

Effects of marine reserve protection on spiny lobster (*Jasus edwardsii*) abundance and size at Tonga Island Marine Reserve, New Zealand

R.J. DAVIDSON^a, E. VILLOUTA^b, R.G. COLE^{c,*} and R.G.F. BARRIER^d

^a *Davidson Environmental Ltd., Nelson, New Zealand*

^b *Department of Conservation, Wellington, New Zealand*

^c *National Institute of Water and Atmospheric Research Ltd., Nelson, New Zealand*

^d *Department of Conservation, Nelson, New Zealand*

ABSTRACT

1. Diving surveys were undertaken to investigate the effects of marine reserve protection on spiny lobster (*Jasus edwardsii*) populations at Tonga Island Marine Reserve, northern South Island, New Zealand over a 2 year period from December 1998 to December 2000.

2. Spiny lobsters were 2.8 times more abundant overall, and mean size was 19 mm carapace length larger in shallow transects and 28 mm carapace length larger in deep transects, in the marine reserve than at adjacent fished sites. That pattern was evident despite very high variability within sites, and among sites within areas.

3. Large reproductive males were 10 times more abundant within the reserve compared to adjacent fished areas, suggesting that more eggs would be fertilized in the reserve than on the adjacent fished coast.

4. Estimates of size-specific fecundity, combined with abundances of females, suggested that almost nine times more eggs would be produced in the reserve than in fished areas.

5. Diving and commercial trapping investigations found weak trends in spiny lobster abundance consistent with gradients at reserve borders. Tagging investigations near those borders led to only one resighting of a tagged spiny lobster.

6. We estimate that the mean abundance of spiny lobster in the reserve has increased by 22%, 5 years after its establishment, indicating an annual population increase of 4.4%. Over the same period, abundance of spiny lobster outside the reserve has declined by 2.9% per annum.

7. Based on known spiny lobster movements, we suggest that marine reserves of more than 10 km length should be given priority over smaller reserves. Smaller reserves will, however, protect part of the population for at least a portion of their lifespan.

8. Previous studies of movement of *J. edwardsii* suggest that spillover from the reserve should occur, and as population density increases we predict that more spiny lobsters will move out from the reserve. Copyright © 2002 John Wiley & Sons, Ltd.

KEY WORDS: spiny lobster; temperate reefs; marine reserve; *Jasus edwardsii*; dispersal; spillover; New Zealand

*Correspondence to: National Institute of Water and Atmospheric Research Ltd., PO Box 893, Nelson, New Zealand.
E-mail: r.cole@niwa.cri.nz

INTRODUCTION

Fully protected marine reserves offer insights into the effects of harvesting on populations of marine organisms (e.g. Babcock *et al.*, 1999; Edgar and Barrett, 1999; Cole *et al.*, 2000; Willis *et al.*, 2000; Davidson, 2001). There is currently widespread interest in the use of such areas as a fishery management tool (e.g. Plan Development Team, 1990; Holland, 2000). Those interests centre on the possibility of larval export and spillover, or direct emigration of harvestable individuals from reserves (Rowley, 1994). Information on such effects is derived from few areas, and there are also few time series to indicate how rapidly effects might become discernible (Jones *et al.*, 1993; but see Kelly *et al.*, 2000). More empirical studies of reserve effects are required to assess the utility of reserve systems for augmenting fisheries.

In order to assess spillover, information on movement rates in relation to reserve borders, and the amount of time spent by the targeted species beyond reserve boundaries is required. There are several examples where spillover from reserves has either been directly measured (Alcala and Russ, 1990; Kelly *et al.*, 1999; Kelly, 2001) or is perceived to occur (Ballantine, 1991). Low abundances within reserves close to borders on contiguous shores (e.g. Cole, 1994; Willis *et al.*, 2000) are consistent with spillover (individuals within the reserve but near reserve boundaries may be susceptible to harvesting). Spillover from reserves depends critically on movement rates, and both modelling (e.g. Johst and Brandl, 1997) and empirical (e.g. Fonseca and Hart, 1996) studies in other systems suggest that dispersal may be a function of density. An increase in density of previously harvested organisms over time has been observed within numerous marine reserves (e.g. Kelly *et al.*, 2000). That may indicate population growth within, and the potential for emigration from, a marine reserve.

The long planktonic life of spiny lobsters (>9 months) means that local abundance is decoupled from recruitment, and there is evidence that larval supply may be linked to oceanography in complex ways (e.g. Chiswell and Booth, 1999). Individuals in southern New Zealand *Jasus edwardsii* populations are thought to undertake large migrations around the coast, particularly in the Stewart Island–Fiordland area (McKoy, 1983; Annala and Bycroft, 1993), but those and other studies suggest that most longshore movements are less than 5 km (Annala, 1981; McKoy, 1983; Annala and Bycroft, 1993). New Zealand *J. edwardsii* also undertake complex onshore–offshore migrations associated with moulting and reproduction (MacDiarmid, 1991; Booth, 1997; Kelly *et al.*, 1999, 2000; Kelly, 2001).

Spiny lobsters are intensively fished in many areas (Lipcius and Cobb, 1994). Several studies have shown abundances and sizes of spiny lobsters to be greater in protected areas than in near-by fished areas (e.g. MacDiarmid and Breen, 1993; Edgar and Barrett, 1999; Kelly *et al.*, 1999, 2000). Those findings suggest that some lobsters remain within unfished areas, but there is also evidence that migrations may cross reserve borders (e.g. Kelly *et al.*, 2000; Kelly, 2001). There is also recent evidence that egg production may be limited in intensively fished populations that lack large males (MacDiarmid and Butler, 1999).

The creation of numerous marine reserves throughout New Zealand has offered the opportunity to investigate the populations of many species in unharvested situations (Creese and Cole, 1995; Department of Conservation, 2001a). Few published studies from marine reserves in more southern areas exist (but see Davidson and Chadderton, 1994; Cole *et al.*, 2000; Davidson, 2001) despite there being six reserves in the South Island (Creese and Cole, 1995; Department of Conservation, 2001a). Comparisons of reserve effects among areas for the same species are rare (but see Edgar and Barrett, 1999; Kelly *et al.*, 2000). We sought to extend the geographic range over which investigations of marine reserve effects on *J. edwardsii* have been carried out.

METHODS

Study area

Tonga Island Marine Reserve is adjacent to the Abel Tasman National Park, northern South Island, New Zealand (Figure 1; centred on Tonga Island, 40° 53' S, 173° 04' E). It has been a marine reserve since November 1993, covers 1835 ha, and extends 10.5 km alongshore and 1852 m offshore (1 nautical mile) (Department of Conservation, 2001b). The subtidal environment has been described in Davidson and Chadderton (1994). Briefly, the reef comprises granite boulders up to 5 m high, which provide extremely high rugosity and the reef slopes to meet muddy sand at depths of about 12–15 m in most areas. There are small areas of isolated reef close to shore, and sandy beaches occasionally interrupt the boulders. The coast supports a relatively low biomass of seaweed, and high densities of grazing gastropods and sea urchins. Historically, the area was fished by potting and provided moderate catches in winter (V. King-Turner, commercial spiny lobster fisher, pers. comm.). It appears that relatively little illegal fishing occurs in the reserve, and recreational scuba diving is uncommon.

Surveys of abundance, size and sex ratio

Sampling was carried out during six surveys (December 1998, February 1999, May 1999, November 1999, March 2000, December 2000). During each survey, we sampled seven sites within the reserve and six sites outside the reserve (Figure 1). However, at one control site (site 2, Totaranui), no spiny lobsters were counted on any occasion. We considered that the absence of lobsters at site 2 reflected poor habitat quality, and we eliminated it from density calculations (leaving 5 control and 7 reserve sites). During each survey the

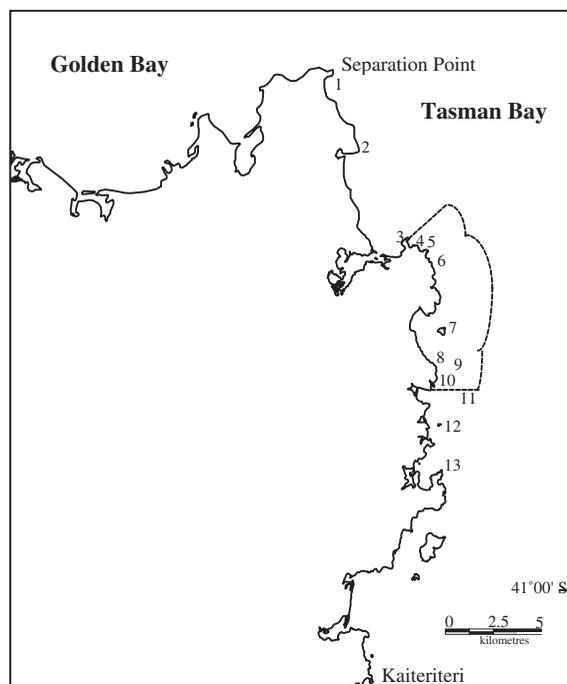


Figure 1. Map of Abel Tasman coast, showing sampling sites and reserve boundaries. Edge effect sampling was done between Foul Point (site 8) and the reserve boundary.

abundance, size and sex of spiny lobsters were sampled in 25×4 m transects ($n = 12$ transects per site). The transects were depth-stratified so that at each site six transects were counted at a depth of 6–7 m, and six were counted at 10–11 m (in December 2000, five replicate transects rather than six were sampled at each depth at each site) (see Figure 2). Transects were haphazardly placed and oriented within the depth stratum. At each site, two divers each independently counted three deep and three shallow transects (thus each diver counted six transects), using a dive torch to search crevices and under boulders, and to estimate spiny lobster sizes and confirm sex. A core group of three divers were involved in most of the surveys, and slates with scale markings were used to estimate sizes (carapace lengths, CL, in 20 mm intervals) during each count. Some spiny lobsters were unable to be sized because they were deeply concealed beneath boulders, and hence numbers of lobsters in density and size data do not correspond. Underwater visibility was at least 2 m during counts, and the transect tape was used to assist estimations of transect width.

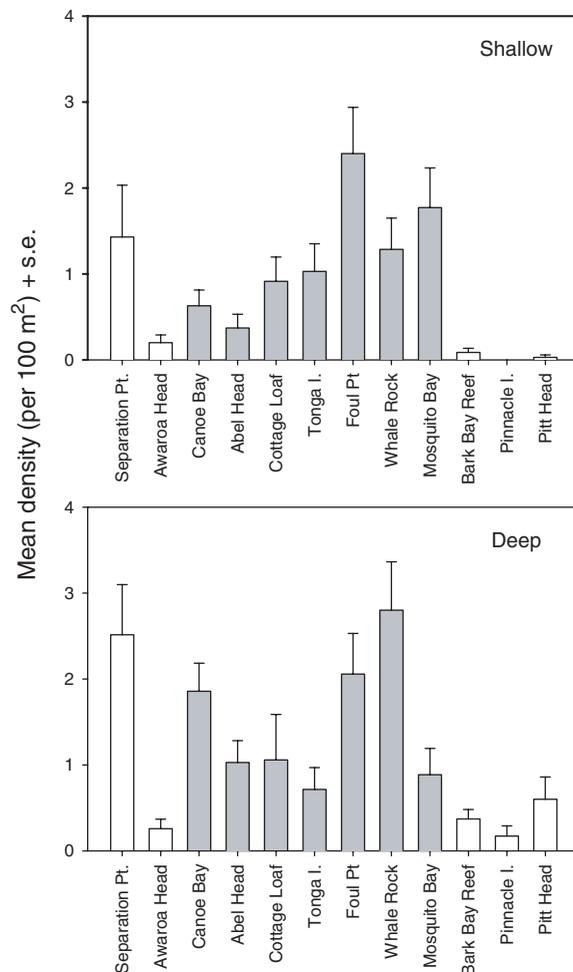


Figure 2. Mean density (per 100 m²) of spiny lobster *J. edwardsii* pooled across all sample occasions, in shallow (6–7 m) and deep (10–11 m) depth strata. Reserve sites are represented by shaded bars, control fished sites are not shaded. Error bars are 1 S.E., $n = 35$ transects per site.

Estimation of recovery rates

To investigate the time-course of recovery, we compared spiny lobster densities (pooled across sites within protection status) collected in December 1994 (12 months after the reserve was gazetted) from varying numbers of transects (between four and 12 per site) at five reserve and five control sites, with the results of our main investigation (pooled across all sampling occasions). Transect sizes in 1994 were 30×4 m, but were scaled to 100 m^2 ($25 \text{ m} \times 4 \text{ m}$) for comparison with the present study. To eliminate seasonal effects, we also separately compared the December 1994 data with the December 1998 and December 2000 data. We make both month-specific and overall comparisons to accommodate possible variation due to timing of seasonal events.

Estimates of egg production

We used a size-specific fecundity equation for *J. edwardsii* (fecundity = $0.169 \text{ CL}^{3.0091}$, MacDiarmid, 1989) to compare the estimated egg production for females between reserve and non-reserve areas. To do this, we pooled abundances of female lobsters across all surveys, in an attempt to render the results as robust as possible. We calculated the number of eggs produced by a female of the midpoint of each size class via the regression equation above, multiplied that value by the number of females for reserve and control areas (having scaled for sampling effort), and summed over all size classes, to obtain a ratio of the number of eggs produced by females inside the reserve versus females outside the reserve. Thus, we took the number of females in each size class ≥ 90 mm CL for reserve and non-reserve areas, multiplied it by the size-specific fecundity from the regression equation, and summed to estimate total egg production for the two areas, having scaled by five control sites/seven reserve sites (0.857) to account for the unequal sampling effort.

Estimation of spillover rates

Sampling at the southern edge of the reserve was undertaken to indirectly assess spillover by describing gradients of abundance into the reserve from the reserve border in more detail. We wished to focus on a gradient where abundances were high, so sampling was done at the southern end of the reserve (between sites 8 and 10; Figure 1). Fishing pressure was high there, because of ease of access. Our surveys entailed both potting with commercial spiny lobster pots and diver counts along a gradient from the reserve edge into the reserve. The fished coast outside and south of the reserve is interrupted by several sandy bays, and is unsuitable for a gradient sampling design, and therefore the gradient extended into the reserve, rather than beyond the boundary. Potting was done during September 1999 as part of a tagging study (see below). On each of two nights (16 and 17 September), a total of 25 pots was set. Five pots baited with miscellaneous fish heads were set in each of five contiguous intervals of ca. 200 m long-shore extent from the reserve southern boundary. The commercial fisher (who had fished the area prior to reserve establishment) set pots at sites he considered would provide good catches within each interval; these included one site with two pots at depths of 17–18 m, but that reef spur was linked to the main area by contiguous reef. Otherwise, pots were set at 10–12 m depth. All spiny lobsters caught were tagged after being measured and sexed, and released at the site of capture ($n = 31$; size range = 96–180 mm CL).

Further scuba surveys were carried out along the same area of coast at 100, 300, 500, 700, 900 and 1100 m into the reserve in December 1999 and March 2000, using the same tape transect sampling technique described above. Diver counts were made at the midpoint of each of the potting distance strata. Three replicate transects were sampled at each of 5 m and 6–7 m depths. Depths were constrained as rock habitat did not extend below 7 m at some sampling sites, but depth stratification was primarily used to distribute diver effort and maximize likelihood of resighting tagged lobsters.

During March 1999, scuba divers caught, tagged (using plastic antenna tags — MacDiarmid *et al.*, 1991), and released 29 spiny lobsters between 100 and 180 mm CL at five sites throughout the reserve. During the two subsequent surveys (November 1999 and March 2000) divers also recorded the presence of tags and recorded tag numbers. Preliminary trials with sonic tags found they were unable to be detected among the dense granite boulders, and having lost several expensive tags we stopped deploying them.

RESULTS

A total of 658 spiny lobsters was counted in the reserve, whereas 198 were counted at control sites. Overall, abundances within the reserve (mean = 1.34 individuals per 100 m², S.E. = 0.11, $n = 490$ transects) were almost 2.8 times greater than those at control sites (mean = 0.48 individuals per 100 m², S.E. = 0.07, $n = 350$ transects) pooled across all six surveys. Analysis of densities, produced statistically significant effects for Survey, Site(Status), and Depth*Site(Status) (Table 1). The main effect of Status was not statistically significant ($P = 0.0878$, d.f. = 1, 10). The mean square for Status was relatively large, but the test against the large Site (Status) effect was relatively weak. Differences among surveys were predicted from prior studies, and we interpret the Depth*Site(Status) effect as reflecting first the large power of the test (d.f. = 10, 746) and second a moderate effect of variable spatial patterns of differences among depths, probably a result of no lobsters being seen in some combinations.

Abundances at Separation Point (site 1) were consistently the highest of all the control sites (Table 2). There was no consistent trend among reserve sites, though Foul Point (site 8) and Whale Rock (site 9) had abundances that consistently ranked highly (Table 2). In the shallow depth stratum, few spiny lobsters were counted outside the reserve (control mean = 0.35 individuals per 100 m², S.E. = 0.13, $n = 175$ transects; reserve mean = 1.20 individuals per 100 m², S.E. = 0.14, $n = 245$ transects) (Figure 3). Differences between reserve and control areas were less clear in the deep depth stratum, although abundances at reserve sites were nearly twice those at controls (control mean = 0.78 individuals per 100 m², S.E. = 0.15, $n = 175$ transects; reserve mean = 1.49 individuals per 100 m², S.E. = 0.16, $n = 245$ transects) (Figure 3). Abundances

Table 1. Analysis of variance for lobster densities

Factor	d.f.	MS	Denom. d.f.	Denom. MS	<i>F</i> value	<i>P</i> value
<i>Survey</i>	5	26.3	50	4.9	5.4	0.0005
Status	1	120.3	10	33.6	3.6	0.0878
Survey*Status	5	3.1	50	4.9	0.64	0.6701
Depth	1	26.6	10	9.4	2.8	0.1226
Survey*Depth	5	0.6	746	4.0	0.16	0.9765
Status*Depth	1	1.2	10	9.4	0.12	0.7318
Survey*Status*Depth	5	2.0	746	4.0	0.49	0.7856
<i>Site (Status)</i>	10	33.6	11	10.2	3.3	0.0301
Survey*Site(Status)	50	4.9	746	4.00	1.22	0.1507
<i>Depth * Site (Status)</i>	10	9.4	746	4.0	2.34	0.0101
Error	746	4.00				
Total	839	SS = 3954				

Design is four factor, partly nested (3 orthogonal fixed factors — Survey, Status, Depth), with a further random factor (Sites) nested within Status (indicated by Site (Status)). d.f. = numerator degrees of freedom, MS = mean square, Denom. d.f. = denominator degrees of freedom (term against which the factor is tested), *F* value is calculated statistic from MS/Denom. MS, *P*-value is probability of obtaining observed value of *F* or larger if the null hypothesis of no difference is true. Italicized factors have *P*-value < 0.05.

Table 2. Mean density (numbers per 100 m²) and standard errors for spiny lobster *J. edwardsii* sampled from the Tonga Island Marine Reserve and control sites. $n = 12$ replicate transects per site per survey, except December 2000, when $n = 10$

Site no.	Site	Treatment	Dec. 1998	Feb. 1999	May 1999	Nov. 1999	March 2000	Dec. 2000
1	Separation Point	Control	0.33 (0.26)	1.5 (0.72)	0.92 (0.67)	1.83 (0.89)	2.17 (1.19)	5.7 (1.7)
2	Totaranui	Control	0	0	0	0	0	0
3	Awaroa Head	Control	0	0.42 (0.26)	0	0.42 (0.19)	0.17 (0.17)	0.4 (0.2)
4	Canoe Bay	Reserve	0.17 (0.11)	1.08 (0.40)	1.83 (0.42)	0.67 (0.26)	1.83 (0.81)	2.0 (0.5)
5	Abel Head	Reserve	0.08 (0.08)	0.25 (0.13)	1.58 (0.43)	0.67 (0.41)	0.08 (0.08)	1.7 (0.6)
6	Cottage Loaf Rock	Reserve	0.17 (0.11)	2.58 (1.54)	0.58 (0.26)	0.42 (0.23)	1.25 (0.55)	0.9 (0.4)
7	Tonga Island	Reserve	0	0.75 (0.25)	1.08 (0.67)	0.67 (0.33)	1.42 (0.66)	1.4 (0.7)
8	Foul Point	Reserve	2.58 (1.05)	2.58 (0.89)	1.67 (0.62)	1.75 (0.82)	2.17 (1.03)	2.7 (0.9)
9	Whale Rock	Reserve	1.42 (0.78)	2.17 (1.35)	1.83 (0.58)	1.58 (0.54)	2.58 (0.83)	2.8 (1.0)
10	Mosquito Reef	Reserve	0.33 (0.19)	1.33 (0.68)	1.33 (0.66)	1.67 (0.78)	0.92 (0.62)	2.6 (1.0)
11	Bark Bay Reef	Control	0.17 (0.11)	0.33 (0.14)	0	0.17 (0.11)	0.17 (0.11)	0.6 (0.3)
12	Pinnacle Island	Control	0	0	0.08 (0.08)	0.08 (0.08)	0	0.4 (0.4)
13	Pitt Head	Control	0	0	0.08 (0.08)	0.17 (0.17)	1.17 (0.71)	0.5 (0.2)

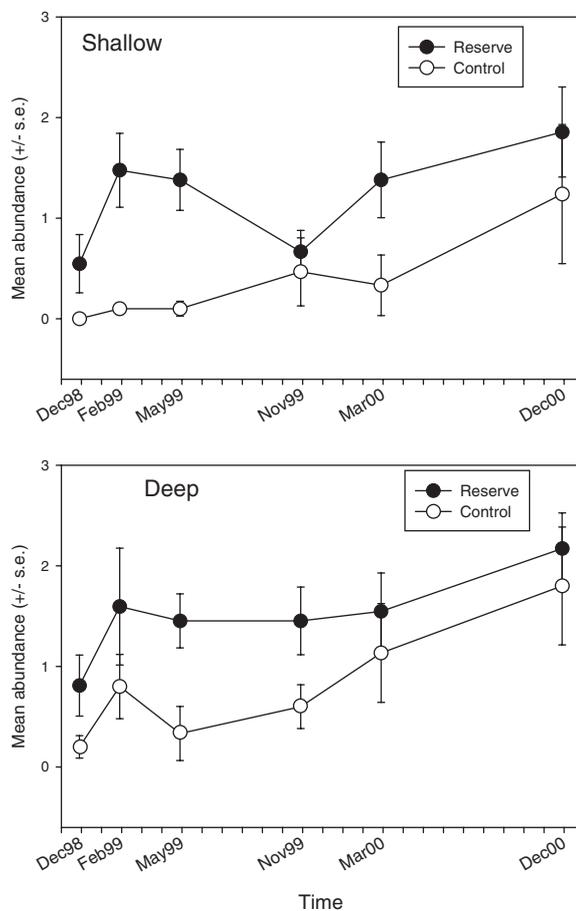


Figure 3. Mean density (per 100 m²) of spiny lobster *J. edwardsii* through time in shallow and deep depth strata. Reserve sites are represented by filled symbols, control fished sites are open. Error bars are standard errors, $n = 6$ transects per site per depth stratum per survey. Note that a control site (site 2), where no lobsters were counted, is excluded.

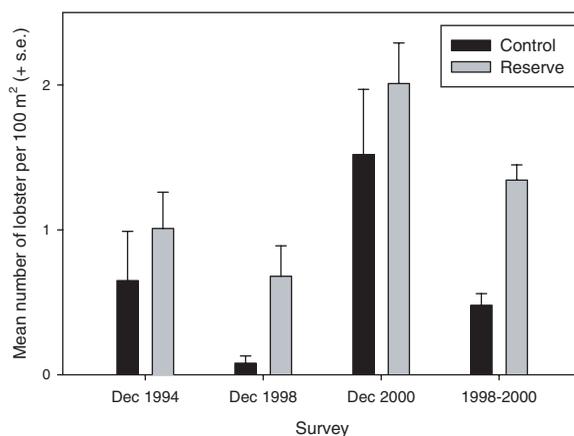


Figure 4. Mean abundances of spiny lobsters *J. edwardsii* pooled across 5 sites for each of control and reserve areas in 1994, and 12 sites (5 control, 7 reserve) in 1998/2000. Sample sizes varied among sites; totals of 35 control transects and 39 reserve transects were counted in 1994, while 350 control transects and 490 reserve transects were counted in 1998/2000. Densities in 1994 have been adjusted from per 120 m² to per 100 m². Error bars are 1 S.E.

were highly variable, both within and among sites. Variance component analysis (Proc Varcomp, SAS — SAS Institute Inc., 1989) of the untransformed densities indicated that the variance among replicate samples (4.24, S.E. = 0.21) was more than eight times greater than that among sites (0.51, S.E. = 0.24).

The pattern of differences between reserve and control sites differed among surveys (Figure 4). Comparing the same sample months (i.e. December 1994, 1998, 2000) the December 1994 and December 2000 surveys showed small differences between reserve and control areas, whereas the December 1998 showed a marked difference. Pooling across the 3 surveys, after 5 years (1994–1999, the midpoint of our study) the increase of abundance within the reserve (i.e. pooling all reserve sites across all 1998–2000 surveys) was 0.22, or 22% of the 1994 value. Thus, we estimate that abundance has increased on average at 4.4% per year. Abundances outside the reserve may have declined by about 12% over the same period, but we also draw attention to the high variability among surveys.

The largest spiny lobsters (estimated 220 mm CL — all size references are to the upper class limit) were found in the reserve in both deep and shallow water (Figure 5). Mean lobster carapace length in reserve shallow counts was 113 mm, whereas mean carapace length in the fished areas was 94 mm. In deep counts, the reserve mean carapace length was 132 mm, compared to 104 mm for fished areas. In shallow water at control sites only one male (out of a total of 15) was larger than 140 mm CL, while nearly one quarter (24%) of those in shallow reserve samples were greater than that size. For the deep counts, 42% of males were larger than 140 mm CL in the reserve, whereas 16% of males were in that size range at control areas. The legal size limits for harvesting correspond to about 95 mm CL for males and 100 mm CL for females, indicating that much greater fractions of the population are of harvestable size in the reserve than outside. Almost all of the large (> 140 mm CL) spiny lobsters sampled at control sites were observed at Separation Point (site 1), the least accessible (and presumably least fished) control site.

With the exception of juveniles in the May 1999 survey, more spiny lobsters in all size–sex categories were counted in the reserve (Figure 6). The most obvious difference between reserve and control occurred for reproductively mature males, abundances of which were consistently more than ten times higher in the reserve than outside.

The sex ratio (of females to males) in shallow strata was 0.65 : 1 in reserve sites and 0.71 : 1 in control sites. The sex ratio in deep strata was 0.53 : 1 at reserve sites and 1 : 1 at control sites. Based on the size-

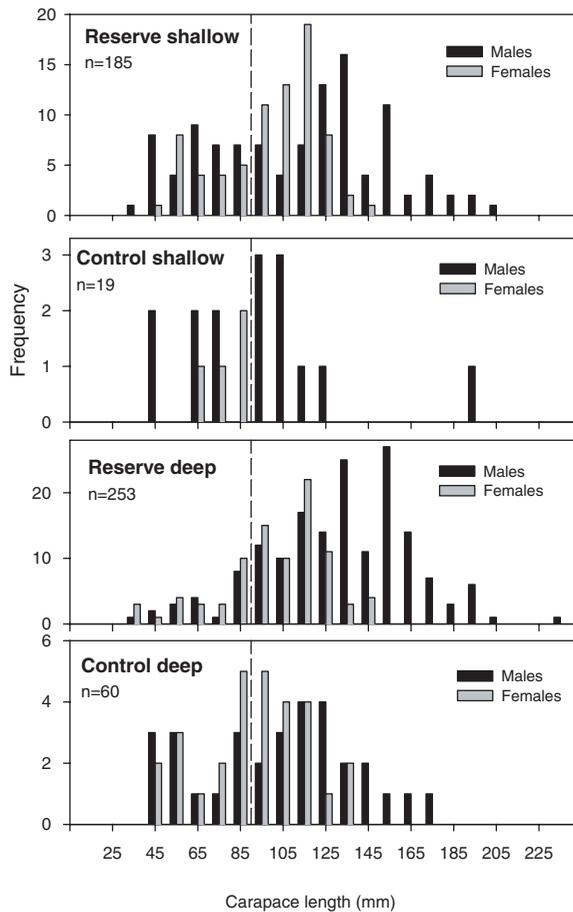


Figure 5. Size–frequency distributions of spiny lobster *J. edwardsii* for shallow and deep transect samples, pooled across sites within reserve and control treatments, and across all surveys. Sizes are estimated carapace length (mm), and males are represented by solid bars, females by shaded bars. Dashed line indicates transition from juvenile to adult.

specific fecundity equation and the number of females ≥ 90 mm CL length combined for all six surveys, we estimated that the ratio of reserve-to-control fecundities was 9.2 : 1. Thus, we estimate that about nine times as many eggs would be produced from the reserve than from the equivalent length of fished coast.

There were clearly low abundances of spiny lobster near the reserve edge and higher abundances 1100 m into the reserve in both scuba surveys (Figure 7A). However, those trends were neither linear nor continuous (several sites in the reserve had no spiny lobsters).

The catches from pots set over the gradient extending into the reserve from the southern nearshore border showed a trend for increasing catch further from the border into the reserve (Figure 7B), but that trend was weakened by the high variability in catches among pots at the site furthest into the reserve. There, one pot site had all of the spiny lobsters caught, so that although the value for one potting site (number 22 of 25) was very high, the mean for the five potting sites grouped into a location (corresponding to the diving observations) was low.

We tagged 60 spiny lobsters (31 by potting and 29 while diving) in the reserve during March 1999, but resighted only one, during the March 2000 sampling, at Whale Rock (site 9). Despite focused searching our attempts to directly estimate spillover were unsuccessful.

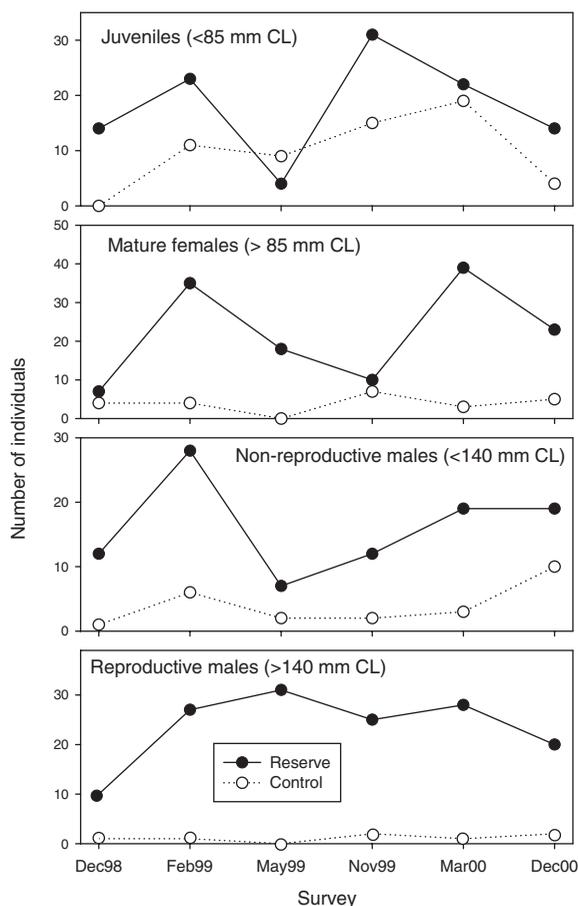


Figure 6. Number of individuals in size and sex classes, for pooled reserve (●) and pooled control (○) sites, plotted against time. Size at sexual maturity from MacDiarmid (1989).

DISCUSSION

Our study showed clear marine reserve effects on abundance and size of *J. edwardsii* at Tonga Island Marine Reserve. We failed to detect direct evidence (resighting of tagged individuals) of migration or spillover due to methodological difficulties. However, there was a pattern of abundance consistent with residency, as abundances were higher within the reserve and the lobsters were larger. There was also a weak pattern consistent with an edge effect, as lower abundances occurred close to the reserve border inside the reserve, though habitat quality could also account for that pattern.

Kelly *et al.* (2000) estimated the increase in population abundance of spiny lobsters in northern marine reserves to be about 9% per year. Our estimate of 4.4% per year for Tonga Island Marine Reserve, based on two sets of abundance data 5 years apart, is smaller. Note that the initial difference, some 13 months after reservation, may not reflect the true pre-reserve situation. The density inside the reserve increased only moderately between 1994 and 1999–2000, while the density outside the reserve declined by approximately 2.9% per year. The decline in abundance outside the reserve could be due to increased fishing effort outside the reserve over time (and proximity of fished areas to the most popular launching ramp), possibly

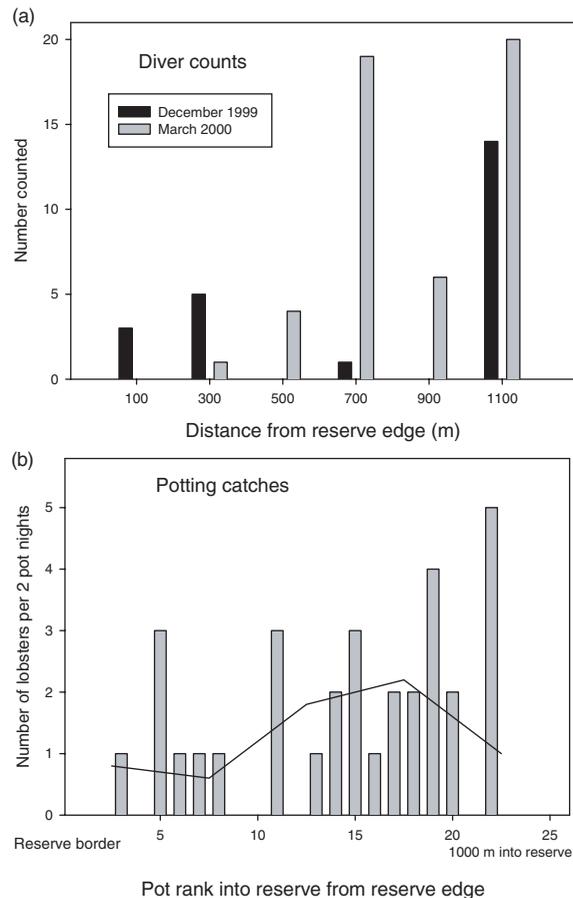


Figure 7. (a). Number of spiny lobsters *J. edwardsii* counted in transects in December 1999 and March 2000, at varying distances from the southern reserve boundary to Foul Point (site 8, Figure 1). See Figure 1 for location of reserve border. (b). Number of spiny lobsters *J. edwardsii* captured in pots set at varying distances from the southern reserve boundary in September 1999. Catches are pooled across two nights' sets, bars represent the catches from the individual pots, while the line plot is the catch for separate groups of five pots (i.e. 1–5, 6–10, ...). Pots were not evenly spaced (the fisher set pots at appropriate sites), but the total range covered (1000 m) is similar to that in the diving exercise.

influenced by displacement of fishing effort due to the presence of the reserve. Our data included the abundances of under-sized spiny lobsters (<100 mm CL), which we do not expect to be affected by reserve status. It is possible that rates of population increase inside southern marine reserves may be slower than in northern reserves, as Kelly *et al.*'s (2000) greatest estimate of rate of increase was 12.2% per annum (for spiny lobsters greater than 100 mm CL in shallow transects). Absolute abundance at Tonga Island Marine Reserve is also somewhat lower than that in northern marine reserves. Because abundances remained similar throughout the 1999/2000 surveys, those estimates of abundance are fairly reliable (they are based on 350 (control) and 490 (reserve) transects, or 84000 m⁻² of reef surveyed).

Several fisheries-related studies in southern New Zealand have suggested that a small portion of the population of spiny lobsters undertakes large-scale migrations. Annala (1981) suggested that near Gisborne most (97% of tag recoveries) *J. edwardsii* moved less than 5 km within a period of 504 d, while at Stewart Island 87% of tag recoveries over the 6 year study were recorded within 5 km of release sites (McKoy, 1983). Studies in Fiordland found that 90% of tag recoveries over the 3.5 year study were recorded within

5 km of the release site (Annala and Bycroft, 1993). However, McKoy (1983) noted evidence that immature females and small males migrated round southern New Zealand, and Annala and Bycroft (1993) found the same pattern for the same parts of the population, with some evidence of directional northward migration. Although each of these studies found some long-distance movements, all three studies provide data consistent with marine reserves of >10 km longshore extent being able to protect a relatively high proportion of spiny lobsters. (We note that Tonga Island Marine Reserve includes approximately 10.5 km of coast.) Based on those tagging studies and the more recent investigations of Kelly *et al.* (1999, 2000) and Kelly (2001), a proportion of the spiny lobster population will move from inside to outside (i.e. spillover) for any reserve. Demonstrating that spillover of spiny lobsters occurs using abundance and tagging studies is difficult, however, because of their patchy distribution, varying behaviour over time, cryptic behaviour and the complex habitats that they occupy (e.g. Kelly, 2001).

One difficulty with interpreting the count data lies with varying accessibility of some individuals to visual census. The reef at most sites on the Abel Tasman coast comprises boulders stacked on boulders, affording considerable shelter, and requiring considerable care during surveys. During the January–May period large male spiny lobsters were highly visible, frequently moving toward divers aggressively when encountered (see Figure 1 of Kelly *et al.*, 1999). At that time—peaking in March–April—they are thought to be mating and defending areas against other males (e.g. MacDiarmid, 1994). There is thus the potential for misinterpreting apparency or visual prominence as abundance (e.g. studies of fishes—Cole, 1994; Kulbicki, 1998; Willis *et al.*, 2000). The survey during which there was the greatest difference between reserve and non-reserve counts was December 1998 (Figure 4), outside the likely time of greatest likely apparency effects. Lobsters are relatively immobile, and easier to sample than fish, and hence only under-counts during times of cryptic behaviour could influence the results. Careful searching by divers in all surveys minimized errors, but we emphasize changes in behaviour over time (both seasonally, and as a response to protection over several years) as a potential difficulty for workers in other locations.

Reproductive effects of marine reserve protection were evident (greater abundances and sizes of females) and implied (greater abundances and sizes of males, hence mating success effects — MacDiarmid and Butler, 1999) from our results. We calculated the number of eggs available to be fertilized to be much greater in the reserve than at control sites, which is consistent with the study of Kelly *et al.* (2000). Given those estimates of fecundity, a 10 km marine reserve has egg output equivalent to an unprotected coastline of 92 km length. The greater numbers of large males found at reserve sites than at control sites further suggests that reproductive output from the reserve is likely to be higher than from the nearby coast, as large males are more likely to successfully fertilize female spiny lobsters (MacDiarmid and Butler, 1999). Egg output is greatly increased compared to adjacent fished reef, although the lengthy larval life of spiny lobsters (Booth and Phillips, 1994) means that it is very unlikely that larvae from reefs in Tonga Island Marine Reserve would return to reefs even regionally (Caputi, 1993). Eggs produced from such a small area are unlikely to have an appreciable effect on recruitment because of the large area of coast that is unprotected.

Our study was based on the expectation that offshore migrations would occur at Tonga Island in the way described at Leigh, northeastern New Zealand (MacDiarmid, 1991; Kelly *et al.*, 1999, 2000). However, we found no indication that such migrations did in fact occur. Temporal patterns in shallow and deep counts tended to parallel one another, rather than demonstrating reciprocal patterns (see Figure 3). Though our tagging investigations were unable to estimate movement, spiny lobster in the Abel Tasman area are unlikely to move offshore. Trawlers working the area prior to it being declared a reserve did not catch spiny lobsters offshore on sediments at any time during more than 10 years (V. King-Turner, pers. comm.), and the commercial returns would have provided a strong incentive to locate such aggregations. Demonstrating that offshore movements do *not* occur requires much more effort than showing that they *do*; though we have not demonstrated that such movements do not occur, we consider it sufficiently supported to discuss possible reasons for lack of movements in the next paragraph.

MacDiarmid (1991) noted that large annual changes in density, sex ratio, and size distribution occur along depth gradients for all species in the *Jasus lalandi* group. Why might *J. edwardsii* remain on reefs on the Abel Tasman coast? MacDiarmid (1991) further suggested that timing, depth range, and horizontal extent of those movements could be expected to vary among areas, due to variations in timing of moulting and reproduction, and the depth ranges of suitable habitats and major prey species. Our results may reflect (a) the relatively short distances between shallow and deep areas on reefs on the Abel Tasman coast, (b) the reef edge being at depths of only about 15 m in many areas, and (c) the abundance of food on reefs relative to its abundance on sediments. Spiny lobsters may move out over sediments to obtain access to populations of bivalves owing to the high costs of mating activity (Kelly *et al.*, 1999). The very high abundances of grazing gastropods and echinoids on the reefs of the Abel Tasman coast (Davidson and Chadderton, 1994) may be sufficient to supply the dietary requirements of the spiny lobsters. Beds of dog cockles *Glycymeris laticostata* and *G. modesta* and morning star shells *Tawera spissa* occur in sediments but are localized and most soft shore areas support low numbers of large food items (Davidson, 1992). The reefs of the Abel Tasman coast generally do not extend far offshore and it may be that the short reef widths (perpendicular to shore) (almost always < 100 m, usually < 50 m) are such that relatively small movements can accommodate the dietary requirements of spiny lobsters, and that it is unnecessary for them to remain offshore (cf. Kelly *et al.*, 1999).

Our study has shown similar effects of reserve protection on populations of spiny lobster to those in more northern New Zealand populations; Tonga Island Marine Reserve clearly retains spiny lobsters. Although the rate of increase in density appears less than those described elsewhere, the major effects are for increased sizes of spiny lobsters and greater abundances. As most large individuals were males, and those large individuals have greatest mating success (MacDiarmid and Butler, 1999), operational sex ratio was also different inside reserve than outside. This study adds further evidence that spiny lobster populations on reefs may be greatly changed by harvesting.

ACKNOWLEDGEMENTS

Thanks to P. Braggins, R. Dickson, A. Pande, L. Richards, D. Tindale, N. Alcock, the Department of Conservation staff at Motueka and Marahau: B. Franklin, S. Fowler, L. Higginson, K. Lynch and S. Houston, the DOC hut wardens Margaret, Chris, and Andrew for their hospitality at Anchorage, V. King-Turner, K. Barton, and the crew of F.V. Tranquil Image for assistance with potting, A. Baxter of Department of Conservation Nelson, and S. Kelly for comments on the manuscript. We are also grateful to J. Boubee and G. James of NIWA, who lent us equipment. This study was supported by Department of Conservation 'Blue Package' funding, with the exception of the December 2000 survey which was provided to the Nelson/Marlborough Conservancy by the Biodiversity Package-Marine Reserve funding, as part of the New Zealand Biodiversity Strategy. We especially thank A. Baxter (Nelson) and C. Wishart (Motueka) for operational support. We particularly thank two referees (Drs Cockcroft and Mayfield), one anonymous referee and the editor (J. Baxter) for their helpful reviews of the manuscript.

REFERENCES

- Alcala AC, Russ GR. 1990. A direct test of the effects of protective management on abundance and yield of tropical marine resources. *Journal du Conseil International pour l'Exploration de la Mer* **46**: 40–47.
- Annala JH. 1981. Movements of rock lobsters (*Jasus edwardsii*) tagged near Gisborne, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **15**: 437–443.
- Annala JH, Bycroft B. 1993. Movements of rock lobsters (*Jasus edwardsii*) tagged in Fiordland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **27**: 183–190.
- Babcock RC, Kelly S, Shears NT, Walker JW, Willis TJ. 1999. Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series* **189**: 125–134.
- Ballantine WJ. 1991. Marine reserves for New Zealand. Leigh Laboratory Bulletin 25, University of Auckland, Auckland, 186pp.
- Booth JD. 1997. Long distance movements in *Jasus* spp. and their role in larval recruitment. *Bulletin of Marine Science* **61**: 111–128.

- Booth JD, Phillips BF. 1994. Early life history of spiny lobster. *Crustaceana* **66**: 271–294.
- Caputi N. 1993. Aspects of spawner–recruit relationships with particular reference to crustacean stocks; a review. *Australian Journal of Marine and Freshwater Research* **44**: 589–607.
- Chiswell SM, Booth JD. 1999. Rock lobster *Jasus edwardsii* larval retention by the Wairarapa eddy off New Zealand. *Marine Ecology Progress Series* **183**: 227–240.
- Cole RG. 1994. Abundance, size structure, and diver-oriented behaviour of three large benthic carnivorous fishes in a marine reserve in northeastern New Zealand. *Biological Conservation* **70**: 93–99.
- Cole RG, Villouta E, Davidson RJ. 2000. Direct evidence of limited dispersal of the reef fish *Paraperis colias* (Pinguipedidae) within a marine reserve and adjacent fished areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* **10**: 421–436.
- Creese RG, Cole RG. 1995. Marine conservation in New Zealand. *Pacific Conservation Biology* **2**: 55–63.
- Davidson RJ. 1992. A report on the intertidal and shallow subtidal ecology of the Abel Tasman National Park, Nelson. Department of Conservation Occasional Publication No. 4, 161pp.
- Davidson RJ. 2001. Changes in population parameters and behaviour of blue cod (*Paraperis colias*; (Pinguipedidae) in Long Island–Kokomohua Marine Reserve, Marlborough Sounds, New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems* **11**: 417–435.
- Davidson RJ, Chadderton WL. 1994. Marine reserve site selection along the Abel Tasman National Park coast, New Zealand: consideration of subtidal rocky communities. *Aquatic Conservation: Freshwater and Marine Ecosystems* **4**: 153–167.
- Department of Conservation. 2001a. Marine reserves. <http://www.doc.govt.nz/Conservation/Marine-and-Coastal/Marine-Reserves/index.asp> 22 November 2001.
- Department of Conservation. 2001b. Tonga Island Marine Reserve. <http://www.doc.govt.nz/Conservation/Marine-and-Coastal/Marine-Reserves/Tonga-Island.asp> 22 November 2001.
- Edgar GJ, Barrett NS. 1999. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *Journal of Experimental Marine Biology and Ecology* **242**: 107–144.
- Fonseca DM, Hart DD. 1996. Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos* **75**: 49–58.
- Holland DS. 2000. A bioeconomic model of marine sanctuaries on Georges Bank. *Canadian Journal of Fisheries and Aquatic Sciences* **57**: 1307–1319.
- Johst K, Brandl R. 1997. The effect of dispersal on local population dynamics. *Ecological Modelling* **104**: 87–101.
- Jones GP, Cole RG, Battershill CN. 1993. Marine reserves: do they work? In *Proceedings of the Second International Temperate Reefs Symposium, 7–10 January 1992, Auckland, New Zealand*. Battershill CN, Schiel DR, Jones GP, Creese RG, MacDiarmid AB (eds). NIWA Marine: Wellington; 29–45.
- Kelly S. 2001. Temporal variation in the movement of the spiny lobster *Jasus edwardsii*. *Marine and Freshwater Research* **52**: 323–331.
- Kelly S, MacDiarmid AB, Babcock RC. 1999. Characteristics of spiny lobster, *Jasus edwardsii*, aggregations in exposed reef and sandy areas. *Marine and Freshwater Research* **50**: 409–416.
- Kelly S, Scott D, MacDiarmid AB, Babcock RC. 2000. Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biological Conservation* **92**: 359–369.
- Kulbicki M. 1998. How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. *Journal of Experimental Marine Biology and Ecology* **222**: 11–30.
- Lipcius RN, Cobb JS. 1994. Ecology and fishery biology of spiny lobsters (chapter 1). In *Spiny Lobster Management*, Phillips BF, Cobb JS, Kittaka J (eds). Blackwell Scientific: London.
- MacDiarmid AB. 1989. Size at onset of maturity and size dependent reproductive output of female and male spiny lobsters *Jasus edwardsii* (Hutton) (Decapoda, Palinuridae) in northern New Zealand. *Journal of Experimental Marine Biology and Ecology* **89**: 191–204.
- MacDiarmid AB. 1991. Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster *Jasus edwardsii* on a coastal reef in northern New Zealand. *Marine Ecology Progress Series* **70**: 129–141.
- MacDiarmid AB. 1994. Cohabitation in the spiny lobster *Jasus edwardsii* (Hutton, 1875). *Crustaceana* **66**: 341–355.
- MacDiarmid AB, Breen PA. 1993. Spiny lobster population change in a marine reserve. In *Proceedings of the Second International Temperate Reef Symposium, 7–10 January 1992, Auckland New Zealand*. Battershill CN et al. (eds). NIWA Marine, Wellington; pp 47–56.
- MacDiarmid AB, Butler MJ. 1999. Sperm economy and limitation in spiny lobsters. *Behavioral Ecology and Sociobiology* **46**: 14–24.
- MacDiarmid AB, Hickey B, Maller RA. 1991. Daily movement patterns of the spiny lobster *Jasus edwardsii* (Hutton) on a shallow reef in northern New Zealand. *Journal of Experimental Marine Biology and Ecology* **147**: 185–205.

- McKoy JL. 1983. Movements of rock lobsters, *Jasus edwardsii* (Decapoda: Palinuridae), tagged near Stewart Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **17**: 357–366.
- Plan Development Team. 1990. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic. NOAA Technical Memorandum NMFS-SEFC-261. 40pp.
- Rowley RJ. 1994. Marine reserves in fisheries management. *Aquatic Conservation: Marine and Freshwater Ecosystems* **4**: 233–254.
- SAS Institute Inc. 1989. *SAS/STAT Users Guide, Version 6, 4th ed. vol. 2*, SAS Institute Inc.: Cary, NC, 846pp.
- Willis TJ, Miller RB, Babcock RC. 2000. Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series* **198**: 249–260.