

Indirect effects of protection from exploitation: patterns from populations of *Evechinus chloroticus* (Echinoidea) in northeastern New Zealand

Russell G. Cole*, Dominic Keuskamp**

Leigh Marine Laboratory, University of Auckland, PO Box 349, Warkworth, New Zealand

ABSTRACT: The influence of predators on populations of the sea urchin *Evechinus chloroticus* in northeastern New Zealand was investigated by comparing densities, population size structure, and crevice occupancy in marine reserve ('protected') and exploited locality pairs. There was no overall difference in sea urchin density between protected and exploited localities, but population size structures were generally more bimodal in the protected localities. Size-related patterns of crevice occupancy did not vary consistently between protected and exploited locality pairs. The effects of protection were most pronounced in the Cape Rodney - Okakari Point (CROP) Marine Reserve, where relative to the adjacent fished area (1) sea urchin densities were ~3 times lower, (2) size structures were more bimodal, and (3) sea urchins remained crevice-bound to larger sizes (~40 mm test diameter). Sea urchin transplant experiments showed higher losses of 30 to 40 mm test diameter *E. chloroticus* at a protected locality than a fished locality. Tests of adult sea urchins were heavier at sites in the reserve relative to the fished reference area. We suggest that predatory fishes, which were larger and more numerous in the reserve, were the cause of the differences. A strong bimodal size structure persisted and density declined over 10 yr at one site in CROP Marine Reserve. We suggest that generalising from reserve studies to exploited areas may lead to erroneous conclusions.

KEY WORDS: Echinoid · Marine reserve · Predation · Refuge · Carnivorous fishes · Grazing

INTRODUCTION

Sea urchins are influential benthic grazers in shallow temperate reef systems. Dense populations of these echinoids create and maintain areas devoid of brown macroalgae and dominated by coralline algae (reviewed by Lawrence 1975, Lawrence & Sammarco 1982, Schiel & Foster 1986). As a consequence, the factors that regulate sea urchin populations have been widely studied. The roles that predators of sea urchins play in altering reef habitat structure have been the topic of considerable debate (e.g. Miller 1985, Foster & Schiel 1988, Aronson 1990, Elner & Vadas 1990,

Scheibling 1996). In the northeastern Pacific sea otter predation has been shown to have a major effect on populations of sea urchins, and ultimately on assemblage structure (Estes et al. 1978, Breen et al. 1982, Estes & Duggins 1995). Similar top-down control of echinoids by fishes on tropical reefs can cause marked community-level habitat changes (e.g. McClanahan et al. 1996). However, clear empirical evidence to support a similar role for predation by non-mammalian predators on subtidal temperate reefs does not yet exist (reviewed by Harrold & Pearse 1987, Scheibling 1996).

Localised aggregations of sea urchins ('feeding fronts') may alter habitat boundaries by intensively grazing areas (Foreman 1977, Schiel 1982, see review by Harrold & Pearse 1987), while behavioural changes may be sufficient to alter grazing intensity in other systems (Ebling et al. 1966, Dean et al. 1984, Ebeling et al. 1985, Harrold & Reed 1985). Storms may directly kill exposed sea urchins (Cowen et al. 1982, Harris et

*Present address and address for correspondence: NIWA, PO Box 893, Nelson, New Zealand.
E-mail: r.cole@niwa.cri.nz

**Present address: School of Biological Sciences, Flinders University of South Australia, GPO Box 2100, Adelaide SA 5001, Australia

al. 1984, Ebeling et al. 1985, Lawrence 1996) and/or alter supply of drift algae (Ebeling et al. 1985, Harrold & Reed 1985). Both mechanisms can restrict sea urchins to refugia and reduce grazing pressure (preceding references). A relationship between predators, sea urchin behaviour and grazing pressure postulated in Nova Scotia (e.g. Bernstein et al. 1981, 1983, Mann et al. 1984) was later criticised by Vadas et al. (1986). The nature of predator effects on sea urchin behaviour remains unclear (Scheibling 1996).

In addition to exhibiting behavioural variability, regular echinoids are phenotypically plastic (see review of Ebert 1996). Some species have a relatively larger feeding apparatus (Aristotle's lantern) where food is limited (e.g. Ebert 1980, Black et al. 1982, Levitan 1991, McShane & Anderson 1997). Levitan (1992) used museum collections of echinoid tests and jaws to address long-term change in food availability. Levitan (1991) concluded that in a diadematid urchin the test shrank around the jaws, thus increasing the relative size of the feeding apparatus (see Constable 1993). Different echinoid taxa express these changes differently, with the Diadematidae changing test size more rapidly than other families (Levitan 1991).

The endemic echinometrid *Evechinus chloroticus* is the dominant grazer on shallow northeastern New Zealand reefs (Andrew 1988) and at sufficient density maintains areas of 'coralline flats' at ~5 to 10 m depth (Ayling 1981, Andrew & Choat 1982, Choat & Schiel 1982). This habitat is defined by the absence of large brown macroalgae and presence of crustose coralline algae (Ayling 1978, Andrew & Choat 1982), but also supports abundant fish predators of *E. chloroticus* (Choat & Ayling 1987). Palinurid lobsters are abundant in macroalgal stands inshore and offshore of the coralline flats habitat (MacDiarmid 1991), but they are thought to have minimal impact on *E. chloroticus* populations on coralline flats (Andrew & Choat 1982, Andrew & MacDiarmid 1991). Coralline flats have persisted for decades at one well-studied site, where Andrew & Choat (1982) enhanced survivorship of juvenile echinoids by excluding predators. They suggested that although present densities of fishes were insufficient to alter habitat distribution, fish predation may have been responsible for bimodal size structures of *E. chloroticus* on coralline flats.

Most studies of *Evechinus chloroticus* in northeastern New Zealand were conducted in the Cape Rodney to Okakari Point (CROP) Marine Reserve, which has been protected from exploitation since 1975 (Ballantine 1991). This is one of several areas in New Zealand protected by 'Marine Reserve' or 'Marine Park' status (Creese & Cole 1995). They vary in spatial extent and have been protected for varying periods, but there is increasing evidence that abundances of exploited

organisms, including predators of sea urchins, are higher in protected areas than in adjacent fished areas (McCormick & Choat 1987, Cole et al. 1990, MacDiarmid & Breen 1993). In many of the studies that detected effects of predators on sea urchin populations, human exploitation of these predators ultimately determined predation intensity (e.g. Breen & Mann 1976, Bernstein et al. 1981, Mann 1982, Tegner & Levin 1983). Manipulating large, mobile predators on spatially and temporally relevant scales remains impractical (Estes 1995). However, areas protected from human exploitation have recently been used to assess the influence of predation on sea urchin populations (e.g. Sala & Zabala 1996).

To investigate the influence of variation in fish predator density on populations of *Evechinus chloroticus*, we examined the density, size structure, and shelter occupancy of sea urchin populations among several localities in northeastern New Zealand including the 3 longest-established marine protected areas (MPAs) in the country. In addition, sea urchin morphological characteristics and predator abundance and size structure were compared between fished and protected localities at Leigh. Survivorship of small *E. chloroticus* transplanted among sites in those localities was compared. Long-term measurements of sea urchin population parameters were made at one well-studied site in CROP Marine Reserve.

METHODS

Sea urchin density, size structure and crevice occupancy. *Evechinus chloroticus* populations were sampled for density, population size structure, and crevice occupancy by SCUBA diving at 6 localities in northeastern New Zealand. Four coastal localities were sampled: Tawharanui Marine Park (protected) and eastern Kauri Island (fished) in 1996, CROP Marine Reserve (protected) and Coastal Leigh (fished) in 1997 (Fig. 1). Size and crevice occupancy data from Poor Knights Is. Marine Reserve (protected, and sampled in 1992) are also presented and compared with data from the Mokohinau Is. (fished, sampled in 1996) (Fig. 1). Choat & Ayling (1987) recorded similarities in the fish faunas of those offshore island groups. Five sites on coralline flats (depth 5 to 10 m) were sampled at all localities except at offshore islands, where logistics restricted sampling to 4 sites. All sea urchins in 1 m² quadrats (n = 20) were counted and at least 60 individuals were measured while diving at each site (more than 400 were measured for each locality). Measurements of test diameter (TD) were made to 1 mm with vernier calipers. Although we have measured *E. chloroticus* as small as 3 mm TD during sampling, and

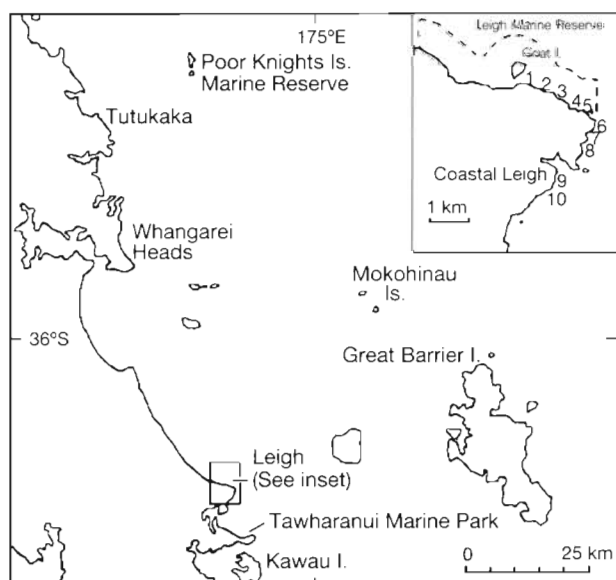


Fig. 1. Location of sampling localities on the northeastern coast of New Zealand. Numbers indicate sites sampled at Leigh. In CROP Marine Reserve: 1 = Waterfall Reef, 2 = Tower Rock, 3 = Tabletop, 4 = Onespot, 5 = Rodney Cove; at Coastal Leigh: 6 = Rodney South, 7 = Drift Bay, 8 = Vee Bay, 9 = Nordic and 10 = Penguin St.

regularly found 5 mm TD *E. chloroticus* at monitoring sites, we are confident that animals larger than 10 mm TD were quantitatively sampled. For each individual measured in quadrats, we also recorded whether or not it occupied a crevice. Densities of 'exposed' *E. chloroticus* (those not occupying crevices) were analysed. Where it was impossible to remove small individuals without crushing them, their test diameters were estimated to 5 mm by holding the scale of the calipers next to the urchin. Keuskamp (1997) showed marked differences in population size structure of *E. chloroticus* between sandstone and greywacke reefs (western and eastern areas of the CROP reserve respectively) so we concentrated on eastern reefs, which have the same rock type as those at Coastal Leigh.

One site in CROP Marine Reserve, Waterfall Reef, was sampled repeatedly for density (1988 to 1997, 28 measures), size structure and crevice occupancy (1990 to 1997, 26 measures) using the method described above.

Sea urchin morphometry. We compared structural characteristics of *Evechinus chloroticus* in protected and unprotected areas near Leigh, to ascertain whether differences existed between localities in lantern size and test weight. Ten *E. chloroticus* in the size range 55 to 65 mm TD were collected from coralline flats habitat at each of the 5 sites at CROP Marine Reserve and Coastal Leigh to examine morphometry. The sea urchins were returned to the laboratory, where TD was

measured to 1 mm, and following dissection, wet weight of the test (with lantern and viscera removed) was also measured. Following cleaning in 5% sodium hypochlorite for 48 h to remove organic material, lengths of 3 haphazardly chosen demipyrramids per lantern were measured to 0.1 mm with vernier calipers according to the method of Levitan (1992).

Sea urchin transplant. Short-term survivorship of small *Evechinus chloroticus* was compared experimentally at the protected and fished Leigh localities. *E. chloroticus* in the size class 30 to 40 mm TD were the largest to be consistently crevice-bound at CROP Marine Reserve sites but were commonly found on open substratum at Coastal Leigh (Cole 1993, this study). Sea urchins of this size were therefore transplanted from Coastal Leigh to CROP Marine Reserve. A fully-crossed design, with reciprocal transplants from reserve to fished sites, was impractical, because of low densities of 30 to 40 mm individuals in the protected area. It is possible that some sea urchins migrated out of the area. Exposed *E. chloroticus* move in the order of 1 to 2 m per night in the coralline flats habitat (Andrew & Stocker 1986), though this information probably pertains to slightly larger individuals.

Four transplant trials were carried out: 2 between Drift Bay (fished) and Waterfall Reef (protected) in April 1997 and 1 from Vee Bay (fished), to each of Onespot and Tower Rock (protected) in August 1997 (see Fig. 1). At each site 2 areas of coralline flats were selected, within which 2 concentric squares of areas 16 and 36 m² were marked with plastic tags nailed to the substratum. The experimental area was then exhaustively searched for all sea urchins ~30 to 40 mm TD, which were collected and removed several hundred metres away. Clearing the area in this manner obviated the need for individual tagging (and assessment of tagging artifacts), which is problematic for this species (Dix 1970b), and only marginally decreased overall density in the plots.

For each transplant, exposed *Evechinus chloroticus* of 30 to 40 mm TD were collected from the fished site, measured and (1) transported to the protected site or (2) returned to the source site as controls. Mean test diameter of each group ($n = 20$) ranged from 33 to 38 mm. In each 16 m² quadrat all 20 individuals were placed in crevices. Sites were revisited each day that weather permitted and the plots were carefully searched for all 30 to 40 mm sea urchins, noting the number in the central quadrat and the border area (the difference between the 2 allowing some assessment of movement). Experiments were run for at least 4 d and until further observations were restricted by weather.

Fish density and size structure. In December 1997 populations of predatory fishes were surveyed at 5 sites in CROP Marine Reserve and 5 sites at Coastal

Leigh (the same ones used in sea urchin population surveys). Potential fish predators of *Evechinus chloroticus* were counted in 25×5 m transects ($n = 10$), counted as the tape was laid with a 10 m lead-in sector, in which fish were not counted (as in Cole et al. 1990, Cole 1994). Eight fish species (*Parapercis colias*, *Pagrus auratus*, *Cheilodactylus spectabilis*, *Upeneichthys lineatus*, *Notolabrus celidotus*, *Notolabrus fucicola*, *Chironemus marmoratus*, and *Parika scaber*) were sampled, and their total lengths were estimated *in situ*. Feeding details and references to autecological studies of those species may be found in Choat & Ayling (1987), but *a priori* we identified the first 3 above-named as being of special interest because they were more abundant and larger in the reserve (McCormick & Choat 1987, Cole et al. 1990).

RESULTS

Sea urchin density, size structure and crevice occupancy

There was no clear overall difference in density of exposed *Evechinus chloroticus* between protected and fished localities (Fig. 2). Densities were on average 3 times higher at Coastal Leigh sites relative to CROP Marine Reserve, but were similar among Kawau I. and Tawharanui sites. Greatest densities were recorded from Coastal Leigh sites, and the least abundant populations were found in CROP Marine Reserve. Densities of *E. chloroticus* varied markedly among sites within localities, with densities at Coastal Leigh and CROP Marine Reserve sites being more similar than at other localities.

The sizes of *Evechinus chloroticus* measured in the 6 localities ranged from 3 to 112 mm. Maximal sizes were >100 mm at offshore island localities and >85 mm on the coast, except at Coastal Leigh, where the largest *Evechinus* measured was 76 mm. Size structures were consistently more bimodal and had lower proportions of exposed individuals at protected than at fished localities (Fig. 3). These contrasts were most distinct at the Leigh localities, where the Coastal Leigh modal size class corresponded to the trough in the CROP Marine Reserve size structure. Size structures at Coastal Leigh and Kawau I. were similar, but there was a slightly higher representation of the smaller size classes at Coastal Leigh.

Size-related patterns of shelter occupancy differed inconsistently between protected and fished localities (Fig. 4).

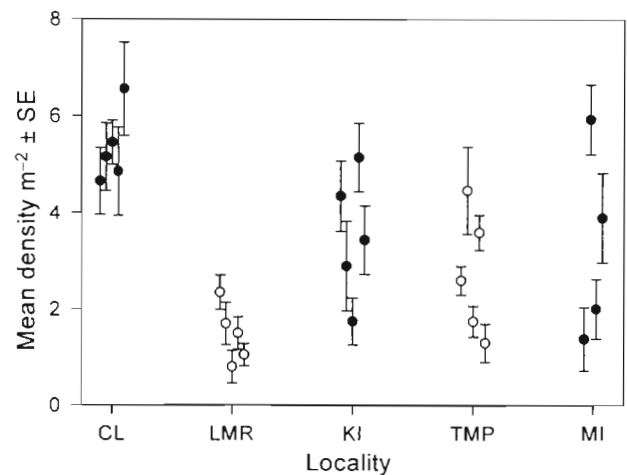


Fig. 2. *Evechinus chloroticus*. Densities of exposed individuals at protected (○) and fished (●) localities in northeastern New Zealand, measured in 1 m^2 quadrats ($n = 20$). Localities are: CL = Coastal Leigh, LMR = CROP Marine Reserve, KI = Kawau Island, TMP = Tawharanui Marine Park, MI = Mokohinau Islands. Five sites sampled at all localities, except MI, where 4 sites were sampled. See Fig. 1 for locations

Evechinus chloroticus occupied crevices to ~20 mm larger TD in CROP Marine Reserve than at Coastal Leigh. Crevice occupancy was closely matched at Tawharanui and Kawau I. At the protected Poor Knights Is., *E. chloroticus* were found exposed on the substratum at ~10 mm smaller than those at Mokohinau Is. (the opposite pattern to that at Leigh localities). Sea urchins at the offshore island groups were crevice-bound at larger sizes than those at coastal localities.

Waterfall Reef

There was a general trend of decreasing density at Waterfall Reef through time, from ~4 m^{-2} in 1988 to

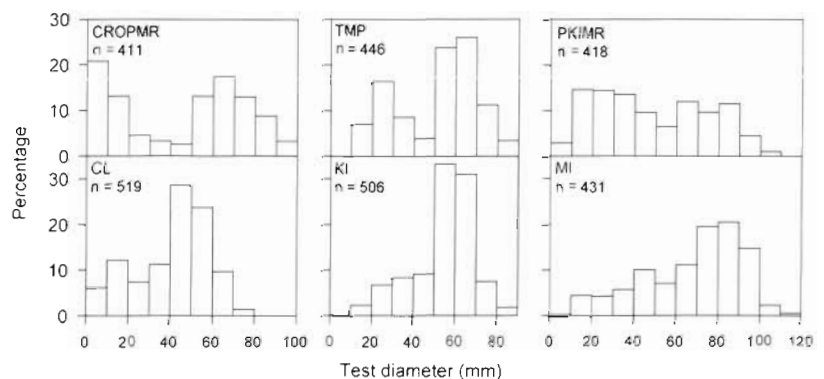


Fig. 3. *Evechinus chloroticus*. Population size structures at protected (upper panels) and fished (lower panels) localities. PKIMR = Poor Knights Is. Marine Reserve; other abbreviations for localities in Fig. 2 legend

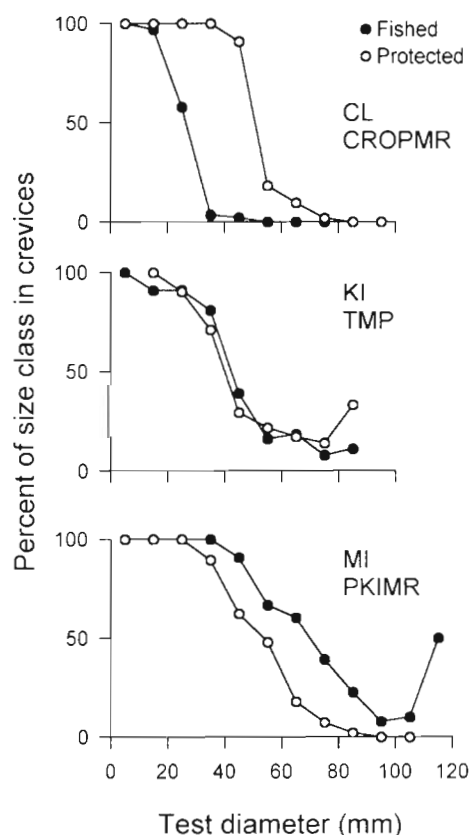


Fig. 4. *Evechinus chloroticus*. Percentage of size classes occupying crevices in protected and fished localities. PKIMR = Poor Knights Is. Marine Reserve; other abbreviations for localities in Fig. 2 legend. Sample sizes as in Fig. 3

$\sim 1 \text{ m}^{-2}$ in 1997 (Fig. 5). However, the decline through that period was similar in magnitude to the variation among samples within a single day. The size structure of the Waterfall Reef *Evechinus chloroticus* population was remarkably stable from 1990 to 1997 and strongly bimodal, with a persistently low proportion of 30 to

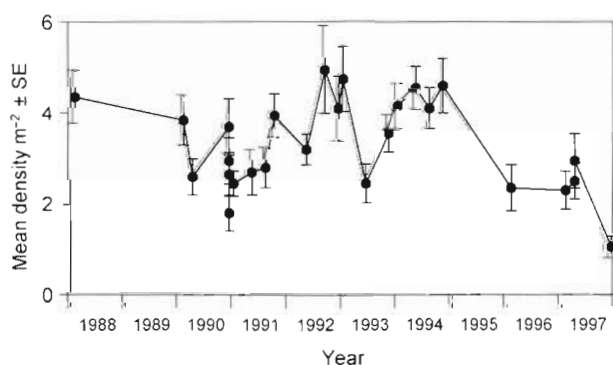


Fig. 5. *Evechinus chloroticus*. Density at Waterfall Reef coralline flats, CROP Marine Reserve, 1988–1997 measured by 1 m^2 quadrats, $n = 20$

50 mm individuals (Fig. 6). (Only 12 of the 28 samples, at approximately 8 mo intervals, are shown here for clarity). The position of the upper mode of 60 to 70 mm did not change, whereas recruitment (measured by the appearance of the smallest size classes) was seasonally recurrent but fluctuated in intensity among years. The size-related pattern of shelter occupancy was also consistent through time: over 90% of all *E. chloroticus* $< 40 \text{ mm}$ sampled at Waterfall Reef were crevice-bound from 1990 to 1997.

Sea urchin morphometry

Test weight was consistently greater for sea urchins from CROP Marine Reserve than for Coastal Leigh, but jaw length did not vary systematically with reserve status (Table 1).

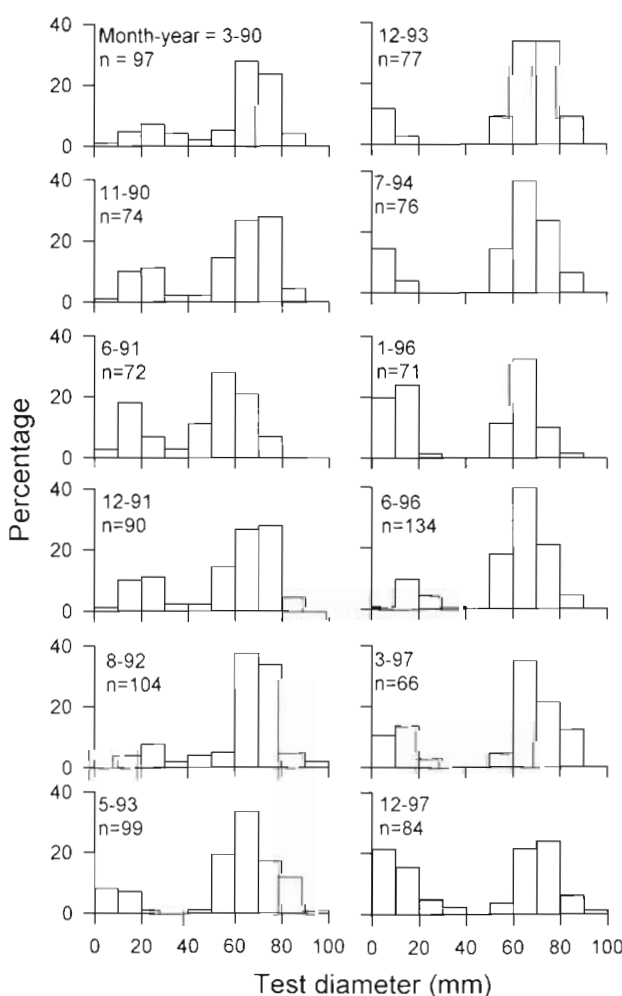


Fig. 6. *Evechinus chloroticus*. Population size structure at Waterfall Reef coralline flats, CROP Marine Reserve, 1990–1997

Table 1. *Evechinus chloroticus*. Morphological characteristics of sea urchins at protected and fished sites at Leigh. Values are mean (SE), $n = 10$ *E. chloroticus* per site. Sea urchins of 55 to 65 mm test diameter were used for the comparison, but due to low abundances of that cohort at Tower Rock, some larger individuals were used there. The lowest 2 rows give the mean (SE) pooled across all individuals from all sites within each level of protection. All values to 1 decimal place

Site	Test weight (g)	Pyramid length (mm)
Marine Reserve		
Waterfall	48.3 (1.6)	15.7 (0.1)
Tower Rock	64.0 (1.5)	15.3 (0.1)
Tabletop	54.1 (2.0)	15.1 (0.2)
Onespot	52.6 (2.4)	13.9 (0.1)
Rodney Cove	49.6 (1.0)	15.2 (0.1)
Coastal Leigh		
Rodney South	43.8 (1.3)	15.0 (1.0)
Drift Bay	41.8 (1.3)	15.0 (0.1)
Vee Bay	35.5 (1.3)	14.2 (0.1)
Nordic Bay	38.1 (0.8)	14.6 (0.2)
Penguin St.	40.9 (1.5)	14.5 (0.1)
Protected	53.7 (1.1)	15.0 (0.1)
Fished	40.0 (0.7)	14.7 (0.1)

Sea urchin transplants

A critical assumption in the transplants was that migration to and from the plots did not unduly influence results. The degree of dispersal of *Evechinus chloroticus* from the central 16 m² plot varied among trials at each site. However, very few sea urchins of transplant size were ever seen beyond the 36 m² area, so abundance in this larger plot was used for the analysis of the experiment.

At all sampling times, mean abundance of transplanted small *Evechinus chloroticus* in plots was lower at protected than at fished (control) sites, and in both Waterfall Reef (Reserve) trials (Fig. 7A) and at Tower Rock (Reserve) (Fig. 7B), mean abundance of transplants consistently declined through time. Numbers at the Onespot (Reserve) site (Fig. 7C) fluctuated conspicuously among samples, probably because diver observations were hindered there by rough weather on some sampling dates. Abundances of *E. chloroticus* in control plots generally remained high, with >80% remaining in any one plot at the conclusion of the experiment. The magnitude and rate of decline was greatest at Waterfall Reef (Reserve), where means of ~13% (first trial) and 3% (second trial) of transplanted sea urchins remained in plots after 4 to 5 d (vs 95% for both controls). We were unable to directly attribute sea urchin disappearances to fish predation; no direct observations of predation were made and remote video observations of the plots at Waterfall Reef (Reserve) and Rodney South (fished)

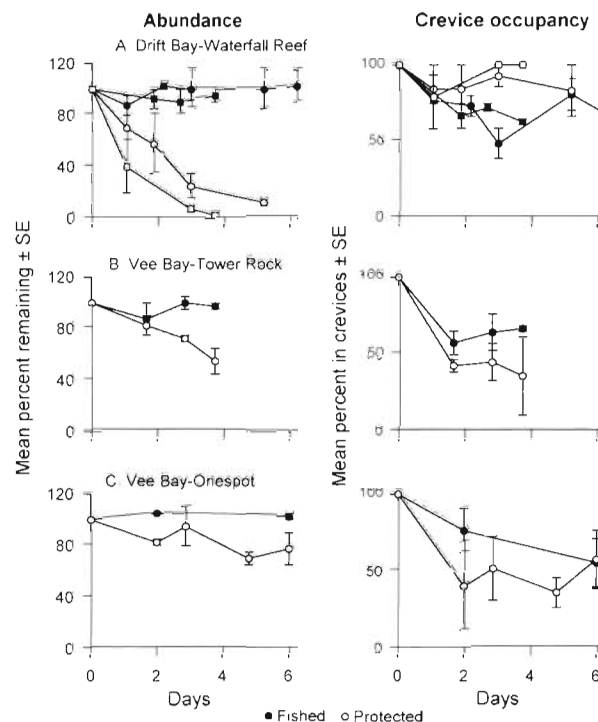


Fig. 7. *Evechinus chloroticus*. Abundance and crevice occupancy following transplants between fished and protected sites at Leigh. (A) Drift Bay to Waterfall Reef (Trial 1 = circles, Trial 2 = squares), (B) Vee Bay to Tower Rock, (C) Vee Bay to Onespot. Initial $n = 20$. Open symbols: transplants from fished to protected sites; filled symbols: control transplants from fished back to fished sites

(1 daylight h per plot in second trial) also revealed no predatory strikes.

There was no clear trend in shelter occupancy of transplanted *Evechinus chloroticus* between protected and fished sites. For the Tower Rock (Reserve) and Onespot (Reserve) trials, crevice occupancy was lower at the reserve sites than at the control sites for almost all sampling dates (Onespot [Reserve] and Vee Bay [fished] values had converged by the last sample) (Fig. 7B, C). In both Waterfall Reef (Reserve) trials, the opposite pattern occurred: shelter occupancy was greater on all sampling dates in plots at the reserve site (Fig. 7A).

Fish density and size structure

Carnivorous fishes were more abundant and larger on coralline flats in CROP Marine Reserve relative to Coastal Leigh (Fig. 8, Table 2). Pooled fish density was over 9 times greater in the protected area (Fig. 8A), and the differences were further emphasised when the 3 species (*Parapercis colias*, *Pagrus auratus*, and *Cheilodactylus spectabilis*) most likely to consume

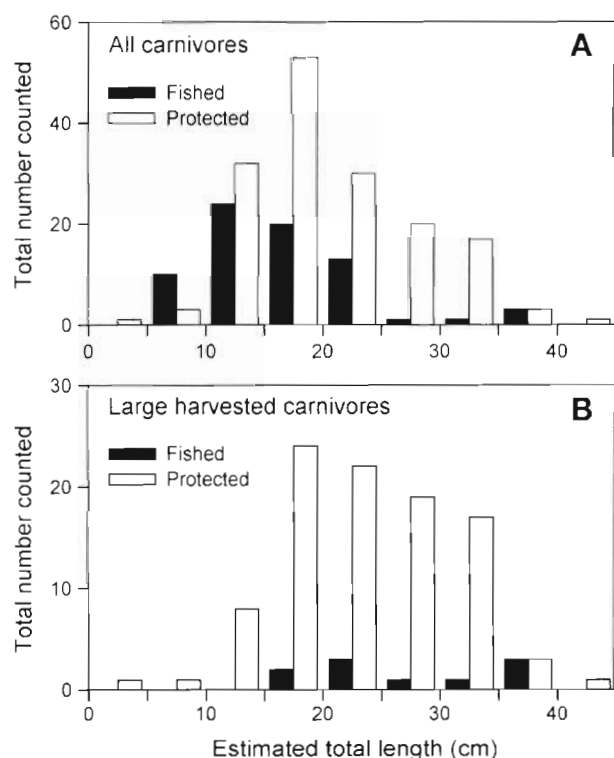


Fig. 8. Combined population size structure of (A) all carnivorous fishes and (B) combined *Pagrus auratus*, *Parapercis colias* and *Cheilodactylus spectabilis* derived from transect counts at CROP Marine Reserve and Coastal Leigh

small *Evechinus chloroticus* were considered as a group (Fig. 8B). Those 3 species were also more consistently present in the reserve than outside (Table 2), with only the monacanthid *Parika scaber* being slightly more abundant outside the reserve than inside.

DISCUSSION

The initial sea urchin population surveys suggested that variation in density, size structure and shelter occupancy of *Evechinus chloroticus* could not be solely attributed to the protection status of localities. Although all 3 MPAs in the survey have been protected from exploitation for over 10 yr, there are a number of important differences among them. Anecdotal evidence suggests that Tawharanui Marine Park, administered by a different authority to the 2 marine reserves, has been illegally fished more than the nearby CROP Marine Reserve, possibly because of the latter's higher public and scientific profile (S. Kelly pers. comm.). Probably for this reason, abundances of exploited fishes (T. J. Willis unpubl. data) and spiny lobsters (S. Kelly unpubl. data) appear to be much lower at Tawharanui than at Leigh. The 2 offshore island groups share a fish fauna distinct from coastal northeastern New Zealand by virtue of their position in the path of the East Auckland current (Choat & Ayling 1987, Choat et al. 1988). That fauna comprises mainly large labrids which are not exploited, and size structures of fishes suggest that the Mokohinau Is. may have more large (>300 mm) fish than the Poor Knights Is. (Fig. 3 of Choat & Ayling 1987). A direct effect of *E. chloroticus* harvesting at exploited sites is unlikely. Harvesting is of low intensity and predominantly targets intertidal/shallow subtidal populations (Mead 1996).

The strong contrast in population densities, size structures and shelter occupancies between the protected and fished Leigh localities was initially suggestive of a 'reserve effect'. Three lines of evidence consistent with direct and indirect effects of reserve

Table 2. Densities of carnivorous fishes for protected and fished sites at Leigh. Mean (SE) densities of 8 potential carnivores in 25 × 5 m (n = 10) transect counts at each site. The lowest 2 rows give the mean (SE) pooled across all urchins from all sites within each level of protection. -: not present; all values to 1 decimal place

Site	<i>Parapercis colias</i>	<i>Pagrus auratus</i>	<i>Cheilodactylus spectabilis</i>	<i>Upeneichthys lineatus</i>	<i>Notolabrus celidotus</i>	<i>Parika scaber</i>	<i>Chironomus marmoratus</i>	<i>Notolabrus fucicola</i>
Marine Reserve								
Waterfall	0.4 (0.2)	2.4 (0.7)	0.2 (0.1)	2.2 (0.9)	0.6 (0.2)	0.1 (0.1)	-	-
Tower	0.3 (0.2)	0.2 (0.2)	0.5 (0.3)	0.2 (0.1)	0.6 (0.2)	-	-	-
Tabletop	1.0 (0.4)	0.3 (0.2)	0.5 (0.2)	0.2 (0.1)	0.6 (0.2)	-	-	-
Onespot	-	0.9 (0.2)	2.1 (0.5)	0.6 (0.3)	0.5 (0.2)	-	-	-
Rodney Cove	0.7 (0.3)	0.1 (0.1)	-	0.6 (0.3)	0.2 (0.1)	-	-	-
Coastal Leigh								
Rodney South	-	-	0.4 (0.2)	-	0.4 (0.2)	0.3 (0.2)	0.1 (0.1)	0.1 (0.1)
Drift Bay	0.2 (0.1)	-	-	0.1 (0.1)	0.2 (0.1)	-	-	-
Vee Bay	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	1.0 (0.3)	-	-	-	-
Nordic Bay	-	-	-	1.9 (1.2)	0.4 (0.2)	-	-	-
Penguin St.	-	0.1 (0.1)	-	1.2 (0.8)	0.4 (0.2)	-	0.1 (0.1)	-
Protected	0.5 (0.1)	0.8 (0.2)	0.7 (0.2)	0.8 (0.2)	0.5 (0.1)	0.0 (0.0)	-	-
Fished	0.1 (0.0)	0.0 (0.0)	0.1 (0.0)	0.8 (0.3)	0.3 (0.1)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)

protection derive from Leigh studies. First, predatory fish densities appeared to be higher in the reserve (McCormick & Choat 1987, Cole et al. 1990, this study). Second, over the last 10 yr the density of *Evechinus chloroticus* has declined at several sites in the reserve (Cole 1993). Third, substantial changes in habitat distribution, particularly decreases in the extent of urchin-dominated coralline flats, have occurred (Cole 1993, Shears & Babcock unpubl. data, R. Cole pers. obs.). Although the exploited area, Coastal Leigh, has not been as intensively studied as CROP Marine Reserve, extensive coralline flats existed at all sites examined, and have done so since at least 1992 (Shears & Babcock unpubl. data, authors' pers. obs.).

One consistent trend that emerged from the population survey was the more bimodal nature of *Evechinus chloroticus* size structures from protected localities. The integration of recruitment, growth and mortality into sea urchin population size structures limits speculation on the causes of this variation, particularly from point samples (Ebert et al. 1993). As *E. chloroticus* growth is slow and variable (Walker 1981, Andrew & Choat 1985, Kerrigan 1987), and individuals can live for at least 10 yr (Walker 1977), neither mode in bimodal size structures represents a single year class. The long-term information from Waterfall Reef clearly showed regular recruitment to a stable, strongly bimodal size distribution, indicative of size-specific rates of growth or mortality (Ebert et al. 1993). *E. chloroticus* size distributions at other CROP Marine Reserve sites sampled in previous years have similarly been bimodal (Kerrigan 1987, Cole 1993), whereas previous samples of size structure from Coastal Leigh have been almost universally unimodal (Cole 1993). (Andrew & Choat 1982 presented evidence for stable bimodality in *E. chloroticus* size distributions at Waterfall Reef soon after the reserve was established; however, the temporal variability among those distributions was not seen in this study).

There are 2 non-mutually exclusive explanations for the low representation of the 30 to 50 mm group in the populations at Leigh. The trough between modes may result from accelerated growth, if greater access to macroalgal food occurs when the crevice-dwelling habit is abandoned (e.g. Himmelman 1986). The influence of growth on population size structures is speculative in the absence of size-specific age or growth data. Estimating long-term growth rates of *Evechinus chloroticus* of a range of sizes with tetracycline mark-recapture would be profitable (cf. McShane & Anderson 1997), but the large sample sizes that would need to be marked (and later destroyed) would conflict with the reserve status of the best-studied localities.

The data of Walker (1981) suggest that *Evechinus chloroticus* of 30 mm TD are 2 yr old, with subsequent year classes being 40, 50 and 55 to 60 mm TD. These

size-age data do not suggest that the trough in the size frequency distributions is due to enhanced growth. A remarkable acceleration of growth rate (cf. Andrew & Choat 1985) would be necessary to 'speed' individuals through 30 mm of test growth (30 to 60 mm) without being detected in samples. Levitan (1992) found relatively larger lanterns in food-deprived echinoids. In regressions of log lantern weight on log total weight for *E. chloroticus* from coralline flats and vegetated habitats, Cole (1993) found a higher intercept value for the coralline flats, as expected from similar studies elsewhere (review of Ebert 1996). Thus the absence of differences in relative jaw size between reserve and Coastal Leigh sites in our study is not consistent with more rapid growth in the protected area. Our transplant experiment suggests that size-specific variation in mortality is a more likely explanation than growth for the trough in the size structures.

Evechinus chloroticus' morphometric parameters also varied between reserve and fished sites. Variation in test morphology among sea urchin populations or species has previously been attributed to variation in wave exposure (e.g. Dix 1970a, Lewis & Storey 1984, Drummond 1993, 1994, McShane & Anderson 1997). However, the protected and fished coasts of Leigh have similar aspects and are exposed to storms from similar quarters (predominantly the northeast) (e.g. McCormick & Choat 1987). Selective mortality of juvenile *E. chloroticus* with thin tests via predation or increased calcification induced by sublethal attacks (Edwards & Ebert 1991) could produce the greater test weights in CROP Marine Reserve.

The implication from our study is that higher abundances of predators within CROP Marine Reserve are the causal agent of bimodal size frequency distributions. Bimodality of sea urchin population size structures is most frequently linked to predation (e.g. Tegner & Dayton 1981, Andrew & Choat 1982, Tegner & Levin 1983, Scheibling & Stephenson 1984, Himmelman 1986, Scheibling & Raymond 1990, Andrew & MacDiarmid 1991, Ojeda & Dearborn 1991). The most likely predators of small sea urchins are the fishes we found to be more abundant and larger in the marine reserve. The size range of *Evechinus chloroticus* which may be consumed by fishes is unknown, although remains of individuals >30 mm have been found in the guts of *Pagrus auratus* caught at Goat Island (T. Willis pers. obs.). Further, we believe that the fish count data underestimate the abundance of the largest *P. auratus*, which swim in midwater, and thus were not sampled by benthic transects. The suggestion that fish predators influence population size structure of *E. chloroticus* populations at Leigh localities is supported by the results of the sea urchin transplants and the contrasting patterns of shelter occupancy between localities. The

rapid loss of individuals, particularly at Waterfall Reef, strongly suggests that exposed 30 to 40 mm TD sea urchins are vulnerable to predation. The smaller losses that occurred over 4 to 5 d at Tower Rock and Onespot are still significant if integrated over longer time scales. Spiny lobsters are uncommon on coralline flats (Andrew & Choat 1982, Andrew & MacDiarmid 1991) and while the influences of crabs, starfish and octopus are unknown, they are not conspicuous in the habitat (Andrew & Choat 1982, authors' pers. obs.).

Small echinoids commonly occupy cryptic microhabitats (e.g. Tegner & Dayton 1977, Bernstein et al. 1981, Tegner & Levin 1983, Scheibling & Raymond 1990), and increased predation on abandonment of refuge is inferred to produce bimodality (e.g. Andrew & MacDiarmid 1991, Scheibling & Hamm 1991). We are uncertain to what degree attrition and learning contribute to the persistence of 20 to 50 mm TD *Evechinus chloroticus* in crevices within the marine reserve. If *E. chloroticus* in CROP Marine Reserve emerge from crevices at the same size as those at Coastal Leigh, individuals in the 20 to 50 mm size range could be restricted to crevices by direct mortality of exposed individuals or a behavioural response to (1) the presence of predators (e.g. Bernstein et al. 1981, Tegner & Levin 1983, Vadas et al. 1986, Scheibling & Hamm 1991), (2) sublethal predation (e.g. Carpenter 1984), or (3) damaged conspecifics (Mann et al. 1984, Parker & Shulman 1986). Data from Tutukaka (R. Cole unpubl. data) and observations at several other sites (e.g. Whangarei Heads) (see Fig. 1 for locations) suggest that emergence of *E. chloroticus* from crevices at small sizes is a widespread feature of unprotected areas in northeastern New Zealand. By recording crevice occupancy in the transplant experiments we aimed to address differences in behaviour, but the results were inconclusive due to the short duration of the experiments, and may have been influenced by handling effects.

Andrew & Choat (1982) excluded predators from small areas of coralline flats at Waterfall Reef 4 yr after protection was established and found that *Evechinus chloroticus* <30 mm TD were more abundant in cages than in uncaged areas. While they considered this to be evidence for a predation effect, they concluded that predation was insufficient to reduce urchin densities or eliminate the coralline flats habitat. Like Andrew & Choat (1982) we have no conclusive evidence that predation by fishes is responsible for the decline in abundances seen in this study. Present densities of predators at Leigh may be sufficient to alter densities, size structures and microhabitat distribution of *E. chloroticus*. Nevertheless, events at the habitat level are equivocal; losses of coralline flats habitat in CROP Marine Reserve have not been confined to areas where fish predators are most abundant (Cole 1993, 1994)

and Waterfall Reef has high densities of those fishes but remains as coralline flats. The intensity of *E. chloroticus* recruitment to Waterfall Reef may be the reason for the persistence of intensely grazed habitat despite severe predation pressure; Keuskamp (1997) suggested higher settlement occurred there than at other reserve sites.

The use of MPAs to study predation effects directly is a relatively recent development. Sala & Zabala (1996) and Sala (1997) examined mortality of a sea urchin in areas of varying fish abundance. Those studies found lower survival of tethered sea urchins at sites with high fish densities, though in both studies artifacts (of tethering and diver responsiveness respectively) may have confounded the experiment. This approach has also been used in Kenya (e.g. McClanahan & Muthiga 1989), where there is strong evidence that predation by fishes has a cascading influence on coral reef community structure (McClanahan et al. 1996). Such trophic cascades, while relatively well-known in freshwater habitats (e.g. Wooster 1994, McIntosh & Townsend 1996) appear to be less common in the marine environment. In a recent review, Menge (1997) found that indirect effects emerged as rapidly as direct ones in rocky intertidal systems (e.g. Wootton 1995). Jones et al. (1993) reviewed the evidence for trophic cascades from marine protected areas, and suggested that long-term studies would be required. Unfortunately, habitat-level differences between protected and fished areas at Leigh are only being documented now, 20 yr after the reserve was established (Shears & Babcock unpubl. data).

Further ecological research in northeastern New Zealand needs to be undertaken outside marine reserves. There is already concern about the limited geographic range from which experiments have been done, and the dangers of extrapolating from reserve studies to other areas (Cole 1993). While reserves offer numerous advantages for researchers (Creese & Jeffs 1993), studies in reserves may not be relevant for management of non-reserve areas. Numerous marine reserves have been created by the New Zealand Government's Department of Conservation (see Table 2 of Creese & Cole 1995), giving an opportunity to assess both the direct effects of harvesting, and the generality of the cascading effects described here. These reserves could function as predator addition experiments at large spatial scales, provided adequate data are collected to document changes in population abundances, sizes and habitat distributions. Studies in marine protected areas can go beyond Hutchings' (1996, p. 960) 'dominant question': 'What are the effects of fishing on the behaviour, life history, and population biology of exploited fishes?' to address ecosystem level effects of human harvesting.

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