

Interrelations between sea urchins and spiny lobsters in northeastern New Zealand

N. L. Andrew*, A. B. MacDiarmid**

University of Auckland Marine Laboratory, R. D. Leigh, New Zealand

ABSTRACT: The interrelation between the sea urchin *Evechinus chloroticus* and the spiny lobster *Jasus edwardsii* was investigated in the shallow subtidal zone of rocky reefs in northern New Zealand. Both species were found in large numbers in the Shallow Broken Rock habitat. During the day spiny lobsters and sea urchins were spatially segregated on a small scale. Movement patterns of spiny lobsters indicate that sea urchins are accessible to nocturnally foraging lobsters. Laboratory experiments demonstrated that large lobsters ate all sizes of sea urchins. All sizes of lobster ate small sea urchins (< 50 mm TD) in preference to larger sea urchins. The provision of herbivorous gastropods (also eaten by lobsters) and shelter for sea urchins did not mean that more larger sea urchins were eaten. The removal of large brown algae or sea urchins and gastropods from areas of reef did not cause significant reductions in the daytime density of *J. edwardsii*. We argue that differing micro-habitat requirements of the 2 species mean that large abundances of *E. chloroticus* are unlikely to depress *J. edwardsii* densities. The necessary experiments to test this hypothesis are discussed.

INTRODUCTION

There has been continuing controversy over the role that clawed (Nephropidae) and spiny (Palinuridae) lobsters play in shaping patterns of density, size-frequency and behaviour in sea urchin populations on temperate rocky reefs (e.g. Breen & Mann 1976, Bernstein et al. 1981, 1983, Tegner & Levin 1983, Miller 1985, 1987, Keats 1986, Vadas et al. 1986, Breen 1987, Garnick 1989). Sea urchins can produce enormous and lasting changes in the species composition of communities on shallow rocky reefs (see Lawrence 1975, Lawrence & Sammarco 1982, Pringle 1986, Schiel & Foster 1986, Andrew 1988 for reviews). At its most extreme, grazing by sea urchins leads to the removal of large brown algae from extensive areas of reef and the maintenance of more structurally simple habitats (see above reviews).

The interrelations between lobsters and sea urchins are complex. Increases in the abundance of sea urchins have been correlated with diminished catches of lob-

sters, leading to the hypothesis that predation by lobsters regulates the density of sea urchins (e.g. Breen & Mann 1976, Wharton & Mann 1981, Tegner & Levin 1983). The negative effects of sea urchins on the abundance of lobsters are thought to be primarily mediated through loss of habitat and consequent reductions in regional productivity (Chapman 1981, Wharton & Mann 1981), or through competition for shelter (Garnick 1989).

Explanation of the relations between sea urchins and lobsters has not been greatly advanced by the great imbalance in the type and quality of information gathered on the 2 groups of organisms. The characteristics of many sea urchin populations have been described and experimental tests done on several spatial and temporal scales appropriate to the resolution of this debate (see above reviews). The ecology and population dynamics of lobsters are less well understood and their abundance is often inferred from the catch statistics of regional fisheries (e.g. Breen & Mann 1976, Mann 1977, Wharton & Mann 1981, Tegner & Levin 1983). In few instances has the density of lobsters been estimated by direct observation in the field (e.g. Cooper et al. 1975, Davis 1977, Pollock 1979, Smith & van Nierop 1986, Barkai & Branch 1988, MacDiarmid 1991). Until recently, the foraging behaviour and ecology of lobsters has also received relatively little attention (but

Present addresses:

* New South Wales Department of Agriculture and Fisheries, Fisheries Research Institute, PO Box 21 Cronulla, NSW 2230, Australia

** Fisheries Research Centre, PO Box 297, Wellington, New Zealand

see Herrnkind et al. 1975, Elner & Campbell 1987, Jernakoff 1987, Jernakoff et al. 1987, Lawton 1987, MacDiarmid et al. in press). The imbalance in the quality of information available between sea urchins and lobsters must, at least in part, be due to the biology of lobsters; it is difficult to quantify patterns and do experiments on highly mobile species subject to commercial fishing.

There have been few field-based experimental tests of hypotheses concerning the relationship between the densities of lobsters and sea urchins and the results of such experiments have been contradictory (e.g. Bernstein et al. 1983, Vadas et al. 1986). Laboratory experiments have repeatedly demonstrated that lobsters are capable of eating sea urchins (e.g. Elner 1980, Tegner & Levin 1983, Mann et al. 1984). Demonstrations of capability, while necessary, are not sufficient evidence from which to claim that these predators control sea urchin populations in nature.

In northeastern New Zealand, the palinurid lobster *Jasus edwardsii* and the echinometrid sea urchin *Evechinus chloroticus* co-occur in shallow water habitats on rocky reefs. Both species have been the subject of intensive study (MacDiarmid 1987, 1989, 1991, MacDiarmid et al. in press; see Andrew 1988 for review of studies on *E. chloroticus*). In this paper we bring together, for the first time, data on the density and distribution patterns of these species. This information is combined with experiments in the laboratory and the field that explore the relationship between the 2 species and herbivorous gastropods, also eaten by *J. edwardsii*.

METHODS AND RESULTS

Study area

The field work was done within the Cape Rodney to Okakari Point Marine Reserve. The reserve contains populations of sea urchins and spiny lobsters that have been undisturbed by commercial and recreational fishing since 1976 (Ballantine 1987). In northeastern New Zealand, high densities of *Evechinus chloroticus* (hereafter *Evechinus*) and *Jasus edwardsii* (hereafter *Jasus*) co-occur only in Shallow Broken Rock (SBR) habitat. This habitat is found in shallow water (less than ca 6 m) and has a highly complex topography, with many large boulders overlying the basal rock substratum (Choat & Schiel 1982). Laminarian and fuclean algae cover the tops of boulders and ridges but are scarce in the gullies between them where sea urchins are abundant (Schiel 1982, MacDiarmid et al. in press). Three locations with large areas of SBR habitat were chosen for the descriptive phase of the study: Martin's Rock, Inner Waterfall, and Inner Tabletop (Fig. 1).

Abundance

During May 1984, the densities of *Evechinus*, several species of large brown algae and herbivorous gastropods were estimated by counting all individuals within 20 haphazardly placed 1 m² quadrats within the SBR habitat at Martin's Rock, Inner Waterfall, and

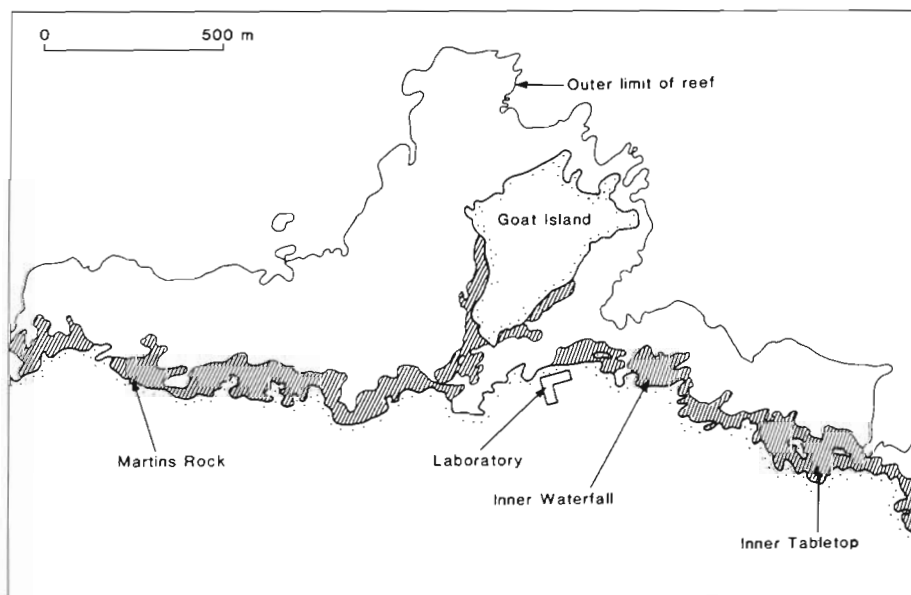


Fig. 1. Central portion of the Cape Rodney to Okakari Point Marine Reserve, New Zealand. Shown is the outer limit of the rocky reef and (hatched) the areal extent of the Shallow Broken Rock habitat. Locations of the 3 study sites and the Leigh Marine Laboratory are also shown

Table 1. Densities of most abundant large benthic organisms at the 3 study locations in May 1984. Data are presented as mean \pm SE, $n = 20$. The coefficient of dispersion (COD) is given for *Jasus* and *Evechinus*. * Significant deviation from unity at $p < 0.05$ with 19 df. The density of *Jasus edwardsii* presented per 100 m² and the density of *Evechinus chloroticus*, gastropods and macroalgae is per 1 m²

Species	Inner Tabletop	Inner Waterfall	Martin's Rock
<i>Jasus edwardsii</i> (total)	7.5 \pm 1.41	10.8 \pm 2.46	14.7 \pm 5.96
(COD)	(5.2)*	(11.8*)	(48.4*)
males	2.1 \pm 0.46	4.9 \pm 1.28	4.4 \pm 1.56
females	5.4 \pm 1.07	6.0 \pm 1.29	10.3 \pm 4.42
<i>Evechinus chloroticus</i> (total)	13.2 \pm 1.42	12.1 \pm 1.36	3.2 \pm 0.83
(COD)	(3.3*)	(3.1*)	(4.3*)
adults	8.8 \pm 1.00	9.5 \pm 1.20	1.5 \pm 0.49
Gastropods			
<i>Cookia sulcata</i>	3.1 \pm 0.42	1.9 \pm 0.35	0.8 \pm 0.21
<i>Trochus viridus</i>	7.1 \pm 0.99	3.3 \pm 0.63	0.4 \pm 0.20
<i>Cellana stellifera</i>	6.2 \pm 0.84	4.9 \pm 0.75	0.8 \pm 0.39
<i>Cantharidus purpureus</i>			
(benthic)	0.7 \pm 0.34	0.2 \pm 0.10	0.2 \pm 0.11
(on <i>Ecklonia</i>)	2.7 \pm 0.43	9.4 \pm 1.12	2.8 \pm 0.52
Macroalgae			
<i>Ecklonia radiata</i>	0.1 \pm 0.10	2.8 \pm 1.00	3.3 \pm 1.13
<i>Carpophyllum maschalocarpum</i>	0	0.1 \pm 0.10	0
<i>C. angustifolium</i>	0	1.0 \pm 0.36	0
<i>Sargassum sinclairii</i>	0.2 \pm 0.2	0	1.0 \pm 0.65

Inner Tabletop. The small gastropod *Cantharidus purpureus* was found in relatively large numbers both on the substratum and on the laminae of the stipitate alga *Ecklonia radiata*. Densities were therefore estimated both in the benthic quadrats used for other species and as the number per individual *Ecklonia* plant ($n = 20$). Small sea urchins greater than 10 mm test diameter (TD) may be reliably found in the field. Quadrats were not placed on the sides or tops of large boulders. All *Evechinus* were measured to the nearest millimetre. The densities of *Jasus* were estimated using 20 randomly placed 10 \times 10 m transects. All *Jasus* observed were counted, sexed, and their size visually estimated to the nearest 5 mm carapace length (CL; see MacDiarmid 1991 for details of this method). Data transformations were done prior to analyses of variance as required by Cochran's test for heterogeneity of variance (Snedecor & Cochran 1980) and these are indicated where appropriate.

The density of *Evechinus* varied significantly among the 3 locations ($F_{(2,57)} = 19.77$, $p < 0.01$; Table 1). There were significantly fewer *Evechinus* at Martin's Rock than at either Inner Waterfall or Inner Tabletop (Student-Neumann-Keuls, SNK, tests, $p < 0.05$): densities at the latter 2 locations did not significantly differ ($p > 0.05$). The abundance of large brown algae (all species pooled) was inverse to that found for *Evechinus*. There were significantly fewer large brown algae at Inner Tabletop than at either of the other locations ($F_{(2,57)} = 5.70$, $p < 0.01$; Table 1). No signifi-

cant difference in the abundance of large brown algae was found between Inner Waterfall and Martin's Rock ($p > 0.05$).

The combined density of gastropods also significantly varied among locations ($F_{(2,57)} = 19.77$, $p < 0.01$). There were significant differences in the abundance of gastropods among all 3 locations (SNK tests). For all 4 species investigated there was a trend toward decreasing mean abundance of gastropods in the benthic quadrats from Inner Tabletop to Martin's Rock (Table 1). The small densities of *Cantharidus purpureus* in benthic quadrats (a mean of less than 1 m⁻² in all cases) contrasted with the relatively high number found amongst the laminae of *Ecklonia* plants, especially at Inner Waterfall (Table 1).

There was a significant negative correlation (data pooled across locations) between the density of *Evechinus* and large brown algae ($r_{(58)} = -0.41$, $p < 0.01$), and between gastropods and large brown algae ($r_{(58)} = -0.34$, $p < 0.01$). There was a positive correlation between the abundance of *Evechinus* and gastropods ($r_{(58)} = 0.46$, $p < 0.01$).

The abundance of *Jasus* in May 1984 did not significantly differ among locations ($F_{(2,57)} = 0.68$, ns; Table 1). There was large variability in the density of spiny lobsters among transects within locations. In one transect at Martin's Rock, superficially no different from others in the area, there were 120 lobsters; a density of 1.2 lobsters m⁻². At all locations there were more females than males (Table 1).

Dispersion and segregation

Coefficients of dispersion (COD) indicated that *Evechinus* was clumped at 1 m² and *Jasus* at 100 m² during day-time sampling (Table 1). The degree of clumping differed among locations and between species (Table 1). Spiny lobsters were more clumped than sea urchins.

Association between the species was described by correlation between the density of sea urchins and spiny lobsters, and by a nearest neighbour technique. This latter technique was used to remove the influence of the scale-dependent nature of sample-unit based descriptors of association. Quadrats of 9 m² were used for correlation analyses between *Evechinus* and *Jasus*. This size was a compromise between the optimal size of transect used to estimate the abundance of *Jasus* (MacDiarmid 1991) and an area small enough for all *Evechinus* to be reliably counted. The entire Inner Tabletop area has been mapped in detail (MacDiarmid 1991). From this map 40 plots of 9 m² were chosen from randomly selected coordinates. Within each plot all spiny lobsters and sea urchins were counted. Only sea urchins greater than 35 mm TD were included in this analysis because smaller sea urchins could not be reliably found in such a large area. The number of large brown algae in these quadrats was also counted. Sampling was done during daylight as *Jasus* were too mobile to sample at night.

The densities of *Jasus* and *Evechinus* were not correlated within 9 m² areas ($r = -0.26$, ns, $n = 40$). There was great variability in the density of *Evechinus* in quadrats that contained no *Jasus* (Fig. 2). There were no *Jasus* in 24 of the 40 quadrats, and the density of *Evechinus* in these quadrats ranged from 7 to 135 individuals per quadrat.

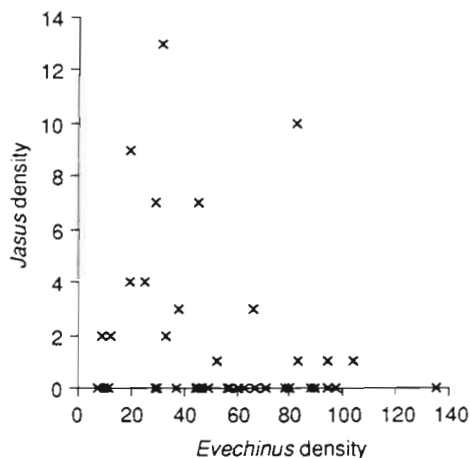


Fig. 2. *Jasus edwardsii*. Day-time density as a function of the density of *Evechinus chloroticus*, in 9 m² quadrats at Inner Tabletop reef, $n = 40$

The 'scale-free' descriptor of association used was Pielou's (1960) measure of segregation. Segregation is a measure of the likelihood that an individual will have a conspecific as its nearest neighbour. If individuals of the 2 species are segregated in space then they will have a greater probability of having a conspecific as their nearest neighbour than an individual of the other species. Framed in this way the data may be analysed using a contingency table, with segregation being synonymous with dependence. Pielou's formulation of this test required the random selection of individuals of each species to be used as 'base' individuals (individuals from which distances to nearest-neighbours are made). Because of the high density of *Evechinus* relative to *Jasus* within the 9 m² plots it was not possible to randomly select individual sea urchins. The following technique was therefore used to select 'base' individuals. For *Evechinus*, within each of the 40 plots described above, one 1 m² quadrat was randomly selected by coordinates and all sea urchins within that area assigned a number. Two individuals were then randomly selected from this group. This sampling procedure biased the sampling toward an unsegregated result as the random selection of areas (and individuals therein) would tend to select isolated sea urchins rather than those in clumps. All *Jasus* within the 9 m² plots were enumerated and one 'base' individual was randomly selected from each plot. *Evechinus* and *Jasus* at Inner Tabletop were significantly segregated in space ($\chi^2 = 59.4$, $p < 0.01$). Individuals of both species were more likely to have a conspecific as their nearest-neighbour than an individual of the other species.

Size-frequency distributions

The size-frequency distributions of *Evechinus* were bimodal at all 3 locations (Fig. 3). At all locations there was a peak in frequency between 15 and 40 mm TD (Fig. 3). All sea urchins in this size-class were cryptic. A trough in the size-frequency distribution of all 3 populations occurred between 40 and 54 mm TD. Bimodality was most extreme at Inner Tabletop where no sea urchins between 40 and 49 mm TD were found. Individuals in this size range become increasingly less cryptic, and begin to occur openly over the substratum. The second, and larger, peak was made up of sea urchins > 55 mm TD (Fig. 3).

The size-frequency distributions of *Jasus* at all locations had 3 modes (Fig. 4). The first peak was made up of lobsters < 90 mm CL, and comprised both males and females. The second peak was comprised mainly of females between 100 and 140 mm CL. The third peak, of individuals larger than 150 mm CL, was made up almost exclusively of males.

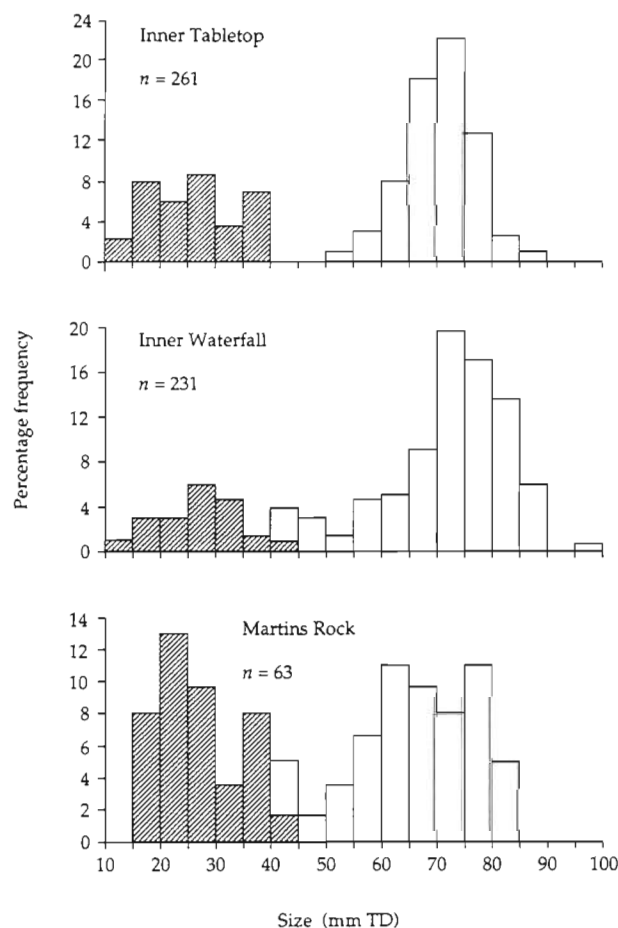


Fig. 3. *Evechinus chloroticus*. Size-frequency distributions at the 3 study sites. Hatching indicates that proportion of each size-class that was found within crevices as opposed to occurring openly on the substratum

Movement

Direction and distance moved by *Evechinus* were estimated by triangulation (Underwood 1977). Twenty sea urchins were haphazardly selected at each location and tagged with colour-coded sleeves of electrical wire fitted over a spine. In order to estimate the degree of periodicity of movement, the positions of tagged individuals were plotted on the morning of 15 May 1984 (between 08:00 and 10:00 h) and in the afternoon of the same day (15:30 to 17:30 h). Their positions were plotted again the following morning.

There were no significant differences among locations in the net distance moved by individuals between morning and evening on the same day ($F_{(2,57)} = 2.47$, ns). The mean net distance moved by sea urchins between morning and afternoon on the same day, pooled across locations, was 8.6 cm (SE = 0.93, $n = 60$).

When the positions of individuals were compared over a 24 h period, there were, again, no significant

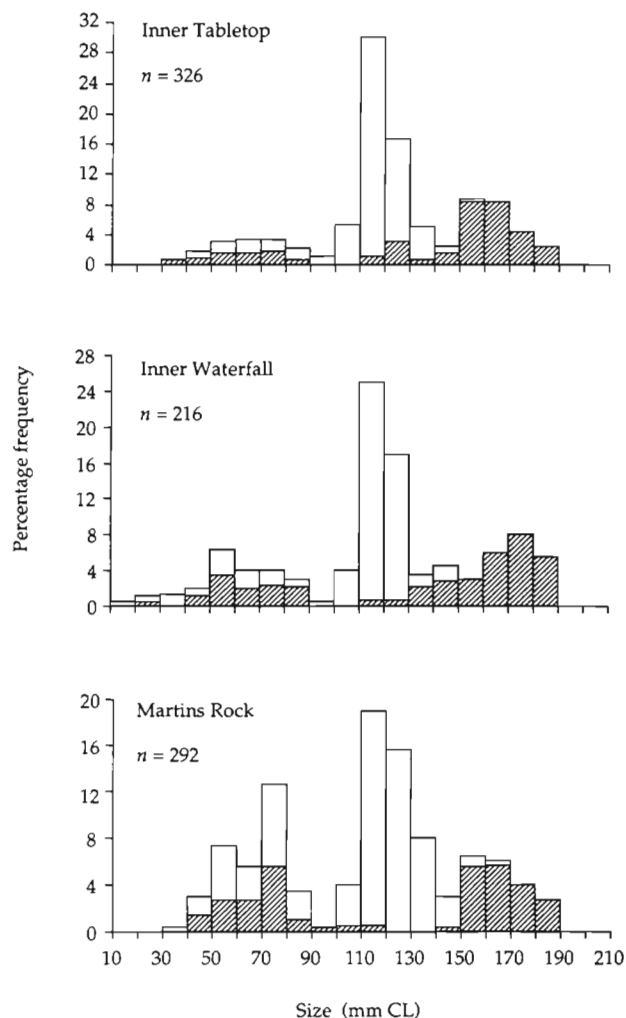


Fig. 4. *Jasus edwardsii*. Size-frequency distribution at the 3 study sites. Hatching indicates that proportion of each size-class that were males

differences among locations in the net distance moved ($F_{(2,57)} = 0.62$, ns). The mean net distance moved overnight, pooled across locations, was 34.2 cm (SE = 4.05, $n = 60$). Of the 60 individuals whose positions were plotted, 16 moved less than 10 cm over the 24 h period. Of these 16 individuals, 11 originally were attached to pieces of drift *Ecklonia*, and none of these moved off the *Ecklonia*. The remaining 5 individuals that did not move were deep in cracks or crevices. All individuals originally exposed and not attached to drift algae moved at least 10 cm overnight. The hypothesis of non-random movement of sea urchins was tested using the circular statistic Z (Batschelet 1981). The null hypothesis of random movement could not be rejected at any location (Table 2), which suggests that individual sea urchins were responding to very localised cues rather than larger phenomena such as swell direction or water currents.

Table 2. *Evechinus chloroticus*. Summary of circular and arithmetic (net distance moved) statistics for movement of sea urchins from 3 locations. $n = 60$ for all arithmetic statistics. All distances moved are shown in cm

Location	n	r	Circular			Arithmetic	
			Angle	Z	Prob.	Mean	SE
Inner Tabletop	19	0.33	337	2.05	ns	33	7.8
Inner Waterfall	20	0.29	305	1.66	ns	29	5.7
Martin's Rock	18	0.17	114	0.54	ns	40	8.0

Laboratory experiments

All laboratory experiments described were done at the Leigh Marine Laboratory between March and early June 1984. Lobsters and sea urchins were collected from adjacent reefs immediately prior to the experiments. The tanks shared the same continuous supply of seawater and were $1.5 \times 1.2 \times 0.3$ m in dimension. Several experiments were done and each will be described separately. Because female *Jasus* moult and do not feed at the time of year these experiments were done (MacDiarmid 1991), only males were used.

Limits on size of sea urchins eaten

The first experiment was designed to provide preliminary data on the size range of *Evechinus* eaten by spiny lobsters. Four size-classes of *Evechinus* were chosen for this experiment: 10–29, 30–49, 50–69, and 70–90 mm TD. *Jasus* were arbitrarily divided into 4 size-

ment began on 6 March 1984 and ran for 40 d, the second lasted 56 d and ran between 11 January and 6 March 1985. Survivorship was monitored every second day and any dead sea urchins were removed from the tanks. An a priori decision was made to end the experiments when no spiny lobster had fed for 1 wk.

The largest *Jasus* ate all sizes of sea urchins (Table 3) and did so within 14 d of the beginning of the first trial. In the second trial 20% of sea urchins remained uneaten at the end of the experiment, all > 50 mm TD. In both trials all sea urchins ≤ 29 mm TD were eaten in the first 2 d. All sea urchins between 30 and 49 mm TD were eaten within 6 and 22 d respectively. The smallest size-class of lobsters ate only the smaller sea urchins, and did not successfully attack the larger sea urchins in the 30–49 mm TD size-class (Table 3). Small *Jasus* (40–69 mm CL) consumed only 57.5% of sea urchins in the first trial and 75% in the second (Table 3). The order in which *Jasus* ate *Evechinus* suggested that, when available, sea urchins were consumed in order of increasing size.

The method used by *Jasus* to attack *Evechinus* varied with the size of both the lobster and sea urchin. The largest lobsters ingested the entire sea urchin. In tanks with *Jasus* > 130 mm CL only 1 of 40 tests was left at the end of the first trial and none remained at the end of the second; the rest were completely consumed (Table 3). The smallest (< 30 mm TD) sea urchins were picked up and held in the first walking legs and maxillapeds while being crushed by the mandibles. Typically, *Jasus* attacked *Evechinus* larger than 50 mm TD by upturning them and piercing the peristomial mem-

Table 3. *Jasus edwardsii* and *Evechinus chloroticus*. Summary of results from the 2 trials of the 'size limits' experiment. Data from the second trial are presented in brackets beside those for the first trial. Shown for each size-class of *Jasus* are: percentage of *Evechinus* eaten, sizes of largest *Evechinus* eaten, percentage of tests remaining after attack, and percentage of tests that were intact (i.e. entry was via the peristomial membrane only). Sizes of *Evechinus* are in mm TD

Size of <i>Jasus</i> (mm CL)	% of urchins eaten	Largest urchin eaten	% Tests left	% Tests left intact
> 130	100 (80)	89 (85)	3 (0)	0 (0)
100–130	58 (75)	77 (75)	9 (3)	100 (0)
70–99	75 (78)	74 (74)	70 (23)	77 (86)
40–69	43 (33)	65 (34)	40 (39)	88 (100)

classes: 40–69, 70–99, 100–130, and > 130 mm CL. Five individuals of each size-class of spiny lobster (one size-class per tank) were placed in a tank with 10 of each size-class of sea urchins. Shortage of tanks large enough to accommodate spiny lobsters meant that this experiment had to be done in 2 trials in order to replicate the experimental treatments. All treatments were present in both trials and treatments were randomly allocated to tanks. The first trial of the experi-

ment began on 6 March 1984 and ran for 40 d, the second lasted 56 d and ran between 11 January and 6 March 1985. Survivorship was monitored every second day and any dead sea urchins were removed from the tanks. An a priori decision was made to end the experiments when no spiny lobster had fed for 1 wk.

Influence of shelter on consumption of *Evechinus*

In the field, sea urchins less than ca 35 mm TD are cryptic (Fig. 3), which serves to lower their availability to spiny lobsters. In light of this information, an experiment was designed to test whether the availability of juvenile *Evechinus* affects the rate at which larger sea urchins were preyed upon. Five spiny lobsters (110 to 140 mm CL) were used per tank. This size range represents the majority of lobsters in the SBR habitat (Fig. 4). Ten *Evechinus* of each of the size classes previously described were placed in each tank. In 2 of the 4 tanks shelter was provided in the form of broken concrete building blocks. The 2 smaller size classes of *Evechinus* (10–29 and 30–49 mm TD) used these building blocks as shelters. The experiment was run in 2 trials, each lasting 4 d. Treatments were randomly assigned to tanks in each trial. At the completion of each trial all lobsters except one per tank were returned to the field. One individual was retained per tank as it was found that the presence of a 'calm' individual provided a steadying influence on freshly caught specimens.

Differences in the number of sea urchins surviving were analysed by 2-factor analyses of variance with the factors Shelter (fixed, +/–) and Trial (nested within Shelter). The analysis was repeated for each of the 5 size-classes of *Evechinus*. In all cases there was no

approximating that in the field, did not mean that lobsters ate significantly more larger sea urchins (Table 4A).

Influence of gastropods on consumption of *Evechinus*

Information on the diet of *Jasus* (J. McKoy & C. Wilson, N.Z. Fisheries Research Centre, pers. comm.) suggests that herbivorous gastropods may be an important component of the diet of spiny lobsters. To test whether the presence of herbivorous gastropods affected the rate at which *Evechinus* were eaten by *Jasus*, the 'shelter' experiment was repeated, this time with gastropods in all tanks. Three species of gastropod were chosen for this experiment: *Cookia sulcata*, *Trochus viridus*, and *Cantharidus purpureus*, all of which were abundant within the SBR habitat (Table 1). These gastropods, along with sea urchins in size-classes as described for the previous experiment, were placed in tanks with 5 lobsters (110 to 140 mm CL). Five individuals of each species of gastropod and size-class of sea urchin provided in each tank.

The experiment used the same 2-factor design as before: Shelter (fixed, +/–) and Trials (nested within Shelter). This experiment was run in 3 trials. Again, there was no significant difference among trials ($p > 0.25$) and they were pooled for further analysis

Table 4. Percentage of *Evechinus chloroticus* and gastropods in laboratory experiments. A: Survivorship of *Evechinus* in the 'shelter' experiment, no gastropods present; B: survivorship of *Evechinus* and gastropods in the 'gastropod' experiment. Data are presented as mean survivorship after 4 d (\pm SE, $n = 6$). Sizes of *Evechinus* are in mm. ** Significant ($p < 0.01$ by F -test) differences in survivorship between treatments. All other tests were non-significant

Species/size	A		B	
	Shelter	No shelter	Shelter	No shelter
<i>Evechinus</i>				
10–29 mm TD	72 \pm 4.7	** 10 \pm 4.1	73 \pm 4.2	** 0 \pm 0
30–49	72 \pm 8.5	** 28 \pm 4.8	73 \pm 4.2	** 10 \pm 6.8
50–69	80 \pm 0	83 \pm 6.3	80 \pm 5.2	60 \pm 10.3
70–90	88 \pm 6.3	95 \pm 5.0	83 \pm 8.0	80 \pm 8.9
<i>Cookia sulcata</i>	–	–	27 \pm 4.2	20 \pm 5.1
<i>Trochus viridus</i>	–	–	0 \pm 0	7 \pm 6.6
<i>Cantharidus purpureus</i>	–	–	0 \pm 0	0 \pm 0

significant effect attributable to Trial ($p > 0.25$) and trials were therefore pooled for further analysis ($F_{(1,4)}$) and presentation ($n = 4$).

The presence of shelter significantly increased the survivorship of small (< 50 mm TD) *Evechinus* (Table 4A). The presence of shelter did not completely prevent predation on these smaller sea urchins as an average of 28 % of both the 10–29 and 30–49 mm TD size-classes were eaten (Table 4A). The relative non-availability of the 2 lower size classes, a situation

($F_{(1,6)}$) and presentation ($n = 6$). The experimental procedures used were the same as for the 'shelter' experiment described above.

The presence of gastropods in tanks with shelter had little effect on the survivorship of small *Evechinus* (Table 4B). As in the previous experiment, the reduced availability of the 2 smaller size-classes of *Evechinus* in tanks with shelter did not mean that significantly more of the larger sea urchins were eaten, even in the presence of gastropods (Table 4). Gastropods were not

observed in the shelters and were eaten at similar rates in tanks with and without shelter (Table 4B). All *Cantharidus purpureus* and *Trochus viridus* were eaten within 2 d.

Spiny lobsters attacked *Cookia sulcata* by chipping away the lip of the shell until they gained access to tissue behind the operculum. The majority of uneaten *C. sulcata* at the completion of the experiment had part of their shell chipped in this manner. Those that remained were invariably the largest in each tank and, overall, had a mean shell length of 41.3 (SE = 1.91, $n = 14$). We did not observe how *Cantharidus purpureus* or *Trochus viridus* were attacked.

Field experiment

The influence of the removal of prey species and macro-algae on the abundance of *Jasus* was investigated by field experimentation. Twelve 100 m² plots within the SBR habitat were chosen in the eastern part of the marine reserve that contained large numbers of spiny lobsters, sea urchins and macro-algae. In 4 plots all sea urchins and gastropods, with the exception of the limpet *Cellana stellifera*, were removed. In another 4 plots, all large brown algae (*Ecklonia radiata*, *Sargassum sinclairii*, and *Carpophyllum* spp.) were removed. The remaining 4 plots were left untouched. Treatments were randomly assigned to plots.

Differences in the abundance of algae and prey were analysed by 2-factor analyses of variance: Treatment (fixed) and Plot (nested within Treatment). The abundances of algae and prey were estimated by 10 haphazardly tossed 1 m² quadrats within each of the experimental plots. Differences among treatments and plots were analysed at the beginning of the experiment. These analyses used all 3 treatments (control, algal-removal, prey-removal), giving (2,9) df for the *F*-test on Treatment and (9,108) df for the test on Plot. Analyses of these variables at the end of the experiment used only 2 of the treatments, giving (1,6) and (6,72) df for the *F*-tests. Differences in the abundance of prey species (gastropods and sea urchins) were not sought in plots from which they were excluded. The abundance of spiny lobsters was estimated as numbers per plot. Differences in the abundance of lobsters were analysed by a single factor analysis of variance using all 3 treatments [giving (2,9) df both at the start and end of the experiment].

At the beginning of the experiment, total numbers of spiny lobsters were counted, and the volume of available shelter in each plot estimated. The size of potential shelters was estimated by measuring the height, width, and depth of all caves, crevices, and holes judged to be suitable for sheltering lobsters larger than 50 mm CL.

Correlations were tested between the number of lobsters and shelter, total prey abundance, and sea urchin abundance in each of the experimental plots. Large brown algae and prey species were removed from appropriate plots several days after these initial counts, and the clearances maintained monthly thereafter. The experiment ran from August 1984 to January 1985. Total numbers of spiny lobsters in each plot were counted at monthly intervals, and the density of prey species and large brown algae were estimated in August and October 1984, and January 1985.

At the beginning of the experiment, the abundance of spiny lobsters and the volume of shelter in a plot were significantly correlated ($r_{(10)} = 0.63$, $p < 0.05$). There was no significant relationship between the initial density of *Jasus* and the initial density of sea urchins ($r_{(10)} = 0.38$, ns), *Jasus* and large brown algae ($r_{(10)} = 0.12$, ns), and *Jasus* and total prey species ($r_{(10)} = 0.38$, ns).

The removal of large brown algae or prey did not influence the abundance of *Jasus* over the 5 mo experimental period (Fig. 5). There was no significant difference in the abundance of spiny lobsters among experimental treatments in August 1984 ($F_{(2,9)} = 0.52$, ns) or January 1985 ($F_{(2,9)} = 0.72$, ns). All treatments showed similar increases in abundance from initial levels to peak densities in October 1984, and then density declined in all treatments until the end of the experiment (Fig. 5). The size-frequency and sex ratio of spiny lobsters in the experimental plots showed the same seasonal changes as described for other areas of SBR habitat (MacDiarmid 1991).

At the beginning of the experiment there were no significant differences in the abundance of large brown algae among treatments ($F_{(2,9)} = 3.37$, ns, square-root transformed). At the end of the experiment, in January

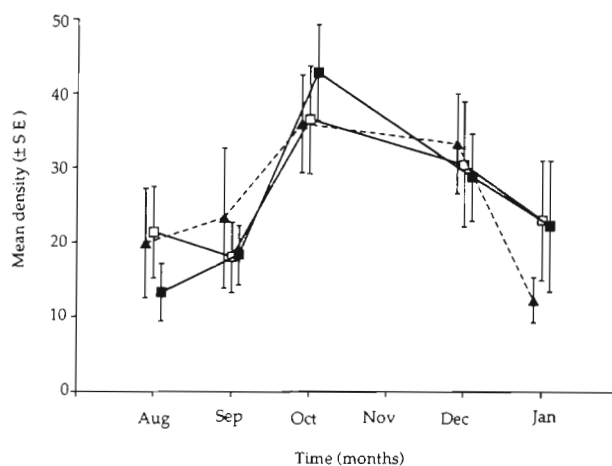


Fig. 5. *Jasus edwardsii*. Mean abundance (\pm SE, $n = 4$) per 100 m² through time in response to experimental treatments. (□) Controls; (▲) prey removals; (■) algal removals

1985, the abundance of large brown algae in the prey removal plots had risen to be significantly greater than in the control plots ($F_{(1,6)} = 6.96$, $p < 0.05$; Fig. 6). These differences were over and above significant differences among plots in the abundance of large brown algae, both at the start of the experiment ($F_{(9,108)} = 3.72$, $p < 0.001$; Fig. 6), and between the control and prey removal treatments at the end ($F_{(6,72)} = 2.80$, $p < 0.05$; Fig. 6).

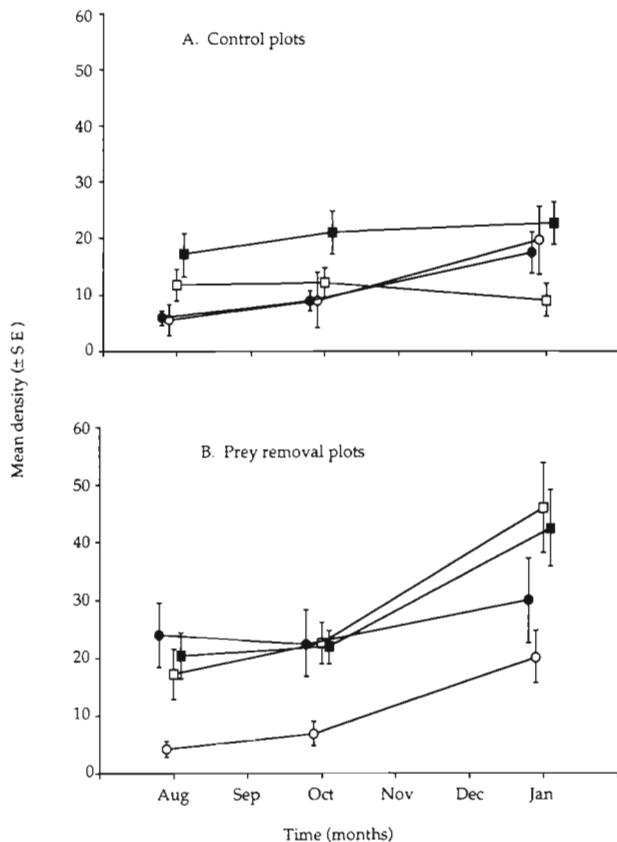


Fig. 6. Mean abundance ($n = 10$) of large brown algae in each of 4 plots from (A) Control and (B) Prey-removal treatments as a function of time. Shown are results for each of the 4 replicate plots

At the beginning of the experiment there were significant differences in the combined abundance of prey species among treatments ($F_{(2,9)} = 2.80$, $p < 0.05$; Fig. 6).

At the beginning of the experiment there were significant differences in the combined abundance of prey species among treatments ($F_{(2,9)} = 9.49$, $p < 0.01$; Fig. 7). At the end of the experiment there were no significant differences between the algal removal treatments and control plots ($F_{(1,9)} = 0.35$, ns; Fig. 7). The combined abundance of prey species significantly differed among plots, both at the start of the experiment ($F_{(9,108)} = 3.18$, $p < 0.01$) and at its end, in January 1985 ($F_{(6,72)} = 5.24$, $p < 0.01$; Fig. 7).

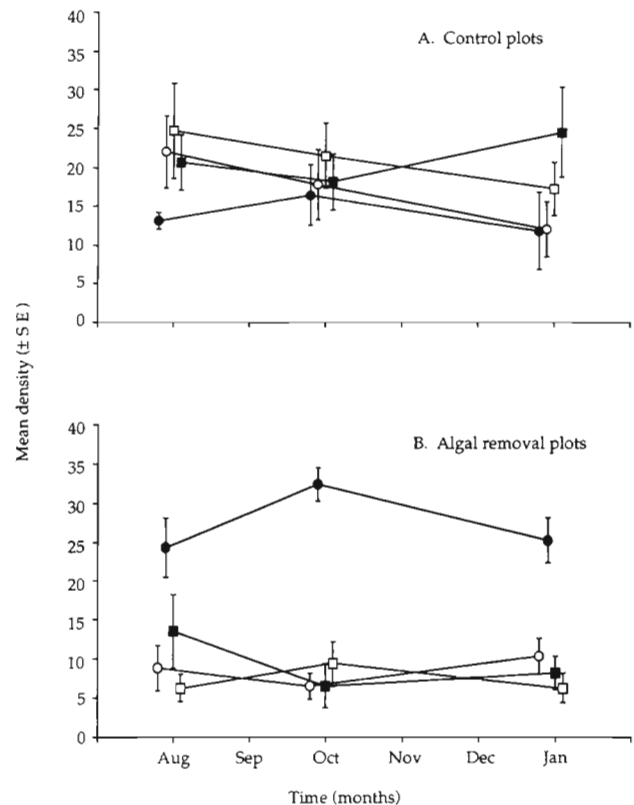


Fig. 7. Mean abundance ($n = 10$) of prey species in each of 4 plots from (A) Control and (B) Algal-removal treatments as a function of time. Shown are results for each of the 4 replicate plots

DISCUSSION

Before assessing the impact of predation by lobsters on populations of sea urchins it must first be established that the 2 species co-occur, that movements bring individuals of the species into contact, and that the sea urchin is a natural prey of the lobster. In northeastern New Zealand these necessary preconditions are satisfied in the SBR habitat. In this habitat both species are abundant and although segregated in space, are separated only by small distances. During daylight hours *Jasus* were found beneath boulders and in large crevices. *Evechinus* occupied both open areas of reef and the basal substratum among large boulders. These day-time patterns of distribution were relatively static as both species moved relatively little during the day. Both species were active at night, and *Jasus* in particular was capable of moving considerable distances [median of 41 m per night (MacDiarmid et al. in press)]. Spiny lobsters move predominantly along gutters and across boulder fields; areas where sea urchins were most abundant. We conclude that sea urchins were within the foraging range of spiny lobsters in the SBR habitat.

The net movement of *Evechinus* reported in this study in the SBR habitat was about half that described in the barrens habitat (Andrew & Stocker 1986). These data are consistent with 2 hypotheses: first, that sea urchins move greater distances in habitats with no lobsters than in those in which lobsters are abundant (e.g. Bernstein et al. 1981, 1983, Tegner & Dayton 1981, Tegner & Levin 1983, Mann et al. 1984, Vadas et al. 1986); second, that sea urchins are more active in areas where large brown algae are scarce (see also Mattison et al. 1977, Russo 1979, Harrold & Reed 1985, Andrew & Stocker 1986, Vadas et al. 1986). In the Sediment Flat habitat, which has abundant macroalgae, but no spiny lobsters, Andrew & Stocker (1986) found rates of movement of *Evechinus* similar to that observed in the SBR habitat in this study. We suggest that, given the cessation of movement of sea urchins when they encounter drift algae, these differences in the movement rates of sea urchins between the barrens and SBR habitat are largely due to the relative abundance of macroalgae rather than spiny lobsters.

We have established that *Jasus* can consume *Evechinus* in the laboratory. Moreover, broken sea urchin tests were often found in the dens of spiny lobsters, and the remains of *Evechinus* are common in the stomachs of lobsters from the marine reserve (J. L. McKoy & C. Wilson pers. comm.). The method of attack described here for *Jasus* is similar to that outlined by Tegner & Levin (1983) for *Palinurus interruptus* and stronglylocentrid sea urchins. Small sea urchins were completely consumed, whereas larger sea urchins were broken open and most of the skeletal material left uneaten. The presence of gastropods did not greatly influence the rate at which small sea urchins were consumed. The small gastropod *Cantharidus purpureus* was also eaten quickly. In the SBR habitat *C. purpureus* were most abundant on the laminae of the laminarian alga *Ecklonia radiata*. In other habitats this species is usually exposed on the substratum (Andrew & Choat 1982). It would be profitable to explore any relationship that may exist between the survivorship of *C. purpureus* and the availability of *E. radiata* as a refuge from predation by *Jasus*.

What evidence is there for a regulatory effect by *Jasus* on the abundance of *Evechinus*? Spiny lobsters are scarce in areas of barrens habitat where *Evechinus* are found in great numbers and sea urchins are largely absent from *Ecklonia* forests and on reefs deeper than approximately 12 m where spiny lobsters are abundant (Ayling 1978, Andrew & Choat 1982, 1985, Choat & Schiel 1982, MacDiarmid 1987). This pattern is also consistent with interpretations that do not rely on a regulatory role for lobsters (see Vadas et al. 1986, Garnick 1989 for recent discussions). Few juvenile sea urchins are found in *Ecklonia* forests and in deep

water, and experimental translocation of juvenile *Evechinus* into those habitats results in very high mortality (Andrew & Choat 1985).

The large trough in the size-frequency distributions of populations of sea urchins noted in this and previous studies (Andrew & Choat 1982, Choat & Schiel 1982) coincides with the ontogenetic shift in behaviour of juvenile *Evechinus* from being cryptic to being exposed. Andrew & Choat (1982) argued that the bimodality in sea urchin size-frequency distribution found in the barrens habitat they studied was largely attributable to benthic-feeding predatory fishes, which are also present in the SBR habitat (MacDiarmid 1989). Similar bimodality, also attributed to predation, has been observed in the size-frequency distribution of *Strongylocentrotus franciscanus* (Tegner & Dayton 1981, Tegner & Levin 1983). Andrew & Choat (1982) argued that predation by fishes was insufficient to lead to the disappearance of the barrens habitat. *Jasus* were not found in this habitat (MacDiarmid 1987) and were not observed to forage in these areas (Andrew & Choat 1982, pers. obs.).

The laboratory experiments described here indicate that any regulatory effect that *Jasus* may have on the abundance of *Evechinus* is most likely to occur as sea urchins lose their cryptic habit. For *Evechinus* smaller than 50 mm TD there is refuge in size only from the smallest spiny lobsters. The cryptic habit of *Evechinus* less than ca 40 mm TD greatly reduces the availability of these sea urchins to a range of predators, including spiny lobsters. As sea urchins between 40 and 50 mm TD move out into the open they greatly increase their vulnerability to predation, and over 80 % of *Jasus* were capable of taking *Evechinus* within this size range. In the areas sampled over 90 % of sea urchins greater than 50 mm TD are found openly on the substratum and therefore were vulnerable to attack from at least 45 % of spiny lobsters (individuals larger than 120 mm CL).

The effects of predation by *Jasus* on *Evechinus* will be constrained by temporal variations in the abundance and feeding behaviour of lobsters. *Jasus* undergo seasonal inshore-offshore movements in relation to moulting and reproduction (MacDiarmid 1991). The estimate of abundance of *Jasus* given here is close to the 3 yr average for this site (1982 to 1985, 8.61 ± 0.76 per 100 m²; MacDiarmid 1987). The greatest densities of both mature female and male lobsters in the SBR habitat coincide with the times they moult; females in May and males in October (MacDiarmid 1989, 1991). Spiny lobsters do not feed for up to 44 d before and 34 d after they moult (Zoutendyk 1988). The greatest impact spiny lobsters can be expected to have on populations of sea urchins in the SBR habitat will be in spring (from juveniles and mature females), and in summer from all sizes and sexes of lobster.

The fine-scale segregation of *Jasus* and *Evechinus* within this habitat may be produced by differing microhabitat requirements of the species and/or predation. Spiny lobsters do not spread out evenly over the reef at night as they forage, but rather remain non-randomly dispersed in response to topographic features (MacDiarmid et al. in press). Predation would be expected to be greatest close to the day-time shelters of lobsters, thereby producing 'halos' in which sea urchins are less abundant. In the present study we found no negative correlation between the 2 species on a scale of 9 m², making it impossible to separate any effect *Jasus* may have on the dispersion of *Evechinus* from microhabitat preferences. Both processes would cause an increase in the variance associated with estimates of the mean abundance of sea urchins.

Results from the field experiment reported here suggest that the abundance of spiny lobsters is largely determined by the availability of suitable shelter. Neither the extra habitat complexity provided by large brown algae nor the availability of sea urchins and gastropods appeared important in determining the local abundance of spiny lobsters at a scale of 100 m². This conclusion suggests that the model proposed by Garnick (1989) for the inverse abundance patterns of sea urchins and clawed lobsters in Nova Scotia (Canada) is not appropriate to northeastern New Zealand. Garnick argues that, because of their generalized diet, food is unlikely to be a limiting resource for *Homarus americanus*. He proposes that observed patterns of abundance are better explained by variations in the availability of shelter and that shelter is a more likely limiting resource for this solitary dwelling species. Although we have no experimental evidence to support or refute such a model in northeastern New Zealand, we suggest that the gregarious nature of *Jasus* (MacDiarmid 1987) and the differing microhabitat requirements of *Evechinus* and *Jasus* are sufficient that competition for shelter would not be limiting.

Clearly spiny lobsters eat *Evechinus* but we suggest that predation by *Jasus* is not of sufficient magnitude to substantially alter sea urchin population size and the structure of the SBR habitat. The necessary test to reject the hypothesis that *Jasus* has a substantial impact on the abundance of *Evechinus* remains undone. Such a test would require the experimental exclusion of lobsters from a number of areas large enough for adult sea urchins to forage normally (ca 25 m²), for a period of at least 1 yr. Like other researchers, we found this requirement logistically unfeasible. Until such an experiment has been done in this system, the direct effects of predation by *Jasus* on *Evechinus* remain undescribed.

Based on the present study and others on the ecology of sea urchins and spiny lobsters in northeastern New

Zealand, we suggest that changes in the abundance of one species (for whatever reason) would not lead to changes in the local abundance of the other. Differing microhabitat requirements of sea urchin and spiny lobsters would act to dislocate any relationship between the abundance of the 2 species. In areas with sufficient shelter for spiny lobsters, both species may be abundant. However, the more restrictive shelter requirements of *Jasus* means that they are not found in areas where sea urchins may be abundant.

Acknowledgements. We thank Laura Stocker and Barbara Hickey for assistance in the field and Tom Wustenburg for providing a continuous supply of seawater. The manuscript was improved by the constructive comments of Mike Kingsford. We thank the University of Auckland's Marine Laboratory at Leigh for support. N.L.A. was funded by the Management Division of the N.Z. Ministry of Agriculture and Fisheries. A.B.McD. was funded by a research grant from the N.Z. Ministry of Agriculture and Fisheries, Fisheries Research Centre.

LITERATURE CITED

- Andrew, N. L. (1988). Ecological aspects of the common sea urchin, *Evechinus chloroticus*, in northern New Zealand; a review. N.Z. J. mar. Freshwat. Res. 22: 415–426.
- Andrew, N. L., Choat, J. H. (1982). The influence of predation and conspecific adults on the survivorship of juvenile *Evechinus chloroticus* (Echinoidea: Echinometridae). Oecologia (Berl.) 54: 80–87.
- Andrew, N. L., Choat, J. H. (1985). Habitat related differences in the growth and survivorship of juvenile echinoids. Mar. Ecol. Prog. Ser. 27: 155–161.
- Andrew, N. L., Stocker, L. J. (1986). Dispersion and phagokinesis in the echinoid *Evechinus chloroticus* (Val.). J. exp. mar. Biol. Ecol. 100: 11–23.
- Ayling, A. M. (1978). Cape Rodney to Okakari Point Marine Reserve: a biological survey. University of Auckland Marine Laboratory, Leigh, New Zealand. University of Auckland Bindery.
- Ballantine, W. J. (1987). New Zealand's course for marine reserves. New Scientist. 1563: 54–55.
- Barkai, R., Branch, G. M. (1988). Energy requirements for a dense population of rock lobsters *Jasus lalandii*: novel importance of unorthodox food sources. Mar. Ecol. Prog. Ser. 50: 83–96.
- Batschelet, E. (1981). Circular statistics in biology. Academic Press, London.
- Bernstein, B. B., Schroeter, S. C., Mann, K. H. (1983). Sea urchin (*Strongylocentrotus droebachiensis*) aggregating behaviour investigated by a subtidal multifactorial experiment. Can. J. Fish. Aquat. Sci. 40: 1975–1986.
- Bernstein, B. B., Williams, B. E., Mann, K. H. (1981). The role of behavioural responses to predators in modifying urchins' (*Strongylocentrotus droebachiensis*) destructive grazing and seasonal foraging patterns. Mar. Biol. 63: 39–49.
- Breen, P. A. (1987). Comments on 'Seaweeds, sea urchins, and lobsters: a reappraisal' by R. J. Miller. Can. J. Fish. Aquat. Sci. 44: 1807–1809.
- Breen, P. A., Mann, K. H. (1976). Destructive grazing of kelp by sea urchins in eastern Canada. J. Fish. Res. Bd Can. 33: 1278–1283.
- Chapman, A. R. O. (1981). Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's bay, eastern Canada. Mar. Biol. 62: 307–311.

- Choat, J. H., Schiel, D. R. (1982). Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. *J. exp. mar. Biol. Ecol.* 60: 129–162
- Cooper, R., Ellis, R., Serfling, S. A. (1975). Population dynamics, ecology and behaviour of spiny lobsters *Panulirus argus* of St John, Virgin Islands, U.S.A. Part 3: Population estimation and turnover rates. *Nat. Hist. Mus. Los Angeles City Sci. Bull.* 20: 23–30
- Davis, G. E. (1977). Effects of recreational harvest on a spiny lobster *Panulirus argus* population. *Bull. mar. Sci.* 27: 223–236
- Elner, R. W. (1980). Predation on the sea urchin (*Strongylocentrotus droebachiensis*) by the American lobster *Homarus americanus* and the rock crab (*Cancer irroratus*). In: Pringle, J. D., Sharp, G. J., Caddy, J. F. (eds.) Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal harvesting. *Can. Tech. Rep. Fish. Aquat. Sci.* 954: 48–65
- Elner, R. W., Campbell, A. (1987). Natural diets of lobster *Homarus americanus* from barren ground and macroalgal habitats off southwestern Nova Scotia, Canada. *Mar. Ecol. Prog. Ser.* 37: 131–140
- Garnick, E. (1989). Lobster (*Homarus americanus*) population declines, sea urchins, and 'barren grounds': a space-mediated competition hypothesis. *Mar. Ecol. Prog. Ser.* 58: 23–28
- Harrold, C., Reed, D. C. (1985). Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* 66: 1160–1169
- Herrnkind, W. F., Vanderwalker, J., Barr, L. (1975). Population dynamics, ecology and behaviour of spiny lobsters *Panulirus argus* of St John, U.S. Virgin Islands: habitation and patterns of movement. *Nat. Hist. Mus. Los Angeles City Sci. Bull.* 20: 31–45
- Jernakoff, P. (1987). Foraging patterns of juvenile western rock lobsters *Panulirus cygnus* George. *J. exp. mar. Biol. Ecol.* 113: 125–144
- Jernakoff, P., Phillips, B. F., Maller, R. A. (1987). A quantitative survey of nocturnal foraging distances of the western rock lobster *Panulirus cygnus*. *J. exp. mar. Biol. Ecol.* 113: 9–21
- Keats, D. W. (1986). Comment on 'Seaweeds, sea urchins, and lobsters: a reappraisal' by R. J. Miller. *Can. J. Fish. Aquat. Sci.* 43: 1675–1676
- Lawrence, J. M. (1975). On the relationships between marine plants and sea urchins. *Oceanogr. mar. Biol. A. Rev.* 13: 213–286
- Lawrence, J. M., Sammarco, P. W. (1982). Effects of feeding on the environment: echinoidea. In: Jangoux, M., Lawrence, J. M. (eds.) Echinoderm nutrition. A. A. Balkema, Rotterdam, p. 499–519
- Lawton, P. (1987). Diel activity and foraging behaviour of juvenile American lobsters, *Homarus americanus*. *Can. J. Fish. Aquat. Sci.* 44: 1195–1205
- MacDiarmid, A. B. (1987). The ecology of *Jasus edwardsii* (Hutton) (Crustacea: Palinuridae). Ph.D. thesis, University of Auckland, New Zealand
- MacDiarmid, A. B. (1989). Moulting and reproduction of the spiny lobster *Jasus edwardsii* (Decapoda: Palinuridae) in northern New Zealand. *Mar. Biol.* 103: 303–310
- MacDiarmid, A. B. (1991). Seasonal changes in depth distribution, sex ratio and size frequency of the spiny lobster *Jasus edwardsii* on a coastal reef in northern New Zealand. *Mar. Ecol. Prog. Ser.* 70: 129–141
- MacDiarmid, A. B., Hickey, B., Maller, R. A. (in press). Daily movement patterns of the spiny lobster *Jasus edwardsii* (Hutton) on a shallow reef in northern New Zealand. *J. exp. mar. Biol. Ecol.*
- Mann, K. H. (1977). Destruction of kelp-beds by sea urchins: a cyclical phenomenon or irreversible degradation? *Helgoländer wiss. Meeresunters.* 30: 455–467
- Mann, K. H., Wright, J. L. C., Welsford, B. E., Hatfield, E. (1984). Responses of the sea urchin *Strongylocentrotus droebachiensis* (O. F. Müller) to water-borne stimuli from potential predators and potential food algae. *J. exp. mar. Biol. Ecol.* 79: 233–244
- Mattison, J. E., Trent, J., Shanks, A., Akin, T. B., Pearse, J. S. (1977). Movement and feeding activity of red sea urchins (*Strongylocentrotus franciscanus*) adjacent to a kelp forest. *Mar. Biol.* 39: 25–30
- Miller, R. J. (1985). Seaweeds, sea urchins, and lobsters: a reappraisal. *Can. J. Fish. Aquat. Sci.* 42: 2061–2072
- Miller, R. J. (1987). Reply to comment by P. A. Breen. *Can. J. Fish. Aquat. Sci.* 44: 1806–1807
- Pielou, E. C. (1960). Segregation and symmetry in two-species populations as studied by nearest-neighbour relationships. *J. Ecol.* 49: 255–269
- Pollock, D. E. (1979). Predator-prey relationships between the rock lobster *Jasus lalandii* and the mussel *Aulacomys ater* at Robben Island on the Cape west coast of Africa. *Mar. Biol.* 52: 347–356
- Pringle, J. D. (1986). A review of urchin/macro-algal associations with a new synthesis for nearshore, eastern Canadian waters. *Monografias Biologicas* 4: 191–218
- Russo, A. R. (1979). Dispersion and food differences between two populations of the sea urchin *Strongylocentrotus franciscanus*. *J. Biogeogr.* 6: 407–414
- Schiel, D. R. (1982). Selective feeding by the echinoid *Evechinus chloroticus*, and the removal of plants from subtidal algal stands in northern New Zealand. *Oecologia (Berl.)* 54: 379–388
- Schiel, D. R., Foster, M. S. (1986). The structure of subtidal algal stands in temperate waters. *Oceanogr. mar. Biol. A. Rev.* 24: 265–307
- Smith, G. B., van Nierop, M. (1986). Abundance and potential yield of spiny lobster *Panulirus argus* on Little and Great Bahama Banks. *Bull. mar. Sci.* 39: 646–656
- Snedecor, G. W., Cochran, W. G. (1980). Statistical methods, 7th edn. Iowa State University Press, Iowa
- Tegner, M. J., Dayton, P. K. (1981). Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Mar. Ecol. Prog. Ser.* 5: 255–268
- Tegner, M. J., Levin, L. A. (1983). Spiny lobsters and sea urchins: analysis of a predator-prey interaction. *J. exp. mar. Biol. Ecol.* 73: 125–150
- Underwood, A. J. (1977). Movements of intertidal gastropods. *J. exp. mar. Biol. Ecol.* 26: 191–201
- Vadas, R. L., Elner, R. W., Garwood, P. E., Babb, I. G. (1986). Experimental evaluation of aggregation behaviour in the sea urchin *Strongylocentrotus droebachiensis*. A reinterpretation. *Mar. Biol.* 90: 433–448
- Wharton, W. G., Mann, K. H. (1981). Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic coast of Nova Scotia. *Can. J. Fish. Aquat. Sci.* 38: 1339–1349
- Zoutendyk, P. (1988). Consumption rates of captive lobster *Jasus lalandii*. *S. Afr. J. mar. Sci.* 6: 267–271