biology (Agrawal et al. 2007).

ACKNOWLEDGMENTS

We thank C. Duffy, R. Russell, and J. Walker for their assistance with diving, and T. Haggitt, S. Kelly, and N. Ward for providing unpublished data. R. Cole, R. Miller, K. Steger, R. Taylor, and E. Villouta provided valuable discussion and comments on earlier versions of the manuscript. We are also grateful to P. Bendle of the vessel *M.V. Norseman* for his help and knowledge of the Poor Knights Islands, and B. Doak and M. Birch for skippering the *R.V. Proteus* to the Mokohinau Islands. Thanks also to staff at the Department of Conservation and Leigh Marine Laboratory for providing logistical support. This study was funded by the New Zealand Department of Conservation Science and Research Unit, under Science Investigation No. 2481. Additional postdoctoral support to N. T. Shears was provided by the University of Auckland's Leigh Marine Laboratory and the New Zealand Foundation of Research, Science and Technology.

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APPENDIX A

Sampling locations and sites in northeastern New Zealand (*Ecological Archives* A018-065-A1).

APPENDIX B

Analysis of environmental variation among locations, and between reserve and fished sites (*Ecological Archives* A018-065-A2).

APPENDIX C

Size frequency distribution of *Evechinus chloroticus* populations at fished and reserve sites at each location (*Ecological Archives* A018-065-A3).

APPENDIX D

Model selection results for exposed sea urchins (*Ecological Archives* A018-065-A4).

APPENDIX E

Model selection results for macroalgal biomass (*Ecological Archives* A018-065-A5).