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Trajectories of spiny lobster *Jasus edwardsii* recovery in New Zealand marine reserves: is settlement a driver?

THEMATIC SECTION
Temperate Marine Protected Areas

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SUMMARY

Monitoring species' response in marine protected areas is important for informing both the management of those areas and the establishment of additional protected areas. Populations of spiny lobsters *Jasus edwardsii* were monitored in eight New Zealand marine reserves for up to 34 years. The populations displayed highly variable responses to protection. While a few showed rapid (within 1–2 years of protection) increases in abundance, others showed little response even after a decade of protection. Some reserves displayed little initial recovery, then a sudden increase following several years of protection, while others displayed significant declines in abundance following initial recovery. Marine reserves located in areas with initially high densities of juveniles tended to have rapid recovery, but aspects of reserve design had no significant influence on the recovery rate. Variability among recovery trajectories also suggests that supply-side dynamics may be a key driver of lobster recovery. Densities of legal-sized lobsters were positively correlated with reserve age, but the abundance of juvenile lobsters increased in all but one reserve, indicating enhanced recruitment, survival and/or movement of juvenile lobsters into reserves. It is important to consider the placement of reserves, with respect to potential levels of larval supply, when establishing marine reserves for either conservation or fisheries management purposes and for evaluating their effectiveness.

Keywords: lobsters, marine protected areas, marine reserves, New Zealand

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INTRODUCTION

The establishment of marine reserves represents a population manipulation experiment on a large spatial scale (Edgar & Barrett 1999). By removing fishing and other extractive pressures, populations of previously-harvested species may be allowed to recover to a more natural state. Such recovery has been reported worldwide, with species density, biomass, size and diversity tending to be higher within reserves than outside (Lester *et al.* 2009). A review of 80 marine protected areas (MPAs) indicated biological responses generally develop within 1–3 years (Halpern & Warner 2002), but there have also been cases where the response to protection has been slow or even absent, despite the apparent release from fishing pressure (see for example Mayfield *et al.* 2005). The reasons for the variability in species' responses to protection are often unclear.

A range of factors may potentially influence the rate of species' recovery in MPAs. The rate may be species-specific, site-specific, time-period specific and mechanism-specific (Russ *et al.* 2005; Molloy *et al.* 2009), with some species potentially taking decades to recover (McClanahan & Graham 2005; Edgar *et al.* 2009; Babcock *et al.* 2010). Aspects such as hydrodynamics, habitat quality, predation intensity and competitive interactions vary spatially, including among marine protected areas (see for example Fernandez & Castilla 2000). In turn, these may influence factors that affect population growth (and therefore recovery trajectory), such as the supply of larvae and adult mortality rate. For example, Shears *et al.* (2006) demonstrated how allowing some recreational harvest of the lobster *Jasus edwardsii* in a marine protected area prevented even partial recovery of the population, which provides an indication of how recovery can be affected by increased mortality rate.

The dynamics of populations outside marine protected areas can have a substantial effect on the recovery of populations within protected areas, as can the harvest regime in place prior to protection (Micheli *et al.* 2004; Baskett *et al.* 2007). Movement of individuals across the MPA boundary, which in turn is affected by factors such as MPA

design (Tewfik & Bene 2003; Tupper 2007; Freeman *et al.* 2009), density-dependent interactions and species' life history characteristics (see Willis *et al.* 2003), will also influence the recovery of the population within the MPA. Protected area size may be particularly important in influencing the recovery of previously-harvested species, with small reserves often failing to provide adequate protection (Parnell *et al.* 2005; Claudet *et al.* 2008). MPAs are thought to be most effective for species with low rates of juvenile and adult movement, with larger MPAs required for species with longer dispersal distances (Botsford *et al.* 2003). By encompassing the movement range of a particular species (including aspects such as diel movement and seasonal migrations) within an MPA, the recovery of that species may be enhanced (Holland *et al.* 1996; Chapman & Kramer 2000). Where MPAs are intended to provide for fisheries enhancement, smaller areas and the placement of boundaries across suitable habitat may allow the export of individuals to be maximized (Hastings & Botsford 2003; Murawski *et al.* 2004; Forcada *et al.* 2009), but would be at the expense of the MPA's effectiveness at protecting the source population (Freeman *et al.* 2009).

When interpreting the recovery trajectories of species within protected areas, the influence of aspects such as adult movement patterns and reserve design are usually better known than the influence of larval supply, which remains unknown for many species. Here, we assess the recovery within New Zealand marine reserves of the spiny lobster *Jasus edwardsii* (Hutton, 1975) (Palinuridae) and assess some factors that may influence recovery trajectories. This species, which supports important commercial, recreational and customary fisheries, has demonstrated increases in size and abundance in Tasmanian (Edgar & Barrett 1999; Barrett *et al.* 2009*a*) and New Zealand marine reserves (MacDiarmid & Breen 1992; Kelly *et al.* 2000; Davidson *et al.* 2002; Shears *et al.* 2006; Pande *et al.* 2008). It has long-lived larvae (spending up to 24 months offshore), with settlement patterns displaying significant spatial and temporal variability (Booth *et al.* 2007*a*; Chiswell & Booth 2008). As adults, movement patterns are similarly variable (MacDiarmid *et al.* 1991; Kelly & MacDiarmid 2003; Kendrick & Bentley 2003; Freeman *et al.* 2009), but are within a range where recovery within existing marine reserves could be expected (Barrett *et al.* 2009*b*). Larval settlement (encompassing the initial puerulus settlement and capture of animals after post-settlement migration; Booth *et al.* 2007*b*) is correlated with recruitment into the fishery (Booth *et al.* 2007*b*), but there has been no study of the implications of variable settlement for unfished populations. In this study, we review the recovery trajectories for *J. edwardsii* within a range of New Zealand marine reserves. We then assess the initial rate of increase in lobster abundance and overall trends in abundance, and consider a number of parameters potentially influencing the observed patterns, including reserve size, length of coastline protected, offshore boundary placement and the initial density of juveniles in the reserve, as a proxy for settlement and subsequent recruitment.

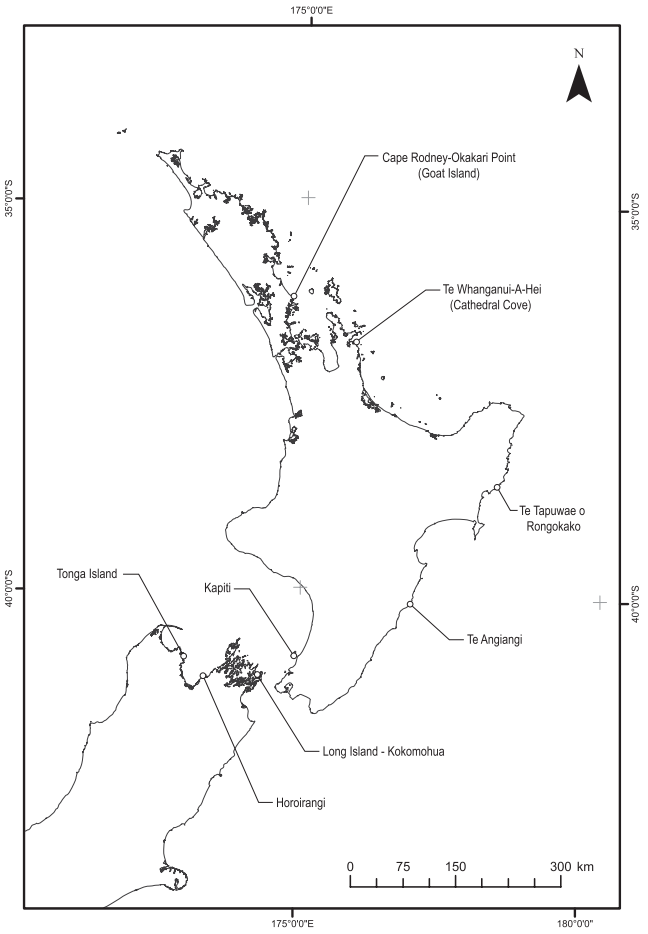

Figure 1 Location of marine reserves included in this study.

METHODS

Study sites

We compiled monitoring data from eight New Zealand coastal no-take marine reserves, five from the North Island and three from the northern end of the South Island (Fig. 1, Table 1). All are in warm-temperate waters and have been placed in the same biogeographic region based on macroalgal presence-absence data (Shears *et al.* 2008). They support broadly similar biological habitats, including shallow rocky reef dominated by large brown macroalgae (Shears & Babcock 2007). The reserves ranged in age from five years (Horoirangi Marine Reserve, established in 2006) to 36 years (Cape Rodney to Okakari Point Marine Reserve, established in 1975) and in size from 446 ha (Te Angiangi Marine Reserve) to 2452 ha (Te Tapuwae o Rongokako Marine Reserve).

Underwater visual census

Underwater visual census methodology was used at all reserves to obtain data on lobster size and abundance. Divers were trained to visually estimate lobster size using an estimate/capture/measure procedure. All surveys

Table 1 Details relating to the age and design of each marine reserve included in this study. Sources of lobster monitoring data were: Te Tapuwae o Rongokako (Freeman 2008); Te Angiangi (Freeman 2008; Department of Conservation, unpublished data 2007–2009); Long Island-Kokomohua (Davidson *et al.* 2009; R. J. Davidson, unpublished data 2010); Kapiti Island (Battershill *et al.* 1993; Stewart & MacDiarmid 2003); Tonga Island (Davidson *et al.* 2002, 2007; R. J. Davidson, unpublished data 2008–2011); Cape Rodney to Okakari Point (Ayling 1978; MacDiarmid & Breen 1992; Kelly *et al.* 2000; Haggitt & Mead 2009*a*); Te Whanganui-a-Hei (Kelly 2000; Kelly *et al.* 2000; Haggitt & Mead 2009*b*); Horoirangi (R. J. Davidson, unpublished data 2006–2011).

Marine reserve	*Year established*	*Size (ha)*	*Approx. length of coastline (km)*	*Min. distance to offshore boundary (km)*
Te Tapuwae o Rongokako	1999	2452	5	3.5
Te Angiangi	1997	446	3	1.85
Long Island-Kokomohua	1993	619	9.8	0.46
Kapiti Island	1992	2167	8.7	1.85
Tonga Island	1993	1835	11.4	1.85
Cape Rodney to Okakari Point	1975	518	5	0.8
Te Whanganui-a-Hei	1993	840	4	1.56
Horoirangi	2006	904	5	1.85

were completed during a similar season (summer or summer/autumn) to reduce seasonal variability and take advantage of more workable sea conditions. Wherever possible, divers recorded carapace length (to the nearest 5 mm) and sex of each lobster within each transect (usually 50×10 m). For some reserves and in some years, only density was recorded (no size or sex data were recorded). Between 3 and 22 sites were surveyed inside and outside each reserve; between 1 and 8 transects were surveyed at each site. All transects were conducted in rocky reef habitat in less than 30 m depth and were located either randomly or haphazardly.

All diver counts of lobsters were converted to numbers per 500 m^2 for analysis. Lobsters that could not be sized were categorized as legal or sublegal based on the relative proportions of measured individuals in those size classes. A legal-sized male has a tail width of at least 54 mm; a female at least 60 mm (equating to carapace lengths of at least 105 mm and 97 mm, respectively; Freeman 2008).

Overall trends in abundance and timing of response

To describe the overall effect of marine reserve protection on lobster densities, we calculated the difference between reserve and non-reserve densities for both legal and sublegal animals over the time series. We then tested for correlation between reserve age and the log reserve:non-reserve ratio using the most recent survey data at each location.

For reserves where a time series of data longer than 10 years existed, we fitted generalized additive models (GAMs) to the density data (using the non-parametric smoother 's') to assess whether reserve age was a significant variable explaining lobster density and then used regression tree analysis (using the function 'rpart' in R; R Development Core Team 2007) to determine when significant changes in lobster density occurred. Regression tree analysis was not undertaken for Cape Rodney to Okakari Point Marine Reserve due to significant gaps in the time series.

The initial rates of increase in density, estimated as the slope of the linear regression fitted to the time series of data for each reserve, were compared using analysis of covariance (R Development Core Team 2007). We included only data collected within the first eight years of the reserve's establishment.

Initial rate of increase in density

Influence of reserve design

The initial rate of increase in density (in total number of lobsters per 500 m^2 per year, and in the number of legal-sized lobsters per 500 m^2 per year) was assessed against reserve size, length of coastline protected and minimum distance to the offshore boundary of the reserve, to establish whether there were any correlations between these variables (Pearson correlations; SPSS 2006).

Influence of recruitment

To provide an estimate of the level of settlement and subsequent recruitment (defined as the addition of individuals to local populations following settlement from the pelagic larval phase to the benthic or demersal early juvenile stage; Caley *et al.* 1996) at each reserve, we calculated the density of sublegal-sized animals within each reserve at or near the time of the reserve's establishment. We then established whether there was any correlation between this initial density of juveniles and the subsequent rate of increase in density of legal-sized animals and in total density.

RESULTS

Overall trends in abundance and timing of response

GAMs fitted to the data indicated that reserve age was a significant variable explaining total lobster density ($p < 0.01$) in all cases, with the exception of Te Tapuwae o Rongokako and Kapiti Island (where there were insufficient data to fit a GAM) and Horoirangi, where a model could not be fitted to the time series data. With the exception of Horoirangi Marine Reserve, there were clear increases in lobster abundance over

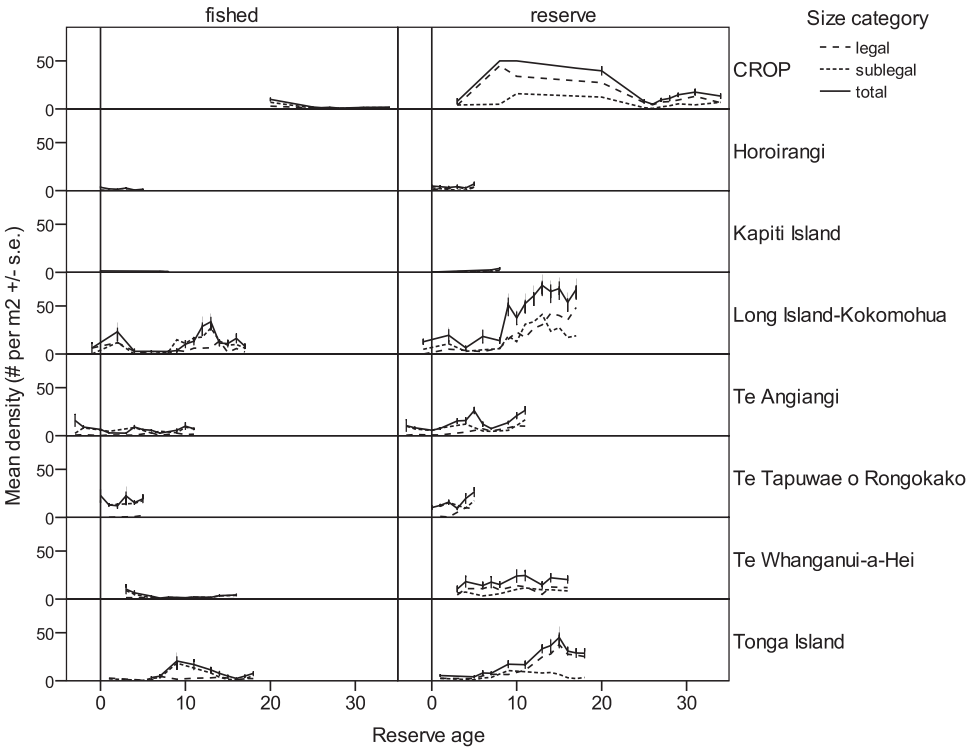

Figure 2 The mean density of lobsters (all sizes, and divided into legal- and sublegal-size categories) within New Zealand marine reserves and at nearby control (fished) sites in relation to the age of the reserve. Error bars have been omitted from the plots for legal and sublegal size categories for clarity.

time within all the reserves we assessed and in the abundance of legal-sized lobsters (Figs 2, 3 and 4). With the exception of Tonga Island, there were also consistent trends over time for the abundance of sublegal-sized lobsters to be higher within marine reserves than outside (Figs 2, 3 and 4).

Initial rates of increase in lobster density were highly variable (Fig. 2). The highest initial rate of increase occurred in Cape Rodney to Okakari Point Marine Reserve, which had an average increase of over 8 lobsters per 500m^2 per year of protection. Te Tapuwae o Rongokako Marine Reserve had the second highest rate, at 2.7 lobsters per 500m^2 per year. The remaining reserves showed only small or no increases in density over this time period (all had a mean rate of less than 1 lobster per 500m^2 per year of protection). There were significant differences among the slopes and intercepts of the regressions between reserve age and lobster density over the initial period for the eight marine reserves (total density: analysis of covariance $F_{15,22} = 7.83$, $p < 0.01$; density of legal-sized lobsters: analysis of covariance $F_{15,18} = 34.81$, $p < 0.01$).

North Island north-east coast

At Cape Rodney to Okakari Point Marine Reserve, there was an initial large increase in density which was sustained for around twenty years. At some point between 1995 and 2000 (after between 20 and 25 years of protection), there was a substantial decline in total (and legal-sized) density of lobsters in this reserve, to a density similar to that recorded in 1978, three years after the reserve's establishment (Fig. 2). At Te Whanganui-a-Hei Marine Reserve, total density was variable, but the overall trend was for a slow increase in density with age. Regression tree analysis indicated that a significant change in density occurred after nine years of protection (in 2002).

North Island east coast

At Te Angiangi and Te Tapuwae o Rongokako Marine Reserves, there was an initial rapid increase in total density, followed by a decline then subsequent recovery (Fig. 2). These patterns mirrored the trends in density of sublegal-sized animals, but the density of legal-sized animals showed a continual increase (Fig. 2). At both reserves, mean density displayed a trend of increasing abundance over the last three years of monitoring with no sign of stabilization. At Te Angiangi Marine Reserve, significant changes in density occurred after 2, 4.5, 5.5, 8 and 9.5 years of protection. These changes were all increases in density, with the exception of the decline between 2003 and 2004 (between five and six years of protection).

North Island south-west coast

Too few data were available from Kapiti Island Marine Reserve to fit a GAM or undertake regression tree analysis. The density of lobsters (total density and density of legal-sized animals) remained low over the eight-year period where monitoring was undertaken (Fig. 2) but slightly higher than at the fished sites monitored (Fig. 3).

South Island

At both Tonga Island and Long Island-Kokomohua Marine Reserves there was an initial period of several years when virtually no change in lobster density took place, followed by a rapid increase and stabilization at approximately

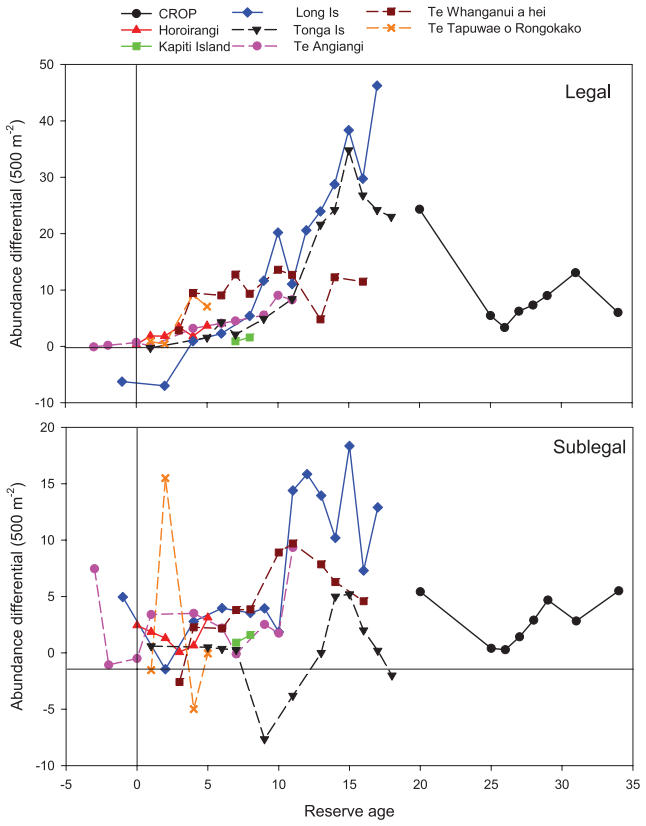

Figure 3 Raw difference in the density of legal- and sublegal-sized lobsters between fished and reserve locations for each year monitoring was undertaken at the eight locations. A value greater than zero indicates a higher density within the reserve; a value less than zero indicates a higher density outside the reserve. CROP = Cape Rodney to Okakari Point.

30 lobsters per 500 m^2 at Tonga Island and at approximately 60 lobsters per 500 m^2 at Long Island-Kokomohua (Fig. 2). At Long Island-Kokomohua, this change was driven firstly by a large increase in the density of sublegal-sized animals, which was followed by a large increase in the density of legal-sized animals (Fig. 2). At Tonga Island, a small increase in density of sublegal-sized animals was followed by a large increase in density of legal-sized animals. At both reserves, regression tree analysis indicated that significant increases in density occurred after 8 and 12 years of protection (in 2001 and in 2005). A small but significant decline also occurred at Tonga Island between 2008 and 2009 (age 15 and 16). No significant changes in lobster density were evident at Horoirangi, after five years of protection (Fig. 2).

Initial rate of increase in density

Influence of reserve design

Even when the exceptionally high (and uncertain; see Discussion) rate of increase calculated for Cape Rodney to Okakari Point Marine Reserve was excluded, there were no significant correlations between the rate of increase in lobster density and reserve size (Pearson correlation coefficients $p = 0.6$ for density of legal-sized and $p = 0.6$ for all lobsters) or length of coastline protected ($p = 0.5$ for legal-sized lobsters and $p = 0.5$ for all lobsters). There was also no significant correlation between the minimum distance to the offshore boundary and the rate of increase in legal-sized lobsters ($p = 0.6$), or in the rate of increase in total density ($p = 0.6$).

Influence of recruitment

When data from Cape Rodney to Okakari Point Marine Reserve were excluded, there was a significant positive correlation between the initial density of sublegal-sized lobsters within the reserve at or near the time of establishment with the rate of increase in total density (Pearson correlation coefficient = 0.89, $p = 0.007$) and in the rate of increase in density of legal-sized lobsters (Pearson correlation coefficient = 0.93, p = 0.002; Fig. 5). When data from Cape Rodney to Okakari Point were included, there were no such correlations ($p = 0.67$ and $p = 0.67$ for the rate of increase in total and legal-sized density, respectively).

DISCUSSION

Long term monitoring has demonstrated that the total abundance of *Jasus edwardsii* and particularly the abundance of large individuals, have increased significantly within most of the marine reserves we compiled data from. This result is consistent with other reported responses of lobsters to protection (Bertelsen & Matthews 2001; Goni *et al.* 2001; Rowe 2002; Wynne & Cote 2007; Pande *et al.* 2008) and demonstrates that marine reserves in New Zealand have been effective to some degree at minimizing the effects of extractive activities on the size and abundance of harvested species. However, we recorded significant variability among reserves in the timing of response to protection, in the recovery trajectories and we also recorded significant increases in the abundance of juvenile lobsters in marine reserves.

Drivers of lobster recovery in New Zealand marine reserves

We found that the rate of increase in large lobsters within marine reserves and the rate of increase in total abundance were best explained by variation in the density of juvenile lobsters, not the properties of the reserves themselves. Reserves that supported high densities of juvenile lobsters at the time of their establishment tended to have more rapid recovery than reserves that initially had lower densities of juveniles. The distinct variability among recovery trajectories and the recovery trajectories themselves, also suggest that supply-side dynamics (larval settlement and subsequent recruitment) are an important driver of lobster population recovery within New Zealand marine reserves.

While we found that reserve properties, such as size, did not influence the initial recovery rate of lobsters, we consider it likely that offshore boundary placement in particular, would

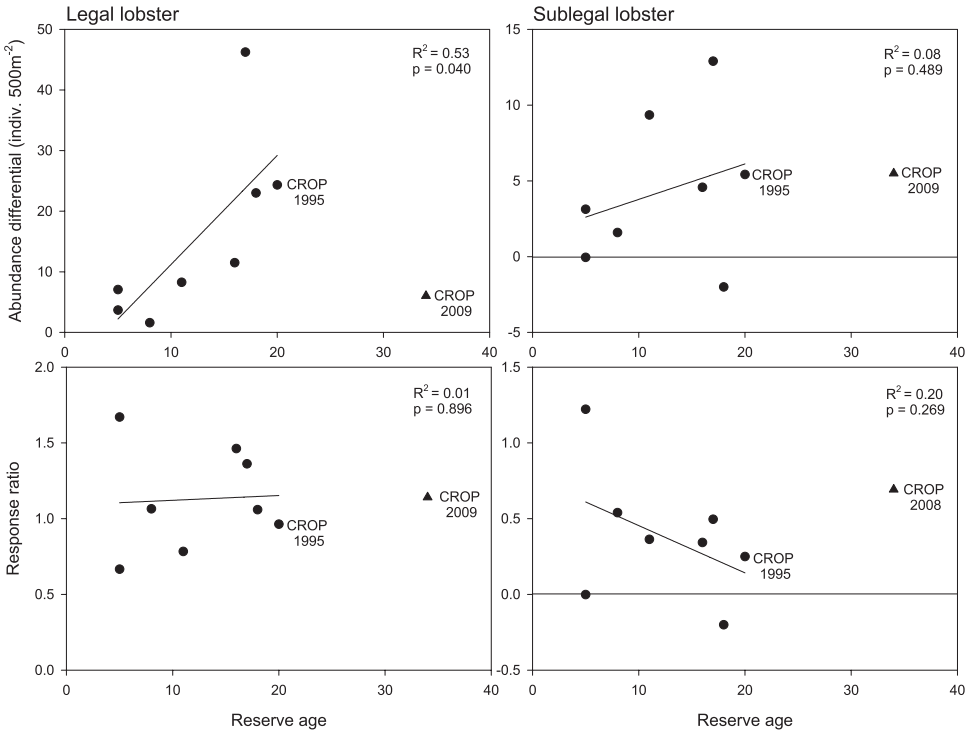

Figure 4 Changes in the density of lobsters within eight no-take marine reserves. Abundance differential is the difference in density between reserve and fished sites; response ratio is the logged ratio of reserve and fished abundance. Data are mean density in the final year of monitoring. For Cape Rodney to Okakari Point Marine Reserve (CROP) we show the data for both 1995 and the final year of monitoring, to demonstrate the influence of the large decline in abundance recorded subsequent to 1995.

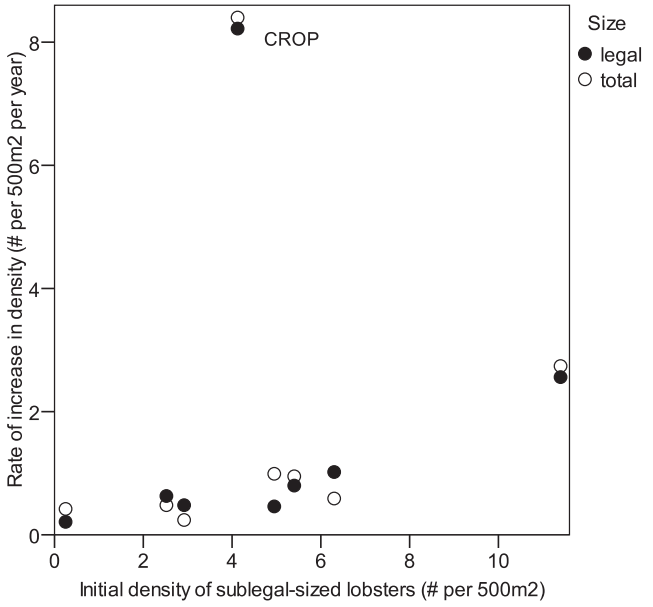

Figure 5 Relationship between the initial density of juvenile lobsters in each marine reserve and the subsequent rate of increase in recovery of legal-sized and total density of lobsters. CROP = Cape Rodney to Okakari Point Marine Reserve.

influence aspects of population recovery. All but one marine reserve in our study (Te Tapuwae o Rongokako) had offshore boundaries located less than 2 km from shore. Te Tapuwae o Rongokako coincidentally had the highest initial density of juveniles, which confounded our analysis. Offshore boundary placement may be particularly important if there are no barriers (such as mud) to seasonal inshore–offshore movement associated with the reserve boundaries (Freeman *et al.* 2009). At Te Whanganui-a-Hei Marine Reserve, Haggitt and Mead (2009*b*) suggested that the decline in abundance of legal-sized animals recorded between 2004 and 2006 reflected a possible emigration across the reserve boundaries, but tagging studies would be required to confirm this. Similarly, targeted fishing of lobster aggregations near the boundary of Cape Rodney to Okakari Point Marine Reserve has been suggested to have contributed to not only a reduction in population growth rate within the reserve, but also a reduction in the number of very large individuals in the reserve population (Kelly *et al.* 2002; Kelly & MacDiarmid 2003). Mature lobsters undertaking offshore migrations as part of their reproductive behaviour crossed the boundary of the marine reserve, but larger lobsters would also have been more susceptible to fishing activity as a result of size-related catchability (Ziegler *et al.* 2002). The decline in both legal- and sublegal-sized lobsters we recorded here coincided with this reported change in fishing effort. This experience has prompted the setting of the offshore boundary further from shore in more recently established marine reserves.

Settlement and recruitment as a driver of recovery

Variation in larval settlement is the most likely driver of the variation we report in the density of juvenile lobsters. Unfortunately, insufficient settlement data exist from other studies to enable a meaningful quantitative test of the relationship between settlement and adult abundance at a local level. With the exception of Te Tapuwae o Rongokako

Marine Reserve, existing puerulus collector sites are over 100 km from the nearest marine reserve (Booth *et al.* 2007*a*) and oceanographic features possibly isolate them further from the reserves. However, at the scale of the fishery management area, 'hotspots' of settlement (such as the North Island's east coast) qualitatively match reserves demonstrating rapid recovery in lobster abundance. A correlation between juvenile abundances and larval settlement would require (1) density-independent survival of settlers, and (2) minimal post-settlement movement on the spatial scale of reserves. There is evidence that the abundance of juveniles can reflect settlement pulses (Booth *et al.* 2001), but factors such as the availability of shelter and habitat quality are also important (Herrnkind & Butler 1997). High larval settlement will therefore not always lead to high juvenile abundance at the site level, due to the influence of post-settlement processes (Frusher *et al.* 2000).

Periodically high larval settlement events may be a particularly important driver of recovery in marine reserves situated in areas that receive generally low background levels of settlement. Puerulus settlement has been correlated with adult abundance in both Tasmania (Gardner *et al.* 2001) and New Zealand (Booth *et al.* 2001; Booth *et al.* 2007*b*) but the implications for unfished populations and for interpreting population recovery have not previously been described. Firstly, sudden changes in lobster density in several reserves coincided with recorded heavy settlement events. The marked increases in density displayed in both Long Island-Kokomohua and Tonga Island Marine Reserves in 2002, eight years after the reserves' establishment and following the trend of virtually no change in density over the previous years, followed a strong pulse of puerulus settlement in 1991–1992 reported by Booth *et al.* (2007*a*). Similarly, trends in juvenile abundance at Te Angiangi and Te Tapuwae o Rongokako Marine Reserves tended to track puerulus settlement patterns (Booth *et al.* 2007*a*). At some locations, total lobster abundance mirrored the abundance of sublegal-sized animals, suggesting that populations comprised predominantly of sublegal-sized animals may be strongly influenced by low levels of larval settlement. In contrast, unfished populations may be more resilient to fluctuations in factors such as larval supply and recruitment variability that affect population abundance, due to a large 'residual' population of legal-sized animals that would be reduced if the area was fished. This resilience may result in more stable populations of targeted species within protected areas than in fished areas (Babcock *et al.* 2010).

The correlation between the rate of increase in lobster density and the initial density of juveniles within that reserve suggests that productive populations may be predisposed to a higher rate of recovery. Marine reserves located in areas of low background larval settlement are dependent on not just the enhanced survival of legal-sized lobsters, but on immigration of adults to allow population recovery. If the density in the surrounding area is low, or there is a low likelihood of adults moving into the reserve (due to proximity, or boundary permeability), the rate of increase in recovery is likely to be low. If there is little movement of adults across the boundary of a reserve, the population is entirely dependent on larval settlement and subsequent recruitment. If the reserve population receives both adult immigrants and larval recruits, then (depending on the rate of these), the rate of recovery within the reserve may be enhanced. An important aspect is that because of the long larval lifespan of this and many other marine species, recruitment and adult abundance are decoupled, with larvae produced from the adult population potentially settling thousands of kilometres from their source (Lipcius *et al.* 2001; Chiswell & Booth 2008). If recruitment fails, the local population within a marine reserve could decline to extinction, regardless of how fecund the population is. The patterns of larval settlement, recruitment and cross-boundary movement are therefore important not only for interpreting the recovery trajectories of protected populations, but also for planning protected areas for either conservation or fisheries enhancement purposes.

The very rapid rate of increase in density at Cape Rodney to Okakari Point Marine Reserve is unusual, and considerable uncertainty surrounds this. Firstly, although this reserve was established in 1975, it was not fully enforced until approximately two years later. The density recorded in 1978 (MacDiarmid & Breen 1992) is therefore likely to better reflect the density at the time of the reserve's establishment, rather than the density after three years of protection. Additionally, there was a pulse of recruitment recorded in late 1978 at nearby Tawharanui Marine Reserve and at Mimiwhangata Marine Park (Shears *et al.* 2006), just after the first biological survey of Cape Rodney to Okakari Point Marine Reserve was undertaken (Ayling 1978). The timing of the first survey at Cape Rodney to Okakari Point Marine Reserve may explain why the initial density of juveniles was unusually low relative to the high rate of increase in density recorded subsequently.

Recovery of juvenile lobsters in marine reserves

In addition to increases in the abundance of legal-sized lobsters following protection, we also recorded significant increases in the abundance of juvenile lobsters (which are not taken in commercial or recreational fisheries). There are four possible explanations for this: enhanced recruitment or settlement within the marine reserves; immigration of sublegal-sized animals into reserves; removal of sublegal-sized animals outside reserves through illegal fishing or customary fishing; and enhanced survivorship of juvenile lobsters within reserves. Spiny lobsters, including *J. edwardsii*, are highly social animals (Butler *et al.* 1999; MacDiarmid 1994) and the presence of conspecifics may encourage an individual to settle or move into and remain in a reserve where the density of adults is higher (although habitat-related factors such as shelter availability may be more important; Booth 2001). The mortality rates of small juveniles may also be lower where they cohabitate with high densities of larger individuals, through enhanced protection from predators. In such cases, densities within marine reserves may increase exponentially

rather than linearly (Willis *et al.* 2003). There is some evidence for movement of sublegal-sized animals into New Zealand marine reserves (Kelly & MacDiarmid 2003; Freeman 2008) but no evidence that the rate of this movement is higher than the rate of movement out of reserves.

We know of no evidence to suggest that illegal fishing or legal removal of juvenile lobsters is occurring at a level that would explain the distinct differences between reserve and fished areas across the spatial scale we studied. While indirect effects of fishing on condition of sublegal-sized lobsters have been documented (Freeman & MacDiarmid 2009) and incidental mortality of sublegal-sized animals is incorporated into lobster stock assessments (see Breen *et al.* 2009), fishing-related incidental mortality of sublegal-sized lobsters in New Zealand has not been quantified. However, modelling studies have demonstrated that fishery interactions with spiny lobsters that are not retained by fishing gear can have significant impacts on population abundance (DiNardo *et al.* 2001; Parsons & Eggleston 2007).

CONCLUSIONS

Lobster populations demonstrated significant variability in their responses to protection in New Zealand marine reserves. While aspects of reserve design, such as size and boundary placement, had no significant influence on the initial recovery rate of lobsters, we found that high densities of juveniles were associated with high recovery rates. In addition, we found that densities of juvenile lobsters, along with densities of legal-sized lobsters, were usually enhanced within marine reserves relative to fished locations. Further studies of adult movement patterns and of puerulus settlement, recruitment and juvenile mortality rates in and around marine reserves, are required to better understand the enhanced density of juvenile lobsters and the link between the supply of juveniles and population recovery within New Zealand marine reserves.

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