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The Ecology of Spiny Lobsters (*Jasus edwardsii*) on Fished and Unfished Reefs

Debbie Joanne Freeman

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Abstract

Knowledge of the interactions among species and communities is vital for their management and protection. Increasingly, the role of marine protected areas in this regard is being recognised, primarily because of the potential for previously-harvested species to increase in density and biomass, and the linkages among species to be restored.

Monitoring and research was conducted within and surrounding two marine reserves on the east coast of the North Island of New Zealand – Te Tapuwae o Rongokako, near Gisborne, and Te Angiangi, south of Napier. The aim was to describe the biological characteristics of spiny lobsters (*Jasus edwardsii*) in the absence of fishing, and to describe the effects of fishing and protection on lobster populations and the communities of which they are a component.

Diver and pot surveys showed that lobsters were significantly more abundant within the reserves than in the surrounding fisheries and that the populations were comprised of a larger proportion of legal-sized individuals. Higher female fecundity within Te Tapuwae o Rongokako Marine Reserve compared with the surrounding fishery was proposed to be primarily a result of increased availability of large males within the reserve. The impact of the fishery on lobsters was also evidenced in the lower tail width to carapace length ratio of the fished population compared to the population within Te Tapuwae o Rongokako Marine Reserve, due to the minimum legal size for *Jasus edwardsii* in New Zealand being based on tail width.

The largest tagging study ever to be conducted in a New Zealand marine reserve showed that sublegal male lobsters within Te Tapuwae o Rongokako Marine Reserve were growing on average faster than the same sized individuals outside the reserve, potentially as a result of the effects of handling and/or size-selective fishing. A decrease in growth rate over time was recorded in male lobsters within the reserve, which coincided with an increase in catch per unit effort and may indicate that density-dependent effects are operating. Distinct seasonal movements of tagged lobsters were recorded, with the vast majority of movements taking place within reefs. Where the boundaries of the reserve crossed reef habitat, significant movement of lobsters across the boundaries occurred.

Lobsters within Te Tapuwae o Rongokako Marine Reserve not only exhibited cannibalistic behaviour but foraged during the day, including on intertidal reef platforms at high tide, potentially as a behavioural response to increased competition for food – behaviour not
previously reported for this species. Outside the reserve, lobster bait apparently provided an alternative protein source but despite this supplementation of diet, these lobsters were in poorer nutritional condition, as evidenced by their lower body weights relative to carapace length and tail width for both sexes. Lobsters outside the reserve were also significantly more affected by a bacterial infection associated with handling, than lobsters within the reserve.

These findings have significant implications for fisheries management and for the design and management of marine protected areas (MPAs). This study demonstrates that many of the biological parameters used in evaluating harvest strategies in the New Zealand lobster fishery may be biased unless collected from populations with a natural size structure, such as may occur within marine protected areas.
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Chapter 1  General Introduction

The impacts of fishing and other human activities on the marine environment are increasingly being recognised. In addition, there is a continuing recognition that fisheries management needs to take into account the impacts of fishing on the wider ecosystem. Ecosystem-based fisheries management, and management of the environmental effects of fishing, are becoming increasingly entrenched in Government policy, including that of New Zealand (Ministry of Fisheries, 2005).

The effects of fishing range from direct impacts on the target species, through to impacts on non-target and bycatch species, habitats and indirect impacts on communities of which the target species are components (Dayton et al., 2002). Management of such effects includes not only good management of the target stock, but other initiatives including fishing method restrictions, observer programmes, imposition of non-target species bycatch limits, the use of bycatch mitigation devices and the establishment of marine protected areas or MPAs (Ministry of Fisheries, 2005; Tegner & Dayton, 1999).

Fisheries management has a long history of dedicating closed areas for specific purposes, from short-term closures to protect species during spawning, to permanent closures to protect certain species or life history stages from particular fishing methods (Ward & Hegerl, 2003). Along with long-term monitoring, spatial closures and / or MPAs are essential for studying the effects of fishing through comparative and baseline purposes and for conducting mega-scale experiments (Mayfield, 2006). In fact the study of no-take areas has been suggested to be the only way of determining the true ecosystem effects of fishing (Tegner & Dayton, 2000). Studies of unfished populations also provide the opportunity of obtaining information on the biological characteristics of target species without the bias introduced by selective fishing mortality (Buxton et al., 2006).

Managing species and changing the abundance, size, sex and age structure of key species by imposing different management regimes has implications for community structure. As has been demonstrated in northeastern New Zealand, changes in species distribution and abundance within no-take MPAs, as a result of removing human harvesting, have the potential to alter the structure of the community of which they are a component (Babcock et al., 1999; Shears & Babcock, 2002). In addition, several studies have demonstrated how human harvesting activities outside protected areas can influence community structure (Lindberg et al., 1998; Moreno, 2001; Sharpe & Keough, 1998). Long-term ecological monitoring is a key method utilised to describe such
changes in community structure. The community changes described for kelp forest communities in Nova Scotia (e.g. Johnson & Mann, 1988) and for the shallow reef communities within the Cape Rodney to Okakari Point Marine Reserve in northeastern New Zealand (Babcock *et al.*, 1999) were mostly based on the monitoring of community structure over many years. Manipulations of the distribution and abundance of key species have also proven to be vital in the assessment of the ecological roles of particular species (e.g. Villouta *et al.*'s, 2001 study on the effects of urchin removal). Investigations of the behaviour and feeding ecology of key species are also important tools in the description of trophic interactions (e.g. the study by Scheibling *et al.*, 1999 on sea urchin feeding aggregations).

If we can understand how species interact, there exists the potential to determine how changing the distribution and/or abundance of one or more species (as occurs in the marine environment through human harvesting activities) can influence community structure. For example, if there are particular species that are of interest or importance (e.g. a species of fisheries value), then the effect of a particular management regime on these species could potentially be assessed. Studies of the interactions among species in unfished areas, where species abundance may be at a more natural level, can therefore inform management decisions in fished areas.

No-take marine reserves are just one of a number of tools available to provide protection of the marine environment. Marine reserves commonly increase the density, biomass and average size of target species within their borders (Halpern, 2003; Rowley, 1994), depending on a number of factors, including the design of the reserve, its location, species assemblages and their characteristics, compliance and external pressures such as pollution and weather. It has been suggested that only complete and permanent protection from fishing can protect the most sensitive habitats and vulnerable species (Roberts *et al.*, 2005) and that partial closures may be ineffective as conservation tools (Denny & Babcock, 2004).

Provided that adequate enforcement is in place, marine reserves may not only protect and preserve the life within their boundaries, but also sustain and even enhance fishery yields in the surrounding area (Halpern & Warner, 2003; Sale *et al.*, 2005). A number of studies have shown that marine reserves can supplement surrounding fished stocks to some degree (e.g. Gell & Roberts, 2003a; Russ *et al.*, 2004), but their ability to increase total fishery yield varies (e.g. Gerber *et al.*, 2002). In terms of New Zealand marine reserves, it has been suggested that their impacts on fishers are at worst neutral (Babcock, 2003) and that early claims that marine reserves increase yields may have been exaggerated.
Reserves intended to provide fisheries benefits ("enhance reserves") must be designed so that they supply fished areas with adults and juveniles (Russ & Alcala, 1996) and larvae (Shanks et al., 2003) via spillover. It has been suggested (Halpern & Warner, 2003; Hastings & Botsford, 2003) that reserves intended to provide such fisheries benefits through reducing the exploitation rate should be as small as possible to maximise larval export and allow sufficient adults to “spill” across reserve boundaries to provide opportunities to “fish the edge”, but that fisheries and conservation goals may not necessarily be in conflict.

However, the interaction between the need to harvest and the need to protect has historically been and remains controversial. The effects of marine protected areas on surrounding fisheries (both positive and negative) are debated every day in various forums worldwide, as are, conversely, the need for protected areas as a way of mitigating the direct and indirect effects of fishing and other activities on marine biodiversity. The mechanisms by which the various stakeholders can work together to implement the right kind of management to achieve both benefits for fishing and for conservation, remain a key focus area for resource managers and the community.

1.1 The spiny lobster, *Jasus edwardsii*

The spiny lobster, *Jasus edwardsii* (also known as red crayfish, koura or rock lobster; Figure 1-1), is the most common of four palinurid lobster species found in New Zealand waters and is present on reefs and light foul along New Zealand’s coast, reaching its northern limit at the Three Kings Islands and its southern limit at the subantarctic Auckland Islands (Booth & Webber, 2001; Kensler, 1967). They are also found on shallower seamounts within New Zealand’s Exclusive Economic Zone and on seamounts in the Tasman Sea (Booth & Webber, 2001). The species is more abundant on the east coast than on the west coast of the North Island of New Zealand and in general, becomes more abundant with increasing distance south (Kensler, 1967). Smith et al. (1980) studied genetic variation in *J. edwardsii* from New Zealand and *J. novaehollandiae* from Australia and concluded that they may be conspecifics. Based on the genetics and biology of the two (including morphology, colour and life history characteristics), Booth et al. (1990) concluded that the two species should be referred to as a single species – *J. edwardsii*. In Australia, *J. edwardsii* is a conspicuous component of rocky reef communities in South Australia, Victoria and Tasmania and supports important commercial and recreational fisheries in those States (Haddon & Gardner, 2007; Linnane et al., 2006a, 2006b).
*J. edwardsii* is a predominantly nocturnal animal (Booth, 1986; Meyer-Rochow & Tiang, 1984; Williams & Dean, 1989) and has been reported to have a varied natural diet comprised primarily of molluscs and other invertebrates (Booth, 1986). In northeastern New Zealand, the interactions among lobsters (and other predators), sea urchins and macroalgae have been the subject of considerable research. Long-term monitoring and experimental research have demonstrated that lobsters and other predators can have significant effects on sea urchin populations, which in turn affect macroalgal communities. In marine protected areas, where previously-harvested predators such as lobsters have increased in abundance and biomass, kelp (*Ecklonia radiata*) forests have replaced what were “barren” areas, because of the removal of herbivorous sea urchins (*Evechinus chloroticus*) by predators (Babcock *et al*., 1999; Shears & Babcock, 2002, 2004). Such trophic cascades have been reported for other temperate reef communities with lobsters as a key component (e.g. Mann, 1982). In addition, the role of spiny lobsters in structuring soft sediment communities has been recognised (Langlois *et al*., 2005b).

Spiny lobsters are not only important predators in New Zealand rocky reef communities and soft sediment habitats adjacent to reef, but are also themselves important prey species. *J. edwardsii* is a known prey species of a number of predatory fish, including rig (*Mustelus lenticulatus*) (M. Francis, NIWA, pers. comm.), blue cod (*Parapercis colias*), hapuka / groper (*Polyprion oxygeneios*) and southern dogfish (*Squalus acanthias*). Ballantyne (comment in Pike, 1969) and Thomson (in Pike 1969) noted that at that time, it was common to catch blue cod and groper with lobsters in their guts, with whole lobsters up to 12 inches in length recorded in the guts of groper. Pike (1969) found that 80% of southern dogfish he had recently examined from Cape Campbell had lobster remains in their stomachs. Marine mammals are also potential predators of lobsters. For example, Yaldwyn (1958, cited in Kensler, 1967) recorded *J. edwardsii* remains in seal vomit from the subantarctic Auckland Islands and seals are a known predator of lobsters in commercial pots in South Australia (McKenzie *et al*., 2005). Octopus can cause significant mortality of lobsters caught in pots and in many cases they are the primary predator of lobsters in traps, particularly of large lobsters (Brock & Ward, 2004; Hunter *et al*., 2005).

*J. edwardsii* is one of a number of lobster species that exhibits complex behaviours associated with cohabitation and reproduction, which vary with lobster size, sex and season (Kelly *et al*., 1999; MacDiarmid, 1994). Aggregation in this species has been demonstrated to be chemically-mediated and has implications for lobster survival (Butler *et al*., 1999). Their movement patterns also vary seasonally, in relation to moulting, mating and feeding (Kelly, 2001; MacDiarmid *et al*., 1991) and migrations of significant distances have been described (e.g. McKoy, 1983).
Female *J. edwardsii* become mature at different sizes around New Zealand, primarily as a response to sea temperature. Mating occurs shortly after the female moult (between December and July, McKoy, 1979), the eggs are extruded and then attached to setae on the pleopods beneath the female’s tail. Eggs are carried for 3-6 months and are released upon hatching between August and November (Booth, 1986; McKoy & Leachman, 1982). Larvae develop through a series of stages and can remain in the plankton for up to 2 years (Chiswell & Booth, 1999; Lesser, 1978; NIWA, 2006). They settle during the puerulus stage, most commonly during winter and early spring (Booth, 1986; Booth *et al*., 2000a). The intensity of settlement varies considerably around the New Zealand coast and one of the highest settlement areas is the East Coast North Island region (Booth *et al*., 2000b).

The high productivity of lobster populations on the North Island’s East Coast is partly attributable to the hydrodynamics of the coast (e.g. Chiswell & Roemmich, 1998), which contributes to the observed high settlement rates of lobster pueruli (e.g. Booth *et al*., 2000b; Booth *et al*., 1999). However, other factors operate, resulting in more rapid growth rates and smaller size at the onset of maturity. Gisborne lobsters are capable of growing to about 38 mm carapace length within one year of settlement and to about 58 mm within two years (McKoy & Esterman, 1981). This growth rate is significantly higher than a number of other New Zealand localities. In addition, female lobsters near Gisborne become sexually mature younger and at a smaller size compared with lobsters from other localities, with females from Gisborne populations becoming mature from 72 mm carapace length, or 3-5 years of age (Annala *et al*., 1980). Booth *et al*. (1999) suggested that unless fishing pressure reduced breeding stocks to very low levels, shelter and food limitations would be important along the southeast North Island coast, because of the much higher reproductive potential of these populations.

A variety of factors are known to affect the population dynamics of lobsters, including latitude, water temperature, food availability (abundance and quality), shelter availability, habitat availability and quality, and mortality. In terms of *Jasus edwardsii*, the activity of fishing probably has the greatest non-environmental influence on this species in New Zealand waters, with a number of potential direct and indirect effects (Breen, 2005).

### 1.2 Site description

The Gisborne lobster fishery remains one of the most important of New Zealand’s fisheries. Lobsters are New Zealand’s third-largest seafood export earners and the commercial harvest from
the Gisborne fishery (CRA3, between East Cape and the Wairoa River) has a landed value of $5.3 million, with a regional asset value of nearly $80 million in 2003 (National Rock Lobster Management Group, 2005a; Statistics New Zealand, 2005).

Following the introduction of individual quotas in 1990, lobster catches in the Gisborne fishery declined and the total quota could not be caught (Breen & Kendrick, 1997). The lobster stock contained many undersized lobsters, but few legal-sized lobsters. Of concern also, were mortality of sublegal lobsters through handling, octopus predation in pots and illegal take. A variety of measures were introduced, including a shortened season, a reduction in the TACC (total allowable commercial catch), a prohibition on taking females during June, July and August, and a reduction in the minimum legal size from 54 mm to 52 mm tail width for male lobsters in the commercial fishery from June to August. An increased CPUE (catch per unit effort) and lobster size were said to reflect the management package’s success (Breen & Kendrick, 1997). Recently, significant concern has been raised over a subsequent decline in CPUE (Haist et al., 2005) and the TACC was reduced by 42% in 2005 to ensure sustainability (National Rock Lobster Management Group, 2005a).

The concept of a no-take marine reserve within the CRA3 area was first suggested in 1990 by the Combined Gisborne Underwater and Fishing Clubs (Gisborne Underwater Club, Lottin Point Mariners’ Association, Gisborne-Tatapouri Sports Fishing Club and the Gisborne Surfcaster’s Association). Local Maori hapu Ngati Konohi expressed deep concern about the state of the marine environment in their rohe, in particular the abundance of harvestable species, and in 1998, after nearly a decade of discussion and consultation, made a joint application with the New Zealand Department of Conservation for Te Tapuwae o Rongokako Marine Reserve (Department of Conservation & Ngati Konohi, 1998). Te Tapuwae o Rongokako Marine Reserve (Figure 1-2) was established in November 1999, following a public submission process. During the submission process, strong opposition was voiced by lobster fishermen, quota owners and organisations representing their interests and legal action by way of a judicial review was undertaken following the establishment of the reserve.

Located on the east coast of the North Island of New Zealand, Te Tapuwae o Rongokako was New Zealand’s 16th marine reserve and at 2452 hectares, remains one of the largest marine reserves on the mainland coast. It protects approximately 5 km of coastline, extending up to 5 km (2.7 nautical miles) offshore to over 40 m depth. A variety of marine habitats are enclosed within the reserve boundaries, representative of the coastal and marine environment between East Cape and Mahia Peninsula (Figure 1-3).
In terms of its general marine conservation objectives, the New Zealand Government seeks to “protect a full range of natural marine habitats and ecosystems to effectively conserve marine biodiversity, using a range of appropriate mechanisms, including legal protection” (Department of Conservation & Ministry for the Environment, 2000). In relation to existing marine reserves, Section 3 of the Marine Reserves Act (1971) states that: they shall be preserved as far as possible in their natural state; the marine life of the reserves shall as far as possible be protected and preserved; and the value of the marine reserves as the natural habitat of marine life shall as far as possible be maintained. The application document for Te Tapuwae o Rongokako Marine Reserve states the following objective for the reserve: “To preserve in their natural state for the scientific study of marine life a range of marine habitats that are so typical of those found on the east coast of North Island between Mahia Peninsula and East Cape that their preservation is in the national interest” (Department of Conservation & Ngati Konohi, 1998). Ngati Konohi have also identified the following objective (Department of Conservation et al., 2005), relating to Te Tapuwae o Rongokako Marine Reserve: “Protection and restoration of local area for education, as a kohanga¹, for spillover and a comparison”. Therefore, the objectives for the establishment of Te Tapuwae o Rongokako Marine Reserve are both conservation and fisheries-related, which may or may not conflict.

Te Angiangi Marine Reserve, located on the Central Hawke’s Bay coast (Figure 1-4), was established two years earlier than Te Tapuwae o Rongokako, in August 1997 (Department of Conservation, 1994). It protects 446 hectares of coastal and marine habitats that are representative of the region. Although it is over 200 km from Te Tapuwae o Rongokako, it is the closest no-take marine reserve to Te Tapuwae o Rongokako and contains many of the same species and communities, although there are some differences, explained by the latitudinal difference between the two regions. North of Mahia Peninsula, the main oceanic influence on the coast is the southward flowing East Cape Current; south of Hawke Bay, the coast is also influenced by the cooler, northward flowing Wairarapa Counter Current (Barnes, 1985; Chiswell, 2002; Chiswell & Roemmich, 1998; Heath, 1985). Nevertheless, as the closest marine reserve to Te Tapuwae o Rongokako, it provides for the comparison between factors such as species recovery rates and population structures.

¹ Translation from Maori: Nest, Nursery
1.3 Objectives

The objectives of this thesis are to:

1. Describe the biological characteristics of lobsters, *Jasus edwardsii*, in the absence of fishing.
2. Describe the effects of protection on lobster populations and communities of which they are a component within Te Tapuwae o Rongokako Marine Reserve.
3. Describe the direct and indirect effects of fishing on lobster populations through the comparison of a fished and an unfished population.

A number of key lobster population parameters are explored in order to achieve these objectives. In Chapter 2, I describe the distribution and abundance patterns of lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve, and also compare the observed patterns with those within and surrounding Te Angiangi Marine Reserve. In Chapter 3, the growth rates of lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve are described, through a tagging study. The movement patterns of these tagged lobsters are described in Chapter 4, including an analysis of the cross-reserve boundary movements of lobsters and the spatial patterns in lobster size and abundance in relation to the reserve boundaries. Chapter 5 comprises studies of the feeding ecology of lobsters within and surrounding the marine reserve, to establish the diet of lobsters and their trophic relationships with other species. Chapter 6 explores several potential indirect effects of lobster fishing, including the incidence of disease and effects on reproductive parameters.

I hypothesise that density-dependent interactions (as a result of potential increased lobster abundance and biomass within the reserve) will result in decreased growth rates and increased movement within the reserve, with relatively more movement of lobsters from the reserve than into the reserve. I also expect lobsters within the reserve to have a reduced nutritional condition and reduced reproductive output, due to increased competition for preferred food sources. I also expect that lobsters within the reserve will exhibit a decreased incidence of characteristics known to be related to handling during fishing activity.

The General Discussion of this thesis describes the key findings and explores the mechanisms operating to create the observed results, and the implications of the results for the management and protection of the New Zealand marine environment.
Figure 1-1 The spiny lobster, *Jasus edwardsii.*
Figure 1-2  Map showing the locations of Te Tapuwae o Rongokako and Te Angiangi Marine Reserves, on the east coast of the North Island of New Zealand.
Figure 1-3 Map showing the location of Te Tapuwae o Rongokako Marine Reserve and other localities mentioned in the text.
Figure 1-4  Map showing the location of Te Angiangi Marine Reserve and other localities mentioned in the text.
Chapter 2  The Distribution and Abundance Patterns of *Jasus edwardsii* on Fished and Unfished Reefs

2.1 Introduction

A variety of factors can potentially affect the distribution and abundance of lobsters, ranging from environmental factors to the particular social behaviour of the species. On a large scale, environmental factors such as latitude, water temperature and hydrodynamics are the primary influences of lobster distribution and abundance. For example, *Jasus edwardsii* is more abundant on the east coast of New Zealand than the west coast and in general, becomes more abundant with increasing distance south (Kensler, 1967).

On a smaller scale, the availability and quality of food, habitat and shelter can alter the distribution and abundance patterns of lobsters. For example, habitat preference by juvenile *Panulirus argus* is strongly influenced by food abundance, with juveniles choosing complex, food-rich habitats (Herrnkind & Butler, 1986). Similarly, *Panulirus guttatus* are more dense on good-quality compared with poorer-quality reefs (Wynne & Cote, 2007). Berry & Smale (1980) suggested that the size of the *Panulirus homarus* population off the South African coast could be limited by the amount of reef habitat in the nearshore zone where its food organism occurs.

The availability of shelter within a lobster’s preferred habitat may also limit the population. For example, the abundance of *Panulirus marginatus* is influenced by the amount of vertical relief and the height of bank summits (Polovina *et al.*, 1995). Habitat limitation may affect the size structure of populations of *Homarus gammarus* (Howard, 1980) through changes in moulting frequency and density-dependent mortality of large lobsters (Addison, 1986). The supplementation of habitat through the use of artificial shelters could be useful in areas where habitat is limiting (Jensen *et al.*, 1994), but the quality of shelters available may be important in determining shelter fidelity (Lozano-Alvarez *et al.*, 2003).

The distribution and abundance of lobsters may also vary on a temporal scale, in relation to the moulting and reproductive cycles of the species. *Jasus edwardsii* are known to make seasonal movements inshore and offshore (Gardner *et al.*, 2003; Kelly, 2001; Kelly *et al.*, 1999; MacDiarmid *et al.*, 1991), although these patterns are not consistent over regional spatial scales (e.g. Davidson *et al.*, 2002; Linnane *et al.*, 2005). Other spiny lobsters make similar migrations associated with reproduction (e.g. *Panulirus cygnus*, Phillips, 1983).
One of the factors that may have an overriding effect on the distribution and abundance of lobsters is mortality – either natural or human induced. In terms of human-induced mortality, fishing has the potential to reduce the population density of lobsters significantly. For example, in a two-day recreational fishing event off Florida, fishers reduced the population density of lobsters (*Panulirus argus*) by 79-95% (Eggleston et al., 2003). Shears et al. (2006) demonstrated how allowing some recreational harvest of lobsters (*Jasus edwardsii*) in a marine protected area prevented the population from even partial recovery following cessation of commercial fishing. Spatial targeting of fishing effort can also alter the distributional patterns of lobsters (Bell et al., 2005; Bello et al., 2005).

Lobster fishing not only reduces the density of lobsters, but can also alter their population structure through the selective removal of particular individuals from the population. Selection may not only be for a particular size, but also a particular sex, age, condition or reproductive status. Iacchei et al. (2005) demonstrated how recreational and commercial fishing impacted on not only the biomass of lobsters (*Panulirus interruptus*) but also the sex ratio. Similarly, fishing for *Jasus edwardsii* in some fisheries management areas in New Zealand and Australia is biased towards either male or female lobsters, primarily because of specific fisheries regulations (such as a prohibition on landing berried females and differences in minimum legal sizes), but also because of seasonal changes in catchability (Breen et al., 2005b; Prescott et al., 1997).

The establishment of marine reserves represents a population manipulation experiment at a vast spatial scale (Edgar & Barrett, 1999). By removing harvesting pressure, lobster populations may recover to a more natural state. Such recovery generally involves an increase in abundance and size of lobsters within protected areas (Childress, 1997; Edgar & Barrett, 1999) and these changes have been reported worldwide for a range of species, including *Homarus americanus* (Rowe, 2002), *Panulirus argus* (Bertelsen & Matthews, 2001; Cox & Hunt, 2005), *Panulirus guttatus* (Wynne & Cote, 2007), *Palinurus elephas* (Goni et al., 2001) and *Jasus lalandii* (Mayfield et al., 2005).

The response of *Jasus edwardsii* to protection has been studied throughout its Australasian range. Edgar & Barrett (1999) reported increases in lobster size and abundance in Tasmanian marine reserves, with an increase in the biomass of legal-sized lobsters of over 20 times in the largest marine reserve studied. In New Zealand, lobsters have also been found to be larger and more abundant within marine reserves in comparison with fished sites (Davidson et al., 2002; Kelly et al., 2000b; MacDiarmid & Breen, 1992; Shears et al., 2006).
However, the extent to which marine reserves can provide protection to lobster populations is dependent on a number of aspects relating to the location and design of the marine reserve. For example, small marine reserves have been suggested to be ineffective at protecting Caribbean spiny lobsters, *Panulirus argus*, due to the dispersal of lobsters from closed areas and their subsequent harvest (Eggleston & Dahlgren, 2001). Stockhausen & Lipcius (2001) used a modelling approach to confirm this, describing how large marine reserves would be more effective than small reserves at protecting this species. The suitability of habitat is also important, as shown for *Panulirus argus* and *P. guttatus* (Acosta & Robertson, 2003) and *Jasus lalandii* (Mayfield *et al.*, 2005).

Changes in population structure may in turn result in changes in the small-scale distribution patterns of lobsters, due to size- and density-dependent intraspecific interactions. *Jasus edwardsii* is one of several spiny lobster species that exhibits ontogenetic changes in sociality and spatial distribution (Butler *et al.*, 1999; MacDiarmid, 1994). Studies of natural populations of *J. edwardsii* and laboratory experiments were utilised by Butler *et al.* (1999) to demonstrate that as early benthic juveniles, *J. edwardsii* are solitary animals, but become social and aggregate as they grow larger. A size-specific response to chemical cues of other lobsters facilitated these changes in aggregation. Larger lobsters were found to benefit from aggregation through an increase in survival, but no such advantage was found for small lobsters.

There are a number of methods available to investigate the distribution and abundance patterns of lobsters. They include direct observation (through the use of divers or remote video cameras) and the use of nets and traps. Direct observation provides the best description of population structure, as every individual in the population, or sample of the population, can potentially be sampled. In contrast, lobsters sampled using traps or nets may be influenced by catchability, which refers to the probability of capture per unit effort (Morgan, 1974). The catchability of lobsters can be influenced by a number of factors, including lunar phase, sea conditions, the lobsters’ reproductive and nutritional status, bait type, pot type and occupancy of the pot (including other lobsters, bycatch and predators).

In this study, I describe the distribution and abundance patterns of *Jasus edwardsii* within and surrounding two marine reserves: Te Tapuwae o Rongokako Marine Reserve (near Gisborne), and Te Angiangi Marine Reserve (in Hawke’s Bay), using two different methods. The aim of this study is to describe the extent to which the cessation of fishing has influenced the population structure, distribution and abundance patterns of lobsters at both locations. It is hypothesised that
lobsters within the two marine reserves will be more abundant and the populations will contain more large individuals than adjacent fished areas. It is also expected that due to a male-biased fishery, the sex ratio of lobster populations in unfished areas will be more even than in fished areas.
2.2 Methods

2.2.1 Sampling strategy

Diver transects and pot surveys were used to describe the density, population structure (size and sex composition) and fine-scale distribution patterns of lobsters on reefs within and surrounding Te Angiangi and Te Tapuwae o Rongokako Marine Reserves, with both methods being employed at Te Tapuwae o Rongokako. Reef habitat from throughout the two reserves and at comparable fished areas adjacent to the reserves was sampled over several years to enable the description of any differences in lobster distribution and abundance between fished and unfished reefs over time. Diver surveys were conducted only during summer months between January and April (to reduce seasonal variability and to take advantage of the more workable sea conditions), whereas the pot surveys included a seasonal component.

2.2.2 Diver training

Prior to the lobster surveys, all divers were trained to visually estimate the carapace length (distance from the base of the antennal platform to the posterior margin of the carapace, to the nearest 5 mm) of lobsters using an estimate / capture / measure procedure. At least 30 lobsters were sampled by each diver during these training sessions and these sessions were repeated annually. Prior to capture, the sex of each lobster was also visually assessed, determined by the presence or absence of chelae on the fifth walking legs (females – chelae present; males – chelae absent) and / or pleopods (females – biramous pleopods; males – uniramous pleopods). The average error and bias in estimating carapace length was calculated for each diver. Divers were required to estimate the carapace length to within 5 mm.

2.2.3 Gisborne

2.2.3.1 Diver surveys

Diver surveys, to obtain data on the density and population structure of lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve, were completed from January to April, between 2001 and 2005. Two depth strata were surveyed (<15 m and 15-29.9 m) and all transects were located on rocky reef. The shallow stratum was comprised of mixed brown algal (Carpophyllum spp and Ecklonia radiata) habitat and the deep stratum was predominantly sparse.
kelp (*Ecklonia radiata*) forest habitat, with a conspicuous sponge community. Transects were positioned haphazardly within each depth stratum in an attempt to sample at least 15 transects within each depth stratum at each location each year, and to sample from throughout the reef habitat within each stratum. However, some parts of the reefs were unable to be sampled due to consistent poor underwater visibility and navigational hazards.

Transects were 50 x 10 metres, to ensure comparability with lobster research being undertaken in other New Zealand marine protected areas (e.g. Kelly *et al.* 2000b) and in accordance with previously-established guidelines for monitoring this marine reserve (Freeman, 2001c). Each 50x10 m transect was sampled by two divers. The first diver swam the tape measure out to 50 m and then sampled a 5 m strip of rocky reef habitat on one side of the tape measure. As this was happening, the second diver sampled the 5 m strip on the other side of the tape measure. This second diver then wound in the tape measure, ensuring that he/she did not overtake the first diver. The transects were completed in a haphazard direction, with the divers only altering their course to ensure that the transect remained within the correct depth stratum and so that at least 90% of the transect crossed rocky reef.

Utilising a torch where necessary, each diver estimated the carapace length (to the nearest 5 mm) and recorded the sex of each lobster within the transect. In some cases, lobsters were too deep within crevices to be sexed, but where possible their carapace length was visually estimated.

Adverse sea conditions, in particular poor underwater visibility, consistently prevented the completion and on occasions the initiation of diver surveys in any one year. Therefore, the level of replication varied considerably among locations and years (Table 2-1, Figure 2-1).

Density measurements for lobsters were also recorded during separate 100x4 m reef fish transects carried out between January and April from 2000 (approximately two months subsequent to the establishment of the marine reserve) to 2004. These transects were undertaken in accordance with previously established guidelines for monitoring this marine reserve (Freeman, 2001c). In 2000 and 2003, these transects provided the only lobster density data, as adverse sea conditions prevented the dedicated lobster transects being undertaken in these years. Table 2-2 provides the number of transects where density measurements of lobsters were able to be collected during the fish count transects. No estimates of lobster size were collected during these fish counts.

During the lobster surveys completed in 2004 and 2005, divers also recorded the size and sex of lobsters for each group of lobsters sampled along the transects to obtain data on group
composition. A total of 242 groups of lobsters were sampled within the reserve and 230 outside the reserve.

2.2.3.2 Pot surveys


The location and number of pots set depended on a number of factors, including weather and sea conditions, the vessel used and the presence of other fishing gear. Where possible, reef habitat from a range of depths throughout the marine reserve and within approximately 3 km of the reserve’s boundary was sampled (Figure 2-2) during each survey period (approximately every three months). Approximately 50 pots were sampled per day, which provided a manageable workload for the vessel and personnel. With the exception of the first surveys in November and December 2003, sampling was undertaken over a period of up to 5 consecutive days (weather permitting), which usually enabled adequate sampling of the entire reef within the reserve and within 3 km of the reserve’s boundary.

Three different types of lobster pots were used: standard commercial pots, ¾-sized standard pots and fine mesh pots. The standard pots were commercial HRC (Hurricane Reinforcing Concrete) pots used widely in the New Zealand lobster fishery. They were of 52 mm mesh, occasionally with a finer mesh on the underside of the pots to minimise damage to the lobsters when the pots were brought on board the boat. A number of ¾-sized pots were used, mainly in winter 2004. These were also of 52 mm mesh, but were ¾ of the width of the standard pots and were easier to handle on the vessels used during this period. A small number of fine mesh pots were also used in an attempt to catch lobsters below the minimum legal size limits (54 mm tail width for males; 60 mm tail width for females). These were standard HRC pots, covered in 25 mm plastic mesh.

Pots were baited with seasonally available fish, usually locally-sourced, including gurnard, snapper, tarakihi, barracuda, kingfish, cardinalfish, jack mackerel, blue moki and trevally. Bait type was recorded for every pot sampled, where possible.

It was intended that all pots be set overnight. On rare occasions, adverse sea conditions prevented pots from being lifted after 24 hours of soak time and so a small number of pots had
48-hour soak times. Pots were generally set in groups of 3 to 7, depending on the extent and complexity of the reef being sampled and were generally no less than 100 m apart. In order to minimise stress and injury to the lobsters, the pots were brought on board the boat without shaking them to remove undersize individuals. In addition, any lobsters with their tail or appendages hanging outside the pot were removed or repositioned before setting the pot on the boat.

The weather and sea conditions were recorded for every day of sampling, and for the days previous to sampling. For every pot set, the time, depth, pot type and GPS position to the nearest metre were recorded.

For every lobster caught, apart from those that had been eaten by octopus, sex and tail width (measured to the nearest 0.1 mm in a straight line between the tips of the primary spines on the second segment of the tail) were recorded. Generally those lobsters that had been preyed upon by octopus were unmeasurable, or had some body parts (e.g. cephalothorax) missing (Brock & Ward, 2004). All bycatch and lobster mortality was recorded.

### 2.2.4 Hawke’s Bay

Between 1999 and 2005, 50x10 m diver transect counts of lobster density were surveyed within Te Angiangi Marine Reserve and at Pourerere, north of the reserve. Sampling was undertaken in accordance with previously established protocols for monitoring this marine reserve (Freeman, 2001a) and to ensure comparability with research being undertaken in other New Zealand marine protected areas (e.g. Kelly et al. 2000b). Lobster carapace length (visual estimate) and sex were recorded wherever possible. Surveys were conducted during the summer months of January and February and transects were located in two depth strata within kelp forest (*Ecklonia radiata* / *Lessonia variegata*) habitat (Table 2-1, Figure 2-3).

In 1999, 2001, 2003 and 2005, lobsters were also counted during a separate survey for reef fish (Freeman, 2001a). During these surveys, all lobsters within a 100x4 m area of rocky reef were counted, but their size and sex were not recorded (Table 2-2).

Previously-collected (1995-1998) data on lobster distribution and abundance were also available for analysis (Department of Conservation, unpubl.). In 1995 (two years prior to the reserve’s establishment), 10x10 m quadrat counts of lobster abundance were completed within the proposed marine reserve and at Pourerere. Lobster carapace width (visual estimate, to the nearest
5 mm) and sex were recorded for most individuals sampled. During 1996 and 1998, 50x10 m transects were surveyed within the marine reserve and at Pourerere, and lobster carapace length and sex were recorded.

Adverse sea conditions prevented any lobster surveys from being initiated in 1997 and 2000, and from being completed in 2001 and 2003.

In 2005, divers recorded the size and sex of lobsters within each den (where possible) to obtain data on group composition. A total of 185 groups of lobsters were sampled along transects within the reserve and 48 along transects outside the reserve.

2.2.5 Data recording and analysis

Generally, divers only estimated carapace length, while only tail width was measured for most lobsters caught in pots. To enable mean size to be compared among the diver and pot catches, previously collected data relating tail width to carapace length were utilised to convert carapace length to tail width. For males, tail width = 9.32 + 0.43 x carapace length ($r^2 = 0.92; n=6210$; tail width range 35.4-77.1 mm; carapace length range 65.5-176.4 mm); for females, tail width = 4.03 + 0.57 x carapace length ($r^2 = 0.82; n=2051$; tail width range 33.8-69.6 mm; carapace length range 55.3-117 mm) (unpubl.). A legal-sized male (tail width of at least 54 mm) from the sample area was determined to have a carapace length of at least 104.5 mm, and a legal-sized female (tail width of at least 60 mm) a carapace length of at least 97 mm.

To establish the relationship between carapace width and length, lobsters retained within holding tanks were sampled in September 1999 (Department of Conservation, unpubl.). Sex, carapace width and carapace length were recorded for 38 individuals (22 females and 16 males). Additional data collected in 1995 (an additional 6 males and 11 females) were also used to establish a relationship between carapace length and width, and this subsequently enabled carapace width data from transects in Hawke’s Bay in 1995 to be utilised.

Counts of lobsters from the same depth stratum, location and year obtained from the lobster and fish counts were converted to numbers per 500 m$^2$ for analysis and graphical display.

Data collected during the pot surveys undertaken in November and December 2003 were recorded by an observer on data sheets specifically designed for the project. Subsequent data were recorded using a custom-designed database programme (DataPlus CE Host software),
loaded on to a handheld field computer (Allegro CE, Juniper Systems). This programme provided continuous error checking (through restrictions on values permitted to be entered in each data field) and therefore improved data accuracy. All depth data were corrected for tidal height.

Statistical analyses were undertaken using SPSS and R software (R Development Core Team, 2007).
2.3 Results

2.3.1 Abundance

Because there was strong evidence for overdispersion in the diver count data from Te Tapuwae o Rongokako Marine Reserve (highly skewed towards smaller values), a quasipoisson distribution was specified for the generalised linear model. There was a marginally non-significant change in variance when the interaction between status (reserve or non-reserve) and year was excluded from the model (p=0.05) and this interaction term was retained in the model. Outside the reserve, the density of lobsters was relatively constant and high, with no apparent trend over time (Figure 2-4). Within the reserve there was an overall 2.5 fold increase in the density of lobsters over the sampling period, from 10.2 lobsters per 500 m$^2$ (s.e. = 2.6) in 2000, to 26.4 per 500 m$^2$ in 2005 (s.e. = 5.2) (Figure 2-4). This increase in density occurred primarily as a result of an increase in lobsters in less than 15 m depth (Figure 2-5), but the increase in abundance was not steady, with a large decline in density between 2002 and 2003, followed by a subsequent large increase.

For Te Tapuwae o Rongokako Marine Reserve:  
\[
\text{density} = e^{-310.15} \times e^{(0.156211 \times \text{year})},
\]

For the fishery surrounding the reserve:  
\[
\text{density} = 0.000175 \times e^{(0.005711 \times \text{year})},
\]

where density is in individuals per 500 m$^2$.

There was no significant correlation between the mean number of lobsters per pot (from pot surveys) and the mean number of lobsters per 500 m$^2$ (from diver surveys) for the two summers (03/04 and 04/05) for which data were available from both fished and reserve locations (Figure 2-6). However, the individual diver transects and pot locations did not usually overlap and so the catchability of lobsters in a particular area could not be assessed.

A total of 55,403 lobsters (plus 343 packhorse lobsters, *Sagmariasis verreauxi*) were caught during pot surveys within and surrounding Te Tapuwae o Rongokako Marine Reserve. Table 2-3 provides the mean catch per unit effort (CPUE) for the three different types of pots used over the three year survey period.

Following data exploration, catch data were divided into “summer” and “winter” months – “summer” months including data from November to March, and “winter” months including data from May to September (Figure 2-7). The mean CPUE was significantly greater for standard-sized pots than the smaller pots (two-tailed $t$-tests, $p<0.05$ for both February and June). Therefore, only CPUE data from standard-sized pots are presented here.
Catches from standard-sized pots within Te Tapuwae o Rongokako Marine Reserve were consistently higher than those outside the reserve, with the average CPUE reaching 46 times higher within the reserve than outside (Figure 2-7).

A distinct difference in the catch between summer and winter months was evident, at least for the 15-29.9 m and 30-44.9 m depth strata. The CPUE within these depth strata peaked during the summer months, then declined in the winter months (Figure 2-7). These seasonal changes were apparent both within and outside the marine reserve, although the changes outside the reserve were much less marked. No such seasonal pattern was apparent for depths <15 m within the reserve, but there was a distinct decline in CPUE in consecutive winters in this depth stratum within the reserve.

Overall (all depth strata combined), there was an increase in mean CPUE in the reserve from 11.2 kg in summer 03/04 to 14.4 kg in summer 06/07 – an increase of 1.1 kg per year. This was mostly the result of increases in the 30-44.9 m depth stratum. The number of legal-sized lobsters per pot in the reserve (all depth strata combined) increased from 16.5 per pot in summer 03/04 to 18.8 per pot in summer 06/07 – an increase of 0.8 per pot per year. Outside the reserve, the mean number of legal-sized lobsters per pot during the summer months (all depth strata combined), ranged between 0.7 and 1.5 per pot.

During summer, males were caught in similar numbers throughout the depth range sampled (0-45 m), but in winter, males were caught almost exclusively in depths less than 15 m. The number of females per pot remained relatively stable over time, but the average number of females per pot was consistently higher in the <15 m depth stratum within the reserve, and in all seasons except winter 2005 outside the reserve (Figure 2-8).

The legal-sized catch within and outside the reserve was predominantly males, with only 18 out of the 1888 standard-sized pots set during the summer months containing more than 5 legal females. Analysis of the number of legal-sized males per standard pot over consecutive summers (all depth strata pooled), specifying a quasipoisson distribution (due to overdispersion) and fitting a generalised linear model, showed that both year and status (reserve or fished) were significant factors (p<0.05), but that there was no significant interaction between year and status (p=0.8).

For Te Tapuwae o Rongokako Marine Reserve:  
# legal males per pot = e^{-66.42169} x e^{0.03456xyear}.

For the surrounding fishery:  
# legal males per pot = e^{-69.15609} x e^{0.03456xyear}.
Within Te Angiangi Marine Reserve, the mean density of lobsters estimated using divers increased over time, reaching a peak of 26.2 lobsters per 500 m$^2$ in 2003, six years after the reserve’s establishment (Figure 2-9). A significant decline in density occurred within the reserve between 2003 and 2004, and again between 2004 and 2005. Outside the reserve, density was variable over time, but, like the reserve, there was a decline in density between 2003 and 2004, and 2004 and 2005. Because there was strong evidence for overdispersion in the diver count data for Te Angiangi (highly skewed towards smaller values), a quasipoisson distribution was specified for the generalised linear model. There was a significant interaction between status (reserve or fished) and year ($p<0.01$) and this interaction term was retained in the model.

For Te Angiangi Marine Reserve: $\text{density} = e^{-74.5352} \times e^{(0.03844 \times \text{year})}$.

For the fishery surrounding the reserve: $\text{density} = e^{263.93095} \times e^{(-0.13107 \times \text{year})}$,

where density is in individuals per 500 m$^2$.

As shown in Figure 2-10, the two marine reserves showed similar patterns in the density of lobsters as a function of reserve age, with an increase following reserve establishment, reaching a peak of approximately 26 lobsters per 500 m$^2$ six years after establishment. In Te Tapuwae o Rongokako Marine Reserve, there was a distinct decline in density between the third and fourth year, with a subsequent increase between the fourth and fifth year. There was a large decline in lobster density in Te Angiangi Marine Reserve after the sixth year of protection and in the last year of monitoring (2005) the mean density of lobsters was similar to what it was one year after this reserve’s establishment.

2.3.2 Size

Analysis of data from small and standard-sized pots from within Te Tapuwae o Rongokako Marine Reserve in February and June 2003 showed that there was no significant difference between the mean sizes of either male or female lobsters caught in these pot types (univariate ANOVA, $p>0.05$). Therefore, size data from small and standard-sized pots were pooled.

There was, however, a significant difference between the size of lobsters caught in the fine mesh pots and those from the 52 mm mesh pots (i.e. standard and small pots) (Figure 2-11), particularly for females. Significantly more small females were caught using the fine mesh pots compared with the 52 mm mesh pots. The difference between the size range of males caught
using the two different mesh sizes was not so marked, although more very large males (over 70 mm tail width) were caught in the 52 mm mesh pots.

Size frequency histograms for lobsters surveyed by divers and pots revealed right shifts over time in the histograms for males within Te Tapuwae o Rongokako Marine Reserve (Figures 2-12, 2-13). This change was less marked for females (Figures 2-14, 2-15) and even after six years of protection, the proportion of female lobsters larger than legal-size (60 mm tail width) caught within the marine reserve was still relatively low compared with the proportion of males larger than legal size (54 mm tail width).

The mean sizes of male and female lobsters sampled by divers (Figure 2-16) varied over time, but were higher within Te Tapuwae o Rongokako Marine Reserve in 2004 and 2005 than in previous years. There was a gradual increase in mean male size outside the reserve.

The mean tail width of males caught by pots within the reserve increased from 58.2 mm to 60.8 mm over the 3 year survey period, but significant decreases in the mean tail width occurred during the winter months at all depth strata surveyed (Figure 2-17). This pattern was less clear outside the reserve. In contrast to males, the mean size of female lobsters in pot catches tended to increase during the winter months, particularly outside the reserve (Figure 2-17), but there was no change in the mean female size within the reserve over the 3 year survey period. Within the reserve, the largest males tended to be caught in shallow depths during both summer and winter months, and this difference among depth strata was most obvious in winter. Outside the reserve, no clear pattern in male size with depth was evident. The largest females were most commonly caught in depths less than 15 m, both within and outside the reserve, during summer and winter months.

In Hawke’s Bay, the size frequency histograms for male and female lobsters within Te Angiangi Marine Reserve showed distinct shifts towards the right over time (Figures 2-18, 2-19). The mean size of lobsters sampled by divers increased following the reserve’s establishment, reaching a peak in 2004 (Figure 2-20). There was a distinct decline in the mean size of males and females, both inside and outside the reserve, between 2004 and 2005 (Figure 2-20). However, sample sizes, in terms of the number of lobsters sized and sexed, were small in 2004. The mean sizes outside the reserve showed similar patterns to those within the reserve, but the means within the reserve were usually higher than those outside.
2.3.3 Sex ratio

At Gisborne, the percentage of males recorded by divers increased over time and was always higher within the marine reserve than at the fished location. In the last survey (2005) the percent males was similar within and outside the reserve, with the sampled population being approximately 1:1 males:females (Figure 2-21).

There was a marked difference between the percent males caught using the fine mesh and 52 mm mesh pots within Te Tapuwae o Rongokako Marine Reserve, with significantly more females being caught in the fine mesh pots. The percent males caught using fine mesh pots was comparable to the percent males recorded during the diver surveys. Using data from only standard pots (as a greater depth range was sampled using these pots), the sex ratio of the pot catch remained stable in the deepest depth stratum surveyed (30-44.9 m), with the catch consistently being comprised almost entirely of males (Figure 2-22). There were fluctuations in the sex composition of the catches in the shallower depths, but no consistent pattern was evident. There were, however, clear reductions in the percentage of males in the catch outside the reserve in the winter months of 2005 and 2006 (Figure 2-22).

In Hawke’s Bay, the percent males recorded during diver surveys varied with time and location, with no consistent or significant effects of either year or location (reserve versus fished).

2.3.4 Small scale distribution and abundance patterns

The diver surveys completed during summer/autumn 2004 and 2005 showed that the lobster groups within Te Tapuwae o Rongokako Marine Reserve were significantly larger than outside the reserve and that males comprised a greater proportion of lobsters in groups within the reserve than outside (two-tailed t-tests, p<0.05; Figures 2-23, 2-24). There was no difference in lobster group size or sex ratio between Te Angiangi Marine Reserve and the corresponding fished location.

At both Gisborne and Hawke’s Bay, the mean number of groups per 500 m² was significantly higher within the marine reserves than outside and there were also more groups per 500 m² at Gisborne than Hawke’s Bay (univariate ANOVA, p<0.05).

Within Te Tapuwae o Rongokako Marine Reserve, there was a significant positive correlation between an individual male’s size and the total number of lobsters in a group, and between the
size of the largest male in the group and total number per group (Pearson correlation, p<0.05), but not between individual male size and the percentage of males in their group (Table 2-5). In Te Angiangi Marine Reserve, there was a significant negative correlation between individual male size and the total number of lobsters per group, but no significant correlation between the size of the largest male in the group and total group size, or between individual male size and percent of males per group.

At Gisborne, there were significant positive correlations between female size and the percentage of males within that group, and between female size and the total number of lobsters per group, both inside and outside the reserve (Pearson correlation, p<0.05). Conversely, at Hawke’s Bay, there was a significant negative correlation between individual female size and the total number of lobsters per group, both inside and outside the reserve. There was no significant correlation between individual female size and the percentage of males per group, either inside or outside Te Angiangi Marine Reserve (Table 2-5).
2.4 Discussion

Diver and pot surveys provided insights into the distribution and abundance patterns of lobsters within and surrounding two East Coast North Island marine reserves. Significant differences in patterns of abundance and in population structure were apparent over time and between protected and fished locations, as well as between the two regions. Lobster abundance has increased significantly within the reserves and the populations within the reserves have a significantly higher proportion of large individuals. The significantly higher research catch rates within Te Tapuwae o Rongokako Marine Reserve than in the surrounding fishery, along with increases in the abundance of legal sized lobsters in both marine reserves and comparable densities of lobsters within and surrounding Te Angiangi prior to implementation of protection, strongly suggest that the increases are due to the cessation of fishing.

2.4.1 Response to protection

Taking into account the caveats relating to the comparisons of population structure and abundance from pot surveys (see below), lobsters within Te Angiangi and Te Tapuwae o Rongokako Marine Reserves have demonstrated responses to protection, with increases in the abundance and proportion of legal-sized individuals. Such responses to protection have been recorded for other spiny lobster species (e.g. *Palinurus elephas*, Goni et al., 2001) and also for *Jasus edwardsii* throughout its Australasian range (Edgar & Barrett, 1997, 1999; MacDiarmid & Breen, 1992).

Kelly et al. (2000b) estimated the rate of increase in lobster (*Jasus edwardsii*) density in four northeastern New Zealand marine protected areas to be between 3.9% and 9.5% per year, depending on depth. The initial rates of increase recorded in my study were significantly higher than these, but there was considerable variability in the diver counts and significant declines took place in both marine reserves over the study period. The higher initial rate of recovery in the two reserves I studied is likely to be partially explained by the higher larval settlement and recruitment rate along this piece of coastline compared with northeastern New Zealand (Booth et al., 2004). Differences in the level of compliance among the marine protected areas may also contribute to differences in recovery rate. Spatial variation in movement rates between reserve and fished areas, and reserve design may also explain differences in recovery rate, and this is explored in Chapter 4.
Research catches within Te Tapuwae o Rongokako Marine Reserve were up to 46 times higher (in terms of CPUE) than outside the reserve, four years after the reserve’s establishment. There was little difference in the total number of lobsters caught per pot between reserve and fished locations. However, because the pots only effectively sampled legal-sized lobsters (due to their mesh size, 52 mm), only the abundance of legal-sized individuals can reliably be estimated. The differences in CPUE between reserve and fished locations are a reflection of differences in size and abundance, with more legal-sized lobsters being caught in the reserve over time, and these lobsters being on average larger than legal-sized individuals outside the reserve. Between consecutive summers in the reserve, there was a relatively low rate of increase in CPUE, in the number of legal-sized lobsters caught per pot and in the number of legal-sized males caught per pot. Assuming that the CPUE and the number of legal-sized lobsters per pot were similar within and outside the reserve prior to its implementation, these low rates suggest either that the rate of increase within the reserve has not been constant since its establishment (this is supported to some extent by the diver data), or that the pot catches provide a conservative measure of the actual legal-sized biomass within the reserve (discussed further below). According to the fitted generalised linear model, the reserve would have had to be over 70 years older than it actually is to reach the mean number of legal males per pot predicted by the model.

A large reduction in lobster density occurred within Te Tapuwae o Rongokako Marine Reserve between 2002 and 2003. However, with no size data available from 2002 and only limited data from 2003, it is not clear what proportion of the population declined. The large reduction in the density of lobsters in Te Angiangi Marine Reserve between 2003 and 2005 is also noteworthy. Unfortunately, there are no size data from Te Angiangi in 2003 and so it is unclear what proportion of the population was reduced. However, in 2004, no males less than 100 mm carapace length and no females less than 65 mm carapace length were observed within the 8 transects completed within the reserve, which suggests that the reduction in density observed over that period was in the juvenile proportion of the population.

Previous studies have used a range of carapace lengths to represent legal-sized *Jasus edwardsii* (95 mm, Davidson et al., 2002; 100 mm, Kelly et al., 2000b; 95 mm, Shears et al., 2006). In my study, I measured the carapace lengths and tail widths of over 8000 lobsters and found that a legal female (tail width 60 mm) typically had a carapace length of around 97 mm; a legal male (tail width 54 mm) typically had a carapace length of around 105 mm. When determining the density and biomass of legal sized lobsters, using a carapace length that is too small would result in overestimation of the density and biomass estimates of legal-sized lobsters.
In Gisborne, commercial fishers are permitted to land and retain male lobsters with a tail width of at least 52 mm during the months of June, July and August. Therefore, my estimates of the CPUE for these months (which are based on 54 mm lobsters) are underestimates. Keeping the minimum legal size constant enabled temporal changes to be more clearly elucidated. During May, no lobsters are permitted to be landed in the fisheries management area surrounding Te Tapuwae o Rongokako Marine Reserve. It could be expected that because of the lack of fishing pressure outside the marine reserve during this time, the mean CPUE could be higher. However, for the two surveys conducted during May, the CPUE was the lowest of any surveys. This is likely due to the fact that this is the breeding season for lobsters in the Gisborne area, which affects their catchability as discussed below. The large reduction in the percentage of males observed in the catches during the winter months of 2005 and 2006, primarily outside the reserve, may be explained not only by a reduction in their catchability, but also by the fact that the Gisborne fishery is primarily a winter fishery for males.

2.4.2 Small scale distribution patterns

The patterns of cohabitation described for the summer months within and outside Te Angiangi and Te Tapuwae o Rongokako Marine Reserves were not consistent. Whereas in Gisborne larger males and females tended to reside in larger groups, in Hawke’s Bay the opposite pattern was observed. The development of aggregation behaviour in *Jasus edwardsii* has been demonstrated to coincide with the response to chemical cues in larger lobsters (Butler *et al.*, 1999) but it has also been previously found that very large males tend to be more solitary (MacDiarmid, 1994). This may explain the negative correlation between lobster size and group size at Te Angiangi, where very large lobsters are more common. In addition, the sizes of groups in Hawke’s Bay, both inside and outside the reserve, were much smaller than in Gisborne, with many more solitary animals of both sexes. There was no significant correlation between individual male size and group size outside the reserves, probably because the size range of males outside the reserves was relatively narrow. In Gisborne, large females tended to reside in groups with higher percentages of males and also in larger groups. This pattern was consistent both inside and outside the marine reserve. No such pattern was found in Hawke’s Bay, again because the groups tended to be a lot smaller than in Gisborne.

As well as being larger in size (in terms of number of individuals), groups in Gisborne were also more common, with a higher density of groups in Gisborne than in Hawke’s Bay, both within and outside the reserve. Whether this reflects behavioural differences between regions, the availability of dens or is a function of lobster density is unclear. Behavioural differences between
regions are unlikely and there is little apparent difference between the two regions in terms of den availability (pers. obs.). Davis & Dodrill (1989) suggested that the occupancy rate of dens for *Panulirus argus* reflected the nature of the available shelter, e.g. gregariousness could relate to the size of the den. No apparent differences among the physical sizes of dens within Te Angiangi and Te Tapuwae o Rongokako Marine Reserves have been observed (pers. obs.). Therefore, it is likely that there were more groups and larger groups in Te Tapuwae o Rongokako simply because Te Tapuwae o Rongokako Marine Reserve supported more lobsters in 2005 than did Te Angiangi. These differences in lobster distribution could have implications for their prey species, with the distribution and abundance of prey species potentially being affected near large aggregations of lobsters. This potential is explored in Chapter 5.

In Gisborne, lobster groups within the reserve had a higher percentage of males than outside the reserve. In addition, the overall sex ratio within the reserve was more even than outside the reserve. This likely reflects the fact that the Gisborne commercial fishery is a male-biased fishery (Sullivan, 2004) and the sex ratio within the reserve is probably returning to a more natural value. Such changes in group structure and the population structure in general have implications for the reproductive potential of populations within marine reserves (MacDiarmid & Butler, 1999; MacDiarmid & Kittaka, 2000; MacDiarmid *et al.*, 2000). The reproductive potential of female lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve is investigated in Chapter 6.

### 2.4.3 Seasonal changes in distribution and abundance

The strong seasonal patterns in the depth distribution of female and male lobsters in Te Tapuwae o Rongokako as inferred from the pot survey data are consistent with the inshore – offshore movements undertaken by this species in association with moulting and reproduction. The observed seasonal patterns are also likely to have been affected by temporal changes in catchability, as discussed below.

The mean CPUE and number of lobsters per pot (in particular males) reduced dramatically in winter at depths greater than 15 m, but remained relatively stable at depths less than 15 m. The decline in CPUE between consecutive winters in this depth stratum is likely to be due to changes in sampling effort in very shallow water (<5 m). In winter 2004, calm seas permitted sampling in very shallow depths in the reserve, which yielded large catches of large lobsters. The following winters, the sea conditions did not allow the same degree of sampling in that depth range.
Large male lobsters (>70 mm tail width) were generally more abundant in shallow depths (<15 m) in both summer and winter, but in winter an influx of smaller animals seemed to occur from greater depths. This agrees with previously published research, showing that male density peaks in shallow water in September / October during the moult, and on deep patch reefs in December subsequent to moulting (Kelly, 2001; Kelly et al., 1999; MacDiarmid, 1991; McKoy & Leachman, 1982). Ziegler et al. (2002a, 2002b) found that the densities of large Jasus edwardsii remained constant, but that the densities of smaller animals changed on a seasonal basis. Similarly, Kelly (2001) found that not all male lobsters migrated into deeper water after moulting, with some maintaining a relatively stable depth distribution.

Females were caught more frequently during the summer months than during winter – this pattern was most obvious at depths less than 15 m, where females (in particular large females) were consistently caught more frequently. In northeastern New Zealand, female Jasus edwardsii are most dense in shallow areas (0-10 m) in April / May (during the breeding season) and in deep areas (17-25 m) in August / September when they release their egg clutches (Kelly, 2001; Kelly et al., 1999; MacDiarmid, 1991; McKoy & Leachman, 1982). In Gisborne during the winter months, mature females are bearing eggs then releasing their clutches, which reduces their catchability and therefore representation in pot catches (see below). Females were rarely caught at depths over 15 m, which likely reflects changes in catchability rather than actual changes in distribution.

2.4.4 Sampling timing and methods

Lack of comparable protected areas and of data collected prior to protective measures being put in place prevents a reliable assessment of the effects of protection on species (Underwood 1992, cited in Goni et al., 2001). The collection of data prior to the establishment of Te Angiangi Marine Reserve therefore provides increased ability to detect changes that may be attributable to protection and also strengthens the argument for any changes within Te Tapuwae o Rongokako Marine Reserve being attributable to protection, since the two reserves are comparable in biogeography (Walls, 2006). In addition, given that the first diver survey was completed just two months subsequent to the establishment of Te Tapuwae o Rongokako, that data is likely to be comparable to any pre-reserve survey.

The key limitation with the use of divers for surveying lobsters (and any other species) at these locations is its labour intensive nature (in particular at Te Tapuwae o Rongokako given the relatively large size of the marine reserve) and the frequently poor sea conditions, particularly
underwater visibility, which rarely exceeded 3 metres over the study period. An additional problem at Gisborne is that many of the lobsters within the marine reserve and in the surrounding fishery were at depths that are not conducive to safe scuba diving.

Although pots provided a more rapid and economical survey method for lobsters at Gisborne, there are issues relating to how representative the pot catch was of the actual population. The assumption that catch per unit effort is proportional to the density of the stock under consideration only holds true if the probability of capture of every member of the population remains constant (Morgan, 1974). However, lobster trapping is a notoriously biased sampling method. This “catchability” can change on a seasonal basis due to factors such as water temperature, molting and mating (Annala & Bycroft, 1984; Frusher & Hoenig, 2001; Taggart et al., 2004; Waddington et al., 2005; Ziegler et al., 2003; Ziegler et al., 2002a; Ziegler et al., 2002b).

As well as catchability, catch rates are typically affected by factors such as soak time, pot saturation, the physical habitat, temperature, water motion, pot design, diurnal and lunar cycle, bait and the life cycle of the target species (Miller, 1990). In this study, factors such as soak time were kept as constant as possible, with only a very small number of pots having soak times of greater than 24 hours. Variability in factors such as water temperature was inherent in the sampling given its seasonal nature. There was unavoidable variability in the sea and weather conditions, and also lunar cycle, but this variability was reduced as much as possible, by altering the timing of sampling. In order to minimize pot competition (Aedo & Arancibia, 2003; Bell et al., 2001; Jernakoff & Phillips, 1988), pots were rarely set closer than 100 metres apart. Pot saturation (where pots become “saturated”, with no additional animals able to enter the pots and be sampled) was observed to be a potential problem sampling within Te Tapuwae o Rongokako Marine Reserve, where large numbers of lobsters were observed to congregate around a full pot (pers. obs.). If the density and size composition of lobsters within the reserve continues to change, this problem may need to be addressed in the future, perhaps through the use of larger pots or pots with larger entrances.

In this study, data from fine-mesh pots were found to be more comparable with data from dive surveys than the pots used in the commercial fishery (52 mm mesh), which tended to over-sample males, in particular larger males. The ability of the fine mesh pots to retain small lobsters, in particular females, provides one explanation for this.
Changes in the catchability of lobsters can affect our ability to compare populations with significantly different compositions, for example fished and unfished populations (Frusher et al., 2003; Goni et al., 2003a; MacDiarmid, 1994). Chittleborough (1974) suggested that dominance would intensify when the level of food supply was depressed, whether relative (depending on the density of lobsters) or absolute (reflecting fluctuations in the populations of prey species). Such intensification of dominance may become apparent in marine protected areas as the densities of particular species change. Although the pot data from this study suggested a strong population bias towards males, data from the diver surveys suggested that this may have been an artefact of sampling using pots. Pots tended to over-sample males, in particular large males, likely due in part to their inability to retain small lobsters (less than 52 mm tail width), particularly females.

The diver estimates of abundance suggested that the population of lobsters within Te Tapuwae o Rongokako Marine Reserve increased by 34% between 2004 and 2005. Using CPUE as a proxy for density, the pot surveys completed around the same time (February 2004 and March 2005) suggested that the population had increased by around 18% over that period. This suggests that the potting estimates may be more conservative than those derived from diver surveys, despite the apparent selectivity for large lobsters. Buxton et al. (2006) similarly found that estimates of Jasus edwardsii abundance derived from pot surveys were more conservative than diver surveys for lobsters within Maria Island Marine Reserve.

2.4.5 Conclusions

This study has demonstrated that in the absence of fishing, lobster populations can increase in density and biomass, due to the increase in the abundance and size of legal-sized lobsters. Within Te Angiangi and Te Tapuwae o Rongokako Marine Reserves, recovery was rapid during the first few years of protection, with density increasing at a rate higher than previously reported for other New Zealand marine protected areas. These increases in density and biomass suggest the potential for density dependent interactions, which may influence population dynamics such as growth, reproduction, movement patterns and feeding ecology. These factors are explored in subsequent chapters.
Table 2-1 Replication levels for lobster transects completed by divers within and surrounding Te Tapuwae o Rongokako Marine Reserve (Gisborne) and Te Angiangi Marine Reserve (Hawke’s Bay). Size and sex data were recorded for all lobsters sampled, where possible.

<table>
<thead>
<tr>
<th>Region</th>
<th>Year</th>
<th>Location</th>
<th>Depth Range</th>
<th>&lt;15 m</th>
<th>15-29.9 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gisborne</td>
<td>2001</td>
<td>Marine reserve</td>
<td>7</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fished</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2002</td>
<td>Marine reserve</td>
<td>2</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>Marine reserve</td>
<td>5</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fished</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>Marine reserve</td>
<td>6</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fished</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hawke’s Bay</td>
<td>1995</td>
<td>Marine reserve</td>
<td>16</td>
<td>17</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fished</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>Marine reserve</td>
<td>10</td>
<td>10</td>
<td>10</td>
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<tr>
<td></td>
<td></td>
<td>Fished</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>Marine reserve</td>
<td>14</td>
<td></td>
<td>13</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fished</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>Marine reserve</td>
<td>16</td>
<td></td>
<td>8</td>
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<tr>
<td></td>
<td></td>
<td>Fished</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>2002</td>
<td>Marine reserve</td>
<td>14</td>
<td></td>
<td>8</td>
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<td></td>
<td></td>
<td>Fished</td>
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<tr>
<td></td>
<td>2004</td>
<td>Marine reserve</td>
<td>8</td>
<td></td>
<td>6</td>
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<tr>
<td></td>
<td></td>
<td>Fished</td>
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<tr>
<td></td>
<td>2005</td>
<td>Marine reserve</td>
<td>30</td>
<td></td>
<td>7</td>
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<tr>
<td></td>
<td></td>
<td>Fished</td>
<td></td>
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<td>15-29.9 m</td>
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</tr>
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<td>2000</td>
<td>Marine reserve</td>
<td>7</td>
<td>15</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Fished</td>
<td>7</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2001</td>
<td>Marine reserve</td>
<td>11</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fished</td>
<td>8</td>
<td>19</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2002</td>
<td>Marine reserve</td>
<td>12</td>
<td>4</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Fished</td>
<td>9</td>
<td>6</td>
<td></td>
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<tr>
<td></td>
<td>2003</td>
<td>Marine reserve</td>
<td>7</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fished</td>
<td>6</td>
<td>3</td>
<td></td>
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<tr>
<td></td>
<td>2004</td>
<td>Marine reserve</td>
<td>11</td>
<td>19</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Fished</td>
<td>12</td>
<td>18</td>
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<tr>
<td>Hawke’s Bay</td>
<td>1998</td>
<td>Marine reserve</td>
<td>19</td>
<td>2</td>
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<td></td>
<td></td>
<td>Fished</td>
<td>16</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>1999</td>
<td>Marine reserve</td>
<td>18</td>
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<tr>
<td></td>
<td></td>
<td>Fished</td>
<td>17</td>
<td></td>
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<tr>
<td></td>
<td>2001</td>
<td>Marine reserve</td>
<td>12</td>
<td>4</td>
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<td></td>
<td></td>
<td>Fished</td>
<td>15</td>
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<tr>
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<td>16</td>
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<td>Fished</td>
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<td>Marine reserve</td>
<td>17</td>
<td>1</td>
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<tr>
<td></td>
<td></td>
<td>Fished</td>
<td>18</td>
<td>2</td>
<td></td>
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</table>
Table 2-3  Mean catch per unit effort (kg of legal lobsters per pot lift), standard error and number of pot lifts completed for each depth stratum for each survey completed within and surrounding Te Tapuwae o Rongokako Marine Reserve, for the three pot types. Data in each cell are mean (s.e.), n. Pot types: Std = standard; Sml = small.

<table>
<thead>
<tr>
<th>Location</th>
<th>Season</th>
<th>Date</th>
<th>Pot Type</th>
<th>Depth Range (m)</th>
<th>Depth Range (m)</th>
<th>Depth Range (m)</th>
</tr>
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<tr>
<td></td>
<td></td>
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<td>&lt; 15</td>
<td>15 - 29.9</td>
<td>30 - 44.9</td>
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<tr>
<td>Fished</td>
<td>Summer 03/04</td>
<td>Nov 03</td>
<td>Std</td>
<td>0.9 (0.3), 8</td>
<td>1.4 (0.6), 7</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Dec 03</td>
<td>Std</td>
<td>0.6 (0.1), 44</td>
<td>0.8 (0.1), 42</td>
<td>0.4 (0.3), 4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Feb 04</td>
<td>Fine</td>
<td>0.5 ( ), 1</td>
<td>0.2 (0.1), 17</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Std</td>
<td>0.2 (0.1), 17</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter 04</td>
<td>June 04</td>
<td>Std</td>
<td>0.6 (0.1), 43</td>
<td>0 ( ), 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Aug 04</td>
<td>Sml</td>
<td>0 (0), 3</td>
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<tr>
<td></td>
<td></td>
<td>Std</td>
<td>0.9 (0.4), 24</td>
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<td>Summer 04/05</td>
<td>Nov 04</td>
<td>Std</td>
<td>0.7 (0.1), 89</td>
<td>0.8 (0.1), 45</td>
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<td>Winter 05</td>
<td>May 05</td>
<td>Std</td>
<td>0.2 (0.0), 69</td>
<td>0.1 (0.1), 6</td>
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<td>Summer 05/06</td>
<td>Nov 05</td>
<td>Std</td>
<td>0.3 (0.2), 8</td>
<td>0.5 (0.1), 46</td>
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<tr>
<td>Winter 06</td>
<td>May 06</td>
<td>Std</td>
<td>0.1 (0.0), 67</td>
<td>0.1 (0.1), 13</td>
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<td>Summer 06/07</td>
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<td>0.6 (0.1), 44</td>
<td>1.3 (0.4), 40</td>
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<tr>
<td>Reserve</td>
<td>Summer 03/04</td>
<td>Nov 03</td>
<td>Std</td>
<td>8.1 (0.7), 70</td>
<td>14.7 (1.4), 43</td>
<td>13.3 (2.2), 21</td>
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<td></td>
<td></td>
<td>Dec 03</td>
<td>Fine</td>
<td>4.2 (0.5), 15</td>
<td>12.5 (1.5), 4</td>
<td>11.1 ( ), 1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Std</td>
<td>8.9 (0.4), 134</td>
<td>13.9 (0.9), 108</td>
<td>13.7 (1.8), 32</td>
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Table 2-4  Number of lobsters measured by season, year, pot type, depth, and sex within and outside Te Tapuwae o Rongokako Marine Reserve.

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Table 2-5  Pearson correlation coefficients for factors describing lobster group structure. Correlations are significant at the 0.05 level. NS = not significant.

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**Figure 2-1** Distribution of sampling effort (using divers) within and outside Te Tapuwae o Rongokako Marine Reserve, where size and sex data were recorded (a) and where only density data were recorded (b).

(a)
Figure 2-2  Distribution of sampling effort (using commercial lobster pots) within and surrounding Te Tapuwae o Rongokako Marine Reserve, by season.
Figure 2-3  Distribution of sampling effort (using divers) within and outside Te Angiangi Marine Reserve, where size and sex data were recorded (a) and where only density data were recorded (b). a)
Figure 2-4 Mean density of lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve, from diver surveys, showing n (number of transects).
Figure 2-5  Density of lobsters, from diver surveys, within and surrounding Te Tapuwae o Rongokako Marine Reserve, in less than 15 m depth and between 15 and 29.9 m depth, showing n (number of transects).
Figure 2-6  Mean number of lobsters per pot (standard pots only) versus density from dive surveys, within and surrounding Te Tapuwae o Rongokako Marine Reserve. Data shown are from summer 03/04 and summer 04/05 only and the two depth strata are separate (<15 and 15-29.9 m). Grey symbol = fished; black symbol = reserve.
Figure 2-7  Mean CPUE (kg legal lobsters per pot, for standard pots; males and females pooled) in 3 depth strata, within and outside Te Tapuwae o Rongokako Marine Reserve.
Figure 2-8  Box plot of the number of female and male lobsters per pot (standard pots only), set within and outside Te Tapuwae o Rongokako Marine Reserve.
Figure 2-9 Mean density of lobsters inside and outside Te Angiangi Marine Reserve, estimated during diver transects, showing n (number of transects). The vertical line indicates when the reserve was established.
Figure 2-10  Mean density of lobsters within Te Tapuwae o Rongokako Marine Reserve and Te Angiangi Marine Reserve, as a function of reserve age.
**Figure 2-11** Box plots for sizes of male and female lobsters caught using either fine-mesh pots, or pots with 52 mm mesh (standard and small pots), within Te Tapuwae o Rongokako Marine Reserve. Box plots show the median, interquartile range (box), outliers (open circles; values between 1.5 and 3 box lengths from the upper / lower edge of the box) and extreme cases (asterisk; values more than 3 box lengths from upper / lower edge of box).
**Figure 2-12** Size frequency histograms (% frequency) for male lobsters within and outside Te Tapuwae o Rongokako Marine Reserve, sampled using divers. Vertical lines are the approximate carapace lengths of legal-sized male lobsters (104.5 mm). There are no data from the “fished” location in 2002. Note size is carapace length.
Figure 2-13 Size frequency histograms (% frequency) for male lobsters caught within and surrounding Te Tapuwae o Rongokako Marine Reserve (small and standard pots pooled). Sample sizes are given in Table 2-4. Note size is tail width. The vertical line indicates the minimum legal size of 54 mm.
Figure 2-14  Size frequency histograms (% frequency) for female lobsters sampled using divers within and surrounding Te Tapuwae o Rongokako Marine Reserve. Vertical lines are the approximate carapace lengths of legal-sized female lobsters (97 mm). There are no data from the “fished” location in 2002. Note size is carapace length.
Figure 2-15  Size frequency histograms (% frequency) for female lobsters, small and standard pots pooled, caught within and outside Te Tapuwaewae o Rongokako Marine Reserve. Sample sizes are given in Table 2-4. Note size is tail width. The vertical line indicates the minimum legal size of 60 mm.
Figure 2-16 Mean sizes of female and male lobsters, surveyed using divers, within and surrounding Te Tapuwae o Rongokako Marine Reserve. There are no data from the “fished” location in 2002, or from either location in 2003.
Figure 2-17  Mean tail width of females and males, divided into depth strata (data from standard and small pots pooled), within and outside Te Tapuwaewae o Rongokako Marine Reserve.
Figure 2-18  Percent size frequency (CL) histograms for male lobsters surveyed by divers within and outside Te Angiangi Marine Reserve. The vertical lines are the approximate carapace lengths of legal-sized male lobsters (104.5 mm). Note that the reserve was established in 1997 and so the 1995 and 1996 distributions are from the area prior to implementation of protection.
Figure 2-19  Percent size frequency (CL) histograms for female lobsters surveyed by divers within and outside Te Angiangi Marine Reserve.  Vertical lines are the approximate carapace lengths of legal-sized female lobsters (97 mm).  Note that the reserve was established in 1997 and so the 1995 and 1996 distributions are from the area prior to implementation of protection.
Figure 2-20  Mean size (CL) of female and male lobsters estimated during dive transects within and outside Te Angiangi Marine Reserve. The vertical line indicates when the reserve was established.
Figure 2-21  Mean percent males sampled during diver surveys, within and surrounding Te Tapuwae o Rongokako Marine Reserve, between 2001 and 2005. There are no data from the “fished” location in 2002, or from either location in 2003.
Figure 2-22  Mean percent males per standard-sized pot within and outside Te Tapuwae o Rongokako Marine Reserve.
Figure 2-23  Box plot of the total number of lobsters per group, within and outside Te Tapuwae o Rongokako Marine Reserve (Gisborne) and Te Angiangi Marine Reserve (Hawke’s Bay) (males, females and unknown sex pooled). Box plots show the median, interquartile range (box), outliers (open circles; values between 1.5 and 3 box lengths from the upper / lower edge of the box) and extreme cases (asterisk; values more than 3 box lengths from upper / lower edge of box).

Figure 2-24  Mean % males per group, within and outside Te Tapuwae o Rongokako (Gisborne) and Te Angiangi (Hawke’s Bay) marine reserves. Percentages are of those sexed and exclude dens where no lobsters could be sexed.
Chapter 3    The Growth Rates of *Jasus edwardsii* on Fished and Unfished Reefs

3.1 Introduction

Growth is a fundamental process determining the productivity of the individual organism and the population of which it is a component. Estimates of individual and population growth rates are also key components of fisheries stock assessments. In marine animals, growth can potentially be influenced by a broad range of biotic and abiotic factors, from direct environmental influences such as water temperature and salinity, to intraspecific interactions and the indirect effects of population density and environmental conditions on growth, through their influence on key resources such as food and shelter.

Because lobsters need to moult in order to grow, growth is incremental rather than continuous, and so overall growth rate is influenced not only by growth increment, but also by moult frequency. A reduction in lobster growth rate may therefore be a result of a reduction in moult frequency, a depressed growth increment, or both (Chittleborough, 1975). A number of factors affect the growth increment and moult frequency of lobsters, including water temperature (Chittleborough, 1975; Punt *et al.*, 1997), food availability and quality (Chittleborough, 1975, 1976), salinity (Field & Butler 1994, cited in Robertson & Butler, 2003), presence of predators (Lozano-Alvarez & Spanier, 1997), stress and injury (Chittleborough, 1975). The growth rate of an individual lobster is also influenced by its sex, age and reproductive state, with growth rates tending to decline with increasing size (e.g. *Panulirus guttatus*, Negrete-Soto *et al.*, 2002). Berry & Smale (1980) showed that the slower growth rates and lower production rates in female *Panulirus homarus* directly matched energy lost to egg production. In addition, the proportion of production being channelled into egg production increased with increasing female size, probably due to increasing relative brood size and the number of broods produced per annum.

Production may also be channelled into limb and tissue replacement, rather than growth, if a lobster is under stress, has an injury or disease. For example, in *Panulirus cygnus*, limb loss decreases growth rate (Brown & Caputi, 1985; Chittleborough, 1975; Melville-Smith & Wing Cheng, 2002) and exposure to air also reduces the growth increment in this species (Brown & Caputi, 1985). Negrete-Soto *et al.* (2002) found from a tagging study that injured *Panulirus guttatus* had smaller moult increments than uninjured individuals. Similar results were reported for *Panulirus argus* (Davis, 1981) and *Panulirus homarus homarus* (Kulmiye & Mavuti, 2005).
Growth in two congeners, *Panulirus gracilis* and *Panulirus inflatus*, appears to be unaffected by the presence of injuries (Briones-Fourzan & Lozano-Alvarez, 2003) but in *Jasus lalandii*, appendage loss negatively affects growth rate (Brouwer et al., 2006; Dubula et al., 2005).

The growth of *Jasus edwardsii*, and the factors affecting growth in this species, have been studied relatively extensively both in New Zealand and Australian waters. The growth rates of Tasmanian populations of *J. edwardsii* vary spatially, with growth rates decreasing from north to south (Punt et al., 1997). Lobsters off southern Tasmania moult just once per year, whereas off northern Tasmania lobsters moult twice per year and tend to have higher annual growth increments (Latour et al., 2003). South Australian *J. edwardsii* also demonstrate significant geographical variation in growth rates (Prescott et al., 1997). In addition, males grow faster than females for all populations around Tasmania (Punt et al., 1997) and around South Australia females grow more slowly after reaching sexual maturity (McGarvey et al., 1999; Prescott et al., 1997). Male *J. edwardsii* living at depths of 20-40 m grow faster than lobsters in deeper water, suggested to be a result of a change in diet with depth (McGarvey et al., 1999; Prescott et al., 1997). The growth of *J. edwardsii* in New Zealand waters has been described (Annala & Bycroft, 1985, 1988; McKoy & Esterman, 1981), with a number of factors, including water temperature and food availability, being proposed as potential factors explaining spatial variation in growth rates.

In lobsters, density is usually positively correlated with mortality and negatively correlated with growth (Cobb & Phillips 1980, cited in Polovina, 1989). In spiny lobsters, density-dependent changes in growth are more likely to be driven by changes in food availability than by any other factor (Pollock, 1995a, 1995b). Such effects of density and/or food availability on growth rates have been described for a number of lobster species, including *Jasus tristani* (Pollock, 1991), *Panulirus cygnus* (Chittleborough, 1975, 1976; Phillips, 1983), *Panulirus ornatus* (Skewes et al., 1997), *Panulirus argus* (Davis & Dodrill, 1989), *Panulirus gilchristi* (Groeneveld, 1997), *Panulirus marginatus* (Polovina, 1989) and *Jasus lalandii* (Newman & Pollock, 1974; Pollock et al., 1997).

The activity of fishing has the potential to reduce the density and biomass of lobsters considerably (e.g. Eggleston et al., 2003). Conversely, in the absence of fishing (such as within marine protected areas) lobsters have been shown to increase substantially in density and biomass (e.g. Bertelsen & Matthews, 2001; Rowe, 2002). Therefore, there exists the potential for significant differences in the growth rates of lobsters between protected and fished locations due to density-dependent effects.
Although a number of factors have been shown to affect the growth of *Jasus edwardsii*, the effects of fishing have never been assessed directly through the study of an unfished reference population. In this chapter, I assess whether the growth rates of *J. edwardsii* vary between populations on fished and unfished reefs, and discuss some of the potential causative factors. I hypothesise that due to the increased abundance and biomass of lobsters within Te Tapuwae o Rongokako Marine Reserve (Chapter 2), the growth rates of lobsters within the reserve will be lower than outside the reserve, due to density-dependent effects.
3.2 Methods

3.2.1 Sampling strategy

The effects of fishing on the growth rates of lobsters were assessed by comparing the growth of tagged lobsters on reefs within a no-take marine reserve, with the growth rates of lobsters on reefs surrounding the reserve. The reefs sampled were similar in their geology and community composition, with the reefs within the marine reserve being representative of reef habitat within the region (Department of Conservation & Ngati Konohi, 1998). Methodology, including tag type and sample sizes, was based on recommendations by Booth (2003), modified by funding availability, approval from the permitting authorities, feasibility and discussions with local lobster fishers.

3.2.2 Lobster sampling and tagging

Potting for lobsters in Te Tapuwae o Rongokako Marine Reserve and adjacent fished areas was undertaken approximately every three months beginning in November 2003, using commercial fishing vessels. Subsequent surveys were undertaken in February 2004, June 2004, August 2004, November 2004, March 2005, May 2005, November 2005, February 2006, May 2006, September 2006 and November 2006 (Table 3-1). The location and number of pots set depended on a number of factors, including weather and sea conditions, the vessel used and the presence of other fishing gear. Where possible, reef habitat from a range of depths throughout the marine reserve and within approximately 3 kilometres of the reserve’s boundary was sampled (Figure 3-1). A total of 3168 pot lifts was completed over the 3-year study period (Table 3-1). Pot positions were determined using GPS with an accuracy of 30 m.

A proportion of lobsters captured during these surveys, in addition to a small number of lobsters caught by divers, were tagged using Hallprint T-bar anchor tags, inserted dorsally between the carapace and tail, either side of the centre line in order to avoid the intestine (Figure 3-2). The tags were positioned as close to the tail as possible to avoid the body cavity. Insertion of the tags into this region of the muscle tissue ensured that the tags were retained during molting. Lobsters of over 70 mm carapace length were tagged using an Avery Dennison Tag Fast tagging gun and TBA tags. A Fine Fabric gun and TBF tags were used for lobsters with a carapace length of less than 70 mm, in accordance with the manufacturer’s recommendations. The tag needle was sterilised in ethanol between animals. Each tag was individually numbered, along with the letters DOC (for Department of Conservation) and the tags also had a short “chew
buffer" on their distal end. After being tagged, lobsters were immediately returned to the sea as close as possible to their capture location.

Data recorded for every tagged lobster included carapace length (measured to the nearest 0.1 mm with vernier callipers, from the antennal platform to the dorsal posterior margin of the carapace along the midline); tail width (measured to the nearest 0.1 mm in a straight line between the tips of the primary spines on the second segment of the tail); sex; and reproductive stage for females (based on the presence (mature) or absence (immature) of setae longer than 6 mm on the endopodites; Table 3-2). The presence of any old or new injuries and the presence and severity of tail fan necrosis (according to Table 3-3) were also recorded.

Every tagged lobster, with the exception of egg-bearing females, also had the distal third of one pleopod clipped using scissors. This ensured that upon recapture, it could be easily determined whether the lobster had moulted and therefore needed to be remeasured upon recapture. Upon recapture, tagged lobsters that had moulted (as indicated by a partially regrown pleopod) were sexed, measured and the pleopod was clipped again. Any change in the presence and severity of tail fan necrosis was recorded, as were any new or old injuries such as missing appendages.

This study was advertised and reported on in local newspapers and magazines, and divers and fishermen were asked to record the tag number, sex, tail width and location of any tagged lobster they observed or caught. Tag reporting forms were provided to all commercial fishermen working in the vicinity of the study site and upon request by members of the public. No reward was offered for providing recapture reports but tagged legal-sized lobsters caught outside the marine reserve were able to be retained by fishermen.

3.2.3 Data analysis

The differences in growth rates among years were analysed using ANCOVA (analysis of covariance) and multi-way ANOVA (S-Plus), using the relationship between either tail width and growth increment, or carapace length and growth increment. For the analysis of growth data, only data from lobsters that had moulted just once within 400 days of being tagged (or last moult) were utilised (as in McKoy & Esterman, 1981). The parameters of the linear regressions relating tail width and growth increment (and carapace length and growth increment) were used to construct von Bertalanffy growth curves (Fabens, 1965). For carapace length, the $t_0$ values (the hypothetical ages at which the lobsters were at zero length) were adjusted to ensure that the
curves crossed the y-axis at approximately 12 mm carapace length, the approximate length at settlement. For tail width, $t_0 = 0$ was used for all curves.

Tag returns from fishermen were not utilised in the analysis of growth, as they tended to provide measurements only to the nearest millimetre. In addition, although measurements were provided, often it was unclear whether or not the individual had moulted. Removing these data from the analysis reduced the available data set considerably, but increased the accuracy of the analysis.

Statistical analyses were carried out using SPSS and S-Plus software.
3.3 Results

3.3.1 Number, size and sex of lobsters tagged

A total of 7466 lobsters was tagged (5225 within the reserve and 2241 from outside the reserve; Table 3-4), mostly during the first surveys in November and December 2003. Within the reserve, males of tail widths between 37.6 and 77.1 mm were tagged (n=3785); outside the reserve, tagged males ranged between 35.4 and 70.3 mm tail width (n=1701). Females tagged in the reserve ranged between 33.8 and 72.4 mm (n=1440); females tagged outside the reserve ranged between 42.4 and 69.3 mm tail width (n=540).

3.3.2 Tag loss

Because all male lobsters that were tagged also had the distal third of one pleopod removed, the loss of tags could be easily distinguished. In addition, the monofilament tag shaft had broken in a large number of cases, usually where the monofilament was being abraded by the movement of the carapace against the tail. In a small number of cases, the numbered section of the tag had been damaged and was illegible. Table 3-5 provides the number of incidences of tag loss. Outside the reserve, 15.6% of all recapture events involved lobsters that had either lost their tag or had their tag broken. Within the reserve, this value was 40.8%. As shown in Figure 3-3, within the reserve there was significant tag loss in lobsters between approximately 58 mm and 70 mm tail width. Lobsters of this size range were rarely encountered outside the reserve and so the majority of tag losses outside the reserve occurred in animals 46-54 mm tail width. Four of seven lobsters with a tail width greater than 62 mm recaptured outside the reserve had lost their tags. Because they had lost their tags, the original capture and release location of these lobsters could not be determined. However, all seven tagged lobsters with a tail width greater than or equal to 58 mm recaptured outside the reserve had initially been tagged and released within the reserve.

Within the reserve, lobsters that had either lost or broken their tag were significantly larger than those that retained their tag intact (univariate analysis of variance, F$_2$, 1641 = 14.22, p<0.01; Student-Newman-Keuls method p<0.05; Figure 3-4). Outside the reserve, the mean size of lobsters that had broken tags was significantly higher than those that had retained their tag or had lost their tag completely (univariate ANOVA, F$_2$, 230 = 6.53, p<0.01, Student-Newman-Keuls method p<0.05; Figure 3-4).
3.3.3 Moulting cycle

Because male lobsters were not only tagged but also pleopod-clipped, it could be determined whether lobsters had moulted in the interval between being tagged and being recaptured, and also between recaptures if a lobster had moulted and been re-clipped at the first recapture. In mature female *J. edwardsii*, moulting coincides with mating and so the presence of eggs beneath the tail of a previously non-egg-bearing female indicates that the lobster has moulted (MacDiarmid, 1989a). Sufficient recaptures of tagged lobsters were obtained to enable the approximate timing of moulting in both males and females to be established.

The majority of female lobsters were tagged at maturity stage 3 (mature, non-egg-bearing stage), and of the tagged females that were recaptured and had moulted (a total of 54), all had been at stage 3 when tagged. Upon recapture, 35 were still stage 3; 1 was stage 2 (immature), and 16 were bearing eggs. Thirty-seven of the total 54 females (69%) that had moulted had done so within 365 days of release. From these recaptures, it was clear that moulting took place around April, with all tagged females tagged prior to April having moulted by May (Figure 3-5).

For males, 346 recaptured tagged lobsters had moulted, 212 of these (61%) within 365 days of release. These were released and recaptured over a wide time period, enabling the timing of moulting to be distinguished (Figure 3-6). It appears from the data that the male lobsters in this study moulted just once per year during the months of August-September. It also appears that the tagged sublegal-sized (<54 mm tail width) males moulted slightly earlier than tagged legal-sized males, as shown in the November and December graphs in Figure 3-6, where the percent moulted is higher for sublegal males in August than for legal males. Interestingly, all of the sublegal-sized males that had moulted before the surveys in August were caught in the marine reserve – none of the 6 sublegal-sized males released outside the reserve during November / December and recaptured the following August had moulted. The graph for November also suggests that a very small proportion of the male population may moult in the summer months some time between November and February - 2 of 94 legal-sized and 1 of 22 sublegal-sized males moulted between November and February. All three of these individuals were caught and released in the marine reserve.
3.3.4 Growth

Table 3-8 shows the number of lobsters tagged, the number of recaptures, the number that had moulted and the number of lobsters that had moulted once within 400 days of being released and therefore provided growth data. The most comprehensive data set is for males from the marine reserve, where 186 individuals yielded growth data. Thirty-eight male lobsters from outside the reserve provided growth data, but as shown in Figure 3-8, all of these were sublegal-sized animals (<54 mm tail width), whereas a range of sizes were recaptured within the marine reserve (Figures 3-7, 3-8). Just two tagged females from outside the marine reserve were recaptured within 400 days of release versus 35 from within the reserve. Within the reserve, recaptured females ranged in size from 51.6 mm to 66.1 mm tail width (original size) (Figures 3-9, 3-10).

Linear regressions were fitted to the raw data for males presented in Figures 3-7 and 3-8. Because the size ranges for reserve and non-reserve animals did not overlap, reserve and non-reserve data were analysed separately. For the reserve, analysis of covariance, using year as a covariate, showed that initial size (either tail width or carapace length) and year were significant main effects, so that there were differences in male growth increment among the 3 years (2004, 2005 and 2006), with the growth increments in 2006 smaller than in previous years. Within each year there was a significant relationship between initial male size and growth increment, with the slope of that relationship being the same for all years (Table 3-9). A second ANCOVA model testing whether there was any interaction between initial size and year was marginally non-significant (p=0.06 for tail width and p=0.07 for carapace length).

There was only sufficient data from outside the reserve to undertake a similar analysis for males for 2004 and 2006. Analysis of covariance showed that there were significant relationships between tail width and growth increment (p<0.05) and carapace length and growth increment (p<0.01) but that year was not significant (p=0.634 for tail width and p=0.227 for carapace length).

For females, there was no significant correlation between initial size and growth increment for either tail width or carapace length (Pearson correlation coefficients, p>0.05) (Figures 3-9, 3-10), but the size range for which growth data were available was limited. Both negative and positive growth increments were recorded – the mean growth increment was -0.3 mm tail width (s.e. = 0.1) and 0.5 mm carapace length (s.e. = 0.2) (reserve and non-reserve data pooled). All of these females were sexually mature when tagged and so the potential effect of reproductive status on growth could not be assessed.
Because outside the reserve only growth data from sublegal males was available, these values were compared with growth data from sublegal males within the reserve. In terms of tail width, it was established that the average growth increment for sublegal (<54 mm tail width) males inside the reserve was significantly higher than the average growth increment for sublegal males outside the reserve (two-sample $t$-test, $p<0.01$). The mean tail width growth increment within the reserve was 2.2 mm (s.e. = 0.3); the mean outside the reserve was 1.0 mm (s.e. = 0.2) (Figure 3-11). In terms of carapace length, the mean growth increment of sublegal-sized males inside the reserve was also higher than outside the reserve (two-sample $t$-test, $p<0.01$). The mean carapace length growth increment within the reserve was 4.7 mm (s.e. = 0.6); the mean outside the reserve was 3.1 mm (s.e. = 0.4) (Figure 3-11). When these data were divided into years, the reduction in sample size and resulting low power of the tests meant that the only statistically significant difference was between the mean tail width growth increment for sublegal males within the reserve and that outside the reserve in 2004 (two-tailed $t$-test, $p<0.01$; Figure 3-12).

When compared with growth increment values for lobsters tagged during 1975-1977 from the same general area (“Gisborne local” site in McKoy & Esterman, 1981), it can be seen that the mean growth rate of lobsters between 90 and 99.9 mm carapace length was higher in the reserve in my study than recorded by McKoy & Esterman (1981) (Figure 3-13). For lobsters between 100 and 109.9 mm carapace length (lobsters at or just below the minimum legal size), the mean growth increment was similar in the reserve to that recorded by McKoy & Esterman (1981), but the mean outside the reserve was lower.

The linear regressions relating initial size and growth increment were used to construct von Bertalanffy growth curves for tagged male lobsters within and outside the marine reserve in 2004 and 2006 (the years for which there were sufficient data for both reserve and fished locations). The parameters for these growth curves are given in Table 3-10. Figures 3-14 and 3-15 show the growth curves for male lobsters from within and outside the reserve, for both 2004 and 2006. Both measures (tail width and carapace length) indicate that 2006 was a year of poorer growth for males inside the reserve but this was not the case for males in the surrounding fishery. However, data from outside the reserve were limited to sublegal-sized animals.

Because the slopes of the regressions relating initial size to growth increment were higher outside the reserve than within the reserve (for example, for carapace length, in 2004 the slope outside the reserve was 3.5 times higher outside than inside the reserve; in 2006, it was 4.6 times higher), the von Bertalanffy curves suggest that the growth rate of male lobsters is higher outside the
reserve than inside the reserve, at least for lobsters with a carapace length less than approximately 100 mm. When compared with the von Bertalanffy curve constructed by McKoy & Esterman (1981) for lobsters tagged in the same general area between 1975 and 1977, the growth rate appears similar between those animals and those tagged outside the reserve in this study (Figure 3-16). My analysis suggests that the male lobsters in the marine reserve have slower initial growth rates with a larger theoretical asymptotic size. However, the curve for the fished site in this study is based solely on recaptures of sublegal-sized lobsters (less than approximately 100 mm CL) and so prediction of the growth rates of larger animals is problematic, as is comparison with growth curves constructed from a wider size range of lobsters (see discussion).

Only three tagged individuals that were recaptured within 400 days had more than 2 premoult injuries and so the potential effect of injury on lobster growth rate could not be assessed. Similarly, just 5 tagged lobsters recaptured within 400 days were recorded to have tail fan necrosis prior to moulting – 3 from the reserve and 2 from outside the reserve – and so the potential effect of disease on growth rate could also not be assessed.


3.4 Discussion

This is the first study in New Zealand where the effects of fishing on the growth of marine animals have been assessed through the study of an unfished population. Tagging of lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve showed that sublegal-sized male lobsters had a faster growth rate within the marine reserve than outside the reserve (particularly just undersized lobsters), but that growth rates for this size class within the reserve were similar to those reported for the same area (prior to reserve implementation) in the 1970s (McKoy & Esterman, 1981). However, analysis of growth data between years suggested that overall, male lobsters within the reserve in 2006 grew more slowly than those in the reserve in 2004. No such difference was apparent outside the reserve.

Of the factors that may have varied between the fished and unfished locations in this study, the most obvious was elevated fishing activity at the fished location. There are direct and indirect effects of this, including persistent removal of the fastest growing individuals, increased handling of lobsters outside the reserve, reduction in lobster density and biomass outside the reserve, and potential reduction in food availability within the reserve (due to higher lobster density and biomass). There may also be differences between locations that are unrelated to reserve status, for example differences in reef topography, extent of reef or hydrographic conditions.

3.4.1 Density-dependent effects on growth

Density-dependent effects on growth have been described for many aquatic and marine species (Bene & Tewfik, 2003; Davey et al., 2006; Johnson, 2006). They have also been described for lobsters. For example, Acosta (1999) suggested that in limited-area or “insular” marine habitats where larval supply is high, the limitation on emigration may lead to elevated population densities and density-dependent regulation of the population. Similarly, Newman & Pollock (1974) suggested that unless rock lobsters could move freely within or between fishing grounds, systematic differences in growth rates could occur in response to the environmental conditions in the immediate vicinity. Regional differences in allometric growth were reported for Homarus americanus, such that lobsters from different locations even had different morphologies (MacCormack & DeMont, 2003). McKoy and Esterman (1981) found that the growth rate of male lobsters (Jasus edwardsii) was highly variable between individuals and areas. They suggested that food limitation may be a factor influencing growth rate of lobsters on Gisborne reefs, on the basis that the catches of lobsters were higher in one of the study areas (“Gisborne local”), indicating a higher population density. Because the density and biomass of lobsters
within Te Tapuwae o Rongokako Marine Reserve was higher than that outside the reserve (Chapter 2), it was hypothesised that density-dependent interactions could be occurring that may result in a reduction of growth rates within the reserve compared with a fished location. Comparison of growth rates across the full size range of lobsters between reserve and fished locations could not be undertaken (due to the lack of legal-sized animals recaptured outside the reserve), but analysis of changes in growth over time for both reserve or fished locations was possible. Within the reserve, male lobsters had higher growth increments in 2004 than in 2006, whereas no difference was apparent outside the reserve. This suggests that the mechanisms operating are highly local, rather than regional and rules out broad environmental fluctuation as a potential cause. The similarity between the reefs within and surrounding the reserve in terms of their geology and community composition (Department of Conservation & Ngati Konohi, 1998; Freeman, 2001b) also provides weight to this argument (see General Discussion). The reduction in growth rate coincided with an increase in the CPUE within the reserve (Chapter 2), which may indicate that density-dependent effects on growth rates were operating within the marine reserve.

Density-dependent growth in this species has been demonstrated previously. Analysis of tagging data from South Australian *J. edwardsii* (McGarvey et al., 1999; Prescott et al., 1997) showed a spatial anti-correlation between male growth rates at 100 mm carapace length and fishery catches by number per unit effort, with a 10% decrease in catch rate corresponding to an increase in growth by weight of 2-5%. In areas where the habitat was highly disaggregated and catches in numbers per pot lift were lowest, growth of lobsters was fastest. This was also an area where puerulus settlement was low. Where reef habitat covered 80% of more of the seafloor and where puerulus settlement was highest, slow growth was recorded.

Although there was no significant change in growth rates detected between 2004 and 2006 outside the reserve, the overall growth rates of sublegal-sized male lobsters outside the reserve were significantly lower than for the same-sized individuals within the reserve and these growth rates were also lower than historical growth rates for this size class (McKoy & Esterman, 1981). The difference between fished and reserve locations is in contrast to what could be expected if density-dependent factors alone were operating. There are a number of potential explanations for this reduction in male growth rate between reserve and fished locations, and over time.

### 3.4.2 Negative effects of fishing on growth rates

The negative effects of fishing on the growth rates of marine animals have been well-described. There are two mechanisms by which this can occur – either through the direct removal or
“selection” of faster-growing animals (which affects the population as a whole), or, through the negative effects of handling, displacement, exposure to air and damage associated with modern fishing practices (which affects individuals).

Fishing for a particular sized individual has been proposed to cause what has been termed “fishing-induced evolution” (Stokes & Law, 2000; Williams & Shertzer, 2005). This occurs through the removal of individuals with traits, such as fast growth, that may have a genetic basis. Such effects of selection have been proven for species including fish (Conover & Munch, 2002; Reznick & Ghalambor, 2005; Walsh et al., 2006). Hazell et al. (2002), Brandao et al. (2004), Pollock et al. (1997) and Cruywagen (1997) described a reduction in somatic growth rate (moult increment) of *Jasus lalandii* over a 25 year period. The widespread reduction in growth rate in this species was suggested to be a result of either a large-scale environmental perturbation (such as anomalous El Nino years), or heavy, size-selective fishing removing individuals genetically predisposed to more rapid growth. Although it is possible that such genetic selection has occurred in the Gisborne region, it would not explain the higher rate of growth in the reserve, due to the wide dispersal of lobster larvae in this region. The difference in growth rates between adjacent populations is not consistent with the wide dispersal of genotypes.

However, persistent removal of faster-growing animals in the fishery would immediately result in a population comprised of animals near the minimum legal size that on average grow more slowly than in a population where the range of growth rates are represented i.e. in an unfished population. Therefore, this could partially explain the lower mean growth rates of sublegal male lobsters in the fishery surrounding Te Tapuwae o Rongokako Marine Reserve. Such an effect could have been exemplified here, because data from fishermen’s recaptures were excluded from the analysis i.e. faster growing tagged individuals outside the reserve may have reached the minimum legal size more quickly than slower growing individuals and were removed from the tagged population by fishers. If this occurred, this would not only reduce the number of tagged legal-sized lobsters available for capture during the research sampling, but also reduce the number of faster-growing animals available for capture and therefore inclusion in my analysis. This may have affected the calculation of average growth rates for lobsters near the minimum legal size limit.

Punt et al. (1997) demonstrated how in fished populations of lobsters there was a tendency for multiple recaptures of tagged animals to represent slow growing animals. This is because a faster growing lobster would reach minimum legal size more quickly and so be retained by a fisherman, whereas a slower growing animal could be caught several times before reaching minimum legal
size. Over a long period of time this could result in a reduction in estimates of average growth rate, as these individuals could be over-represented in tag recaptures. The time frame for the present study was only three years and the most number of times a lobster was recaptured was four times, therefore such over-representation is unlikely to have been an issue. However, this may need to be addressed in any future continuation of this study.

Negative effects on growth rates through handling associated with normal fishing practices have been reported for a number of aquatic and marine species, including crustaceans. Farrell & Leonard (2000) reported negative effects on the growth rates of freshwater crayfish through frequent handling. Harris & Andrews (2005) suggested that the physiological stress experienced by the Norway lobster, *Nephrops norvegicus*, associated with being caught and landed, may in the long term affect their ability to grow and reproduce. Brown & Caputi (1985) demonstrated that after exposure to air, even for only 15 minutes, the growth increment at the first moult of undersize western rock lobster, *Panulirus cygnus*, was significantly reduced. It was also shown that the growth increment of damaged animals returned to the sea was inversely proportional to the number of appendages lost by the animal and that displacement from the lobster’s home range also affected growth rates. Exposure to air, damage and displacement are all factors that may occur repeatedly to sublegal-sized lobsters during normal fishing activity outside protected areas and may have contributed to the reduced growth rate of undersized male lobsters in fished areas in my study. These are effects that can occur within a time frame of months-years, rather than generations, and so corresponds with the age of Te Tapuwae o Rongokako Marine Reserve. Stock assessment models should take into account these depressed rates of growth for males.

The reduction in male growth increment in the reserve between 2004 and 2006 not only coincided with an increase in CPUE (Chapter 2), but also corresponded with an increase in the handling of lobsters within the reserve due to research sampling effort. Whereas the lobsters that had moulted and grown in 2004 had only been subjected to one year of research sampling in the reserve, those that had moulted and grown in 2006 had been subjected to 3 years of research sampling. Most of the male lobsters that provided growth data in 2006 were tagged in November 2005 and so it could not be determined whether in 2006 there was a difference in growth between animals tagged in 2003 and those tagged in 2005. It remains unknown how often lobsters tagged in 2005 had been handled during previous surveys and so the possibility that handling during research sampling explains the reduction in growth between 2004 and 2006 cannot be discounted completely. However, given that: 1) surveys were generally only conducted for around 5 days every 3 months, with pot locations changing daily, 2) relatively few multiple recaptures of tagged lobsters were obtained, and 3) there was no significant change over time in the incidence of tail
fan necrosis (a bacterial infection associated with handling) within the reserve (Chapter 6), it is unlikely that the increased handling as a result of research sampling explains the decline in growth rate within the reserve between 2004 and 2006.

Although this was to date the largest lobster tagging study to be conducted within a New Zealand marine protected area, the availability of data for growth rate analysis was affected by a number of factors, including tag loss, catchability, sampling effort, tag-related mortality and non-reporting of tag recaptures.

### 3.4.3 Tag loss

As in other studies, the present study has demonstrated that Hallprint T-bar tags can be retained through several moulting events over many years (e.g. Stewart, 2003 reported recaptures after over 3000 days). In my study, tagged lobsters were recaptured after up to 3 moults, with lobsters being recaptured after each event. However, significant tag loss did occur. The rate of tag loss in female lobsters could not be determined because not all females were pleopod-clipped as well as tagged. No females bearing eggs at the time of tagging had a pleopod clipped, due to potential adverse effects on the lobster’s ability to aerate and protect her clutch, but all tagged males were clipped. The incidence of tag loss in males was far greater within the marine reserve than outside the reserve, primarily because tag loss was more common in larger lobsters. Overall, nearly 41% of all male recaptures within the reserve involved animals that had either lost their tags or had their tags damaged or broken, with the highest percentage of tag loss occurring in lobsters between 62 and 69.9 mm tail width. Outside the reserve, tag loss in this size range of male lobsters was similar to that within the reserve. Stewart (2003) suggested that tag loss was greater in larger lobsters (*Ibacus peronii*). In contrast, Melville-Smith & Chubb (1997) found that although tag mutilation varied among sites and tended to be higher in areas of high lobster (*Panulirus cygnus*) density, there was no significant effect of lobster size or sex on tag damage. Similarly, Rowe & Haedrich (2001) found that tag-shedding in *Homarus americanus* was not related to either lobster size or sex. In the present study, lobsters were more abundant and on average larger within the reserve than outside (Chapter 2). In addition, lobsters are known to be very social animals, with complex and often agonistic interactions with conspecifics (Debuse *et al.*, 2003). These factors may explain the higher incidence of tag loss within the reserve. It was noted in a number of large lobsters that there was abrasion along the monofilament tag shaft where the carapace rubbed against the tail. This was not as marked in smaller lobsters and may explain why larger lobsters tended to have a higher incidence of tag breakage. Use of tags with a thicker monofilament shaft or ventral tagging may be worthwhile in future studies to reduce the
incidence of tag loss in large lobsters. There was little difference in the incidence of tag loss in sublegal lobsters inside and outside the reserve, which suggests that the higher degree of handling outside the reserve (through normal fishing practices) had little effect on the retention of tags.

When a lobster sheds its tag, or when its tag is damaged, it is obviously impossible to determine the origin of the animal and also impossible to determine where the lobster was when it lost its tag. Therefore, the potential effect of reserve status on the rate of tag loss can only be postulated. However, of those tagged lobsters larger than 58 mm tail width recaptured outside the reserve, all originated from the marine reserve, which infers that those in that size range that had lost their tags also originated from the reserve.

The timing of tagging has been demonstrated to have an effect on tag retention. Comeau & Mallet (2003) recommended tagging lobsters during the intermoult period to minimise tag loss and all lobsters in the present study were tagged during this period.

### 3.4.4 Moult cycle

Because lobsters were not only tagged but also had a pleopod clipped, it could accurately be determined whether a lobster had moulted and therefore grown, and also from recapture events during what time interval that moult event occurred. Only mature females were recaptured during this study and their moulting occurred around April. In tagged males, moultting occurred during August and September, with limited evidence for a second moult. A small number of individuals moulted some time between November and February, but it is unclear whether this was a second moulting for those individuals or a late moult. Within the reserve, there was some evidence that sublegal-sized males moulted slightly earlier than legal-sized lobsters. Such size-dependent moultting has been demonstrated for other spiny lobsters, for example *Palinurus gilchristi* (Groeneveld, 2000). The potential reasons for this can only be postulated, but perhaps larger lobsters require more time to prepare for the moult, or they moult at different times to avoid potential competition or to reduce the effects of predation on the population as a whole. Alternatively it may be that smaller lobsters have a longer moulting period, which narrows in larger individuals (Groeneveld, 2000).

The moult cycles presented here relate only to the size range of lobsters caught during the pot surveys. Because most lobsters were initially caught using pots, lobsters smaller than approximately 46 mm tail width are not well-represented in the samples. McKoy & Esterman (1981) studied lobsters in the same general area as in this study and provided a moult frequency
of 1.6 for lobsters between 80 and 89 mm carapace length and 1.3 for lobsters between 90 and 99 mm carapace length, i.e. some males in these size ranges moulted more than once per year.

### 3.4.5 Growth

Because it could be determined whether or not a lobster had moulted between release and recapture, accurate measures of growth increment were able to be obtained. This prevented problems arising where animals exhibited zero growth. For example, where the incidence of moultng is unknown, a lobster recaptured after a short time will be more likely to have zero growth than one with a long recapture time, so that non-moultng individuals will be overrepresented in growth estimates. But if all zero growth records are excluded, K (average growth constant) may be overestimated, since any true zero growths are excluded from its calculation (Groeneveld, 1997; Ulmestrand & Eggert, 2001). Prescott et al. (1997) noted that when lobsters had only a small moult increment close to the measurement error, it was difficult to distinguish non-moultng individuals from those that had undergone a small moult increment.

Although accurate measures of growth were able to be obtained for male lobsters, the key issue was that the size ranges for which data were obtained were different between the reserve and fished locations. Whereas a large size range of male lobsters was recaptured within the reserve, only sublegal-sized males tagged outside the reserve were recaptured, principally because males larger than this were rare in fished areas. Lobsters that had migrated between the reserve and fished locations (and vice versa) had to be excluded from the analysis of growth, as it was their location of origin that was being tested as potentially influencing growth rate. Growth rates of lobsters recaptured by fishermen were also excluded from the analysis, as it was usually not known whether a lobster had moulted between recaptures, measurements were usually only recorded to the nearest millimetre, and excluding these data reduced potential measurement error between observers.

The use of von Bertalanffy equations to describe the growth rates of crustaceans has been debated, primarily because growth in the length of crustaceans occurs incrementally (through moultng) rather than continuously. However, provided that the data support estimation of an asymptotic length, the von Bertalanffy curve is one of the simplest available to describe growth given the inherent variability associated with tag-recapture data (Maller & DeBoer, 1988). In a review of lobster growth studies, Morgan (1980, cited in McGarvey et al., 1999), concluded that the most adequate description of growth in spiny lobsters was given by the von Bertalanffy relationship. A number of studies have used von Bertalanffy curves to describe growth in *Jasus*

Because the size ranges of lobsters tagged and recaptured outside the reserve were so narrow, the resulting von Bertalanffy growth curves are not as reliable as those for the reserve, where the data range was more extensive. The low growth rates of sublegal-sized lobsters outside the reserve (particularly just sublegal-sized) resulted in von Bertalanffy growth curves with steep slopes and unrealistically low asymptotic sizes. For example, of all the male lobsters for which growth data were available, 198 had tail widths greater than the $L_\infty$ predicted by the growth curve for males from outside the reserve in 2006. Fabens’ (1965) method of fitting von Bertalanffy curves to tag-recapture data is known for its tendency to underestimate $L_\infty$ and overestimate $K$ (Rodriguez-Cabello et al., 2005). The growth curve for non-reserve animals was, however, similar to that produced by McKoy & Esterman (1981) for lobsters from the same general area in 1975-1977. Comparing the reserve growth curve with the growth curve constructed by McKoy & Esterman (1981) suggested that lobsters in the reserve in my study had a slower growth rate than reported in the earlier study but also had a larger (though more realistic) theoretical asymptotic size. However, the size range of lobsters in the 1981 study was narrower than in my study.

Due to difficulties in comparing von Bertalanffy growth curves, because of varying size ranges of lobsters sampled, comparisons between individual size classes of lobsters were much more reliable and form the basis of my conclusions. The growth rates of sublegal-sized males within the reserve were significantly higher, in terms of both tail width and carapace length, than for the same sized lobsters in the surrounding fishery. This was particularly the case for males just below the minimum legal size. Comparing the growth rates of individual size classes, the growth rate of lobsters in the 100 to 109.9 mm carapace length range was the same in the reserve in this study as in McKoy & Esterman’s (1981) earlier study. However, in my study the growth rate of lobsters in that size range in fished areas was lower than that for both the reserve lobsters and those described in the earlier study.

The von Bertalanffy growth curves constructed for male lobsters from the marine reserve (the most comprehensive data set in this study), suggested that they didn’t reach their asymptotic size until they were aged over 30 years old. Although lobsters cannot be aged (but see Maxwell, 2006) they are thought to be relatively long-lived animals and so the age at asymptotic size suggested here seems realistic. In the Gisborne area, male lobsters were thought to be 4.5 to 6 years of age when they reach minimum legal size (Booth, 1986; McKoy & Esterman, 1981). The
growth curve in this study suggests that this age could be closer to 10-15 years of age, at least within the reserve.

The growth rates of females could only be presented for mature individuals tagged and recaptured within the marine reserve. For this size range and maturity, both positive and negative growth occurred in different individuals, with females growing little overall. Shrinkage in lobsters has been reported in other studies, e.g. *Jasus lalandii* (Cockcroft & Goosen, 1995; Goosen & Cockcroft, 1995). They considered that negative growth, or shrinkage at moulting, was a direct result of adverse environmental conditions, rather than a physiological mechanism evolved to overcome defined periods of hardship. Cockcroft & Goosen (1995) suggested that female *Jasus lalandii* sacrifice growth to optimise egg production and that under extreme conditions, the maintenance of body size would take precedence over egg production. Shrinkage, however, was shown to be very small. Kulmiye & Mavuti (2005) described a reduction in female growth increment corresponding with the reproductive season. Prescott et al. (1997) found that the growth rates of mature female *Jasus edwardsii* in South Australia were so low that it took several years for a detectable change in size to be recorded. The same appears to apply for this species within Te Tapuwae o Rongokako Marine Reserve and perhaps the wider region.

### 3.4.6 Effects of tagging on growth

Although tagging is a common method used to assess growth, tagging itself may have an impact on the animal’s growth rate. Several studies have assessed the effects of tagging on crustacean growth and while some studies have found negative effects on growth, factors such as the type of tag, timing of tagging and the handling and stress associated with tagging are important considerations.

Courtney *et al.* (2001) showed that tagging was unlikely to significantly affect the survival rate or growth increments of Scyllarid lobsters, but that it was likely to lower the incidence of moulting. Cooper (1971) and Chittleborough (1974) respectively reported similar results for *Homarus americanus* and *Panulirus longipes cygnus* tagged with the same or similar tags. Phillips *et al.* (1992) suggested that tagging or handling could decrease the growth rates of *Panulirus cygnus*, *P. argus* and *P. ornatus*. Dubula *et al.* (2005) found that negative impacts on growth were absent when *Jasus lalandii* were tagged during the intermoult period. Tagging of tiger prawns did not affect their overall growth rates, but did shorten their intermoult period and reduce their moult increment (Hill & Wassenberg, 1985; Primavera & Caballero, 1992).
The potential effect of tagging on the growth rates recorded in this study cannot be assessed. However, McKoy & Esterman (1981) compared the moult increments of tagged and untagged *Jasus edwardsii* held in aquaria and found no significant difference in the moult increments within each sex. Winstanley (1976), however, reported reduced growth of *J. edwardsii* tagged with dart tags, along with deformities, necrosis and adverse effects on reproduction in females. No such deformities or adverse effects on reproduction were noted in the present study, where T-bar tags were used, although some colouring of the tissue around the point of tag insertion was noted and this is expected with damaged muscle tissue (J. Booth, NIWA, pers. comm.). It is possible that handling associated with tagging or perhaps the tags themselves caused mortality within the tagged population and this rate of tagging mortality cannot be assessed. However, in this study, careful attention was paid to minimising any effects of the tags and tagging procedure on the lobsters. Lobsters were immediately returned to the water after tagging, and if lobsters were required to spend time on board the boat prior to tagging this time generally did not exceed 10 minutes and lobsters were kept moist in a shaded bin during this time. The tag needle was sterilised prior to use and lobsters were only tagged if they had no more than 2 injuries. On very rare occasions, additional injuries occurred, either during the tagging procedure or during recapture.

### 3.4.7 Sampling method

The primary method used to catch and recapture lobsters in this study (potting) may have influenced the growth rates presented. For example, pots tend to select against very large and small lobsters, due to the design of pots and the behaviour of individual lobsters (Miller, 1989). Ziegler *et al.* (2002b) demonstrated that capture had no significant impact on the catchability of tagged small male and female *Jasus edwardsii*. Recaptures of medium-sized and large males were over-represented in their catches, which was suggested to be a result of differences in motivational issues and increased selectivity with lobster size, rather than a history of previous capture. In my study the main implication of catchability was a reduction in the data available for analysis, rather than any effect on the calculation of average growth rate for example.

### 3.4.8 Tag non-reporting

It is known from discussions with fishermen that there was a low level of tag non-reporting outside the marine reserve. This did not affect the overall sample size available for analysis however, as data from fishermen were not used to assess lobster growth. The primary reason for excluding reports from fishermen was that it could often not be determined from the recapture
reports whether or not a tagged lobster had moulted. Without knowing whether a moult event had occurred, the possibility existed that non-moulted individuals would be included in the analysis of growth data. In addition, many fishermen recorded measurements to the nearest millimetre, rather than to the nearest 0.1 mm and there was an unknown degree of measurement error.

### 3.4.9 Conclusions

This study has demonstrated that the growth rates of male lobsters in the Gisborne region may be affected by fishing. The growth rates of male lobsters were lower in the reserve in 2006 than in 2004, and coincided with an increase in CPUE (Chapter 2). No such change in growth rate or CPUE between 2004 and 2006 was recorded outside the reserve. This suggests that density-dependent effects on growth may be occurring within the reserve. However, contrary to expectation, the overall growth rates of sublegal male lobsters were higher within the reserve than outside. The wide dispersal of lobster larvae means that the possibility of fishing-induced evolution explaining the difference in growth rates between adjacent populations can be discounted. However, the direct effect of fishing through the persistent removal of faster growing individuals does provide an explanation for the reduced average growth rate of lobsters just below the minimum legal size. In addition, the indirect effects of fishing, by way of handling during normal fishing activity, should be explored as a potential mechanism contributing to the reduction in the growth rates of individual lobsters in the fishery surrounding Te Tapuwae o Rongokako Marine Reserve.
Table 3-1. The number of pot lifts completed and their location, for every survey month. Data are divided into the three different types of pot used. Std= standard HRC (Hurricane Reinforcing Concrete mesh) pot; sml= ¾ sized HRC pot; fine= standard HRC pot covered in 25 mm plastic mesh.

| Month / Year | Reserve | | | | Fished | | | |
|--------------|---------|---------|---------|-------|---------|---------|---------|
|              | std     | sml     | fine    | TOTAL | std     | sml     | fine    | TOTAL |
| November 2003| 134     |         | 134     | 134   | 15      |         | 15      | 15    |
| December 2003| 274     | 20      | 294     | 90    | 90      |         |         |       |
| February 2004| 95      | 80      | 8       | 183   | 17      |         | 1       | 18    |
| June 2004     | 71      | 92      | 8       | 171   | 44      |         | 44      |       |
| August 2004   | 163     | 1       | 164     | 24    | 3       |         | 27      |       |
| November 2004| 189     | 12      | 201     | 134   |         |         | 134     |       |
| March 2005    | 176     | 10      | 186     | 64    |         |         | 64      |       |
| May 2005      | 163     | 10      | 173     | 75    |         |         | 75      |       |
| November 2005| 151     |         | 151     | 54    |         |         | 54      |       |
| February 2006| 182     |         | 182     | 63    |         |         | 63      |       |
| May 2006      | 170     |         | 170     | 80    |         |         | 80      |       |
| September 2006| 165    |         | 165     | 80    |         |         | 80      |       |
| November 2006| 166     |         | 166     | 84    |         |         | 84      |       |
| TOTALS        | 2099    | 173     | 68      | 2340  | 780     | 47      | 1       | 828   |

Table 3-2. The 6 stages of lobster maturity recorded for all lobsters sampled.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Male (may be sexually mature or immature)</td>
</tr>
<tr>
<td>2</td>
<td>Immature female – no setae on pleopods, or setae less than 6 mm in length.</td>
</tr>
<tr>
<td>3</td>
<td>Mature but non egg-bearing female – setae on pleopods longer than 6 mm in length. No egg mass present.</td>
</tr>
<tr>
<td>4</td>
<td>Mature egg-bearing female. Eggs have no visible eyes.</td>
</tr>
<tr>
<td>5</td>
<td>Mature egg-bearing female. Eggs have visible eyes.</td>
</tr>
<tr>
<td>6</td>
<td>Mature female. Eggs have been released. Traces of eggs may remain on setae; setae appear matted.</td>
</tr>
</tbody>
</table>

Table 3-3. Relative scale of severity of tail fan necrosis recorded for every lobster sampled.

<table>
<thead>
<tr>
<th>Severity of Tail Fan Necrosis</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Necrosis absent. No obvious sign of blistering or blackened areas on any part of the lobster.</td>
</tr>
<tr>
<td>1</td>
<td>Necrosis present. Small (less than 2x2 cm) area of blistering or blackening on telson or uropod.</td>
</tr>
<tr>
<td>2</td>
<td>Necrosis present. Area greater than 2x2 cm showing blistering or blackening. Generally more than one uropod and / or telson affected. Uropod or telson occasionally missing.</td>
</tr>
<tr>
<td>3</td>
<td>Necrosis present. All uropods and telson affected to considerable extent by blistering and / or blackening.</td>
</tr>
</tbody>
</table>
Table 3-4. Number of lobsters tagged, including their location, sex and year / month of tagging.

<table>
<thead>
<tr>
<th>Month / Year</th>
<th>Reserve</th>
<th>Fished</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>November 2003</td>
<td>2123</td>
<td>159</td>
</tr>
<tr>
<td>December 2003</td>
<td>467</td>
<td>859</td>
</tr>
<tr>
<td>January 2004</td>
<td>11</td>
<td>15</td>
</tr>
<tr>
<td>February 2004</td>
<td>36</td>
<td>206</td>
</tr>
<tr>
<td>June 2004</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>August 2004</td>
<td>25</td>
<td>3</td>
</tr>
<tr>
<td>November 2005</td>
<td>642</td>
<td>91</td>
</tr>
<tr>
<td>September 2006</td>
<td>479</td>
<td>106</td>
</tr>
<tr>
<td>TOTAL</td>
<td>3785</td>
<td>1440</td>
</tr>
</tbody>
</table>

Table 3-5. Tag loss in male lobsters tagged within and outside the marine reserve.

<table>
<thead>
<tr>
<th>Location</th>
<th>Tag Condition</th>
<th>No. of Recaptures</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reserve</td>
<td>Tag retained intact</td>
<td>972</td>
</tr>
<tr>
<td></td>
<td>Tag lost completely</td>
<td>544</td>
</tr>
<tr>
<td></td>
<td>Tag broken along shaft or damaged so as to be illegible</td>
<td>126</td>
</tr>
<tr>
<td>Fished</td>
<td>Tag retained intact</td>
<td>195</td>
</tr>
<tr>
<td></td>
<td>Tag lost completely</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>Tag broken along shaft or damaged so as to be illegible</td>
<td>7</td>
</tr>
</tbody>
</table>

Table 3-6. Sample sizes for tagged female lobsters that had moulted and were recaptured within 365 days. Their months of release and recapture are shown.

<table>
<thead>
<tr>
<th>Release Month</th>
<th>Moult Status</th>
<th>January</th>
<th>February</th>
<th>March</th>
<th>April</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>August</th>
<th>September</th>
<th>October</th>
<th>November</th>
<th>December</th>
</tr>
</thead>
</table>
Table 3-7. Sample sizes for tagged male lobsters that had moulted and were recaptured within 365 days of release. Shown are the month of release and month of recapture.

<table>
<thead>
<tr>
<th>Release Month</th>
<th>Moult Status</th>
<th>January</th>
<th>February</th>
<th>March</th>
<th>April</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>August</th>
<th>September</th>
<th>October</th>
<th>November</th>
<th>December</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>moulted</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>not moulted</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>February</td>
<td>moulted</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>not moulted</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
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<td>0</td>
<td></td>
</tr>
<tr>
<td>March</td>
<td>moulted</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>not moulted</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>moulted</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
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<td>0</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<td>13</td>
<td></td>
</tr>
<tr>
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<td>0</td>
<td>0</td>
<td>0</td>
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<td>2</td>
<td>14</td>
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<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>moulted</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>not moulted</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>moulted</td>
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<td>0</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
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<td>not moulted</td>
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<td>0</td>
<td>0</td>
<td>0</td>
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</tr>
<tr>
<td>October</td>
<td>moulted</td>
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<td>0</td>
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<td></td>
</tr>
<tr>
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<td>not moulted</td>
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<td>0</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>November</td>
<td>moulted</td>
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<td>0</td>
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<td>0</td>
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<td>0</td>
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<td>7</td>
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<td>80</td>
<td></td>
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<td>not moulted</td>
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<td>1</td>
<td>0</td>
<td>4</td>
<td>113</td>
<td>1</td>
<td>236</td>
<td></td>
</tr>
<tr>
<td>December</td>
<td>moulted</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>25</td>
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<td>not moulted</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

Table 3-8. Available data for growth rate analysis. Recapture numbers exclude 2 “emigrants” i.e. lobsters that moved out of the reserve. Note that only one of either tail width and carapace length was recorded for a small number of individuals.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Location</th>
<th>No. Tagged</th>
<th>No. Recapture Events</th>
<th>No. Moulted between Recaptures</th>
<th>No. Moulted within 400 Days of Release</th>
<th>No. Moulted within 400 Days and Measured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>Reserve</td>
<td>3785</td>
<td>1001</td>
<td>305</td>
<td>197</td>
<td>186</td>
</tr>
<tr>
<td></td>
<td>Fished</td>
<td>1701</td>
<td>160</td>
<td>41</td>
<td>38</td>
<td>38</td>
</tr>
<tr>
<td>Female</td>
<td>Reserve</td>
<td>1440</td>
<td>97</td>
<td>51</td>
<td>38</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>Fished</td>
<td>540</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>
Table 3-9. Results of ANCOVA for establishing whether a relationship exists between size and growth increment of male lobsters in the marine reserve and whether year has an influence on that relationship.

<table>
<thead>
<tr>
<th>Measure</th>
<th>coefficient</th>
<th>value</th>
<th>std error</th>
<th>T value</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tail width</td>
<td>(intercept)</td>
<td>8.5070</td>
<td>1.0032</td>
<td>8.4800</td>
<td>0.0000</td>
</tr>
<tr>
<td></td>
<td>Year1</td>
<td>-0.4121</td>
<td>0.1940</td>
<td>-2.1236</td>
<td>0.0351</td>
</tr>
<tr>
<td></td>
<td>Year2</td>
<td>-0.0773</td>
<td>0.0875</td>
<td>-0.8839</td>
<td>0.3779</td>
</tr>
<tr>
<td></td>
<td>Tail width</td>
<td>-0.1255</td>
<td>0.0167</td>
<td>-7.5172</td>
<td>0.0000</td>
</tr>
<tr>
<td>Carapace length</td>
<td>(intercept)</td>
<td>16.3176</td>
<td>1.8780</td>
<td>8.6888</td>
<td>0.0000</td>
</tr>
<tr>
<td></td>
<td>Year1</td>
<td>-0.8224</td>
<td>0.3958</td>
<td>-2.0777</td>
<td>0.0391</td>
</tr>
<tr>
<td></td>
<td>Year2</td>
<td>-0.3505</td>
<td>0.1785</td>
<td>-1.9638</td>
<td>0.0511</td>
</tr>
<tr>
<td></td>
<td>Carapace length</td>
<td>-0.1149</td>
<td>0.0158</td>
<td>-7.2509</td>
<td>0.0000</td>
</tr>
</tbody>
</table>

Table 3-10. Parameters of von Bertalanffy growth curves for male lobsters within and outside the marine reserve and for males at the “Gisborne Local” site in McKoy & Esterman (1981). Note that the data set for lobsters tagged outside the reserve in my study contained only sublegal-sized animals.

<table>
<thead>
<tr>
<th>Data Set</th>
<th>Year</th>
<th>Measure</th>
<th>L∞</th>
<th>K</th>
<th>t₀</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>This study Reserve</td>
<td>2004</td>
<td>Carapace length</td>
<td>147.84</td>
<td>0.131</td>
<td>-0.64</td>
<td>136</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tail width</td>
<td>70.22</td>
<td>0.143</td>
<td>0</td>
<td>134</td>
</tr>
<tr>
<td>Fished 2004</td>
<td></td>
<td>Carapace length</td>
<td>148.10</td>
<td>0.071</td>
<td>-1.2</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tail width</td>
<td>72.56</td>
<td>0.070</td>
<td>0</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>2006</td>
<td>Carapace length</td>
<td>105.47</td>
<td>0.466</td>
<td>-0.26</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tail width</td>
<td>57.99</td>
<td>0.159</td>
<td>0</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>2006</td>
<td>Carapace length</td>
<td>106.19</td>
<td>0.330</td>
<td>-0.36</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tail width</td>
<td>53.49</td>
<td>0.362</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>McKoy &amp; Esterman</td>
<td>1975-1977</td>
<td>Carapace length</td>
<td>118</td>
<td>0.29</td>
<td>-0.36</td>
<td>25</td>
</tr>
</tbody>
</table>

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Figure 3-1 Map showing the initial locations of tagged lobsters (a) and the subsequent distribution of sampling effort to obtain recaptures (b).

a)
Figure 3-2. A tagged lobster.
Figure 3-3. The percentage tag loss (either lost completely or broken) in male lobsters recaptured within and outside the reserve, over a range of sizes. Sample sizes are shown for each size range.

Figure 3-4. Mean sizes of recaptured tagged male lobsters that retained their tag intact, had lost their tag completely, or had broken or damaged their tag.
Figure 3-5. Graph showing the percentage of tagged female lobsters that had moulted between being released and being recaptured, separated into the months they were released and recaptured. Only recaptures within 365 days are shown. Sample sizes are given in Table 3-6.
Figure 3-6. Graphs showing for each month that male lobsters were released, the percent that had moulted prior to recapture. Only recaptures within 365 days are shown. Lobsters are divided into sublegal (<54 mm tail width) and legal (54 mm+ tail width) sizes. Sample sizes are given in Table 3-7.
Figure 3-7. Carapace lengths and growth increments for males tagged within and outside the marine reserve, over 3 years. Only data for males that moulted within 400 days of being released are shown.

![Carapace lengths and growth increments for males](image)

Figure 3-8. Tail widths and growth increments for males tagged within and outside the marine reserve, over 3 years. Only data for males that moulted within 400 days of being released are shown.

![Tail widths and growth increments for males](image)
Figure 3-9. Carapace lengths and growth increments for females tagged within the marine reserve, for the two years for which data were available. Only data for females that moulted within 400 days of being released are shown. No data are available for females from outside the reserve.

Figure 3-10. Tail widths and growth increments for females tagged within and outside the marine reserve, for the two years for which data were available. Only data for females that moulted within 400 days of being released are shown.
Figure 3-11. Mean growth increments for sublegal sized (<54 mm tail width) male lobsters within and outside the marine reserve. Growth rates are significantly higher within the reserve than outside, both in terms of tail width and carapace length.

Figure 3-12. Mean growth increments for sublegal sized (<54 mm tail width) male lobsters within and outside the marine reserve in 2004 and 2006.
Figure 3-13. Mean growth increments (showing sample sizes) of lobsters tagged within and outside the reserve, compared with data from lobsters tagged between 1975 and 1977 (“Gisborne local” site in McKoy & Esterman 1981).
Figure 3-14. Von Bertalanffy growth curves (based on carapace length) for male lobsters from within and outside the marine reserve in 2004 and 2006.

Figure 3-15. Von Bertalanffy growth curves (based on tail width) for male lobsters from within and surrounding the marine reserve in 2004 and 2006.
Figure 3-16. Comparison of von Bertalanffy growth curves constructed for tagged male lobsters in this study (reserve and fished locations) and for the Gisborne Local site in McKoy & Esterman (1981).
Chapter 4  The Movement Patterns of *Jasus edwardsii* on Fished and Unfished Reefs

4.1 Introduction

Knowledge of the movement patterns of exploited marine animals is important for a proper understanding of the dynamics of stocks and therefore, their management (Stewart & Kennelly, 1998). The movement patterns of lobsters have been divided into three general categories (Herrnkind, 1980):

1. **Migration**: the movement of a population (or a distinct part of it) within some confined time period and over relatively long distances;
2. **Nomadism**: the wandering of individuals without any clear start and end points; and
3. **Homing**: periodic excursions from shelter to some nearby area, with subsequent return to that shelter or others nearby.

Each of these patterns of movement can be associated with aspects such as feeding, finding shelter, genetic mixing, reproduction or recruitment, and lobsters can exhibit any or all of these patterns at some stage during their life history. Spiny lobsters are known to possess a magnetic map that assists with navigation towards specific areas, such as during homing (Lohmann & Lohmann, 2006). In *Jasus* spp, long distance movements (on a scale of tens to hundreds of kilometres) occur in late juveniles and are generally alongshore, against the prevailing current (Booth, 1997). In *J. edwardsii*, seasonal inshore-offshore movements, which can exceed 5 km, are associated with moulting and reproduction (Booth, 1997; Gardner *et al.*, 2003; Kelly, 2001; Kelly & MacDiarmid, 2003; MacDiarmid, 1991). Nomadism has also been reported in *J. edwardsii* (Annala & Bycroft, 1993; Booth, 1997).

The intensity and nature of movement may be modified by factors such as population density and the availability of resources. As population density increases, competition for resources such as food and shelter may also increase, which may result in compensatory changes in biological variables – a mechanism known as density dependence (Sanchez-Lizaso *et al.*, 2000). Such density-dependent effects have been reported for marine species (Johnson, 2006; Moksnes, 2004; Overholtzer-McLeod, 2004). In terms of lobsters, density-dependence can affect home range size (Chittleborough, 1974) and survival (Morgan, 1974). Prescott *et al.* (1997) suggested that the high density of lobsters in an area of South Australia induced lobsters to migrate, but Gardner *et al.* (2003) found that in areas of very high lobster density and high catch rates around southern
Tasmania, very little movement of lobsters was detected, with a virtual absence of large-scale (over 5 km) movements in that area.

Whether intended for conservation or for fisheries management, marine protected areas function by segregating some local population(s) within their boundaries, where they experience lessened direct human impacts, particularly fishing pressure (Sale & Kritzer, 2003). Marine protected areas can therefore provide an opportunity for previously harvested species to increase in size and abundance (Bohnsack, 1998; Gell & Roberts, 2003b; Halpern, 2003; Roberts & Hawkins, 2000). It has been hypothesised that density-dependent changes in life history characteristics should occur when populations recover within marine protected areas (Kramer & Chapman, 1999; Sanchez-Lizaso et al., 2000) and there is some evidence for such effects. For example, Abesamis & Russ (2005) described density-dependent home-range relocation of fish from a no-take marine reserve. Density-dependent effects on the growth rates of conch in a protected area have also been reported (Bene & Tewfik, 2003).

Although any scale of movement by lobsters, whether it is homing, nomadism or migration (Herrnkind, 1980), has the potential to produce significant movement across the boundaries of marine protected areas, movement across the boundaries may be increased by density-dependent effects. For example, Edgar & Barrett (1999) predicted that an increase in lobster density could, through crowding, increase the movement and so biomass export from Tasmanian marine protected areas. The emigration of organisms from marine protected areas into the surrounding fishery, or “spillover”, has been assessed in a number of studies through the use of tags and transmitters (Attwood & Bennett, 1994; Cole et al., 2000; Eristhee & Oxenford, 2001; Holland et al., 1993; McGarvey, 2004; Parsons & Egli, 2005; Starr et al., 2004).

As well as assessing the movement patterns of animals directly (through tagging for example), analysis of the spatial patterns of species’ size and abundance in relation to the location of the boundaries of marine protected areas can also provide information on movement across the boundaries. This is because while species may increase in abundance within marine reserves, their abundance close to the reserve boundaries may be influenced by fishing pressure adjacent to the protected area, due to increased chance of cross-boundary movement (and therefore susceptibility to harvest) the closer the animal is to the boundary. This may result in gradients of population density and mean size across reserve boundaries with maxima in the centre of the reserve and minima outside the reserve away from the boundary (Abesamis & Russ, 2005; Babcock et al., 2007; Kramer & Chapman, 1999; Murawski et al., 2004). The more effective
spillover is from a reserve, the less pronounced the density gradient across the reserve boundaries should be (Tewfik & Bene, 2003).

But for a fishery to improve from the establishment of a marine reserve through the movement of marine species, emigration from reserves must be greater than immigration into reserves and it must also offset removal from exploitation of protected populations (Roberts & Polunin, 1991; Rowley, 1994). From a different perspective, the effectiveness of protection afforded by an MPA may be limited by the impacts of fishing on species that undergo daily foraging movements or seasonal migrations outside the MPA (Goni et al., 2001). For example, small marine reserves appear to be ineffective in protecting Caribbean spiny lobsters, *Panulirus argus*, in the Florida Keys, due to the dispersal of lobsters from closed areas and their subsequent harvest (Eggleston & Dahlgren, 2001). Stockhausen & Lipcius (2001) found that the establishment of a single large reserve would be more effective in providing fisheries benefits (through fishery yield, larval production and population growth rate) for *P. argus* than several small reserves. However, this applied to a theoretically over-exploited lobster population. The impact of area closures on reduction of exploitation rates will depend strongly on the rate and timing of lobster movement, with slower migration tending to reduce the benefits of an area closure (Gendron & Brethes, 2002). Rowe (2001) suggested that no-take marine reserves could be useful for achieving conservation objectives, but in terms of *Homarus americanus*, because of intense harvesting pressure on surrounding lobster grounds, reserves could only be effective if adult movement occurred at a sufficiently low rate to permit increased adult survival. It has been suggested that priority should be given to identifying areas used by *Jasus edwardsii* during offshore migrations and that depending on the objective of the reserve (either conservation or fisheries management) these areas should either be included within the boundary of a reserve, or the boundaries should be set to limit spillover to sustainable levels (Kelly et al., 2000b).

Analysis of catch data from within Te Tapuwae o Rongokako Marine Reserve and the surrounding fishery in Chapter 2 suggested that seasonal inshore-offshore movements of *Jasus edwardsii* were occurring. It also showed that lobster abundance and size has increased significantly within Te Tapuwae o Rongokako Marine Reserve. In this chapter I aim to describe the short-distance and seasonal movements of lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve, to establish whether any differences exist between fished and unfished populations. I also assess the level of movement of lobsters across the boundary of the reserve, through the analysis of tagging data and spatial data on the abundance and size structure of lobsters in the vicinity of the reserve’s boundaries. I hypothesise that the rate of lobster
movement is higher within the reserve than in the surrounding fishery and that there is a net emigration of lobster biomass from the reserve, due to density-dependent effects.
4.2 Methods

4.2.1 Sampling strategy

To describe the movement patterns of lobsters on fished and unfished reefs, lobsters were tagged within and surrounding a marine reserve, with subsequent pot surveys completed on a seasonal basis to obtain recaptures of tagged lobsters. In addition, a small number of lobsters was fitted with acoustic transmitters. Catch data from pot surveys completed throughout the marine reserve and adjacent to the reserve boundaries, were analysed to determine whether any gradients in catch per unit effort or lobster size existed as a function of distance from the reserve boundaries. The survey design (in terms of aspects such as numbers of lobsters tagged and required recapture rate) were based on recommendations by Booth (2003) and modified in accordance with funding and logistical constraints, permitting requirements and advice from fishing industry representatives, including fishermen.

4.2.2 Tagging

A total of 7466 lobsters was tagged (5225 within Te Tapuwae o Rongokako Marine Reserve and 2241 from outside the reserve), mostly during November and December 2003 (Table 4-1, Figures 4-1, 4-2). A small number of lobsters, from very shallow depths within Te Tapuwae o Rongokako Marine Reserve, were caught by divers and tagged on shore. Lobsters were tagged using Hallprint T-bar anchor tags, inserted dorsally between the carapace and tail, either side of the centre line in order to avoid the intestine and as close to the tail as possible to avoid the body cavity (Figure 4-3). Insertion of the tags into this region of the muscle tissue ensured that the tags were retained during moulting. The tag needle was sterilised in ethanol between animals. Lobsters of over 70 mm carapace length were tagged using an Avery Dennison Tag Fast tagging gun and TBA tags. A Fine Fabric gun and TBF tags were used for lobsters with a carapace length of less than 70 mm. Each tag was individually numbered, along with the letters DOC (for Department of Conservation) and the tags also had a short “chew buffer” on their distal end. Tagged lobsters also had the distal third of one pleopod clipped using scissors, to enable determination of tag loss. After tagging, lobsters were immediately returned to the sea as close as possible to their capture location (using a Garmin Etrex GPS unit, with a margin of error of approximately 30 m).
Table 4-1 provides the number of lobsters tagged, along with the month/year, original location and sex. Data recorded for every tagged lobster included carapace length (measured to the nearest 0.1 mm with vernier callipers, from the antennal platform to the dorsal posterior margin of the carapace along the midline); tail width (measured to the nearest 0.1 mm in a straight line between the tips of the primary spines on the second segment of the tail); sex; and reproductive stage for females (based on the presence (mature) or absence (immature) of setae longer than 6 mm on the endopodites).

This study was advertised and reported on in local newspapers and magazines, and divers and fishermen were asked to record the tag number, sex, tail width and location of any tagged lobster they observed or caught. Tag reporting forms were provided to all commercial fishermen working in the vicinity of the study site and upon request by members of the public. No reward was offered for providing recapture reports but tagged legal-sized lobsters caught outside the marine reserve were able to be retained by fishermen.

4.2.3 Pot surveys

Pot surveys were conducted to obtain recaptures of tagged lobsters and to provide data on the characteristics of the catch (CPUE and size) in relation to the boundaries of the marine reserve. Potting for lobsters in Te Tapuwae o Rongokako Marine Reserve and adjacent fished areas was undertaken approximately every three months beginning in November 2003, using commercial fishing vessels. Subsequent surveys were undertaken in February 2004, June 2004, August 2004, November 2004, March 2005, May 2005, November 2005, February 2006, May 2006, September 2006 and November 2006 (Table 4-2). The location and number of pots set depended on a number of factors, including weather and sea conditions, the vessel used and the presence of other fishing gear. Where possible, reef habitat from a range of depths throughout the marine reserve and within approximately 3 kilometres of the reserve’s boundary was sampled in order to obtain tag recaptures (Figure 4-4). A total of 3168 pot lifts was completed over the 3-year study period (Table 4-2). Pot locations were recorded using a Garmin Etrex GPS with a margin of error of approximately 30 m.

4.2.4 Transmitters

Five Vemco V16 continuous acoustic transmitters (Figure 4-5) were fitted to lobsters within Te Tapuwae o Rongokako Marine Reserve in November 2004. The transmitters were attached to the carapaces of 3 male and 2 female lobsters using a cable tie. Due to the size and weight of the
transmitters (10 g), each lobster was required to weigh in excess of 500 g, or 50 times the weight of the transmitter (as recommended by the manufacturer) and so only relatively large lobsters could be utilised. Details of these lobsters are in Table 4-3.

Regular surveys of the marine reserve were made using a Vemco VH10 directional hydrophone and VR60 ultrasonic receiver, to obtain positional data for each lobster. When the transmitter was located, the GPS position was recorded as close as possible to the position of strongest acoustic signal. The regularity of the surveys depended primarily on weather and sea conditions, in particular water clarity, which affected signal attenuation. The number of animals able to be fitted with transmitters was restricted by the cost of the equipment.

4.2.5 Data analysis

For the assessment of cross-boundary movement, two methods were employed. The first method (A) excludes all recaptures reported by fishermen. The second method (B) uses both my data and data from fishermen. Both methods were used to obtain recapture rates of tagged lobsters, either assuming no tag loss, or taking into account an estimate of tag loss, and all analyses allowed for tagged lobsters that were retained by fishermen.

4.2.5.1 Method A

The recapture rate (R) was calculated for both the marine reserve and fished locations, for lobsters that moved across the reserve boundary (“migrants”) and for those that stayed at their tag / release location (“non-migrants”). R was calculated for each day surveys were conducted, by dividing the number of recaptured tagged lobsters (N) by the number of tags in the water at each location (T) and the number of pot lifts completed each day (P).

\[
R = \frac{100 \times N}{T} / P
\]

4.2.5.2 Method B

The recapture rate (R) was calculated for both the marine reserve and fished locations, for lobsters that moved across the reserve boundary (“migrants”) and for those that stayed at their tag / release location (“non-migrants”). R was calculated as the number of recaptures (N) divided by the number of tags in the water at each location (T) and did not account for fishing effort, as fishermen’s effort was unknown.

\[
R = 100 \times N / T
\]
For both Methods A and B, where T (number of tags in the water) included tag loss, this was estimated for each day surveys were conducted, for fished and reserve locations. The tag loss rate was calculated as the proportion of lobsters that were recaptured that had lost their tags (evidenced by a clipped pleopod but no tag), of the total number of recaptured lobsters that were tagged or had lost their tags. For days where no survey was conducted, the estimated number of tags available for capture was taken as the number estimated on the last survey date. If the estimate for the last survey date was 0, the previous non-zero estimate was used.
4.3 Results

Tagging, transmitters and pot surveys provided detailed information about the movement patterns of lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve. The analysis of movement patterns is divided into two sections: short-distance / seasonal movements, and cross-boundary movements.

4.3.1 Short-distance and seasonal movements

4.3.1.1 Tagging

Of the 7466 lobsters tagged, 1105 were recaptured at least once and 5 individuals were recaptured four more times following their initial tag and release (Table 4-4). The majority of tagged lobsters were recaptured during the regular pot surveys I undertook, but commercial and recreational fishers reported 156 recaptures of 142 individual tagged lobsters. Of these, 35 were kept as catch. An additional 2 records supplied by fishers were excluded from the analysis as they both involved large movements and unrealistic reductions in tail width over time. A further 3 recapture events recorded during my pot surveys were excluded from the analysis as they involved large changes in tail width over time, or changes in sex.

Insufficient data were obtained for legal-sized males from outside the reserve to determine whether there was any significant effect of tag / release location on the distance moved for these lobsters. However, for sublegal-sized males (<54 mm tail width), the frequency distributions for the distance moved between capture events were similar between the reserve and fished locations (Figure 4-6). Overall in the reserve, tagged males smaller than 70 mm tail width were recaptured up to 5856 m from their last capture location, although the majority of distances between captures were less than 1 km (Figure 4-7). Only 3 tagged males over 70 mm tail width (all from the reserve) were recaptured more than 1 km from their last position. Just 3 of the 106 records of female recaptures involved movements of over 1 km between release and recapture. In terms of the maximum displacement from their initial tag location, the largest straight-line distance travelled by a male was 5856 m; for females, it was 4655 m.

There was a significant positive correlation between the number of recapture events and the total distance moved by tagged male lobsters, such that lobsters caught more frequently tended to move larger distances overall (Pearson correlation coefficients: reserve 0.275, fished 0.308;
There were also significant positive correlations between the total time at large and the total distance moved for tagged males and females from the reserve (Pearson correlation coefficients 0.183 and 0.334 respectively; p<0.01), but not from outside the reserve. The maximum total distance moved by a male lobster tagged within the reserve was 8505 m; the maximum total for a male tagged outside the reserve was 4288 m (Figure 4-9). The largest total distance moved by a female tagged within the reserve was 4655 m; for females tagged outside the reserve, the largest total distance was 636 m (Figure 4-9). The vast majority of total distances moved (for males and females, tagged either within or outside the reserve) were less than 1000 m (Figure 4-10). Where the total distance moved was less than 1000 metres, most of these movements were less than 200 metres in extent (Figure 4-11).

Longer distances travelled by male lobsters tended to be associated with significant depth changes, either inshore or offshore (Figure 4-12), with significant positive correlations between the distance moved between subsequent captures and the absolute depth change for males from both the reserve (Pearson correlation coefficient = 0.809; p<0.01) and fished locations (coefficient = 0.587; p<0.01; Figure 4-13). No such correlation was apparent for females (Figures 4-13, 4-14).

The change in depth between capture events provided an indication of exactly when these inshore-offshore movements were made. In addition, changes in the lobsters’ reproductive status and moult stage provided information about whether these events were associated with seasonal movements. For tagged males, most movements undertaken between November and February were to shallower water (Figure 4-15), with little change in depth recorded between February and June. Between June and November, most movement was to deeper water, subsequent to mouling.

Nine tagged males that underwent these seasonal movements demonstrated a degree of homing behaviour, making movements of over 1 km then returning to within 100 m of their initial release site up to two years later. Two of these individuals moved over 2 km before returning to their initial release location.

Tagged female lobsters demonstrated no detectable change in depth over time, with changes in depth rarely being more than 5 m between capture events (Figure 4-16). The coincidence of changes in the reproductive state of females with changes in depth could not be assessed as only one female tagged in a mature, non-egg bearing state was subsequently recaptured bearing eggs and this was over 160 days later, with no change in depth and a displacement of only 19 metres.
Three females tagged while bearing eggs were recaptured after releasing their eggs, but none had undergone any detectable change in location or depth.

4.3.1.2 Transmitters

Movement information from lobsters fitted with transmitters supported the movement patterns inferred by the tagged lobsters. Lobster 5757, a large male, was located only a further 3 times after the initial transmitter deployment in November 2004 (Figure 4-17). The last recorded signal from this transmitter was in February 2005, when the transmitter had been deployed for 3 months. On the first three occasions, this lobster was in very shallow water within the marine reserve (on one occasion it was located by diving in less than 1 m depth, beneath a rock approximately 4 m from shore at low tide). Due to the complexity of the reef habitat in such shallow water, it was found that the hydrophone had to be within just several metres of the transmitter to enable detection and this may have prevented detection on a number of searches.

The two male lobsters caught on deep (30-35 m) reef within the reserve in November 2004 (lobsters with transmitters 5758 and 5759) were able to be detected relatively easily until August 2005 (Figure 4-17). Lobster 5758 was located a further 17 times after the initial deployment; lobster 5759 was located a further 16 times, until the transmitter battery failed. Lobster 5758 remained on the deep reef area until the end of February 2005, when some time over a 12 day period it made a 1600 m movement inshore, to a reef in 10 m depth, where it remained until August 2005. Transmitter 5759 was consistently recorded in the same general area over the 9 month period, and it is unclear whether this was due to lobster mortality or transmitter loss. Attempts to retrieve or check the transmitter were prevented by poor underwater visibility in combination with restricted bottom time for searches by scuba diving at that depth.

Both females fitted with transmitters moved little over the period they were able to be monitored (Figure 4-17). Lobster 5760 was detected 10 times after the initial deployment – the final detection was in May 2005. Lobster 5761 was only detected a further 2 times after deployment, with the last detection being in February 2005. These two lobsters were difficult to track due to their location on a shallow (< 10 m), complex reef system within the reserve. On occasions a signal could be detected with the hydrophone, but a precise location could not be obtained due to noise in the signal from wave action and signal refraction from the reef and suspended sediment in the water column. It was anticipated that the transmitters would be retrieved by divers prior to the females’ moulting period and fitted to new lobsters. However, despite several attempts, poor underwater visibility prevented them from being retrieved.
4.3.1.3  Recaptures of groups of lobsters

On many occasions, lobsters that were caught in the same pot, tagged and released together, were caught during subsequent surveys, again in the same pot. In addition, tagged lobsters that were recaptured together in the same pot were recaptured again on another occasion in the same pot (Table 4-5). Between the two dates, the distance moved was up to over 300 m, with a maximum time at large of over 700 days (Figure 4-18).

There were several instances where between the initial capture and the recapture event, one or more of the tagged lobsters underwent significant movements (Table 4-6). On one occasion, a group of 4 lobsters captured, tagged and released in November 2003 were recaptured together in November 2005, approximately 27 m from their original release position. Between these dates, one of the tagged lobsters was recaptured 1228 m southwest of and 5 m shallower than the initial position, in May 2005. On another occasion, a group of four lobsters caught, tagged and released together in November 2003 were recaptured together in November 2004, 63 m from the initial release position. Between those two dates, one of the tagged lobsters was caught 1503 m northwest of and 20 m shallower than the initial location, in June 2004. There were also four occasions where two lobsters that were caught, tagged and released together in November 2003, were recaptured together in November 2004, close to their initial release location, with at least one of the group being recaptured between the two dates, during winter, up to 2029 m and 28 m shallower than the release location (Table 4-6).

One group of nine lobsters captured, tagged and released together in November 2003 were all recaptured together in the same pot 16 days later, 149 m from their initial capture location. During this time, one of these tagged lobsters was recaptured 302 m from their initial capture location.

In five instances, two lobsters caught, tagged and released together (four pairs of males and one pair of females) were recaptured together twice more. Two of the pairs of tagged males were at liberty for one year, with only small differences among their tag and recapture locations. Another pair was at liberty for two years, again with only a small difference (30-40 m) between their tag and recapture locations. The fourth pair of males was only at liberty for approximately three months, with little change in position. The pair of females was captured in the same pot three times during one month (December 2003), again with only small changes in location.
4.3.2 Cross boundary movement

4.3.2.1 Tagging

Of the 921 lobsters tagged within the reserve that were recaptured at least once, 49 individuals (48 males and 1 female) or 5.3% were recaptured outside the reserve (Table 4-7). The remainder were recaptured within the reserve. Of the 184 lobsters tagged outside the reserve that were recaptured at least once, 9 (all males), or 4.9%, were recaptured within the reserve; one of these lobsters was recaptured within the reserve, then subsequently recaptured outside the reserve. 5.2% of all tagged lobsters that were recaptured had moved across the reserve boundary – the remainder (94.8%) were only recaptured at their initial tag and release location (either reserve or fished).

In order to assess the net movement of lobsters across the reserve boundary, recapture rates of tagged male lobsters from the reserve and fished locations were calculated according to the number of tagged lobsters recaptured and the estimated number of tagged lobsters available to be caught, taking into account removals by fishermen (tagged lobsters that were retained as catch) and the number of pot lifts completed (Method A). Recapture reports from fishermen where tagged lobsters were returned to the water were excluded in this analysis, as their fishing effort was not reported. Assuming no tag loss, the average recapture rate for tagged lobsters that moved out of the reserve (0.000385% per pot, s.e.=0.000184, n=64) was 1.3 times higher than for those that moved into the reserve (0.000292% per pot, s.e.=0.000142, n=67) (Figure 4-19). The average recapture rate for tagged lobsters that stayed out of the reserve (0.021538% per pot, s.e.=0.013702, n=63) was 1.4 times higher than for those that stayed in the reserve (0.015409% per pot, s.e.=0.001491, n=69).

When tag loss was incorporated into this method, the average recapture rate for tagged lobsters that moved out of the reserve (0.000640% per pot, s.e.=0.000294, n=64) was 2.5 times higher than for those that moved into the reserve (0.000251% per pot, s.e.=0.000134, n=69). The average recapture rate for tagged lobsters that stayed in the reserve (0.027093% per pot, s.e.=0.001979, n=69) was 1.1 times higher than for those that stayed out of the reserve (0.024363% per pot, s.e.=0.013511, n=64). No two-tailed t-tests comparing the means of fished and reserve locations were significant (p>0.05).

Because so few tagged male lobsters that moved across the boundary were recaptured during my surveys, additional data from fishermen were also used to assess whether lobsters that moved...
across the boundary were captured at a different rate to those that had not (Method B). For tagged lobsters recaptured by fishermen outside the reserve, on days where recaptures were recorded, the mean recapture rate for lobsters that had not moved out of the reserve (0.1536% per day, s.e.=0.0155, n=57) was 3.3 times higher than for those that had (0.0459% per day s.e.=0.0068, n=32), (Figure 4-20). However, for surveys conducted within the reserve, on days where tagged lobsters were recaptured, the mean recapture rate for lobsters that had not moved into the reserve (0.5394% per day, s.e.=0.0551, n=67) was 44.2 times higher than for those that had (0.0122% per day, s.e.=0.0064, n=66), i.e. the relative likelihood of capturing a lobster that moved out of the reserve was higher than capturing one that moved in, taking into account the number of tagged animals available to be caught. For data from fishermen outside the reserve and from my surveys within the reserve, the mean recapture rates for lobsters that had not moved across the boundary were significantly higher than for those that had (two-tailed t-tests, p<0.05).

When the recapture rates calculated using this method took into account the estimate of tag loss each day, the mean percent recapture rate outside the reserve (fishermen’s data), for lobsters that had not moved out of the reserve (0.1674% per day, s.e.=0.1680, n=57) was only 1.5 times higher than for those that had (0.1137% per day, s.e.=0.0284, n=32) and there was no significant difference between these recapture rates (two-tailed t-test, p>0.05). Within the reserve (my data), the mean recapture rate for lobsters that had not moved into the reserve (0.9325% per day, s.e.=0.0657, n=67) was 78.4 times higher than for those that had (0.0119% per day, s.e.=0.0068, n=62) and there was a significant difference between these mean recapture rates (two-tailed t-test, p<0.05).

The size frequency distributions for male lobsters showed that there was a higher proportion of tagged lobsters of legal size (54 mm+ tail width) recaptured outside the reserve than were actually tagged outside the reserve (Figure 4-21). Analysis of their initial tag and release location showed that of the 25 tagged legal-sized male lobsters recaptured outside the reserve, 16 of these were initially tagged and released within the reserve. An additional 12 lobsters that were initially tagged and released within the reserve were recaptured by fishermen and retained due to their legal size, but actual measurements were not provided. Insufficient tagged females were recaptured outside the reserve to allow comparison of size frequency distributions (Figure 4-22).

Recaptured males that had moved out of the reserve were significantly larger than those that moved into the reserve (two-tailed t-test, p<0.05, Figure 4-23). The mean size of males that moved out of the reserve was 55.8 mm tail width (s.e.=0.8, n=50); the mean size of the males that moved in was 51.6 mm (s.e.=1.3, n=10 ).
Recaptured males that had moved out of the reserve were significantly larger than those that were tagged and recaptured outside the reserve (two-tailed \( t \)-test, \( p<0.05 \), Figure 4-23). The mean size of males that moved out of the reserve was 55.8 mm tail width (s.e.=0.8, \( n=50 \)); the mean size of those that stayed out of the reserve was 51.6 mm (s.e.=0.1, \( n=202 \)). Tagged males that moved into the reserve were significantly smaller than those that were tagged and recaptured within the reserve (two-tailed \( t \)-test, \( p<0.05 \)). The mean size of tagged males that moved into the reserve was 51.6 mm tail width (s.e.=1.3, \( n=10 \)); the mean size of males tagged and recaptured within the reserve was 59.6 mm (s.e.=0.1, \( n=966 \)).

### 4.3.2.2 Analysis of spatial patterns in size and abundance

The catch per unit effort (in kg of legal-sized lobsters per pot) tended to be highest in the centre of the marine reserve and decline towards the northern and southern boundaries, with this pattern most clear in summer (Figure 4-24). Fitting a generalised additive model to the data, using the non-parametric smoother “s” (R Development Core Team, 2007) and pooling all data from standard-sized pots, showed that distance from the reserve boundary was a significant variable (\( p<0.01 \)) explaining catch per unit effort. Regression tree analysis showed that distinct and large increases in CPUE occurred at approximately 334 metres and at 1360 metres into the marine reserve.

Similarly, the mean size of males per pot (which comprised most of the catch) declined towards the reserve boundary, for all seasons and years (Figure 4-25). Fitting a generalised linear model to the pooled data from standard and small pots, using the non-parametric smoother “s” (R Development Core Team, 2007), showed that distance from the reserve boundary was a significant variable explaining the mean size of males per pot (\( p<0.01 \)). Regression tree analysis showed that significant increases in male size occurred at approximately 61, 263 and 921 metres into the marine reserve. Catches outside the reserve but near the reserve boundary were more likely to be unusually high, in terms of the number of outliers and extreme cases (Figure 4-26).

There were four main reef systems within the survey area (Figure 4-27) – one near the southern boundary of the reserve with a small part of the reef within the reserve boundary (Turihuaa Reef); one entirely enclosed within the reserve boundaries (Pariokonohi Reef); one straddling the northern boundary of the reserve (Whangara Reef) and one to the north of Whangara (B5 Reef). Overall (reserve and fished data combined), the catches were significantly higher on Pariokonohi Reef than on any of the other reefs; catches on Whangara Reef were significantly higher than on
Turihaua Reef and B5 Reef, but there was no significant difference between catches on Turihaua Reef and B5 Reef (univariate analysis of variance, p<0.05; Student-Newman-Keuls method, p<0.05; Table 4-8).

For pots set within the reserve, catches were significantly higher on Pariokonohi Reef than on Whangara Reef or Turihaua Reef, and catches on Whangara Reef were significantly higher than on Turihaua Reef (univariate analysis of variance, p<0.05; Student-Newman-Keuls method, p<0.05; Figure 4-28; Table 4-9). For pots set outside the reserve, catches were significantly higher on Whangara Reef than on Turihaua Reef, but there was no significant difference between catches on Turihaua or B5 Reefs, or B5 and Whangara Reefs (univariate analysis of variance, p<0.05; Student-Newman-Keuls method, p<0.05; Figure 4-28; Table 4-10).

Season had a significant effect on catches, with average CPUE tending to be higher in summer than in winter, for either reserve or fished sites within each reef system (univariate analysis of variance, p<0.05; Tables 4-11, 4-12).

4.3.2.3 Effects of habitat distribution on cross-boundary movement

Cross-boundary movements by males tagged and released within the reserve were mostly less than 1500 m in straight-line distance (Figure 4-29), and were usually associated with a change in depth (Figure 4-30).

Nearly all movements across the reserve boundary occurred where the boundary crossed a reef (Figures 4-31, 4-32), with few movements taking place across soft sediment habitat. Of the 1328 total recorded lobster movements, 1309 (98.6%) took place within a reef; the remaining 19 (1.4%) involved movements between two reefs. 1.9% of the 106 female movements involved movement between reefs; 1.4% of the 1222 male movements involved movement between reefs.

On Turihaua Reef, 9 of the total 143 (6.3%) male lobsters that moved within that reef originated from the marine reserve and the sole male that moved away from this reef moved into the marine reserve. On Pariokonohi Reef (located within the reserve), 9 of the 12 (75%) males that moved between reefs crossed the reserve boundary – one of these males moved from Pariokonohi Reef, across Whangara Reef, to B5 Reef. On Whangara Reef, 40 of the 278 (14.4%) males that moved within that reef crossed the reserve boundary between capture events – 8 moved into the reserve and 32 moved out of the reserve. Of those males that moved from Whangara Reef to Pariokonohi
Reef (4 individuals), 1 crossed the reserve boundary. 14 tagged male lobsters moved only within B5 Reef – there were no recorded movements away from B5 Reef.

Of the two females that moved between reefs, one moved between Whangara Reef and Pariokonohi Reef but remained within the reserve; the other moved between Pariokonohi Reef and Turihaua Reef and crossed the reserve boundary. No females that moved within any of the three reefs crossed the reserve boundary.
4.4 Discussion

Tagging, transmitters and the analysis of catch data from within and surrounding Te Tapuwae o Rongokako Marine Reserve revealed detailed information about the movement patterns of lobsters in this area. Distinct seasonal inshore-offshore movements were recorded for male lobsters, associated with the moult cycle of this species. Movements of tagged lobsters across the marine reserve boundary were recorded, with a net export of lobster biomass from the reserve. Movements were associated with reef habitat, with most movements of tagged lobsters taking place within reefs and most movements across the reserve boundary taking place where the boundary crossed reef habitat.

4.4.1 Short-distance and seasonal movements

The majority of recorded movements, for both sexes, were on a scale of less than 1 kilometre, and most of these involved movement of less than 200 metres from their last capture position. Because lobsters are attracted to a baited pot and move towards it, the pot location only provides an approximate location of the lobster’s den. The area of attraction of a baited pot is estimated at approximately 100 m for crustaceans (Aedo & Arancibia, 2003; Jernakoff & Phillips, 1988). In addition, the GPS unit utilised had a margin of error of approximately 30 m. Therefore, these short-distance movements are probably the result of regular excursions to find food, with the baited pots being located within their foraging ranges, making the lobsters susceptible to capture. MacDiarmid et al. (1991) found that the daily movement ranges of this species in northeastern New Zealand were in the order of less than 100 metres, with a median foraging range of 24 metres. The spatial differences among the foraging ranges of lobsters may relate to factors such as topography and food availability and quality, but foraging ranges are also known to vary significantly among individuals within populations (e.g. Jernakoff et al., 1987).

Tagged male lobsters showed clear seasonal changes in their distribution and these changes were supported by lobsters fitted with transmitters. Subsequent to moulting during August and September, tagged males moved offshore, where they were caught at depths up to 43 m. Around February, tagged males that were located offshore moved inshore, where they remained until moulting. These inshore-offshore movements were on a scale of up to 4 km, but were generally in the order of 1-2 km. Large males over 70 mm tail width tended to be more sedentary, with few tagged lobsters of this size moving more than 1 km from their release location. Similarly, Kelly & MacDiarmid (2003) found that smaller lobsters tended to move
longer distances than large lobsters and MacDiarmid et al. (1991) reported that during the mating season, large males tended to move less than smaller males.

Such seasonal movements have been previously reported for *Jasus edwardsii*, but there are some apparent differences among locations. In northeastern New Zealand, male lobsters have been shown to move both inshore and offshore during autumn and spring, and predominantly offshore during winter and summer (Kelly, 2001; Kelly & MacDiarmid, 2003; Kelly et al., 1999; MacDiarmid, 1991). These inshore-offshore movements were of distances up to 1.7 km (Kelly, 2001). Around July, males were reported to move offshore to feed (subsequent to mating), then move back inshore to moult (Kelly et al., 1999; MacDiarmid, 1991). No such movement offshore during winter was observed in the present study. At Tonga Island, near the top of New Zealand’s South Island, Davidson et al. (2002) found no evidence for inshore-offshore migrations. They suggested that the gradient of the reefs, the shallow maximum depth of the reef or the abundance of prey species on the reef may make inshore-offshore migrations along that coast unnecessary. Gardner et al. (2003) reported distinct movements of tagged lobsters back and forth between local areas around Tasmania, associated with male moulting and female larval release.

Female *J. edwardsii* tagged by Kelly & MacDiarmid (2003) in northeastern New Zealand moved offshore towards the end of the egg-bearing season – one of these females then made a return trip back inshore to the original point of release. In addition, site association of females tended to increase with size. In the present study, little movement of tagged females or females fitted with transmitters was found, with no apparent seasonal movement. However, as discussed below, the recapture method may have masked movement patterns.

In terms of the distances moved by lobsters tagged in this study, those tagged within the reserve were recaptured over 4 km from and at depths over 30 m shallower or deeper than their initial release location. Outside the reserve, the distances tended to be shorter and the depth changes less marked. This may be the result of differences in the extent of the reefs between the reserve and fished locations – within the reserve, the main reef extended over 3 km offshore and to over 40 m depth, whereas outside the reserve the reefs were narrower and extended to shallower depths. Booth (1997) suggested that inshore-offshore movements of over 5 km were more likely in areas where the seafloor slopes gently. Similarly, Gardner et al. (2003) found that on the west coast of Tasmania, Australia, where reef areas were more extensive, more tagged *J. edwardsii* moved larger distances.
Previous studies have found that lobsters can display a high degree of site fidelity and also homing behaviour. For example, Lozano-Alvarez et al. (2002) displaced tagged *Panulirus guttatus* up to 200 m from their point of capture and nearly all of these were recaptured back on the same patch of reef where they had been initially captured. Annala & Bycroft (1993) suggested that homing may be occurring for some lobsters (*Jasus edwardsii*), particularly mature females, in Fiordland, New Zealand. In the present study, there was evidence for homing over relatively large distances, with 9 tagged males moving over 1 km from their initial site, then back to within 100 m of that site up to 2 years later. There was also evidence to suggest that tagged lobsters were moving in groups between particular sites, with a number of tagged lobsters being captured, tagged and released together, then caught up to 730 days later, again in the same pot. There were several instances where significant movements had been made by one or more of the group over that period of time. An alternative explanation is that lobsters were moving independently between particular sites and coincidentally being captured on the same occasion, rather than moving together as a group. However, it is well known that spiny lobsters undertake movements, in particular long-distance migrations, in aggregations (e.g. Street, 1971) and this aspect of lobster movement could be explored further at this location.

### 4.4.2 Long distance movement

In this study, just one tagged lobster was captured more than 5 km from its initial tag and release location and this was also the only individual that moved over 5 km between recapture events. Just four tagged lobsters moved total distances of over 5 km, with all of these involving inshore-offshore movements between recaptures.

An absence of long distance movements has previously been demonstrated for this species in this area (Booth, 1997) and contrasts with the southeast, south and southwest of the South Island of New Zealand, for which directed alongshore migrations have been detected (Annala & Bycroft, 1993; McKoy, 1983). Of the 2131 tag recaptures reported in Annala (1981) for the Gisborne region, just 3.1% moved 5 km or more from their initial release site, with no apparent directionality to the movements. Annala & Bycroft (1984) tagged lobsters in offshore areas (90-400 m depth) off the Gisborne coast and found that while a proportion of the tagged lobsters (7%) moved inshore, most were recaptured near their offshore tagging site. Kendrick & Bentley (2003) found that within CRA3 (the fisheries management area within which Te Tapuwae o Rongokako Marine Reserve is located), 94% of recaptured tagged lobsters had moved less than 5 km from their release site. There has been anecdotal evidence of northward movement against the current on
the east coast of the North Island (Booth & Breen 1994, cited in Booth, 1997), but this remains unsubstantiated.

4.4.3 Cross-boundary movements

Analysis of the spatial patterns in size, abundance and catch rates of lobsters showed that the mean size of male lobsters and the catch per unit effort were highest in the centre of the marine reserve, declining towards both the northern and southern boundaries. Very high catches in the centre of the reserve, particularly during the summer months, can be partially explained by the fact that the deepest part of the reef within the reserve is located in the centre of the reserve. This area of deep reef is small relative to the rest of the reef and so the unusually high catches in this area may not solely be a result of longer distance from the reserve boundary. However, the observed patterns in CPUE and in the mean size of males, suggest that there is movement across the reserve boundary by lobsters within approximately 1 km of the boundary, making them vulnerable to fishing (Rakitin & Kramer, 1996; Russ et al., 2003).

In addition, the catch data from outside the reserve boundaries suggested that unusually large catches were more likely to be obtained within approximately 1 km of the marine reserve boundaries than further away, which may infer that legal-sized lobsters are emigrating from the reserve. An alternative explanation may be that normal fishing effort is reduced near the reserve boundary, but this is unlikely. The patterns in CPUE and in the mean size of lobsters in relation to the boundary of Te Tapuwae o Rongokako Marine Reserve are consistent with the patterns predicted by Kellner et al. (2007) for a competitive fishing industry with a “fishing-the-line” component. Under this scenario, the authors suggested that fishermen were altering their fishing effort and focusing on areas near the boundary of the marine reserve in order to maximise CPUE.

The observed patterns in size and abundance in relation to the boundaries of the marine reserve are unlikely to have been generated in response to some other factor (such as environmental gradients), as the reefs studied within and surrounding the reserve were similar in their geology and community composition and the absence of fishing has had a large influence on the population abundance and size of lobsters within the marine reserve (see Chapter 2 and General Discussion of this thesis). However, additional data from other protected areas would help strengthen the conclusion that movement and subsequent susceptibility to fishing is responsible for the observed patterns in and around Te Tapuwae o Rongokako Marine Reserve.
The “edge effects” on lobsters within 1 km of the reserve boundary are similar to those reported for this species in Tasmanian marine reserves by Edgar & Barrett (1999). In that study, as in the current study, a change in mean lobster size occurred rapidly within 1 km of the boundaries of four marine reserves surveyed. Similarly, Davidson et al. (2002) reported gradients in lobster abundance near the boundary of Tonga Island Marine Reserve. These patterns are similar to those described for other lobster species in marine protected areas. The CPUE of Palinurus elephas declined rapidly from the boundaries of a marine reserve in the western Mediterranean and it was suggested that lobster export from the reserve could maintain catches up to 1.5 km from the boundaries (Goni et al., 2006).

Analysis of the catches from each of the four reefs surveyed in this study showed that catches were consistently higher on the reef that was completely enclosed within the marine reserve boundaries (Pariokonohi Reef). However, catches on the non-reserve part of Whangara Reef, which was bisected by the northern boundary of the reserve, were significantly higher than catches on Turihaua Reef, of which a small part was within the reserve boundary. In addition, catches on reef within the reserve boundaries were significantly higher on Whangara Reef than on Turihaua Reef. On Turihaua Reef, catches within the reserve were on average just 3.5 times the catches outside the reserve, whereas as Whangara, the catches were on average 9.5 times higher than outside. This suggests that although the section of Turihaua Reef that is within the reserve boundaries receives some protection, it receives less protection than Whangara Reef, which in turn received less protection than Pariokonohi Reef.

The inference of movement across the reserve boundary through analysis of spatial patterns was supported by what was to date the largest tagging study to be conducted in a New Zealand marine protected area. Tagged lobsters were demonstrated to be moving across the boundary of Te Tapuwae o Rongokako Marine Reserve, with over 5% of all tagged lobsters being recaptured across the boundary of the marine reserve, having either moved into or out of the marine reserve.

Excluding reports by fishermen, it was found that lobsters moving out of the reserve were more likely to be caught than lobsters that moved into the reserve, taking into account removal of tagged lobsters by fishermen (i.e. tagged lobsters retained as catch) and regardless of whether or not tag loss was accounted for. Comparing the recapture rates of tagged lobsters from the reserve and fished locations, using data collected by fishermen outside the reserve and data from my surveys within the reserve, it was found that the recapture rate of lobsters moving out of the reserve was comparable to the recapture rate of lobsters that stayed out of the reserve, whereas there was a very large difference between the recapture rates of tagged lobsters that moved into
the reserve and those that had not, particularly when tag loss was accounted for. When tag loss was incorporated, the recapture rate of lobsters that stayed within the reserve was over 78 times higher than for those that moved into the reserve, whereas the recapture rate of lobsters that stayed out of the reserve was only 1.5 times higher than for those that moved out of the reserve. In addition, lobsters moving out of the reserve were on average larger than those that moved into the reserve, and were also larger than the average size of lobsters outside the reserve. Therefore, a net emigration of lobster biomass from the marine reserve is indicated.

The use of fishermen’s data in the method above assumes that fishermen who reported a tagged lobster were unaware of the original tag and release location of the lobster and were therefore equally likely to report a tagged lobster that originated from the reserve as one that originated from outside the reserve. Because the tags used in this study did not identify the origin of the lobsters, the only clue as to the lobster’s original release location would be if the lobster was unusually large compared with the rest of the catch, as lobsters originating from the reserve were on average larger than lobsters that comprised an average catch outside the reserve. Whether or not this would affect the tag reporting rate is debateable, but probably depends upon the individual fisherman – some may be more likely to report a large tagged lobster, whereas others may be more inclined not to report such a recapture. However, the fact that both methods (using fishermen’s data and using only my data) indicated an export of lobsters from the reserve suggests that selective reporting of tag recaptures was not an important factor.

Only recaptures of tagged males were utilised in the assessment of movement of lobsters across the reserve boundary. This is because only one female was reported to have moved across the boundary and because tag loss could only be reliably estimated for males, as berried females did not have a pleopod clipped during tagging due to potential effects on their ability to retain and aerate their clutch.

Assessment of the movement of lobsters across marine protected area boundaries using tagged animals has been previously used, with varying success (Davidson et al., 2002; Davis & Dodrill, 1989; Rowe, 2001). For *Jasus edwardsii*, several studies have attempted to describe movement across the boundaries of marine protected areas, but quantifying such movement has been difficult. For example, lack of recaptures of tagged lobsters prevented Davidson *et al.* (2002) and Kelly (2002) from assessing spillover of tagged animals from Tonga Island Marine Reserve and Te Whanganui-a-Hei Marine Reserve respectively. McGarvey (2004) presented a method for estimating the emigration rates of species from marine reserves by analysing the recapture rates of tagged animals. A net emigration of 62% per year (in terms of numbers) was estimated from a
lobster sanctuary in South Australia using that method (McGarvey, 2003). Such movement was suggested to be a density-regulating mechanism. Kelly & MacDiarmid (2003) described the movement patterns of tagged *Jasus edwardsii* within and around Cape Rodney to Okakari Point Marine Reserve, northeastern New Zealand. Of the recaptured lobsters, 20% crossed the reserve boundary (either into or out of the reserve) and so an unknown proportion of the population from the reserve was available to supplement fishermen’s catches outside the reserve. The authors suggested that fishing on the reserve boundary was therefore likely to not only reduce the overall size of the protected population and slow its growth, but also reduce the overall mean size of lobsters within the reserve and limit the number of very large individuals within the population, since most of the lobsters moving across the boundary were large.

The movement by lobsters across the boundary of Te Tapuwae o Rongokako Marine Reserve appears to be affected by the distribution of the lobsters’ preferred habitat. The vast majority of recorded movements occurred within reefs, with little movement between reefs. The movement that did take place between reefs was predominantly away from the large reef enclosed by the marine reserve boundaries, which suggests that density- or biomass-dependent interactions may be occurring. If the biomass of lobsters within that reef continues to increase, the rate of emigration from that reef may increase if density-dependent interactions are taking place. Because the northern boundary of this reserve bisected a reef (Whangara Reef), there was a higher degree of movement across this boundary than the southern, where only a small fraction of the reef was within the reserve. Over 14% of the lobsters recorded to move within Whangara Reef crossed the reserve boundary, whereas just 6% of lobsters that moved within Turihaua Reef crossed the reserve boundary. Buxton *et al.* (2006) similarly found that only a small proportion of tagged lobsters moved between reefs, but that movement across sand barriers of up to 500 m was possible.

Population density and mean individual size may be higher in reserves that have a natural barrier between the reserve and non-reserve areas, than where a natural barrier does not exist (Kramer & Chapman, 1999). In fact, Edgar & Barrett (1999) suggested that if the aim of a marine reserve was to conserve biodiversity, then the reserve should use any potential barriers to species movement. If the primary aim was to act as a fish propagation area, then an open boundary (for example one that crosses a reef) may be more desirable. However, a habitat edge may not only indicate a barrier to movement, but the edge itself may provide suboptimal habitat for a particular species or life history stage to occupy. For example, Tewfik & Bene (2003) showed that the spatial pattern of an adult conch population was characterised by low densities along boundaries that coincided with shallow and occasionally emergent bare sand habitats. Goni *et al.* (2006)
suggested that the quality of lobster environment could decline from the centre of the Columbretes Islands Marine Reserve, resulting in a decline in lobster density away from the reserve’s centre.

Patchy habitat can have a significant effect on the movement patterns of lobsters. Acosta (1999) demonstrated that for Panulirus argus, rubble fields can act as a barrier to dispersal between seagrass beds. It was suggested that vegetated substrates may function as movement corridors for juveniles of this species and may facilitate dispersal to areas containing new resources. Other topographic features such as ridges or gutters may also influence the movement patterns of lobsters (Comeau & Savoie, 2002; MacDiarmid et al., 1991; Rowe, 2001; Smith et al., 2001).

It is clear that with regard to Jasus edwardsii, the design of marine reserves and other marine protected areas needs to take into account information about the short and long term movement patterns of this species and the design needs to relate to the objectives of the marine protected area. The behaviour of lobsters around particular habitats means that an increase in biomass within a marine protected area will result in varying degrees of movement from or “spillover” from that area, depending on its design. Therefore, if the aim of the reserve is to conserve biological communities, then the reserve should use any potential barriers to species movement, such as soft sediment habitat in the case of Jasus edwardsii. If the aim is to maximise spillover, then the marine protected area should make use of rocky reef habitat in the placement of its boundaries. In terms of Te Tapuwae o Rongokako Marine Reserve, the design of the reserve (size and location of boundaries) allows the movement of lobsters from the reserve into the surrounding fishery, primarily across the boundaries where they cross rocky reef habitat. By also enclosing another entire reef system, the reserve also allows the recovery of a population of this species within the reserve boundaries, with inter-reef movement (possibly due to density-dependent interactions) supplementing populations near or across the boundaries.

4.4.4 Use of tags and transmitters

A key question regarding the use of tags and transmitters to describe the movement patterns of animals is: do tagged animals behave in a similar way to untagged animals? It is known that tagging crustaceans can have an effect on aspects such as moulting (e.g. Courtney et al., 2001) and mortality (e.g. Primavera & Caballero, 1992), but the influence on their movement patterns is less clear and seems to depend on the handling associated with the tagging procedure, the type of tag / transmitter, and displacement of tagged animals. For example, Jernakoff et al. (1987) found that western rock lobsters (Panulirus cygnus) showed an immediate movement response to the
disturbance associated with having a transmitter attached but that neither the physical presence of
the transmitters nor the signals produced (electromagnetic in that case) affected the number of
animals sheltering during the day or foraging at night. Melville-Smith & Cheng (2002) found
that in that species, those brought ashore to be tagged moved significantly further and faster upon
release than those tagged at sea. Chittleborough (1974) suggested that any displacement of
tagged rock lobsters beyond their normal home range was highly likely to result in abnormal
movements and recommended that when tagging lobsters for studies of movement, they be
returned to their original reef. European lobsters (*Homarus gammarus*) react to the capture and
handling associated with having a transmitter attached by hiding for several days (van der Meeren, 1997).

In *Jasus edwardsii*, tagged animals appear to migrate in a similar manner to untagged animals
(Booth, 1997), although the capture associated with tagging may increase the likelihood of
lobsters moving away within 24 hours of capture (MacDiarmid et al., 1991). In the present
study, all tagged lobsters were returned as soon as possible to their capture location, with
displacement only on the scale of metres. The handling and stress associated with the tagging
and fitting of the transmitters was minimised through holding lobsters out of the water for no
more than 10 minutes and keeping them moist, in a shaded bin prior to tagging.

One problem with the use of acoustic transmitters in this study was that individuals located in
shallow broken reef habitat were difficult to detect. Ramm (1980) noted that in shallow habitats,
where individuals can inhabit reef crevices beneath dense algal beds, the maximum range of
detection of acoustic transmitters can be significantly reduced. Similarly, Kelly et al. (2000a)
found that detection of acoustic transmitters around shallow broken reef was a problem, due to
high signal attenuation in those areas. It was found that in those cases the hydrophone had to be
within 10-15 m of a transmitter to detect a signal and this was the case in the present study also.
In addition, suspended sediment in the water column affected signal attenuation and on occasions
limited my ability to detect the transmitters.

### 4.4.5 Survey methodology

Tagging studies can provide detailed information on time at liberty, distance, direction,
seasonality and rate of movement, and also information on the biology of the species, for
example reproduction, moulting and growth. However, in terms of studying movement,
tag/recapture data can bias results either through the tagging itself causing changes in the natural
behaviour of animals or through spatial or temporal variation in the fishing effort applied to
obtain recaptures. Some factors to consider (from Annala, 1979) include: greater susceptibility of tagged lobsters to capture by pots; changes in catchability; tag loss; higher mortality of tagged lobsters; emigration of tagged lobsters out of the fishing area; and incomplete reporting by fishers.

Lobsters initially caught in pots may be more susceptible to subsequent capture in pots than lobsters initially caught and released by divers (Morgan, 1974). This may be due to either or both of 1) individual lobsters behaving differently, so that the probability of a particular individual being caught in a pot is a property of the individual, or 2) the probability of any individual being caught in a pot depends on its previous history of capture. In my study, the vast majority of lobsters were caught using pots and so the movement patterns described are strictly only representative of lobsters that are usually caught using pots. The key issue with catchability in this study was that proportionally fewer small lobsters, and proportionally fewer females were available to be tagged than are actually present in the population (see Chapter 2).

In describing cross-boundary movement, a number of factors may have biased my estimates, including tag loss, mortality and catchability. From recaptures of lobsters that had lost their tag (as evidenced by a clipped pleopod but no tag), it was known that the rate of tag loss was significantly higher within the reserve than outside. The rate of tag loss could be estimated for each day pot surveys were conducted and incorporated into estimates of the number of tagged animals available to be caught. These estimates were affected by the total number of recaptures each day, which in turn was affected by the distribution of sampling effort. Therefore, estimates of tag loss were quite variable but were the most accurate estimates available. Tag loss also reduced the data set considerably, particularly for lobsters initially tagged within the reserve. Mortality of tagged lobsters (either natural or unreported fishing mortality) and catchability were not incorporated into estimates of cross-boundary movements, as reliable estimates for these factors were not available for both reserve and fished locations. It is known that larger lobsters tend to be more catchable (Miller, 1990) and so it could be expected that lobsters tagged within the reserve would be more catchable than those tagged outside the reserve. This could not only increase the probability of catching a lobster tagged within the reserve relative to one tagged outside the reserve, but also increase the probability of catching a lobster that moved out of the reserve relative to either one that moved into the reserve or one that stayed out of the reserve.

A low tag reporting rate can potentially not only bias movement data (Gardner et al., 2003), but it can also reduce the available data set considerably. In my study, there was a degree of tag non-reporting by fishermen, but its magnitude remains unknown. Six of nine commercial fishing
vessels known to regularly operate within 3 km of the marine reserve boundaries provided 
records of tag recaptures. One way to potentially increase tag returns is to provide a reward, but 
this is not always effective (e.g. Gregory, 1998) and can actually increase the incidence of 
inaccurate records (e.g. Schmalz et al., 2004). In my study, I ensured that fishermen likely to 
capture tagged lobsters were kept informed of the study and also received feedback about the 
growth and movement patterns of tagged lobsters they had reported, in an attempt to maximise 
reporting rate.

As in McGarvey et al. (1999) and Annala (1981), tag releases were not random, but were 
determined in part by where the vessels utilised could operate, and also harvest and release 
substantial numbers of tagged lobsters. This resulted in non-random distribution of tagged 
lobsters, which may have led to a greater susceptibility to capture for some of the tagged lobsters. 
For example, in my study, large catches of large male lobsters were obtained during surveys 
conducted during November and December, particularly within the reserve and at depths greater 
than 30 m. Therefore, these animals were over-represented in the data set of tagged lobsters. 
One advantage of this was that detailed information was obtained about the seasonal movement 
patterns of these animals, but it was at the expense of small and very large males and females, 
which were less catchable and often located in areas (for example very shallow water) that were 
not easily sampled using a vessel and pots.

One issue with the methodology in this study, which has also been a problem in other similar 
studies, is that the results can be biased against long-distance movements. This is because in 
areas where fishing or sampling effort is high, the probability of recapture is also high and tagged 
lobsters are more likely to be caught near their release point, before they have a chance to move 
long distances. For example, Davis & Dodrill (1989) noted that tagged *Panulirus argus* leaving 
Everglades National Park were quickly captured by fishermen, artificially truncating the range of 
their natural movements. In these situations, even if animals disperse randomly, increased 
fishing effort in a particular area may result in an apparent directionality of dispersion that 
doesn’t exist (Annala & Bycroft, 1993; Rowe, 2001). In contrast, if fishing or sampling effort is 
low, the probability of recapture is lower, so if a tagged lobster moved a long distance to an area 
that is not fished or has not been sampled, its movement would go undetected. Similarly, if a 
tagged lobster moved to an area where tag reporting rate was low, its movement may not be 
represented in the data set (Annala & Bycroft, 1993, Gardner et al., 2003), or few tagged animals 
may be caught in a particular area because there is a high probability of capture along the way 
(Hilborn, 1990).
For tagged lobsters and those fitted with transmitters, movements are unlikely to have taken place in a straight line and so the distances and directions have some inaccuracies. Similarly, lobsters may have been tagged or recaptured while undertaking a seasonal or longer-distance movement, which would also bias the distance and direction of movement. Seasonal inshore-offshore movements could only be described when lobsters were captured at least 3 times and only when recapture events took place during different seasons. There were many instances where lobsters were recaptured in almost the same location a year apart, which gave the impression that no movement had occurred. However, given that there were also tagged lobsters that underwent seasonal movements returning to almost the same location a year later, it is likely that the lack of recapture events masked movement in those animals that appeared not to move within a year.

4.4.6 Conclusions

Clear patterns in the movement of lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve were described through the use of tags and transmitters, and the analysis of distribution, size and abundance patterns. Males underwent seasonal inshore-offshore movements, in particular individuals less than 70 mm tail width. Larger male lobsters and females appeared to be relatively sedentary. Cross-boundary movement of lobsters was recorded, with a net emigration of lobster biomass providing a potential supplement to recreational, commercial and customary fishermen. The distribution of rocky reef habitat was demonstrated to be a crucial factor in terms of the movement of lobsters within and between reefs, with important implications for the design of individual marine protected areas and networks.
### Table 4-1  Number of lobsters tagged within and surrounding Te Tapuwae o Rongokako Marine Reserve, between November 2003 and September 2006.

<table>
<thead>
<tr>
<th>Month / Year</th>
<th>Reserve</th>
<th></th>
<th>Fished</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>November 2003</td>
<td>2123</td>
<td>159</td>
<td>246</td>
<td>29</td>
</tr>
<tr>
<td>December 2003</td>
<td>467</td>
<td>859</td>
<td>707</td>
<td>253</td>
</tr>
<tr>
<td>January 2004</td>
<td>11</td>
<td>15</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>February 2004</td>
<td>36</td>
<td>206</td>
<td>6</td>
<td>104</td>
</tr>
<tr>
<td>June 2004</td>
<td>2</td>
<td>1</td>
<td>73</td>
<td>23</td>
</tr>
<tr>
<td>August 2004</td>
<td>25</td>
<td>3</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>November 2005</td>
<td>642</td>
<td>91</td>
<td>239</td>
<td>22</td>
</tr>
<tr>
<td>September 2006</td>
<td>479</td>
<td>106</td>
<td>424</td>
<td>106</td>
</tr>
<tr>
<td>TOTAL</td>
<td>3785</td>
<td>1440</td>
<td>1701</td>
<td>540</td>
</tr>
</tbody>
</table>

### Table 4-2  Number of pot lifts completed within and surrounding Te Tapuwae o Rongokako Marine Reserve. Three different pot types were used: standard commercial pots (“std”), ¾-sized commercial pots (“sml”) and fine mesh pots (“fine”).

<table>
<thead>
<tr>
<th>Month / Year</th>
<th>Reserve</th>
<th></th>
<th>Fished</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>std</td>
<td>sml</td>
<td>fine</td>
<td>TOTAL</td>
</tr>
<tr>
<td>November 2003</td>
<td>134</td>
<td>134</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td>December 2003</td>
<td>274</td>
<td>20</td>
<td>294</td>
<td>90</td>
</tr>
<tr>
<td>February 2004</td>
<td>95</td>
<td>80</td>
<td>8</td>
<td>183</td>
</tr>
<tr>
<td>June 2004</td>
<td>71</td>
<td>92</td>
<td>8</td>
<td>171</td>
</tr>
<tr>
<td>August 2004</td>
<td>163</td>
<td>1</td>
<td>164</td>
<td>24</td>
</tr>
<tr>
<td>November 2004</td>
<td>189</td>
<td>12</td>
<td>201</td>
<td>134</td>
</tr>
<tr>
<td>March 2005</td>
<td>176</td>
<td>10</td>
<td>186</td>
<td>64</td>
</tr>
<tr>
<td>May 2005</td>
<td>163</td>
<td>10</td>
<td>173</td>
<td>75</td>
</tr>
<tr>
<td>November 2005</td>
<td>151</td>
<td>151</td>
<td>54</td>
<td>54</td>
</tr>
<tr>
<td>February 2006</td>
<td>182</td>
<td>182</td>
<td>63</td>
<td>63</td>
</tr>
<tr>
<td>May 2006</td>
<td>170</td>
<td>170</td>
<td>80</td>
<td>80</td>
</tr>
<tr>
<td>September 2006</td>
<td>165</td>
<td>165</td>
<td>80</td>
<td>80</td>
</tr>
<tr>
<td>November 2006</td>
<td>166</td>
<td>166</td>
<td>84</td>
<td>84</td>
</tr>
<tr>
<td>TOTALS</td>
<td>2099</td>
<td>173</td>
<td>68</td>
<td>2340</td>
</tr>
</tbody>
</table>

### Table 4-3  Sex and sizes of lobsters fitted with acoustic transmitters.

<table>
<thead>
<tr>
<th>Transmitter</th>
<th>Sex</th>
<th>Carapace Length (mm)</th>
<th>Tail Width (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5757</td>
<td>male</td>
<td>135.2</td>
<td>68.8</td>
</tr>
<tr>
<td>5758</td>
<td>male</td>
<td>130.3</td>
<td>69.3</td>
</tr>
<tr>
<td>5759</td>
<td>male</td>
<td>133.1</td>
<td>68.0</td>
</tr>
<tr>
<td>5760</td>
<td>female</td>
<td>100.1</td>
<td>68.5</td>
</tr>
<tr>
<td>5761</td>
<td>female</td>
<td>107.0</td>
<td>68.1</td>
</tr>
</tbody>
</table>
Table 4-4  Number of tagged lobsters recaptured and the percent recaptured for each sex and location. Also shown are the total numbers recaptured and the percentage of the total tagged.

<table>
<thead>
<tr>
<th>Release Location</th>
<th>Sex</th>
<th>1 Recapture</th>
<th>2 Recaptures</th>
<th>3 Recaptures</th>
<th>4 Recaptures</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reserve</td>
<td>Male</td>
<td>688</td>
<td>126</td>
<td>20</td>
<td>4</td>
<td>838</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(18.2%)</td>
<td>(3.3%)</td>
<td>(0.5%)</td>
<td>(0.1%)</td>
<td>(22.1%)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>69</td>
<td>13</td>
<td>1</td>
<td>0</td>
<td>83</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(4.8%)</td>
<td>(0.9%)</td>
<td>(0.1%)</td>
<td></td>
<td>(5.8%)</td>
</tr>
<tr>
<td>Fished</td>
<td>Male</td>
<td>156</td>
<td>14</td>
<td>6</td>
<td>1</td>
<td>177</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(9.2%)</td>
<td>(0.8%)</td>
<td>(0.4%)</td>
<td>(0.1%)</td>
<td>(10.4%)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>6</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.1%)</td>
<td>(0.2%)</td>
<td></td>
<td></td>
<td>(1.3%)</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>919</td>
<td>154</td>
<td>27</td>
<td>5</td>
<td>1105</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(12.3%)</td>
<td>(2.1%)</td>
<td>(0.4%)</td>
<td>(0.1%)</td>
<td>(14.8%)</td>
</tr>
</tbody>
</table>

Table 4-5  Table showing the frequency of recapture events that involved recapture in the same pot of lobsters that had initially been caught, tagged and released together. Shown are the group size, frequency of occurrence, the number of times those groups were recaptured together, and the ranges in time at large and distance travelled.

<table>
<thead>
<tr>
<th>Group Size</th>
<th>Frequency</th>
<th>No. Times Captured Together</th>
<th>Range in Time at Large (days)</th>
<th>Range in Distance Travelled (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>101</td>
<td>5 groups captured 3 times; 96 groups captured 2 times.</td>
<td>1-730</td>
<td>1-321</td>
</tr>
<tr>
<td>3</td>
<td>23</td>
<td>2</td>
<td>7-730</td>
<td>8-184</td>
</tr>
<tr>
<td>4</td>
<td>11</td>
<td>2</td>
<td>2-730</td>
<td>20-105</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
<td>2</td>
<td>8-356</td>
<td>27-136</td>
</tr>
<tr>
<td>7</td>
<td>3</td>
<td>2</td>
<td>15-16</td>
<td>27-81</td>
</tr>
<tr>
<td>9</td>
<td>1</td>
<td>2</td>
<td>16</td>
<td>149</td>
</tr>
</tbody>
</table>

Table 4-6  Numbers of tagged lobsters captured together, showing whether any of the group were recaptured between the capture dates and whether there was significant movement by that / those individuals.

<table>
<thead>
<tr>
<th>Group Size</th>
<th>Frequency</th>
<th>Zero Recaptures between Dates</th>
<th>1+ Recaptures between Dates with No Significant Movement (max distance in brackets)</th>
<th>1+ Recaptures with Movement over 300 m (max distance in brackets)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>101</td>
<td>74</td>
<td>22 (191 m)</td>
<td>5 (2029 m)</td>
</tr>
<tr>
<td>3</td>
<td>23</td>
<td>14</td>
<td>7 (174 m)</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>11</td>
<td>8</td>
<td>1 (91 m)</td>
<td>2 (1503 m)</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
<td>3</td>
<td>2 (34 m)</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>3</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>1</td>
<td></td>
<td></td>
<td>1 (302 m)</td>
</tr>
</tbody>
</table>
Table 4-7  Number of tagged lobsters recaptured, and whether they moved within or between the two locations (fished and reserve). * includes one animal that moved into the reserve then back out again.

<table>
<thead>
<tr>
<th>Release Location</th>
<th>Sex</th>
<th>Stayed at Release Location</th>
<th>Moved between Locations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reserve</td>
<td>Male</td>
<td>790</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>82</td>
<td>1</td>
</tr>
<tr>
<td>Fished</td>
<td>Male</td>
<td>168</td>
<td>9*</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>7</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 4-8  Analysis of variance (ANOVA) table for the CPUE of lobsters from pot surveys on the 4 reefs within the survey area. * denotes effect significant at the 0.05 level.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef</td>
<td>3</td>
<td>26233.136</td>
<td>624.162</td>
<td>0.000*</td>
</tr>
<tr>
<td>residual</td>
<td>2875</td>
<td>42.029</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4-9  Analysis of variance (ANOVA) table for the CPUE of lobsters from pot surveys on the unfished sections of the reefs within the survey area. * denotes effect significant at the 0.05 level.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef</td>
<td>2</td>
<td>11356.084</td>
<td>205.391</td>
<td>0.000*</td>
</tr>
<tr>
<td>residual</td>
<td>2098</td>
<td>55.290</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4-10  Analysis of variance (ANOVA) table for the CPUE of lobsters from pot surveys on the fished sections of the reefs within the survey area. * denotes effect significant at the 0.05 level.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef</td>
<td>2</td>
<td>3.526</td>
<td>6.444</td>
<td>0.002*</td>
</tr>
<tr>
<td>residual</td>
<td>775</td>
<td>0.547</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4-11  Analysis of variance (ANOVA) table for the CPUE of lobsters from pot surveys on the fished sections of the reefs within the survey area, divided into summer and winter months. * denotes effect significant at the 0.05 level.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef</td>
<td>2</td>
<td>1.209</td>
<td>2.334</td>
<td>0.098</td>
</tr>
<tr>
<td>Season</td>
<td>1</td>
<td>17.825</td>
<td>34.419</td>
<td>0.000*</td>
</tr>
<tr>
<td>Reef x season</td>
<td>2</td>
<td>0.962</td>
<td>1.857</td>
<td>0.157</td>
</tr>
<tr>
<td>residual</td>
<td>772</td>
<td>0.518</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4-12  Analysis of variance (ANOVA) table for the CPUE of lobsters from pot surveys on the unfished sections of the reefs within the survey area, divided into summer and winter months. * denotes effect significant at the 0.05 level.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef</td>
<td>2</td>
<td>7824.419</td>
<td>154.949</td>
<td>0.000*</td>
</tr>
<tr>
<td>Season</td>
<td>1</td>
<td>394.657</td>
<td>7.815</td>
<td>0.005*</td>
</tr>
<tr>
<td>Reef x season</td>
<td>2</td>
<td>581.741</td>
<td>11.520</td>
<td>0.000*</td>
</tr>
<tr>
<td>residual</td>
<td>2095</td>
<td>50.497</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 4-1 Size frequency distributions of tagged lobsters. Vertical lines are the minimum legal sizes (females 60 mm, males 54 mm).
Figure 4-2 Map showing the original locations of tagged lobsters.
Figure 4-3 A tagged lobster.
Figure 4-4  Distribution of sampling effort (using commercial lobster pots) within and surrounding Te Tapuwae o Rongokako Marine Reserve, by season.
Figure 4-5  A lobster fitted with an acoustic transmitter.
Figure 4-6  Frequency of distance between recapture locations for sublegal (<54 mm tail width) male lobsters initially tagged and released within or outside the marine reserve.
Figure 4-7  Frequency of distance between recapture positions for males initially tagged and released within the marine reserve, by tail width.
Figure 4-8  Mean total distance moved by tagged lobsters recaptured between one and four times subsequent to tagging, for female and male lobsters initially tagged and released either within or outside the marine reserve.

**fished reserve**

<table>
<thead>
<tr>
<th>No. recaptures</th>
<th>Female</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>n=6</td>
<td>n=688</td>
</tr>
<tr>
<td>2</td>
<td>n=1</td>
<td>n=126</td>
</tr>
<tr>
<td>3</td>
<td>n=69</td>
<td>n=20</td>
</tr>
<tr>
<td>4</td>
<td>n=1</td>
<td>n=4</td>
</tr>
</tbody>
</table>

**Mean total distance (m) ± s.e.**

- Female: n=6, n=1, n=69, n=1
- Male: n=688, n=126, n=20, n=4
Figure 4-9 Total distance moved by tagged lobsters, as a function of total time at large, for females and males initially tagged and released within or outside the marine reserve, showing the number of recaptures for each individual.
Figure 4-10 Frequency of total distance moved by recaptured lobsters, initially tagged and released either within or outside the marine reserve.
Figure 4-11 Frequency of total distance moved by recaptured lobsters, initially tagged and released either within or outside the marine reserve, where the total distance moved was less than 1000 m.
Figure 4-12  Depth changes and distance between recapture locations for male lobsters. Depth changes greater than 0 m indicate a move to deeper water; depth changes less than 0 m indicate a move to shallower water.
Figure 4-13 Relationship between distance between recapture locations and the absolute depth change, for lobsters tagged either within or outside the marine reserve.

- **Fished**
  - Female
  - Male

- **Reserve**
  - Female
  - Male
Figure 4-14  Depth changes and distance between recapture locations for female lobsters. Sublegal= <60 mm, legal= 60 mm+. Depth changes greater than 0 m indicate a move to deeper water; depth changes less than 0 m indicate a move to shallower water.
Figure 4-15 Depth changes recorded for recaptured tagged male lobsters, indicating whether moulting had occurred since release. Depth changes greater than 0 m indicate a move to deeper water; depth changes less than 0 m indicate a move to shallower water.
Figure 4-16 Depth changes recorded for tagged female lobsters recaptured within 365 days of release, indicating whether moulting had occurred since release. Depth changes greater than 0 m indicate a move to deeper water; depth changes less than 0 m indicate a move to shallower water.
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Figure 4-18 The time at large and distance moved by groups of lobsters that were initially tagged and released together, or were recaptured together, then again recaptured together. Only data for lobsters tagged during November, December and February are shown.
Figure 4-19  Recapture rates (% per pot) of tagged lobsters caught during my surveys outside the reserve (“fished”) and within the marine reserve (“reserve”). Averages on the left assume no tag loss. Averages on the right incorporate tag loss, estimated by the proportion of recaptures that involved the loss of tags. Both incorporate removals by fishermen.

Figure 4-20  Recapture rates (% per day) of tagged lobsters caught by fishermen outside the reserve (“fished”) and during my surveys of the marine reserve (“reserve”). Averages on the left assume no tag loss. Averages on the right incorporate tag loss, estimated by the proportion of recaptures that involved the loss of tags. Both incorporate removals by fishermen.
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Figure 4-25  Mean male tail width (mm) per pot (52 mm mesh pots only) as a function of distance from the marine reserve boundary. Points to the left of the vertical line are within the reserve; points to the right are outside the reserve.
Figure 4-26  Box plots for CPUE (kg of legal-sized lobsters per pot) outside the marine reserve, as a function of distance from the reserve boundaries (standard-sized pots only). Box plots show the median, interquartile range (box), outliers (open circles; values between 1.5 and 3 box lengths from the upper / lower edge of the box) and extreme cases (asterisk; values more than 3 box lengths from upper / lower edge of box).
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Figure 4-28  Mean catch per unit effort (kg of legal-sized lobsters per pot lift; standard pots only) on the 4 reefs within the survey area, for fished and unfished parts of each reef (note that Pariokonohi Reef is completely enclosed within the reserve).
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Figure 4-30 Frequency of depth changes for males that moved out of the reserve. Depth changes less than 0 m indicate a move to shallower water; depth changes greater than 0 m indicate a move to deeper water. N=27.
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Figure 4-32  Movement patterns of tagged male (a) and female (b) lobsters, divided into size classes and pooled.

a)
Chapter 5  The Feeding Ecology of *Jasus edwardsii* on Fished and Unfished Reefs

5.1 Introduction

The interactions among species play a key role, along with environmental conditions, in determining community structure. In terms of predator-prey interactions, community structure and dynamics can be influenced by the direct removal of species through predation and also by changes in species distribution and abundance through removal of competitors by predators. In some cases, high trophic level consumers initiate chains of interactions that can reach the base of the food web – such multi-trophic interactions have been termed “trophic cascades” (Carpenter *et al*., 1985; Pinnegar *et al*., 2000). The high trophic level consumer may also be classed a keystone predator, or a species whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance (Power *et al*., 1996).

Lobsters can play a significant role in influencing the structure of both subtidal and intertidal benthic assemblages. In some areas, lobsters may play a “keystone” role in the communities of which they are a component. American lobster (*Homarus americanus*) has been suggested to be a controlling predator of urchins (Hagen & Mann, 1992; Mann, 1977), but this has been debated (Elner & Vadas, 1990; Pringle, 1986). Lobsters may also play a keystone role in some southern Californian marine communities. For example, predation by lobsters (*Panulirus interruptus*) on intertidal mussels resulted in the maintenance of a distinctive red algal turf community (Robles & Robb, 1993), with lobsters functioning as keystone predators, on wave-exposed shores of Santa Catalina Island, California (Robles, 1987). A similar role of lobsters has been demonstrated in South Africa. Barkai & Branch (1988) described two stable community states – one dominated by mussels, and another dominated by South African rock lobsters (*Jasus lalandii*) and a dense seaweed flora. It was suggested that the presence or absence of lobsters was fundamental to the maintenance of the two contrasting communities, through the predation effects of the lobsters. A dramatic decline in populations of sea urchins and abalone was recorded along South African coasts in 1994, possibly caused by an influx of lobsters (Tarr *et al*., 1996). Mayfield *et al* (2001) subsequently showed that the intensity of predation by lobsters on sea urchins was sufficient to cause a decline in the abundance of both urchins and abalone. Abalone juveniles had previously been shown to shelter beneath urchins (Mayfield & Branch, 2000).
Lobsters have the potential for significant impacts not only on benthic communities, but also on epifaunal communities. For example, the western rock lobster, *Panulirus cygnus*, can consume up to 200 epifaunal molluscs per night in Western Australian seagrass beds (Edgar, 1990b). This intensity of predation could be responsible for the autumn and winter decline of larger size classes of the primary prey species, a trochid gastropod, and possibly also have an impact on the recruitment of this species (Edgar, 1990b). Andrew & MacDiarmid (1991) noted the frequent occupancy of kelp laminae in northeastern New Zealand by the gastropod *Cantharidus purpureus*, which was eaten in large quantities by the lobster *Jasus edwardsii* in tank experiments where the alga was not available as a refuge. When this and other species of gastropod were tethered to the reef at night, they were consumed by lobsters and other benthic predators, which suggested that their nightly migrations into the kelp forest canopy were potentially a response to benthic predation by lobsters (Freeman, 1998).

The extent of the impact of lobsters on their prey species and the communities of which they are a component depends on a number of factors, including not only diet and consumption rates, but also lobster density, population structure and foraging range. A study of the foraging ranges of *J. edwardsii* in northeastern New Zealand (MacDiarmid et al., 1991) suggested that the impact of *J. edwardsii* on their prey would be limited to near daytime shelters and their low foraging distances could be explained by topographic complexity and availability of food. MacDiarmid (1994) also suggested that the patchy dispersion of *J. edwardsii* among shelters could imply a patchy impact on prey, with predation intensity and distribution changing as the abundance and dispersion of lobsters varies. In urchin-dominated “barrens” areas, where shelters are scarce and lobsters rare during the day, lobsters may have a minimal impact on prey populations (MacDiarmid et al., 1991). In marine protected areas, urchin populations may decline in abundance at around the size they emerge from cryptic habitat and begin to graze on exposed rock surfaces (e.g. Andrew & MacDiarmid, 1991). This decline has been shown to potentially be attributable to increased susceptibility of the urchins to predators such as lobsters (Shears & Babcock, 2002).

Recent research from northeastern New Zealand has shown that changes in populations of predatory species can potentially have large and measurable effects on the distribution and abundance of habitat–forming organisms such as kelp and urchins (Babcock et al., 1999; Shears & Babcock, 2002). The mechanism suggested to operate is a top-down control by predatory fish (snapper, *Pagrus auratus*) and lobsters (spiny lobster, *Jasus edwardsii*) on urchin (*Evechinus chloroticus*) populations, which in turn influences the abundance and distribution of habitat-forming macroalgae (*Ecklonia radiata*). *J. edwardsii* has also been demonstrated to play a role in structuring soft sediment habitats adjacent to reefs (Langlois et al., 2005a; Langlois et al., 2006).
There are a variety of methods available to assess how trophic interactions can operate to alter community structure. Long-term ecological monitoring is a key method utilised to describe such changes. The community changes described for kelp forest communities in Nova Scotia (e.g. Johnson & Mann, 1988) and for the shallow reef communities within the Cape Rodney to Okakari Point (Leigh) Marine Reserve (Babcock et al., 1999) were mostly based on the monitoring of community structure over many years. Manipulations of the distribution and abundance of key species have also proven to be vital in the assessment of the ecological roles of particular species (e.g. Villouta et al.'s, 2001 urchin removal experiments). Investigations of the behaviour and feeding ecology of key species are also important tools in the description of trophic interactions (e.g. Sheibling et al.'s, 1999 study of urchin feeding aggregations).

Marine protected areas have been suggested to be a key tool in the study of trophic interactions, because of the potential for these areas to demonstrate significant changes in previously exploited populations of marine species in comparison with areas where harvesting is permitted (Babcock et al., 1999; Friedlander & DeMartini, 2002; Micheli et al., 2005). Fishing alters the distribution, abundance and population structure of species such as lobsters (Acosta & Robertson, 2003; Eggleston & Dahlgren, 2001; Rowe, 2002) and potentially their prey species (e.g. van Zyl et al., 1998), and therefore there exists the potential for lobsters within marine protected areas to have different effects on their prey species and the communities of which they are a component, through changes in the composition of their diet (e.g. Micheli et al., 2004).

Predation by lobsters can not only affect the distribution and abundance of their prey species, but their diet can also influence aspects of the life history of the lobsters themselves, including growth (Chittleborough, 1975, 1976; Davis & Dodrill Davis & Dodrill, 1989; McGarvey et al., 1999; McKoy & Esterman, 1981; Newman & Pollock, 1974; Phillips, 1983; Pollock, 1995a, 1995b), moulting (Chittleborough, 1975), fecundity and size at onset of maturity (Pollock, 1995a), and behaviour of individual lobsters (Chittleborough, 1975; Thomas et al., 2003). Therefore, dietary studies are crucial in the determination not only of the trophic effects of lobsters, but also in establishing the causes of spatial and temporal differences in lobster life history characteristics.

The abundance and biomass of lobsters have increased substantially within Te Tapuwae o Rongokako Marine Reserve since its establishment (see Chapter 2), coinciding with a reduction in the growth rates of males within the reserve (Chapter 3). In addition, sublegal-sized males within the reserve have the potential to grow more rapidly within the marine reserve than in the
surrounding fishery (Chapter 3). In this Chapter, I assess whether changes in lobster diet, nutritional condition, trophic position or prey species distribution and abundance have taken place within the marine reserve that may have coincided with the observed changes in the lobster population. Specifically, I test the following hypotheses: that to counter potential density-dependent effects on growth and condition, the diet of lobsters within the marine reserve is different from that of lobsters outside the reserve; to maintain nutritional condition, lobsters within the marine reserve extend their foraging activity spatially or temporally in comparison with fished areas; the density of lobster prey species is lower within the marine reserve than in fished areas and increases with distance from major lobster aggregations; and the size distributions of major prey species such as urchins are affected by predation by lobsters within the reserve.
5.2 Methods

5.2.1 Sampling strategy

The feeding ecology of lobsters on fished and unfished reefs was explored by comparing their nutritional condition, diet and trophic position, and by describing the distribution and abundance of their prey species, within and adjacent to a marine reserve.

5.2.2 Nutritional condition

5.2.2.1 Blood sampling

The refractive index of lobster blood, measured using a refractometer, has been demonstrated to be correlated with the total blood protein level, which in turn provides an indication of nutritional condition (Oliver & MacDiarmid, 2001; Ozbay & Riley, 2002). This is because the circulating protein in lobster blood is metabolized and diluted during periods of low food and starvation (Hagerman, 1983).

In order to determine the blood protein content and therefore nutritional condition of lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve, 276 lobsters were collected – 142 from fished areas, and 134 from within the marine reserve (Table 5-1). The lobsters were restrained using elastic cord on a padded board, resting on their dorsal surface, with their tail outstretched. 0.1 ml blood samples were taken from the base of one of the fifth walking legs using a 27 gauge insulin syringe. Exposed mouthparts and gills were kept moist with a spray bottle of seawater while the lobsters were out of the water.

The blood samples were analysed for protein content using a handheld blood / urine refractometer, adjusted to 1.334 on the instrument’s scale using a 3% sodium chloride solution (Moore et al. 2000, cited in Oliver & MacDiarmid, 2001). The higher the refractive index, the higher the blood protein concentration (Oliver & MacDiarmid, 2001). The distal third of one pleopod was removed from each animal using scissors, for moult staging in accordance with the methods described by Musgrove (2000).
5.2.2.2 Morphometrics

There are a number of animal body condition measures that provide an estimate of nutritional state, which can in turn provide a measure of an animal’s physiological state (Jakob et al., 1996).

The nutritional condition of lobsters within and adjacent to the marine reserve was assessed by recording the carapace lengths, tail widths and total body wet weights of lobsters from these locations. Lobsters were weighed on shore, to prevent inaccuracies associated with using electronic scales at sea. A total of 215 lobsters was sampled (Table 5-2). I aimed to sample a range of sizes of lobsters from both reserve and fished locations.

Weight, tail width and carapace length were log transformed and carapace length (CL)-weight and tail width (TW) – weight relationships were described using ordinary least-squares linear regression to fit the coefficients $a$ and $b$ to the equations:

\[
\ln(\text{weight}) = \ln a + b \ln(\text{CL}).
\]
\[
\ln(\text{weight}) = \ln a + b \ln(\text{TW}).
\]

5.2.3 Stable isotope analysis

Samples of marine species were collected from sites within Te Tapuwae o Rongokako Marine Reserve and from locations outside the marine reserve during August 2005. A list of species, sample sizes, sampling locations and tissues analysed is provided in Table 5-3. The selection of species was based on a number of factors, including biomass (e.g. large habitat forming species such as *Ecklonia radiata*) and potential importance in the diet of lobsters (based on published data and data from diet analysis in this study).

For fleshy marine algae, whole plants or pieces of laminae were collected for analysis. For coralline species, pieces of algae were removed from the substrate using a hammer and chisel.

Animals with a hard shell were generally dissected out of their shells, with the exception of very small gastropods, which were analysed whole. Large gastropods, for example abalone / paua (*Haliotis iris*), had a section of muscle tissue removed for analysis. Crustaceans were generally analysed whole, with the exception of lobsters, for which one leg was sampled from each animal and the shell removed from the muscle tissue prior to analysis.
Fish samples were either sections of white muscle tissue (for larger species such as snapper, *Pagrus auratus*) or whole animals (for triplefin species).

Samples were frozen fresh, then oven-dried and ground to a powder prior to analysis. Isotopic abundance analysis for $\delta^{13}C$ and $\delta^{15}N$ was carried out on a Europa Scientific Tracermass isotope analyser at the University of Waikato’s Stable Isotope Unit.

To determine the relative contributions of various food sources to the diet of lobsters, potential food sources (informed by the analysis of lobster foregut contents; see below) were entered into IsoSource mixing model software (Phillips & Gregg, 2003) using where possible, the stable isotope signatures for those food sources from the location being assessed. IsoSource calculates feasible ranges of source contributions by firstly calculating all possible combinations of source proportions that sum to 100%. Then, the predicted isotope values of each mixture are calculated using linear mixing model equations that preserve mass balance (Phillips, 2001). After comparing the isotopic values of computed mixtures with the observed isotope values, the range of combinations that match within a tolerance level is described.

For this study, source increment was set at 2% and tolerance set at 0.01. Lobster stable isotope values were adjusted for fractionation (-3.5‰ of N and -1‰ for C) and ranges of feasible contributions (the combination of source proportions which satisfies isotopic mass balance in the mixing model) were given as 1st to 99th percentile, in accordance with recommendations by Benstead *et al.* (2006).

Trophic positions of species were assessed using the formula provided in Fredriksen (2003), where trophic position = $1 + (\delta^{15}N – 4.4) / 3.8$.

### 5.2.4 Lobster diet analysis

Twenty lobsters (7 females, 13 males) were collected by divers from Te Tapuwae o Rongokako Marine Reserve on the 9th of August 2003. They were collected before dawn, to ensure that digestion of food eaten during nocturnal foraging was not well advanced. Upon collection, lobsters were immediately placed in a seawater / ice slurry, to euthanase the lobsters and to halt the digestive processes. The number of animals sampled from the reserve was considered to be the maximum number able to be removed from the study location (chosen for its safe and relatively easy access during low light conditions) without causing a significant impact to the
population. No lobsters were able to be sampled from a fished location, due primarily to accessibility and safety issues.

Each lobster was measured, sexed and weighed (on shore). The foregut of each lobster was then dissected out, weighed full and the percent fullness of each gut was estimated. The contents were then removed and the foregut weighed empty. The contents were then placed in a 10% formalin in seawater solution.

The contents of each foregut were identified to the lowest possible taxonomic level. Where whole organisms were identifiable, these were counted. Estimates of the contribution of each taxa to the volume of the gut contents were made.

5.2.5 Prey species distribution

5.2.5.1 Intertidal reef communities

To describe changes in the distribution of lobster prey species, intertidal reef platforms within Te Tapuwae o Rongokako Marine Reserve and at two non-reserve locations (Makorori and Turihaua) were surveyed during the period from 11 March 2000 to 9 May 2000, and resampled between 17 April 2003 and 19 May 2003. Three haphazardly-located replicate transects were completed at Makorori Reef and Turihaua Reef and three were completed on the intertidal reef platform (Kaiora Reef) within the marine reserve (Figure 5-1).

A tape measure was laid perpendicular to the shore, beginning from the base of the cliffs or bank at each location, which was generally the position of the extreme high water mark. The GPS position of the landward end of each transect was recorded utilising a handheld GPS.

For each transect, the width of the sandy beach or boulder area was recorded and then at 10-20 m intervals of rocky reef platform thereafter, five haphazardly located 0.25 m² quadrats were sampled (Table 5-4). Sampling was carried out within two hours either side of low tide and the entire width of the reef platform exposed at low water was sampled at each location. This level of replication provided adequate coverage of the three intertidal reefs and ensured completion of all transects when weather permitted over a 2-3 month timeframe (thereby eliminating any potential seasonal variability).
For each quadrat, the following was recorded: percent cover of algae and encrusting or non-motile invertebrates; abundance of all mobile invertebrates; and sizes of macroinvertebrates such as sea urchins / kina (*Evechinus chloroticus*) and gastropods.

For sea urchins (*Evechinus chloroticus*), test diameter (excluding the spines) was recorded to the nearest millimetre. The shell lengths of abalone / paua (*Haliotis* spp) and the shell widths of gastropods including *Cookia sulcata*, *Melagraphia aethiops* and *Turbo smaragdus* were recorded to the nearest millimetre.

5.2.5.2 Sea urchin sampling

The intertidal reef platforms around headlands within and adjacent to Te Tapuwae o Rongokako Marine Reserve are intersected by a large number of pools and narrow channels. During October / November between 2000 and 2004, a number of these channels were surveyed for sea urchins (*Evechinus chloroticus*) within the reserve and at two non-reserve locations, Turihaua and Makorori (Table 5-5, Figure 5-1), to describe the potential effect of lobster predation on sea urchin abundance and population structure. The length of each channel was measured with a tape measure and all urchins located within the channel were measured (test diameter to the nearest millimetre). Transects were also completed in channels along sandstone ramparts on the outer edge of the reef platforms within the reserve (Kaiora Reef) and at Makorori. Transects were completed during spring low tides, but adverse sea conditions prevented completion of surveys in 2004. Where possible, transects were located to provide adequate coverage of the reef at each location, with the number of transects completed dependent primarily on accessibility and reef extent.

5.2.5.3 Communities around lobster dens

During June 2003, five transects were completed perpendicular to a pool located on the intertidal reef platform (Kaiora Reef; Figure 5-1) within Te Tapuwae o Rongokako Marine Reserve, to describe the changes in the reef community as a function of distance from known aggregations of lobsters. This pool was known to support high densities of lobsters and was surrounded by exposed reef platform at low tide. Lobsters had been regularly observed feeding on the reef platform around the pool when covered by the tide, both during the day and at night (pers. obs.). Each transect was 10 metres in length and one 0.25 m² quadrat was sampled every 2 metres along the transect. For each quadrat, the following was recorded: percent cover of algae and encrusting
or non-motile invertebrates; abundance of all mobile invertebrates; and sizes of macroinvertebrates such as urchins (*Evechinus chloroticus*) and gastropods.

### 5.2.5.4 Core samples

Lobsters were regularly observed foraging in a cobble area adjacent to the intertidal reef platform within Te Tapuwae o Rongokako Marine Reserve. This area remained shallowly submerged at low tides. To describe the fauna of this area (and therefore potential lobster prey), nine core samples were collected from this cobble area in July 2003. Core samples were 10 cm in diameter and 10 cm in depth. Samples were sieved in a 2 mm mesh sieve and all organisms identified to the lowest taxonomic level.

### 5.2.6 Lobster daytime distribution

Five haphazardly-located 50x10 m transects were completed across the intertidal reef platform during a daytime high tide in January 2005 to describe the daytime behaviour of lobsters in this habitat within Te Tapuwae o Rongokako Marine Reserve. The size (carapace length) and sex of each lobster was recorded, along with whether the lobster was actively foraging (as evidenced by feeding or scraping at the substrate) or not. This level of replication provided adequate coverage of the intertidal reef platform without the possibility of transect overlap.

At the same time of year during a daytime low tide, a channel intersecting the reef platform was surveyed for lobsters. The depth of this channel at low tides ranged between 1 metre at its shallowest point and 3 metres at its deepest. The channel was searched using divers and the sex and carapace length were recorded for every lobster encountered.
5.3 Results

5.3.1 Nutritional condition

5.3.1.1 Blood sampling

Only data from lobsters at intermoult stage were included in this analysis as too few lobsters in any other moult stage were able to be collected.

A high refractive index indicates a high blood protein concentration (Oliver & MacDiarmid 2001). There was no significant difference between the mean refractive indices of male lobsters within and outside the marine reserve, for either undersized (<54 mm tail width) or legal-sized (greater than 54 mm tail width) lobsters (two-tailed t-tests, p>0.05; Figure 5-2). For females, the mean refractive index of lobsters less than 60 mm tail width was significantly higher within the marine reserve than outside the reserve (two-tailed t-test, p<0.05), but there was no significant difference between the mean refractive index for females 60 mm+ tail width within and outside the reserve.

5.3.1.2 Morphometrics

Analysis of covariance (ANCOVA) showed that there was a significant relationship between female log transformed carapace length and log transformed body weight (raw, untransformed data are in Figure 5-3), but that this relationship depended on area status (reserve or fished) (F2,110 = 719.6, p<0.01). There was also a significant relationship between female log-transformed tail width and log-transformed body weight (raw data in Figure 5-4), and this relationship also depended on area status (F2,110 = 608, p<0.01).

For females within the reserve:

\[
\text{Body weight} = 0.004296 \times \text{CL}^{2.52}
\]
\[
\text{Body weight} = 0.014699 \times \text{TW}^{2.51}
\]
For females outside the reserve:

\[
\text{Body weight} = 0.002009 \times \text{CL}^{2.67} \\
\text{Body weight} = 0.012907 \times \text{TW}^{2.52}
\]

(body weight in grams; carapace length (CL) and tail width (TW) in millimetres).

For males, analysis of covariance revealed that there was a significant relationship between log transformed carapace length and log transformed body weight (raw, untransformed data in Figure 5-3), but that the slopes and intercepts were different between reserve and fished locations (\(F_{3, 98} = 1754, p<0.01\)). There was also a significant relationship between log transformed tail width and log transformed body weight (raw data in Figure 5-4), and the slopes and intercepts were different between reserve and fished locations (\(F_{3, 98} = 1453, p<0.01\)).

For males within the reserve:

\[
\text{Body weight} = 0.000394 \times \text{CL}^{3.05} \\
\text{Body weight} = 0.001581 \times \text{TW}^{3.18}
\]

For males outside the reserve:

\[
\text{Body weight} = 0.014264 \times \text{CL}^{2.25} \\
\text{Body weight} = 0.043718 \times \text{TW}^{2.33}
\]

(body weight in grams; carapace length (CL) and tail width (TW) in millimetres).

5.3.2 Stable isotope analysis

The isotopic signatures for lobster muscle tissue indicated that this species is a high trophic level predator, with calculated trophic positions ranging between 3.2 and 3.9. There was no significant difference in the mean nitrogen signatures or trophic positions between the pooled reserve and pooled fished samples, or between reserve and fished samples within each size class and sex (two-tailed \(t\)-tests, \(p>0.05\) for all tests; Figures 5-5, 5-6). However, the mean carbon signature was slightly but significantly lower in samples from within the marine reserve than in samples from outside the reserve (two-tailed \(t\)-test, \(p<0.01\)). The mean carbon isotopic signature for
samples within the reserve was -16.76 (s.e. = 0.08); the mean from lobster samples outside the reserve was -16.02 (s.e. = 0.18). There was no significant difference in carbon signatures between reserve and fished samples when samples were divided into sexes and size classes (two-tailed t-tests, p>0.05 for all tests).

Because relatively little fractionation of carbon isotopes occurs between a consumer and its prey, a consumer’s δ¹³C signature should be similar to those of its prey species (Stapp et al., 1999). Carbon isotopic signatures of the range of species sampled outside the reserve showed that those lobsters were probably feeding on species including grazing gastropods, urchins and other species deriving their carbon sources predominantly from *Ecklonia radiata* (Figure 5-7). Lobsters also had a carbon signature similar to predatory fish species commonly used as bait in the lobster fishery.

Within the reserve, the carbon signatures of lobsters indicated that they were also feeding on grazing invertebrates such as gastropods and other species deriving their carbon predominantly from *Ecklonia radiata* (Figure 5-8).

Using the modelling software IsoSource, lobster tissue and urchins (*Evechinus chloroticus*) were shown to comprise large feasible contributions to lobster diet within the marine reserve, for both sexes and all size ranges assessed (Tables 5-6, 5-7 and 5-8). The small ranges between minima and maxima indicate that the values provided by IsoSource for these two food sources, or sources with similar signatures, represent relatively well-constrained estimates of the source contribution (Benstead et al., 2006). Gastropods, hermit crabs and coralline turf comprised relatively small feasible contributions to lobster diet within the reserve. Lobster tissue, or a food item with a similar signature, provided a larger feasible contribution to the diet of males between 60 and 65 mm tail width than smaller and larger males, with the feasible contribution ranging between 46 and 50% (1st and 99th percentiles). Lobster tissue was less important as a food source for large males (over 70 mm tail width) than smaller males. Outside the reserve, lobster tissue and urchins were potentially less important food sources, but fish bait, gastropods and hermit crabs became comparatively more important as potential food sources.

When all samples from the reserve were pooled and the average isotopic values inputted into the mixing model, lobster tissue contributed 34 to 42% to lobster diet; urchins contributed between 22 and 42% to lobster diet – both well-constrained estimates (Figure 5-9).
When average isotopic values from samples collected outside the reserve were pooled, lobster tissue, sea urchins and bait contributed between 0 and 40% to lobster diet (Figure 5-10).

5.3.3 Lobster diet analysis

Estimates of foregut fullness ranged from 25 to 100%, with the weight of the foregut, including contents, ranging from 3.5 to 27.2 g, and the weight of the gut contents ranging from 1.8 to 15.1 g.

Foregut contents included a range of algal and invertebrate species – almost exclusively coralline algae (both turfing and non-geniculate species) and coralline algal-dwelling invertebrates (Table 5-9). The most commonly recorded invertebrates (found in every lobster sampled) were gastropod molluscs, with up to 45 whole gastropods being recorded from each gut. Intact gastropods were predominantly rissoid gastropods, which are commonly found in turfing coralline algae (Morton 2004) and other small gastropods including *Turbo* *smaragdus* and *Zebittium exile*. Larger gastropods were generally recorded only as fragments and species such as *Micrelenchus* spp could not be distinguished. Crustaceans were found in 75% of the lobsters sampled and included the pill-box crab (*Halicarcinus innominatus*), hermit crabs (*Pagurus novaezealandiae*), other unidentified crab species and there was also evidence of cannibalism, with the foregut of one lobster containing an intact newly-settled lobster, *Jasus edwardsii*. Some prey items were commonly found in lobster foreguts, but comprised only a small percentage of the total volume of food. These prey items included polychaetes, algae (excluding non-geniculate coralline algae), chitons and bivalves.

5.3.4 Prey species distribution

5.3.4.1 Intertidal transects

Two distinct habitat types were recorded on the three reef platforms surveyed – one comprised predominantly of *Hormosira banksii* and turfing coralline algal species (“*Hormosira / turf*”) and the other with a conspicuous component of *Cystophora torulosa* and *C. retroflexa* (“*Cystophora*”). Quadrats sampled within each of these habitats were compared among the three locations (reserve, Turihaua and Makorori).
There were a number of significant changes in the percent covers and animal densities between 2000 and 2003 at all three locations and in all habitats sampled. However, not all statistically significant changes were particularly significant ecologically.

Between 2000 and 2003 within the marine reserve, the mean percent cover of bare reef within the *Cystophora* habitat increased from 4 to 29% and the mean percent cover of coralline turf decreased from 64 to 35% (Figure 5-11). Similarly, within the *Hormosira* / turf habitat in the reserve, the mean percent cover of bare reef increased from 4 to 11% and the mean percent cover of coralline turf decreased from 78 to 59%. Outside the reserve, there was little change in the mean percent covers of the most common algal species (plus bare reef) at Turihaua, but at Makorori there was a large increase in the percent cover of bare reef in the *Cystophora* habitat (from 18 to 44%; Figure 5-11). Unlike the marine reserve, there was no large concurrent change in the percent cover of coralline turf, but there was a large reduction (from 62 to 27%) in the percent cover of *Cystophora* species in this habitat at Makorori.

The densities of mobile macroinvertebrates were low at all three locations sampled. Of the three most common mobile macroinvertebrates (hermit crabs, *Melagraphia aethiops* and *Turbo smaragdus*), the only instance where the mean density was greater than 4 per 0.25 m² was for *T. smaragdus* in the *Hormosira* / turf habitat at Makorori in 2003 (Figure 5-12). Although there were some statistically significant changes in the density of these species, due to the organisms’ small size the ecological significance of these changes is likely to be minimal.

### 5.3.4.2 Sea urchin sampling

The mean density of urchins (*Evechinus chloroticus*) in channels on the intertidal reef platform within the marine reserve was consistently lower than in channels on the two non-reserve reef platforms sampled (Figure 5-13). The density was also consistently lower in channels in the sandstone rampart within the reserve than at the non-reserve rampart sampled. However, there was no statistically significant difference among the three locations or over time (univariate ANOVA, reef platforms: $F_{2,49} = 3.27$, ramparts: $F_{1,44} = 17.81$, $p<0.05$ for location, Student-Newman-Keuls method $p>0.05$).

There was considerable variation over time in the density of intertidal urchins, particularly on the two non-reserve reefs sampled. The highest density was recorded at Turihaua in 2001, when the mean density was 22.5 individuals per metre of channel (s.e. = 14.9). This mean was influenced by a very high density of 78.7 individuals per metre in one of the channels sampled.
A clear cohort of small urchins (less than 50 mm test diameter) was apparent at all three locations sampled in 2000 and this cohort continued to be apparent over time (Figures 5-14, 5-15). Within the reserve however, this cohort comprised a much smaller component of the total population sampled and the population was also comprised of a wider range in sizes of urchins. Only one urchin with a test diameter greater than 80 mm was ever recorded outside the reserve, whereas urchins of this size were recorded within the reserve in all years with the exception of 2001.

5.3.4.3 Communities around lobster dens

A variety of mobile invertebrates was recorded in quadrats on the intertidal reef platform adjacent to a pool known to support high densities of lobsters. However, the densities of these invertebrates were low in every quadrat sampled, with no effect on the total density of mobile macroinvertebrates (potential lobster prey species) of distance from the lobsters (Figure 5-16; univariate ANOVA, $F_{5, 29} = 0.73$, $p>0.05$). However, the percent cover of coralline turf was significantly lower within 2 metres of lobster dens than between 2 and 10 metres from the dens (Figure 5-17; univariate ANOVA, $F_{5, 29} = 3.37$, $p<0.05$).

5.3.4.4 Core samples

A variety of invertebrates was recorded in 10 cm core samples from the shallow subtidal cobble area adjacent to the intertidal reef platform within Te Tapuwae o Rongokako Marine Reserve (Table 5-10). The gastropods *Zebittium exile* and *Micrelenchus* spp were recorded in all samples, as were polychaetes (unidentified species). The most abundant species was *Zebittium exile*, with a mean density of 34.3 per sample (s.e. = 9.5). The mean density of *Micrelenchus* spp was 26.3 per sample (s.e. = 7.3) and for polychaete species it was 15.3 per sample (s.e. = 2.8). Limpets (at least 3 species combined) averaged 2.6 per sample (s.e. = 0.8); the bivalve *Nucula hartvigiana* averaged 2.6 per sample (s.e. = 0.6) and all other species averaged less than one individual per sample.

5.3.5 Lobster daytime distribution

A total of 128 individual lobsters were recorded on the 5 transects completed across the intertidal platform in Te Tapuwae o Rongokako Marine Reserve during daytime high tides in January 2005. Sixty-seven were males, 52 were females and sex could not be determined for 9 individuals. Of the males, 5 (7.5%) were actively foraging – one of these was feeding on an urchin (*Evechinus chloroticus*) and the remainder were either scraping at the coralline algae
substrate or digging holes in soft sediment patches on the reef platform. No females were observed to be foraging.

Lobsters that were not actively foraging were moving across the reef platform, stopped all activity when disturbed by the observer or retreated into nearby shelter.

Both male and female lobsters found on the intertidal reef platform at high tide during the day were on average significantly smaller than those recorded in the deep channel intersecting the reef platform (two-tail $t$-tests, $p<0.05$; Figure 5-18). The mean size of males recorded on the reef platform was 106.5 mm (s.e. = 4.3); the mean in the channel was 122 mm (s.e. = 1.8). For females, the mean size on the reef platform was 79.8 mm (s.e. = 1.9); in the channel it was 90.1 mm (s.e. = 2.1).
5.4 Discussion

The sampling and analysis undertaken here demonstrated that lobsters within Te Tapuwae o Rongokako Marine Reserve not only had a different diet and nutritional condition from lobsters outside the reserve, but that the ecological effects of their foraging activity on the communities of which they were a component were potentially significant.

5.4.1 Lobster diet

Lobsters in this study were demonstrated through foregut contents analysis to ingest a variety of potential food items, but predominantly coralline algae and coralline algal-dwelling invertebrates. Gastropods and crustaceans comprised the greatest percentage of foregut contents (by volume), with up to 45 intact gastropods being found in the foregut contents along with large volumes of shell fragments. Gastropods and other molluscs are known to be important components of lobster diet. For example, Edgar (1990a, 1990b) found that *Panulirus cygnus* consumed large numbers of gastropods - up to 200 per night. Similarly, Cox *et al.* (1997) found that molluscs constituted 75% of the prey items in the diet of Caribbean spiny lobster (*Panulirus argus*), with gastropods comprising between 57 and 66% of all molluscan prey.

Coralline algae (both turfing and non-geniculate species) were recorded in the foreguts of all but one lobster sampled, with up to 15% of the total foregut volume comprising coralline algae. Whether this was ingested intentionally or incidentally remains unknown. Joll & Phillips (1984) and Edgar (1990a) found that at some sites in Western Australia, lobster (*Panulirus cygnus*) diet was dominated by foliose coralline algae. Castaneda-Fernandez-de-Lara *et al.* (2005) also found coralline algae in the diet of *Panulirus interruptus*. Barkai *et al.* (1996) found that *Jasus lalandii* had limited ability to digest plant tissue and suggested that seaweeds were only incidentally caught. However, Joll & Crossland (1983) found that the calcium in coralline algae was absorbed by the lobster digestive system and suggested that it could be important in post-moult re-mineralization of the exoskeleton. Lobsters may also ingest hard items such as fragments of shell and exoskeleton to facilitate digestion (Barkai & Branch, 1988). The presence of coralline algae in the foreguts of lobsters in the present study could therefore be either intentional (to aid re-mineralization of the exoskeleton or to aid digestion of other prey items) or incidental (ingested while foraging for invertebrates within the coralline algae).
As hypothesised, lobsters within the reserve were demonstrated to have a different diet to those outside the reserve, but the details of these differences were startling and the extent of these differences unexpected. Lobsters are known to be cannibalistic (Barkai & Branch, 1988; Barkai et al., 1996; Griffiths et al., 2000; Joll & Phillips, 1984; Mayfield et al., 2000; Sainte-Marie & Chabot, 2002; Thomas et al., 2003) and there was evidence for cannibalism in this study, both from diet analysis and stable isotope analysis. Stable isotope analysis suggested that lobster tissue, and/or a prey item with the same signature, was an important component of lobster diet within Te Tapuwae o Rongokako Marine Reserve, but less so for lobsters outside the reserve. The isotopic mixing model suggested that lobster tissue could comprise up to 50% (99th percentile) of lobster diet within the reserve, with well-constrained estimates provided for this prey source. Lobsters were also observed on a number of occasions within Te Tapuwae o Rongokako Marine Reserve feeding on other lobsters or lobster appendages (pers. obs.). It is likely that the increased incidence of cannibalism is a direct response to the increase in lobster density and biomass (through the cessation of fishing) and thus is a natural behaviour, although the potential for some other unknown factor to be responsible cannot be completely discounted. This result does suggest that the rate of natural mortality observed within marine reserves is higher than in adjacent fished areas and so suggests that mortality rates included in fisheries population models should be density sensitive. Such mortality within protected areas may have implications for management in New Zealand in terms of reducing the potential for incidental fisheries benefits from MPAs and may also affect the recovery rate of such species within the boundaries of protected areas.

The trophic effects of lobster pot bait on New Zealand coastal and marine ecosystems has been suggested to be small (Breen, 2005), but the effect of bait on lobster productivity is unknown. Bait can enter lobster diet in three ways: consumption by undersized lobsters; consumption by adults that subsequently escape; and consumption of discarded bait. In other fisheries the effect of bait on lobster populations and nearshore benthic communities has been suggested to be quite substantial. For example, Saila et al. (2002) found that bait could potentially support a quarter to a third of American lobster landings from the inshore Gulf of Maine. Grabowski (2005) found that large lobsters derived 33.7 to 54.8% of their tissue from herring bait, with smaller lobsters deriving 10.9 to 12.6% of their tissue from bait. In this study, lobsters outside Te Tapuwae o Rongokako Marine Reserve were found through stable isotope analysis to potentially derive up to 46% of their tissue from fish species utilised as bait in this region. This is a food source that is not naturally available within the marine reserve (with the exception of research sampling and natural mortality of these fish species) and indicates that lobster diet is quite different between reserve and fished locations. These strikingly different sources of protein in the two adjacent
populations will have significant implications for the reef communities. When lobster bait was added into the mixing model for the marine reserve (a hypothetical situation; data not presented here), the only significant change to the feasible contributions was a reduction in the contribution of lobster tissue to their diet – the feasible contributions of other prey species remained relatively unchanged. Therefore, the main implication of the difference in diet is an increase in the natural mortality rate and therefore effect on the density of lobsters within the reserve. This will affect not only the population dynamics of the lobsters, but also have effects on populations of their natural prey species.

It was hypothesised that lobsters within the marine reserve would have different foraging behaviours, spatially and temporally, than has been recorded in fished areas. Evidence to support this hypothesis was produced in this study. *Jasus edwardsii* has been reported to be a nocturnal animal, feeding and moving predominantly at night (Booth, 1986; Williams & Dean, 1989). However, within Te Tapuwae o Rongokako Marine Reserve, lobsters were regularly observed foraging and moving around during the day and a survey of their behaviour revealed that at least 7.5% of the males on the intertidal reef platform during a daytime high tide were actively foraging. This is likely to be an underestimate, as many lobsters retreated when encountered by the survey divers and their behaviour could not be assessed. Many of the lobsters on the intertidal reef platform during the day were in such shallow water that they had to crawl out of the water as they moved between deeper pools and channels; the location of lobsters on the reef platform was often indicated by antennae emerging from the water (pers. obs.). No such behaviour was ever observed outside the marine reserve. The only previous report of substantial daytime activity in shallow water by this species was by MacDiarmid et al. (1991). They found that large, mature males and a smaller proportion of mature females moved among dens searching for mates in depths as shallow as 1-2 m during the height of the mating season in the Cape Rodney to Okakari Point (Leigh) Marine Reserve. In my study, the lobsters recorded on the intertidal reef platform were on average smaller than those in the deep channel intersecting the reef platform, but were still relatively large (males were up to 190 mm carapace length).

Daytime foraging has been reported in other lobster species, for example *Jasus tristani* (Pollock, 1991) and *Panulirus cygnus* (Dall, 1975). However, daytime movements of *J. edwardsii* in clear, shallow water is unusual, given the eye morphology and electrophysiology in this species (Meyer-Rochow & Tiang, 1984) and studies of the effects of light-dark cycles on locomotor activity, which indicated that the species is normally nocturnal (Williams & Dean, 1989). Allan (1979, cited in Williams & Dean, 1989) found that when *J. edwardsii* were repeatedly exposed to direct sunlight for several hours, they were effectively blinded for long periods. It may be that
lobsters within Te Tapuwae o Rongokako Marine Reserve have become adapted to foraging during the day, to take advantage of the abundant food sources on the intertidal reef platform and to help counter potential density-dependent effects. Dall (1975) found evidence of poor nutritional state of juvenile Panulirus cygnus at Seven Mile Beach, Western Australia and observed that these normally nocturnally-feeding animals were foraging during the daylight at that site. No such evidence of poor nutritional state was found for the lobsters feeding during the day in the present study – in fact, lobsters of both sexes within the marine reserve were in better nutritional condition (as evidenced by differences in the relationship between weight and carapace length or tail width) than those outside the reserve. However, the effects of this unusual behaviour on the physiology of the lobsters would be worthy of further research. Lobster foraging on intertidal reef platforms during nocturnal high tides has been recorded in a number of studies (e.g. Panulirus interruptus on southern Californian shores: Robles, 1987; Robles et al., 2001; Robles & Robb, 1993, 1990), but this is the first time daytime foraging on intertidal reef platforms has been reported.

5.4.2 Effect of lobsters on the distribution and abundance of prey species

The foregut contents of lobsters within the marine reserve were generally representative of the potential prey species available. Micrelenchus spp and Zebittium exile, which were commonly recorded on the cobble areas adjacent to the intertidal reef platform within the reserve, were also the most commonly recorded species in lobster foreguts. Coralline turf and turf-dwelling fauna recorded on the intertidal reef platform were also recorded in lobster foreguts, which corresponds with my frequent observations of lobsters foraging in this area at high tide.

It was hypothesised that lobsters within the marine reserve were having a significant effect on their prey species relative to fished areas and so the assessment of the potential impact on lobster prey focused on species commonly found in lobster foreguts and those known from other studies to comprise an important component of lobster diet. Although a number of changes were recorded on the intertidal reefs within and outside the marine reserve between 2000 and 2003, only a few could be said to be ecologically significant. Transects completed within the marine reserve in 2000 and 2003 showed a large change in the covers of bare reef and coralline turf in the two habitats sampled. Large decreases in the percent covers of coralline turf were recorded, with concurrent large increases in the percent cover of bare reef. At Makorori, there was also a large decrease in the cover of bare reef within the Cystophora habitat, but no concurrent decrease in the cover of coralline turf. In contrast, there was a large decrease in the percent cover of Cystophora species in this habitat. These changes at Makorori may be explained by the high
incidence of trampling by people on this reef platform, or perhaps the impact of sedimentation on
the intertidal reef community. Makorori is known for its predisposition to runoff of sediment-
laden water from the adjacent headland and such sedimentation is known to negatively affect
intertidal algal species in New Zealand (Schiel et al., 2006).

One of the hypotheses I aimed to test was that the density of lobster prey species would increase
with distance from aggregations of lobsters. It was found that although the percent cover of
coralline turf was significantly lower within 2 metres of dens containing high densities of
lobsters, the density of mobile macroinvertebrates remained very low up to 10 metres from the
dens. This suggests that either the lobsters have no significant effect on mobile
macroinvertebrates, or that the effect of lobster predation on these species is at a scale of more
than 10 metres. Observations of lobsters feeding on the intertidal reef platform at high tide up to
30 metres from their dens suggest the latter. It may be that coralline algae, which was commonly
found in the diet of lobsters, can be found more readily close to the lobsters’ dens, but they need
to forage more widely to find mobile prey.

The density of intertidal sea urchins was lower within the reserve than at the two non-reserve
reefs sampled and the population was comprised of proportionally fewer small urchins and
proportionally more large urchins. Although this pattern may be explained by predation on
intertidal populations of urchins by lobsters, my ability to detect an effect is partially confounded
by human harvesting of particularly large urchins outside the reserve and sampling within only
one protected area. However, at other sites in New Zealand, predation by lobsters has been
demonstrated to be most intense on urchins 30-40 mm in size (Shears & Babcock, 2002). This
was the size class proportionally less abundant within Te Tapuwae o Rongokako Marine Reserve
than at the two non-reserve locations sampled and so provides support for the hypothesis that
lobsters within the reserve have a significant impact on the population structure of urchins.
Urchins of this size are unlikely to be harvested by humans, due to their low gonad volume and
so this difference between reserve and non-reserve locations may be attributable to predation.
Unfortunately no pre-reserve data on urchin populations were available for analysis. Urchins
were not found in the lobster foregut samples in this study, possibly because the very soft tissue
within the test would be digested rapidly. However, lobsters were observed feeding on urchins
(pers. obs.) and the importance of this species as a prey item of Jasus edwardsii in other areas
(Pederson & Johnson, 2006; Shears & Babcock, 2002) suggests that it is likely to be important in
the Gisborne region too. The output from the isotopic mixing model suggested that urchins (or a
prey species with the same isotopic signature) were important components of lobster diet both
inside and outside the reserve, with well-constrained estimates provided for the marine reserve.
Given the high density of the lobster population within the marine reserve, particularly in the very shallow subtidal, there exists the potential for food limitation. Berry & Smale (1980) suggested that the size of the *Panulirus homarus* population off the South African coast could be limited by the amount of reef in the nearshore zone where its food organism occurs. It was also suggested that excessive surge conditions caused by rough seas could limit feeding activity. Such limitation (both biological and physical) could potentially occur within Te Tapuwae o Rongokako Marine Reserve if the lobster population continues to increase in biomass. It is interesting to note therefore that only in this location were lobsters observed foraging in the intertidal zone and that this activity occurred during the day. Thus, lobsters in Te Tapuwae o Rongokako Marine Reserve may have extended their foraging both spatially and temporally compared with lobsters in fished areas. Certainly, legal-sized individuals undertaking this activity in fished areas would be highly vulnerable to recreational fishers and quickly removed from the population.

### 5.4.3 Survey methods

A number of methods are available for assessing the nutritional state or physiological health of lobsters, including the refractometric method (Oliver & MacDiarmid, 2001; Ozbay & Riley, 2002), the ratio between weight and carapace length (Oliver & MacDiarmid, 2001; Robertson *et al.*, 2000), levels of gastric fluid protein (Dall 1975) and relative weight of digestive gland (Castaneda-Fernandez-de-Lara *et al.*, 2005). The first two of these methods were utilised in the present study and both proved useful for sampling a large number of animals. The morphometric method, which provided a more long-term indication of condition, suggested that the nutritional condition of lobsters within the reserve was higher than for lobsters outside the reserve. Because lobsters of a particular carapace length outside the reserve tended to have smaller tail widths than those within the reserve (see Chapter 6), using solely the relationship between carapace length and body weight would have been inappropriate. This is because many of the lobsters with wider abdomens (and therefore higher body weights) would have been removed from the fished population. However, analysis of the relationship between tail width and body weight also suggested that the nutritional status of lobsters within the reserve was higher than for lobsters outside the reserve.

Although the density of lobster prey species was lower within the marine reserve relative to fished areas, the direct impact of lobsters on their prey species could not be assessed through an experimental approach such as the use of exclusion cages at the study site. The primary reason for not undertaking these experiments was that the exclusion cages were required to be relatively
large, with many replicates (due to the need for cages controlling for cage effect, the effect of small carnivorous fish and also stingrays and eagle rays, which were common on the intertidal reef platform at high tide). In addition, the exposed nature of the reef and use of the reef by the public for recreational purposes precluded such experiments. Therefore, the conclusions able to be drawn are based solely on correlations between observed patterns in the distribution and abundance of lobsters and their prey species.

The analysis of lobster gut contents is notoriously problematic, primarily because of the rapid digestion of gut contents and in particular the rapid digestion of soft-bodied prey items. Given the rapid movement of prey items through the gut of spiny lobsters (e.g. Joll, 1982), Cox et al. (1997) concluded that the gut contents analysed in their study of the diet of the Caribbean spiny lobster (*Panulirus argus*) probably represented prey that each lobster captured during a single night. Newman & Pollock (1974) noted that it was difficult to obtain an unbiased quantitative assessment of diet, given that recognition of organisms without hard parts was difficult and that organisms with hard parts could be overemphasised in the diet due to their persistence in the stomach during and following digestive processes. The analysis of *J. edwardsii* diet here then, is likely to be biased towards those species that contain hard parts and are more slowly digested. Although lobsters were collected prior to dawn in this study, many prey items were already significantly digested and difficult to identify. Any larger organisms such as crabs and large gastropods were in small fragments and it was therefore difficult to identify them and establish the number of individuals present in the foregut. Where hard parts such as chiton radulae, gastropod operculae and polychaete jaws were present, the number of individuals in the lobster foreguts could be established relatively easily, but animals without such hard parts, or animals that were very fragmented, are likely to be underrepresented in the analysis.

While gut contents analysis is useful for describing what is ingested, stable isotope analysis provides an indication of what is actually assimilated (Fry & Sherr, 1984; Gannes et al., 1998). However, stable isotope analysis also has its limitations. One of the key issues with the stable isotope analysis in the present study is that a variety of tissues was analysed, including muscle tissue, gonad and whole animals (including or excluding shells). Different tissues from the same animal can potentially have quite different isotopic signatures (Kurle & Worthy, 2002; Tieszen et al., 1983). Where possible, small invertebrates were removed from their shell prior to analysis, but some (for example microgastropods) could not easily be removed from their shell. However, all invertebrates for which data was inputted into IsoSource, with the exception of hermit crabs, had their shells removed. Lack of an acidification step on samples with a high content of calcium carbonate (for example coralline algae) resulted in a positive bias in δ13C measurements and a
negative bias in δ15N measurements for those species (Jacob et al., 2005), which may have impacted on IsoSource outputs.

In a real food web with various food sources, there is variation in factors such as availability, palatability and productivity and so the minima and maxima feasible contributions produced by IsoSource, rather than the means, are the most informative outputs (Benstead et al., 2006). Well-constrained ranges were provided for some prey species, including urchin and lobster tissue for lobsters from within the marine reserve. However, large feasible ranges were provided for other potential prey species, which is not particularly informative (Benstead et al. 2006). However, no post-processing, in terms of constraining the IsoSource outputs with the results from gut contents analysis, was undertaken in this study, as there was too much variability in the diet data, and stable isotope signatures were not available for all the species identified in the foregut contents. Additional sampling would help to further constrain the modelling outputs. Phillips et al. (2005) suggested that lumping food sources with similar isotopic signatures is an option where there are a number of potential food sources. Some lumping of signatures was undertaken in this study, for example predatory fish species. Conversely, it implies that the feasible proportions provided by IsoSource relate not to a specific food source, but to a specific isotopic signature, which could be shared by a number of food sources. This should be considered when assessing the modelling outputs in this study.

5.4.4 Conclusions

The impact of lobsters on their prey species within Te Tapuwae o Rongokako Marine Reserve is suggested by the sampling undertaken to be potentially significant, particularly considering the high biomass of lobsters within the reserve (Chapter 2). The importance of coralline turf and turf-dwelling fauna in the diet of lobsters is particularly noteworthy and the increase in lobster biomass within the reserve has coincided with a reduction in these species on the intertidal reef platform. The lobster population within the reserve may also suppress the growth of intertidal kina populations, through selective removal of small individuals. Lobster diet within the reserve was shown to comprise a significant component of conspecifics, whereas outside the reserve, lobster bait appears to provide an important alternative protein source. Analysis of their nutritional status suggested that lobsters within the reserve were in better condition than those outside the reserve. Other potential indirect effects of fishing are explored in Chapter Six.
Table 5-1 Sample sizes for lobster blood sampling for protein analysis.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Moul Stage</th>
<th>Size Class</th>
<th>Location</th>
<th>No. Samples</th>
</tr>
</thead>
<tbody>
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<td>Female</td>
<td>Intermoult</td>
<td>60 mm +</td>
<td>Reserve</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>60 mm +</td>
<td>Fished</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>&lt;60 mm</td>
<td>Reserve</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>&lt;60 mm</td>
<td>Fished</td>
<td>90</td>
</tr>
<tr>
<td></td>
<td>Apolysis</td>
<td>&lt;60 mm</td>
<td>Fished</td>
<td>1</td>
</tr>
<tr>
<td>Male</td>
<td>Intermoult</td>
<td>54 mm +</td>
<td>Reserve</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>54 mm +</td>
<td>Fished</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>&lt;54 mm</td>
<td>Reserve</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td></td>
<td>&lt;54 mm</td>
<td>Fished</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>Postmoult</td>
<td>&lt;54 mm</td>
<td>Fished</td>
<td>3</td>
</tr>
</tbody>
</table>

Table 5-2 Sample sizes for lobsters within and outside Te Tapuwae o Rongokako Marine Reserve for which the relationship between carapace length and weight and tail width and weight were calculated.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Location</th>
<th>Sample Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>Reserve</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td>Fished</td>
<td>44</td>
</tr>
<tr>
<td>Female</td>
<td>Reserve</td>
<td>79</td>
</tr>
<tr>
<td></td>
<td>Fished</td>
<td>34</td>
</tr>
</tbody>
</table>
Table 5-3  Samples collected from within and outside Te Tapuwae o Rongokako Marine Reserve for stable isotope analysis.

<table>
<thead>
<tr>
<th>Feeding Strategy</th>
<th>Species</th>
<th>Type</th>
<th>Tissue Analysed</th>
<th>Reserve</th>
<th>Fished</th>
</tr>
</thead>
<tbody>
<tr>
<td>algae</td>
<td><em>Porphyra columbina</em></td>
<td>Intertidal alga</td>
<td>Thallus</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>Ecklonia radiata</em></td>
<td>Subtidal alga</td>
<td>Thallus</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>Cystophora torulosa</em></td>
<td>Intertidal / shallow subtidal alga</td>
<td>Thallus</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>coralline turf</em></td>
<td>Intertidal / subtidal algae</td>
<td>Whole plant</td>
<td>y</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Carphophyllum maschalocarpum</em></td>
<td>Intertidal / subtidal alga</td>
<td>Thallus</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>Hormosira banksii</em></td>
<td>Intertidal alga</td>
<td>Thallus</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td>nongeniculate corallines</td>
<td>Intertidal / subtidal algae</td>
<td>Whole plant</td>
<td>y</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Pterocladia capillacea</em></td>
<td>Intertidal alga</td>
<td>Thallus</td>
<td></td>
<td>y</td>
</tr>
<tr>
<td>plant</td>
<td><em>Zostera capricorni</em></td>
<td>Seagrass</td>
<td>Whole plant</td>
<td></td>
<td>y</td>
</tr>
<tr>
<td>grazer</td>
<td><em>Cookia sulcata</em></td>
<td>Subtidal gastropod</td>
<td>Whole animal</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>Chiton glaucus</em></td>
<td>Intertidal gastropod</td>
<td>Whole animal</td>
<td></td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>Evechinus chloroticus</em></td>
<td>Echinoid</td>
<td>Gonad</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>Trochus viridis</em></td>
<td>Subtidal gastropod</td>
<td>Whole animal</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>Haliotis iris</em></td>
<td>Intertidal / subtidal gastropod</td>
<td>Muscle</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>Melagaphia aethiops</em></td>
<td>Intertidal gastropod</td>
<td>Whole animal</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>Cellana ornata</em></td>
<td>Intertidal gastropod</td>
<td>Whole animal</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>Turbo smaragdus</em></td>
<td>Intertidal / shallow subtidal gastropod</td>
<td>Whole animal (- shell)</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>Chiton pelliserpentis</em></td>
<td>Intertidal gastropod</td>
<td>Whole animal</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td>particle feeder</td>
<td><em>Ophionereis spp</em></td>
<td>Brittlestars</td>
<td>Whole animal</td>
<td>y</td>
<td></td>
</tr>
<tr>
<td>predator</td>
<td><em>Polyprion oxygeneitos</em></td>
<td>Predatory fish</td>
<td>Muscle</td>
<td>y</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Nemadactylus macroopterus</em></td>
<td>Predatory fish</td>
<td>Muscle</td>
<td>y</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Latridopsis ciliaris</em></td>
<td>Predatory fish</td>
<td>Muscle</td>
<td>y</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Pagrus auratus</em></td>
<td>Predatory fish</td>
<td>Muscle</td>
<td>y</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Jasus edwardsi</em></td>
<td>lobster</td>
<td>Muscle</td>
<td>y</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Pagurus novaeezlandiae</em></td>
<td>Hermit crab</td>
<td>Whole animal</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td><em>Plagusia chabrus</em></td>
<td>Crab</td>
<td>Whole animal</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td></td>
<td>Polychaetes</td>
<td>Polychaetes</td>
<td>Whole animals</td>
<td>y</td>
<td></td>
</tr>
<tr>
<td></td>
<td>triplefins</td>
<td>Intertidal / subtidal fish</td>
<td>Whole animal</td>
<td>y</td>
<td></td>
</tr>
</tbody>
</table>
Table 5-4 Replication of 0.25 m$^2$ quadrats within three defined habitats on reef platforms at three locations sampled. No sampling could be undertaken on the sandstone rampart in the reserve in 2000. There is no rampart on the outer edge of the reef platform at Turihaua.

<table>
<thead>
<tr>
<th>Location</th>
<th>Year</th>
<th>Hormosira banksii / coralline turf</th>
<th>Cystophora</th>
<th>Sandstone Rampart</th>
</tr>
</thead>
<tbody>
<tr>
<td>Marine reserve</td>
<td>2000</td>
<td>50</td>
<td>110</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>25</td>
<td>105</td>
<td>35</td>
</tr>
<tr>
<td>Makorori</td>
<td>2000</td>
<td>125</td>
<td>35</td>
<td>65</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>135</td>
<td>25</td>
<td>55</td>
</tr>
<tr>
<td>Turihaua</td>
<td>2000</td>
<td>114</td>
<td>75</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>90</td>
<td>105</td>
<td>n/a</td>
</tr>
</tbody>
</table>

Table 5-5 Replication of intertidal channels within and outside Te Tapuwae o Rongokako Marine Reserve surveyed for sea urchins between 2000 and 2004.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Year</th>
<th>Marine reserve</th>
<th>Turihaua</th>
<th>Makorori</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef platform</td>
<td>2000</td>
<td>4</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2001</td>
<td>4</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2002</td>
<td>4</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>4</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sandstone rampart</td>
<td>2000</td>
<td>5</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2001</td>
<td>5</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2002</td>
<td>5</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>5</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 5-6  Mean stable isotope signatures of lobster muscle tissue, inputted into IsoSource. Nitrogen values have been corrected for fractionation by subtracting 3.5 from the raw values; carbon values were corrected by subtracting 1 from the raw values.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Tail Width</th>
<th>Reserve</th>
<th></th>
<th>Fished</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>δ15N</td>
<td>δ13C</td>
<td>Sample Size</td>
<td>Sample Size</td>
</tr>
<tr>
<td>Male</td>
<td>&lt;54 mm</td>
<td>10.6</td>
<td>-17.88</td>
<td>3</td>
<td>10.58</td>
</tr>
<tr>
<td>Male</td>
<td>54-55 mm</td>
<td>10.52</td>
<td>-18.08</td>
<td>3</td>
<td>10.43</td>
</tr>
<tr>
<td>Male</td>
<td>60-65 mm</td>
<td>11.03</td>
<td>-17.75</td>
<td>3</td>
<td>10.13</td>
</tr>
<tr>
<td>Male</td>
<td>70 mm+</td>
<td>9.99</td>
<td>-17.72</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>&lt;60 mm</td>
<td>10.52</td>
<td>-17.55</td>
<td>3</td>
<td>10.43</td>
</tr>
<tr>
<td>Female</td>
<td>60 mm+</td>
<td>10.25</td>
<td>-17.58</td>
<td>3</td>
<td>10.4</td>
</tr>
<tr>
<td>Pooled</td>
<td></td>
<td>10.48</td>
<td>-17.76</td>
<td>18</td>
<td>10.43</td>
</tr>
</tbody>
</table>

Table 5-7  Isotopic signatures of potential lobster prey species inputted into IsoSource. All species were collected from the location specified. Tissues sampled are listed in Table 5-3.

<table>
<thead>
<tr>
<th>Location</th>
<th>Group</th>
<th>Species</th>
<th>δ15N</th>
<th>δ13C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reserve</td>
<td>Subtidal gastropods</td>
<td><em>Cookia sulcata</em> and <em>Trochus viridis</em> (combined)</td>
<td>8.85</td>
<td>-17.08</td>
</tr>
<tr>
<td></td>
<td>Hermit crabs</td>
<td><em>Pagurus novaezelandiae</em></td>
<td>9.84</td>
<td>-11.83</td>
</tr>
<tr>
<td></td>
<td>Chitons</td>
<td><em>Chiton pelliserpentis</em></td>
<td>6.64</td>
<td>-10.62</td>
</tr>
<tr>
<td></td>
<td>Coralline turf</td>
<td><em>Corallina officinalis</em></td>
<td>6.92</td>
<td>-12.71</td>
</tr>
<tr>
<td></td>
<td>Intertidal gastropods</td>
<td><em>Turbo smaragdas</em></td>
<td>7.53</td>
<td>-14.01</td>
</tr>
<tr>
<td></td>
<td>Sea urchins</td>
<td><em>Evechinus chloroticus</em></td>
<td>8.2</td>
<td>-21.13</td>
</tr>
<tr>
<td></td>
<td>Lobster</td>
<td><em>Jasus edwardsii</em></td>
<td>13.98</td>
<td>-16.76</td>
</tr>
<tr>
<td>Fished</td>
<td>Bait</td>
<td><em>Latridopsis ciliaris, Pagrus auratus, Nemadactylus macropterus</em> (combined)</td>
<td>14.05</td>
<td>-17.08</td>
</tr>
<tr>
<td></td>
<td>Lobster</td>
<td><em>Jasus edwardsii</em></td>
<td>13.93</td>
<td>-16.02</td>
</tr>
<tr>
<td></td>
<td>Hermit crabs</td>
<td><em>Pagurus novaezelandiae</em></td>
<td>9.41</td>
<td>-12.42</td>
</tr>
<tr>
<td></td>
<td>Chitons</td>
<td><em>Chiton pelliserpentis</em></td>
<td>7.27</td>
<td>-11.03</td>
</tr>
<tr>
<td></td>
<td>Coralline turf</td>
<td><em>Corallina officinalis</em></td>
<td>6.6</td>
<td>-13.04</td>
</tr>
<tr>
<td></td>
<td>Subtidal gastropods</td>
<td><em>Trochus viridis</em></td>
<td>9.2</td>
<td>-18.67</td>
</tr>
<tr>
<td></td>
<td>Sea urchins</td>
<td><em>Evechinus chloroticus</em></td>
<td>8.24</td>
<td>-20.41</td>
</tr>
</tbody>
</table>
Table 5-8  IsoSource mixing model output for lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve, based on carbon and nitrogen isotope signatures. No males greater than 70 mm tail width were available for analysis from outside the reserve.

<table>
<thead>
<tr>
<th>Sex and Tail Width</th>
<th>Food Source</th>
<th>Reserve</th>
<th>Fished</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean feasible proportion (%)</td>
<td>Range (1st percentile – 99th percentile)</td>
</tr>
<tr>
<td>Male &lt;54 mm</td>
<td>Subtidal gastropods</td>
<td>9</td>
<td>0-26</td>
</tr>
<tr>
<td>Lobster</td>
<td>41</td>
<td>38-44</td>
<td></td>
</tr>
<tr>
<td>Hermit crabs</td>
<td>4.2</td>
<td>0-14</td>
<td></td>
</tr>
<tr>
<td>Chitons</td>
<td>1.7</td>
<td>0-8</td>
<td></td>
</tr>
<tr>
<td>Coralline turf</td>
<td>3.5</td>
<td>0-10</td>
<td></td>
</tr>
<tr>
<td>Intertidal gastropods</td>
<td>3.4</td>
<td>0-14</td>
<td></td>
</tr>
<tr>
<td>Urchins</td>
<td>37.4</td>
<td>30-44</td>
<td></td>
</tr>
<tr>
<td>Bait</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male 54-55 mm</td>
<td>Subtidal gastropods</td>
<td>11.2</td>
<td>0-32</td>
</tr>
<tr>
<td>Lobster</td>
<td>39.4</td>
<td>36-42</td>
<td></td>
</tr>
<tr>
<td>Hermit crabs</td>
<td>2.9</td>
<td>0-10</td>
<td></td>
</tr>
<tr>
<td>Chitons</td>
<td>1.8</td>
<td>0-6</td>
<td></td>
</tr>
<tr>
<td>Coralline turf</td>
<td>2</td>
<td>0-8</td>
<td></td>
</tr>
<tr>
<td>Intertidal gastropods</td>
<td>3.5</td>
<td>0-12</td>
<td></td>
</tr>
<tr>
<td>Urchins</td>
<td>39.3</td>
<td>30-46</td>
<td></td>
</tr>
<tr>
<td>Bait</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male 60-65 mm</td>
<td>Subtidal gastropods</td>
<td>7.4</td>
<td>0-20</td>
</tr>
<tr>
<td>Lobster</td>
<td>48.6</td>
<td>46-50</td>
<td></td>
</tr>
<tr>
<td>Hermit crabs</td>
<td>3.6</td>
<td>0-10</td>
<td></td>
</tr>
<tr>
<td>Chitons</td>
<td>2</td>
<td>0-8</td>
<td></td>
</tr>
<tr>
<td>Coralline turf</td>
<td>3</td>
<td>0-10</td>
<td></td>
</tr>
<tr>
<td>Intertidal gastropods</td>
<td>2.3</td>
<td>0-10</td>
<td></td>
</tr>
<tr>
<td>Urchins</td>
<td>33.1</td>
<td>26-38</td>
<td></td>
</tr>
<tr>
<td>Bait</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male 70 mm+</td>
<td>Subtidal gastropods</td>
<td>12</td>
<td>0-38</td>
</tr>
<tr>
<td>Lobster</td>
<td>30.4</td>
<td>24-34</td>
<td></td>
</tr>
<tr>
<td>Hermit crabs</td>
<td>5.6</td>
<td>0-20</td>
<td></td>
</tr>
<tr>
<td>Chitons</td>
<td>3</td>
<td>0-12</td>
<td></td>
</tr>
<tr>
<td>Coralline turf</td>
<td>4</td>
<td>0-16</td>
<td></td>
</tr>
<tr>
<td>Intertidal gastropods</td>
<td>6</td>
<td>0-20</td>
<td></td>
</tr>
<tr>
<td>Urchins</td>
<td>39</td>
<td>24-48</td>
<td></td>
</tr>
<tr>
<td>Bait</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female &lt;60 mm</td>
<td>Subtidal gastropods</td>
<td>11.8</td>
<td>0-42</td>
</tr>
<tr>
<td>Lobster</td>
<td>39.7</td>
<td>34-44</td>
<td></td>
</tr>
<tr>
<td>Hermit crabs</td>
<td>4.4</td>
<td>0-18</td>
<td></td>
</tr>
<tr>
<td>Chitons</td>
<td>2.9</td>
<td>0-12</td>
<td></td>
</tr>
<tr>
<td>Coralline turf</td>
<td>3.4</td>
<td>0-12</td>
<td></td>
</tr>
<tr>
<td>Intertidal gastropods</td>
<td>5</td>
<td>0-22</td>
<td></td>
</tr>
<tr>
<td>Urchins</td>
<td>32.7</td>
<td>18-42</td>
<td></td>
</tr>
<tr>
<td>Bait</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sex and Tail Width</td>
<td>Food Source</td>
<td>Reserve</td>
<td>Fished</td>
</tr>
<tr>
<td>-------------------</td>
<td>-------------------</td>
<td>---------</td>
<td>--------</td>
</tr>
<tr>
<td>Female 60 mm+</td>
<td>Subtidal gastropods</td>
<td>13</td>
<td>17.3</td>
</tr>
<tr>
<td></td>
<td>Lobster</td>
<td>35</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Hermit crabs</td>
<td>4.8</td>
<td>12.1</td>
</tr>
<tr>
<td></td>
<td>Chitons</td>
<td>3</td>
<td>9.1</td>
</tr>
<tr>
<td></td>
<td>Coralline turf</td>
<td>4</td>
<td>10.7</td>
</tr>
<tr>
<td></td>
<td>Intertidal gastropods</td>
<td>5.7</td>
<td>13.9</td>
</tr>
<tr>
<td></td>
<td>Urchins</td>
<td>34.6</td>
<td>18.8</td>
</tr>
<tr>
<td></td>
<td>Bait</td>
<td>18.8</td>
<td>0-42</td>
</tr>
</tbody>
</table>

Note: The table shows the mean feasible proportion (%) and the range (1st percentile – 99th percentile) for each food source in the Reserve and Fished areas.
Table 5-9  Gut contents of 20 lobsters collected from Te Tapuwae o Rongokako Marine Reserve. * = this prey item also found in fragments and so maximum number per lobster is conservative.

<table>
<thead>
<tr>
<th>Species Group</th>
<th>Item</th>
<th>Frequency of Occurrence (%)</th>
<th>Mean % Volume (s.e.)</th>
<th>Range in No. Individuals per Lobster (where prey item present)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhodophyta</td>
<td>Coralline turf</td>
<td>90</td>
<td>2.5 (0.7)</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td>Non-geniculate corallines</td>
<td>75</td>
<td>11.3 (5.6)</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td>Unid. red algae</td>
<td>40</td>
<td>0.4 (0.1)</td>
<td>n/a</td>
</tr>
<tr>
<td>Phaeophyta</td>
<td>Unid. brown algae</td>
<td>55</td>
<td>5 (4)</td>
<td>n/a</td>
</tr>
<tr>
<td>Chlorophyta</td>
<td>Unid. green algae</td>
<td>60</td>
<td>2 (1.1)</td>
<td>n/a</td>
</tr>
<tr>
<td>Polychaeta</td>
<td>Unid. polychaetes</td>
<td>45</td>
<td>1.9 (0.9)</td>
<td>1 - 4</td>
</tr>
<tr>
<td>Crustacea</td>
<td><em>Jasus edwardsii</em></td>
<td>5</td>
<td>0.5 (0.5)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Halicarcinus innominatus</em></td>
<td>10</td>
<td>0.3 (0.3)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Pagurus novaezelandiae</em></td>
<td>15</td>
<td>9.4 (6.4)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Unid. ostracod</td>
<td>10</td>
<td>0.4 (0.3)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Unid. crustaceans</td>
<td>55</td>
<td>2.3 (0.9)</td>
<td>1 *</td>
</tr>
<tr>
<td></td>
<td>Pooled crustaceans</td>
<td>75</td>
<td>12.8 (6.2)</td>
<td>1 - 2 *</td>
</tr>
<tr>
<td>Amphineura</td>
<td>Unid. chitons</td>
<td>35</td>
<td>0.4 (0.1)</td>
<td>1 – 5 *</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Unid. bivalves</td>
<td>40</td>
<td>2 (0.7)</td>
<td>1</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>Unid. rissoid gastropods</td>
<td>55</td>
<td>1 - 44</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Zebittium exile</em></td>
<td>15</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Micrelenchus spp</em></td>
<td>60</td>
<td>1*</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Turbo smaragdus</em></td>
<td>25</td>
<td>1 - 5 *</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Unid. limpet</td>
<td>15</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pooled gastropods</td>
<td>100</td>
<td>64.4 (8.3)</td>
<td>1 - 45 *</td>
</tr>
</tbody>
</table>

Table 5-10  Density and frequency of occurrence of invertebrates (>2 mm) sampled in nine 10 cm core samples adjacent to the intertidal reef platform within Te Tapuwae o Rongokako Marine Reserve.

<table>
<thead>
<tr>
<th>Group</th>
<th>Species</th>
<th>Mean Density (s.e. in brackets)</th>
<th>Frequency of Occurrence (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crustacea</td>
<td>Unid. amphipods</td>
<td>0.3 (0.2)</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>Unid. ostracod</td>
<td>0.2 (0.1)</td>
<td>22</td>
</tr>
<tr>
<td>Annelida</td>
<td>Unid. polychaetes</td>
<td>15.3 (2.8)</td>
<td>100</td>
</tr>
<tr>
<td>Platystermites</td>
<td>Unid. flatworms</td>
<td>0.1 (0.1)</td>
<td>11</td>
</tr>
<tr>
<td>Mollusca</td>
<td>Amaurochiton glaucus</td>
<td>0.7 (0.6)</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>Chiton pelliserpentis</td>
<td>0.6 (0.3)</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>Ischnochiton maorianus</td>
<td>0.1 (0.1)</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Barnea similis</td>
<td>0.1 (0.1)</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Cookie sulcata</td>
<td>0.3 (0.2)</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>Crepidula sp</td>
<td>0.4 (0.2)</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>Haliotis iris</td>
<td>0.1 (0.1)</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Unid. limpets</td>
<td>2.1 (0.7)</td>
<td>67</td>
</tr>
<tr>
<td></td>
<td>Micrelenchus spp</td>
<td>26.3 (7.3)</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>Nesting mussel</td>
<td>0.2 (0.1)</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>Nucula hartvigiana</td>
<td>2.6 (0.6)</td>
<td>89</td>
</tr>
<tr>
<td></td>
<td>Paphies subtriangulata</td>
<td>0.1 (0.1)</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Zebittium exile</td>
<td>34.3 (9.5)</td>
<td>100</td>
</tr>
</tbody>
</table>
Figure 5-1 Map showing the location of intertidal reef platforms sampled.
Figure 5-2 Mean blood refractive indices for lobsters within and outside Te Tapuwae o Rongokako Marine Reserve.
Figure 5-3  Plots of lobster carapace length and body wet weight, for female and male lobsters collected from within and outside Te Tapuwae o Rongokako Marine Reserve.

![Carapace Length vs Body Weight](image1)

Figure 5-4  Plots of lobster tail width and body wet weight, for female and male lobsters from within and outside Te Tapuwae o Rongokako Marine Reserve.

![Tail Width vs Body Weight](image2)
Figure 5-5 Isotopic signatures for male lobsters collected from within (filled symbols) and outside (hollow symbols) Te Tapuwae o Rongokako Marine Reserve.

Figure 5-6 Isotopic signatures for female lobsters collected from within (filled symbols) and outside (hollow symbols) Te Tapuwae o Rongokako Marine Reserve.
Figure 5-7  Plot of isotopic signatures for species collected from outside Te Tapuwae o Rongokako Marine Reserve. Signatures for *Jasus edwardsii* are averages. Label font and symbol colour distinguish species.
Figure 5-8 Isotopic signatures for species collected from within Te Tapuwae o Rongokako Marine Reserve. Signatures for *Jasus edwardsii* are averages. Label font and symbol colour distinguish species.
Figure 5-9  Plots of feasible contributions to lobster diet within Te Tapuwae o Rongokako Marine Reserve, from stable isotope signatures. The number of feasible solutions was 36.
Figure 5-10  Plots of feasible contributions to lobster diet outside Te Tapuwae o Rongokako Marine Reserve, from stable isotope signatures. The number of feasible solutions was 688.
Figure 5-11  Percent covers of the main substrates and habitat-forming species at three locations and two habitats sampled in 2000 and 2003. ** denotes two-tailed t-test significant at the 0.01 level; * denotes significant difference at the 0.05 level.

![Graph showing percent covers of substrates and habitat-forming species](image)

Figure 5-12  Densities of three species of mobile macroinvertebrate at three locations and two habitats sampled in 2000 and 2003. ** denotes two-tailed t-test significant at the 0.01 level; * denotes significant difference at the 0.05 level.

![Graph showing densities of mobile macroinvertebrates](image)
Figure 5-13  Density of urchins in intertidal channels in two habitats within and outside Te Tapuwae o Rongokako Marine Reserve between 2000 and 2004. There are no data from Makorori or Turihaua in 2004, and there was no “rampart” habitat at Turihaua.
Figure 5-14  Size frequency distributions of urchins at three locations sampled between 2000 and 2004. There are no data from Makorori or Turihaua in 2004. Only data from transects on the intertidal reef platform are presented.
Figure 5-15  Size frequency distributions for urchins sampled on the ramparts adjacent to the intertidal reef platforms within the reserve and at Makorori between 2000 and 2004. There are no data from Makorori in 2004.
**Figure 5-16** Density of mobile macroinvertebrates as a function of distance from a known high density population of lobsters.

**Figure 5-17** Percent cover of coralline turf as a function of distance from a known high density population of lobsters.
Figure 5-18 Mean sizes of lobsters recorded on the intertidal reef platform during a daytime high tide and in an adjacent channel in the reef platform at low tide.
Chapter 6  Effects of Fishing on Lobster Morphometrics, Disease Incidence and Female Fecundity

6.1 Introduction

Since the physical impact of lobster fishing on the environment through the use of pots or traps is considered to be negligible (Casement & Svane, 1999; Eno et al., 2001), the primary impact of lobster fishing is the direct removal of lobster biomass (Frusher & Buxton, 2006). Fishing for lobsters can significantly reduce the density and biomass of lobsters within an area, depending on local restrictions on fishing methods and catch characteristics. Eggleston et al. (2003) described a reduction in lobster (Panulirus argus) density of up to 95% during a 2-day recreational fishing season in the Florida Keys. In New Zealand under the Quota Management System, fish stocks may be reduced to 20-40% of their virgin biomass in order to boost productivity (Ministry for the Environment, 1998). Over 90% of the legal-sized biomass of Jasus edwardsii has been removed from eastern Tasmania through fishing (Frusher & Buxton, 2006). Such removal of biomass can have significant impacts on not only the dynamics of the fished population, but also on the communities of which that species is a component.

Fishing, including for lobsters, is almost always size- and often sex-selective, as a consequence of minimum legal sizes and restrictions on the harvest of particular components of the population, for example, reproductive females. Removal of particular sized individuals may not only remove their function in a population or community, but also result in removal of their genotypes and therefore result in what has been termed “fishing-induced evolution” (Conover & Munch, 2002; Pollock, 1995a, 1995b; Stokes & Law, 2000; Walsh et al., 2006; Williams & Shertzer, 2005).

Larger adults of many marine species can have disproportionately greater fecundity and may also produce larvae that have better survival (Birkeland & Dayton, 2005; O'Farrell & Botsford, 2006). In Jasus edwardsii, as in other lobsters, female reproductive output increases with female length (Annala & Bycroft, 1987; Kensler, 1968; MacDiarmid, 1989b). In addition, lobsters can exhibit specific behaviours in terms of mate selection and therefore, selective removal of lobsters can not only affect the genetic composition of the population, but also affect mating dynamics. MacDiarmid & Butler (1999) and MacDiarmid et al. (2000, 1999) demonstrated that female J. edwardsii are vulnerable to the non-availability of mates. Similar potential problems in terms of egg production have been described for other crustaceans, including the American lobster,
*Homarus americanus* (Gosselin *et al.*, 2003, 2005), the blue crab, *Callinectes sapidus* (Carver *et al.*, 2005) and spiny king crab *Paralithodes brevipes* (Sato *et al.*, 2005).

Understanding the impact of fishing upon the egg production of a spiny lobster population is crucial to maintaining viable fisheries (Chubb 2000, cited in Goni *et al.*, 2003b). High adult mortality rates, such as occur with fishing, select for earlier maturity or smaller size at the onset of maturity and an increase in size-specific reproduction (Reznick & Ghalambor, 2005). In a number of heavily fished populations of spiny lobsters, a decline in size at onset of maturity (SOM) has been recorded (Wahle, 1997). An explanation for this has been that selective harvesting of large individuals favours reproduction of early-maturing, small individuals that make a larger contribution to future generations than would occur in a virgin population.

Other potential effects associated with lobster fishing include the supplementation of lobster diet with bait (e.g. Grabowski, 2005, Chapter 5 of this thesis), bycatch (e.g. Brock *et al.*, 2007) and injury and mortality of discarded lobsters (e.g. DiNardo *et al.*, 2001).

The incidence of fishing-induced injury, disease and mortality of lobsters, particularly in those animals that are not retained as catch, has been highlighted in a number of studies. For example, Parsons & Eggleston (2005) reported a 27% increase in the density of injured lobsters after a two-day recreational fishing season. Injuries reduced adult abundance and landings significantly (Parsons & Eggleston, 2007) and also increased their susceptibility to predation (Parsons & Eggleston, 2006). Injuries can also affect lobster growth (Chittleborough, 1975; Melville-Smith & Wing Cheng, 2002). In addition, handling, displacement and exposure to air can affect lobster growth (Brown & Caputi, 1985), susceptibility to predation (Brown & Caputi, 1983), stress levels (Taylor & Waldron, 1997) and potentially reproduction (Harris & Andrews, 2005). It is known that stress caused during handling of lobsters causes mortality during live storage (Paterson *et al.*, 2005; Ridgway *et al.*, 2006) and handling mortality of discarded spiny lobsters has been estimated to be up to 77% in some species (DiNardo *et al.*, 2001). Such handling-related mortality has been a concern in the New Zealand lobster fishery (Breen & Kendrick, 1997).

Lobsters, like most species, are susceptible to a variety of pathogens found in the natural environment. For example, incidences of shell and tail disease in lobsters, both in onshore holding facilities and in wild populations, have been reported world wide (e.g. *Homarus americanus*, Castro & Angell, 2000). Some diseases may be increased through the handling and stress associated with fishing or aquaculture. In New Zealand waters, lobsters (*Jasus edwardsii* and *Sagmarias in verreauxi*) and paddle crabs (*Ovalipes catharus*) are susceptible to a form of
shell disease manifested as erosion and blackening of the carapace, tail fan and walking legs, caused by chitinoclastic bacteria (Diggles et al., 2002). Such diseases may not only cause direct mortality, but may also weaken the animal, making them more vulnerable to other sources of mortality (Smolowitz et al. 1992, cited in Castro & Angell, 2000).

The direct and indirect effects of fishing on the population dynamics of species such as lobsters can probably only be assessed through comparison of fished and unfished populations (Babcock et al., 2007; Robertson et al., 2005). Similarly, the effects of the establishment of marine protected areas on the surrounding fishery can probably only be assessed through comparison of fished and unfished areas, including the interaction between the areas.

In Chapter 2, the effect of the establishment of Te Tapuwae o Rongokako Marine Reserve on the density, biomass and population structure of lobsters was described. The growth rates of lobsters on fished and unfished reefs were described in Chapter 3 and the interchange between fished and unfished populations was described in Chapter 4. In Chapter 5 I described the effects of lobsters on their prey species and also assessed the potential effect of lobster bait on lobster diet in a fished and an unfished area. In this chapter, I assess other potential indirect effects of lobster fishing through the study of lobster morphometrics, to establish whether the removal of legal-sized animals based on one aspect of morphology (tail width) results in a population with a different carapace length to tail width relationship than an unfished population. I also assess the incidence of a bacterial infection associated with handling, and describe the reproductive parameters within and outside Te Tapuwae o Rongokako Marine Reserve. I hypothesise that the population of lobsters outside the reserve will be comprised of animals with morphologies affected by the fishing removals of animals with legal-sized tail widths (i.e. survivors will have smaller tail widths relative to carapace length); lobsters outside the reserve will have a higher incidence of tail fan necrosis due to repeated capture and handling before reaching minimum legal size, a smaller size at onset of maturity due to size selection processes, and larger clutches than similar sized lobsters within the reserve, due to increased competition for food within the reserve.
6.2 Methods

6.2.1 Sampling strategy

A number of lobster biological parameters expected to be potentially affected by fishing were studied within and surrounding Te Tapuwae o Rongokako Marine Reserve. Lobsters were sampled from both fished and unfished populations and their morphology, incidence of disease and reproductive output were compared.

6.2.2 Morphometrics

By removing legal-sized individuals based on one aspect of morphology, there exists the potential for differences to exist in the morphometrics of lobsters within and outside protected areas. In the fishery surrounding Te Tapuwae o Rongokako Marine Reserve, lobsters are landed according to tail width measures. To establish whether there was a difference in the relationship between carapace length and tail width between fished and unfished populations in this area, the carapace lengths (measured to the nearest 0.1 mm with vernier callipers, from the antennal platform to the dorsal posterior margin of the carapace along the midline) and tail widths (measured to the nearest 0.1 mm in a straight line between the tips of the primary spines on the second segment of the tail) were recorded for a total of 9464 lobsters caught in pots within and surrounding Te Tapuwae o Rongokako Marine Reserve (Table 6-1). Linear regressions relating carapace length to tail width were calculated for each sex and location, and analysis of covariance (S-Plus) used to describe how tail width related to carapace length and location (either reserve or fished), for each sex.

6.2.3 Incidence of disease

6.2.3.1 Pot surveys

Pot surveys of reef habitat within and surrounding Te Tapuwae o Rongokako Marine Reserve were completed approximately every 3 months between November 2003 and November 2006. The presence and severity of tail fan necrosis was recorded for every lobster sampled (with the exception of those which were dead, as in some cases parts of the dead lobster were missing). The severity of necrosis was recorded on a scale from 0 to 3 (Table 6-2). Lobster sex and tail width were also recorded.
The location and number of pots set depended on a number of factors, including weather and sea conditions, the vessel used and the presence of other fishing gear. Where possible, reef habitat from a range of depths throughout the marine reserve and within approximately 3 km of the reserve’s boundary was sampled (Figure 6-1).

Three different types of lobster pots were used: standard commercial pots, ¾-sized standard pots and fine mesh pots. The standard pots were commercial HRC (Hurricane Reinforcing Concrete) pots used widely in the New Zealand lobster fishery. They were of 52 mm mesh, occasionally with a finer mesh on the underside of the pots to minimise damage to the lobsters when the pots were brought on board the boat. A number of ¾-sized pots were used, mainly in winter 2004. These were also of 52 mm mesh, but were ¾ of the width of the standard pots and were easier to handle on the vessels used during this period. A small number of fine mesh pots were also used in an attempt to catch lobsters below the minimum legal size limit. These were standard HRC pots, covered in 25 mm plastic mesh.

Pots were baited with seasonally available fish, usually locally-sourced, including gurnard, snapper, tarakihi, barracuda, kingfish, blue moki, cardinalfish, jack mackerel and trevally.

It was intended that all pots be set overnight. On rare occasions, adverse sea conditions prevented pots from being lifted after 24 hours of soak time and so a small number of pots had 48-hour soak times. Pots were generally set in groups of 3 to 7, depending on the extent and complexity of the reef area being sampled, and were generally no less than 100 m apart. In order to minimise stress and injury to the lobsters, the pots were brought on board the boat without shaking them to remove undersize lobsters. In addition, any lobsters with their tail or appendages hanging outside the pot were removed or repositioned before setting the pot on the boat deck.

The weather and sea conditions were recorded for every day of sampling, and for the days previous to sampling. For every pot set, the time, depth, pot type and GPS position to the nearest metre were recorded.

6.2.3.2 Tagging

A total of 7466 lobsters was tagged (5225 within Te Tapuwae o Rongokako Marine Reserve and 2241 from outside the reserve), mostly during the pot surveys completed in November and
December 2003. A small number of lobsters, from very shallow depths within Te Tapuwae o Rongokako Marine Reserve, were caught by divers and tagged on shore. Lobsters were tagged using Hallprint T-bar anchor tags, inserted dorsally between the carapace and tail, either side of the centre line in order to avoid the intestine and as close to the tail as possible to avoid the body cavity. Insertion of the tags into this region of the muscle tissue ensured that the tags were retained during moulting. Lobsters of over 70 mm carapace length were tagged using an Avery Dennison Tag Fast tagging gun and TBA tags. A Fine Fabric gun and TBF tags were used for lobsters with a carapace length of less than 70 mm. Each tag was individually numbered, along with the letters DOC (for Department of Conservation) and the tags also had a short “chew buffer” on their distal end. Tagged lobsters had the distal third of one pleopod clipped using scissors, to enable determination of tag loss. After tagging, lobsters were immediately returned to the sea as close as possible to their capture location (using a Garmin Etrex GPS unit, with a margin of error of approximately 30 m). The tag needle was sterilised in ethanol between animals. The severity of tail fan necrosis was recorded for every tagged lobster.

6.2.4 Reproductive output of lobsters

6.2.4.1 Fecundity

The fecundity of female lobsters was assessed for 73 lobsters from within and 33 from outside Te Tapuwae o Rongokako Marine Reserve, caught during the egg-bearing season between May and September. Lobsters between 73 and 100.9 mm carapace length were sampled outside the reserve; lobsters between 65.8 and 103.7 mm were sampled within the reserve.

Captured lobsters were restrained using elastic cord on a padded board, resting on their dorsal surface. Lobster mouthparts and gills were kept moist using a spray bottle of seawater. The egg mass was removed by shaving the setae and attached eggs from the pleopods using a scalpel. Lobsters were then returned to the sea as soon as possible. The procedure generally took less than 3 minutes.

Each lobster was weighed (to the nearest 0.1 gram, including the egg mass) and the egg mass was also weighed separately. Carapace length and tail width (to the nearest 0.1 mm) were also recorded.
Clutch weight, tail width and carapace length were log transformed and carapace length (CL) - clutch weight and tail width (TW) – clutch weight relationships were described using ordinary least-squares linear regression to fit the coefficients $a$ and $b$ to the equations:

\[ \ln(\text{weight}) = \ln a + b \ln(\text{CL}). \]
\[ \ln(\text{weight}) = \ln a + b \ln(\text{TW}). \]

Fecundity (number of eggs produced per lobster) was estimated by using published values for the average number of eggs per gram of clutch (Kensler, 1968) – 4412 eggs per gram (average of 14 individuals in that study).

6.2.4.2 Size at onset of maturity (SOM)

For every female lobster caught during the pot surveys described above under “Incidence of disease”, the stage of sexual maturity was recorded, as evidenced by the presence of setae longer than 6 mm on the pleopods, or by the presence of eggs attached to the setae. Female lobsters with no setae, or with setae shorter than 6 mm, were recorded as being immature.
6.3 Results

6.3.1 Morphometrics

The relationship between carapace length and tail width was significantly different between the marine reserve and fished locations for both male and female lobsters, with both the intercepts and slopes of the fitted linear regressions being different between reserve and fished locations (analysis of covariance: $F_{2, 7298} = 48520$, $p<0.01$ for males; $F_{2, 2160}= 4755$, $p<0.01$ for females). Within the reserve, lobsters above the minimum legal size had on average smaller carapace lengths than the same-sized lobsters outside the reserve (Figures 6-2, 6-3).

The resulting regressions are given in Table 6-3.

6.3.2 Incidence of disease

Tail fan necrosis was found to affect predominantly male lobsters and particularly those within the fished areas. Overall, 1.8% of males caught in pots within the marine reserve were affected by tail fan necrosis (TFN), whereas only 0.4% of females caught within the reserve showed signs of TFN. Outside the reserve, at Turihaua Reef, 17.1% of males and 1.9% of females caught in pots had TFN; at Whangara Reef, 16.6% of males and 2.6% of females caught in pots had TFN. There was considerable variability over time, however, with males at Turihaua and Whangara showing similar patterns in the percent affected by TFN over time (Figure 6-4). Although the percentages of affected males outside the reserve declined over the 3-year survey period, there were clear increases in the percentages affected in early summer, following a decline in late winter. Within the reserve, the percentage affected changed little over the 3-year survey period.

The percentage of females affected by tail fan necrosis was consistently lower over the 3-year survey period than for males, but the percentage affected outside the reserve was usually higher than that within the reserve (Figure 6-5). There was no clear pattern over time in the percentage of females affected by TFN.

Outside the marine reserve, males most commonly showing signs of tail fan necrosis had tail widths of between 50 and 56 mm (Figure 6-6). Overall, over 24% of all males between 52 and 53.9 mm tail width caught outside the reserve had tail fan necrosis. The size frequency...
distributions of male lobsters with or without tail fan necrosis were similar for those caught outside Te Tapuwae o Rongokako Marine Reserve (Figure 6-8). However, for both Turihaua and Whangara, the mean sizes of lobsters showing signs of tail fan necrosis were significantly higher than for lobsters that did not have the disease (two-tailed $t$-test, $p<0.01$ for both locations).

Within the reserve, the proportion affected by tail fan necrosis was relatively consistent across all size classes (Figure 6-7). However, although the sizes of lobsters caught in the reserve without tail fan necrosis were normally distributed, the sizes of lobsters with the disease were distinctly bimodal (Figure 6-8), with a clear peak at between 52 and 54 mm tail width that was not present in the unaffected population.

Over the 3-year survey period, most lobsters within the reserve that had tail fan necrosis had only mild or moderate cases and there was no clear trend over time in the percentages affected (Figure 6-9). Outside the reserve, mild and moderate cases of tail fan necrosis were most common, with the exception of winter 2004, when a relatively high proportion of severe cases of tail fan necrosis was recorded (Figure 6-9).

There was little difference between the recapture rates of tagged male lobsters either with or without tail fan necrosis. Outside the reserve, 151 of 1417 (10.7%) male lobsters tagged without TFN were recaptured at least once; 26 of 281 (9.3%) males tagged when they showed signs of tail fan necrosis were recaptured at least once. Within the reserve, 818 of 3665 (22.3%) of tagged males without TFN were recaptured at least once; 20 of 118 (16.9%) males tagged showing signs of tail fan necrosis were recaptured at least once.

For those males that were tagged and recaptured outside the reserve (and for which information on necrosis incidence was recorded on both captures; $n=140$ capture events), 71% remained free of tail fan necrosis, 13% acquired the disease between captures, 12% lost signs of the disease between captures and 4% still showed signs of necrosis. Within the reserve, of 965 recapture events, 96% remained free of necrosis, 2% acquired the disease, 2% lost signs of the disease and less than 1% still showed signs of the disease. Few tagged male lobsters that were recorded to have moved across the boundary had the severity of tail fan necrosis recorded for both captures. Of the 25 that moved out of the reserve (all males), 22 remained free of necrosis and 3 lost signs of necrosis. Of the 9 that moved into the reserve, 7 remained free of necrosis and 2 lost signs of necrosis.
Of the 5 tagged males that were recaptured four more times after being tagged, 4 still showed no signs of tail fan necrosis (all were tagged and recaptured within the reserve) and one, which was tagged outside the reserve, remained free from necrosis on the first recapture, but subsequent recaptures were made by fishermen and necrosis was not recorded. Of 26 tagged males recaptured 3 times after being tagged, 20 remained free of necrosis on the 3rd recapture; 5 had necrosis on the 3rd recapture (2 of these were tagged and recaptured outside the reserve, 3 were tagged and recaptured within the reserve) and one tagged outside the reserve was recaptured by a fisherman and disease incidence was not recorded.

There were four main reefs within the survey area – one near the southern boundary of the reserve with a small part of the reef within the reserve boundary (Turihaua Reef); one entirely enclosed within the reserve boundaries (Pariokonohi Reef); one straddling the northern boundary of the reserve (Whangara Reef) and one to the north of Whangara (B5 Reef) (Figure 6-10). When data on the incidence of disease in lobsters from each of the reefs was analysed, it was found that the mean percentage of lobsters affected by tail fan necrosis per pot (52 mm mesh pots only) was significantly higher on Turihaua and B5 Reefs than on Whangara Reef, which in turn was significantly higher than on Pariokonohi Reef which is entirely protected (univariate analysis of variance, $F_{3, 2952} = 274.82$, $p<0.01$; Student-Newman-Keuls method, $p<0.05$). For pots set outside the reserve boundaries, there was no significant difference in the percentage of lobsters affected by tail fan necrosis among the reefs (univariate analysis of variance, $F_{2, 768} = 0.485$, $p>0.05$; Figure 6-11). For pots set within the reserve, the incidence of tail fan necrosis was significantly higher on Turihaua Reef (17.3%) than on Whangara Reef (3.2%), which in turn was higher than Pariokonohi Reef (1.2%) (univariate analysis of variance, $F_{2, 2183} = 198.77$, $p<0.01$; Student-Newman-Keuls method, $p<0.05$; Figure 6-11).

When the mean percentage of lobsters per pot affected by tail fan necrosis was assessed as a function of distance from the marine reserve boundary, it was clear that most pots set within the reserve had a low percentage of affected animals. However, pots set near the reserve boundary (but still within the reserve) had a higher percentage of affected animals, particularly within approximately 200 metres of the boundary (Figure 6-12). When the two reserve boundaries are compared (Figure 6-13), it is evident that the percentage of affected animals was on average higher near the southern boundary of the reserve, than near the northern.
6.3.3 Reproductive output

6.3.3.1 Fecundity

Outside the reserve, female egg clutches weighed between 10.1 and 30.9 g; within the reserve, clutches weighed between 10.1 and 65.5 g, over a similar size range of lobsters (Figure 6-14, 6-15). For the size range of lobsters sampled, the females within the reserve showed a much wider range in the weight of the egg mass, with some females producing a clutch that was over 15% of their body weight (Figure 6-16, 6-17). Outside the reserve, the range in percent of body weight was 3–10%; within the reserve it was 4-17%.

Analysis of covariance revealed that there was a significant difference between females in the reserve and those outside the reserve in the relationship between log-transformed carapace length and log-transformed egg mass weight ($F_{2, 103} = 28.61, p<0.01$), and in the relationship between log-transformed tail width and log-transformed egg mass weight ($F_{2,103} = 41.88, p<0.01$).

For females in the marine reserve:

$$\text{Clutch weight} = 0.000439 \times \text{CL}^{2.47}$$
$$\text{Clutch weight} = 0.000241 \times \text{TW}^{2.91}$$

For females outside the reserve:

$$\text{Clutch weight} = 0.025223 \times \text{CL}^{1.53}$$
$$\text{Clutch weight} = 0.014408 \times \text{TW}^{1.85}$$

where clutch weight is in grams and carapace length (CL) and tail width (TW) are in millimetres.

Using previously published values of the number of eggs per gram of clutch enabled a comparison with a previously published size-fecundity relationship for the Cape Rodney to Okakari Point (Leigh) Marine Reserve (MacDiarmid, 1989b). This showed that female fecundity within Cape Rodney to Okakari Point Marine Reserve was similar to that within Te Tapuwae o Rongokakako Marine Reserve for lobsters smaller than 100 mm carapace length, but that above this size, the fecundity was higher within Cape Rodney to Okakari Point Marine Reserve (Figure 6-18). At fished sites outside Te Tapuwae o Rongokakako Marine Reserve, fecundity was lower than either marine reserve. However, as shown in Figures 6-14 and 6-15, there were a number of
females within the reserve that had smaller clutches than similar-sized individuals outside the reserve.

6.3.3.2 Size at onset of maturity (SOM)

Because the sizes of lobsters captured in pots were affected by the mesh size and only 9 females were captured in fine-mesh pots outside the reserve, only data from 52 mm-mesh pots were analysed in determining the size at onset of maturity. However, insufficient lobsters of less than 44 mm tail width were captured either within or outside the marine reserve to establish the size at which 50% of the female population was mature. Just 26 females less than 44 mm tail width were captured in standard-mesh pots outside the reserve, and only 10 within the reserve. The majority of lobsters greater than 44 mm tail width, both within and outside the reserve, were mature.

Although the size at onset of maturity could not be established, the sizes of immature females within and outside the reserve could be compared. The mean size of immature females captured in 52 mm-mesh pots was significantly higher within the marine reserve than outside the reserve (two-tailed t-test, p<0.01). For immature females within the reserve, the mean size was 52.6 mm tail width (s.e. = 0.3, n=168), but the mean size of immature females outside the reserve was 2.4 mm less, at 50.2 mm tail width (s.e. = 0.6, n=68). The smallest immature female caught in a 52 mm-mesh pot within the reserve was 35 mm tail width; outside the reserve it was 37.1 mm tail width. Only 5 immature females were caught in fine-mesh (25 mm) pots outside the reserve and there was no significant difference between the mean size of immature females caught in fine-mesh pots between the reserve and fished locations (two-tailed t-test, p>0.05).

However, because the frequency distribution of tail widths was affected by the fishery (see 6.3.1 above), the carapace lengths of immature females from inside and outside the reserve were also analysed. This reduced the data set considerably, as not all lobsters captured during the pot surveys had both tail width and carapace length measured (26 immature females from 52 mm-mesh pots outside the reserve and 54 from within the reserve; 5 immature females in fine-mesh pots outside the reserve and 5 from within the reserve). There was no significant difference between the mean size of immature females caught either within or outside the reserve, for 52 mm and fine-mesh pots (two-tailed t-tests, p>0.05).
6.4 Discussion

Some potential direct and indirect effects of lobster fishing became apparent through the comparison of a fished and an unfished population. The lobster population outside Te Tapuwae o Rongokako Marine Reserve not only showed signs of size-selection, but had a higher incidence of a disease known to be associated with handling and the females produced smaller egg clutches than the same-sized females within the reserve. There was no evidence for a difference in size-at-onset of maturity between females within or outside the marine reserve.

6.4.1 Size selection

Natural variability in morphology has been previously described in lobsters. For example, Debuse et al. (2001) described variation in exoskeleton damage, claw spines and rostrum teeth in the European lobster Homarus gammarus. These differences were proposed to be a result of variation in population density. Selection through the activity of fishing can also alter the morphology of lobsters in a fished population. It is well-known that exploited stocks typically display truncated size and age distributions, due to targeted removal of larger individuals, which may or may not be due to imposition of minimum harvestable size limits (Conover & Munch, 2002). Such fishing is expected to generate selection on body size (Stokes & Law, 2000) and when the minimum harvestable size dimension correlates with other body dimensions, fishing changes the population composition of those dimensions too.

As expected in this case, removal of lobsters with a tail width greater than the minimum legal size limit, regardless of other body dimensions, has resulted in a population that has smaller tail widths relative to carapace length, than observed in an unfished population. Whereas lobsters in the reserve of a particular carapace length had a range of tail widths, lobsters outside the reserve within the same carapace length range tended to have smaller tail widths, simply because of the removal of legal-sized animals. Such morphological variation near the minimum legal size has been reported in this species and has influenced the selection of data to be inputted into stock assessments (e.g. Haist et al., 2005).

Whether this direct fisheries selection also results in evolutionary selection for lobsters with smaller tails and larger carapace lengths is debatable. Because the likelihood that body size is heritable is not negligible (Stokes & Law, 2000), if fewer lobsters with a particular body shape get to reproduce, then an evolutionary change could be expected over the scale of generations.
Because lobsters in the Gisborne fishery breed a number of times before attaining minimum legal size (Annala et al., 1980), the potential for such evolution is probably small. However, the potential for changes in lobster morphology over time should at least be considered in the management of this species, particularly in areas where exploitation levels are high, and/or where the size at onset of maturity is above the minimum legal size limit. This is important as genetic change caused by fishing is not readily reversed (Reznick & Ghalambor, 2005; Stokes & Law, 2000; Walsh et al., 2006) and could have significant economic consequences. The effects of fishing on the evolution of body size relationships may be reduced however, if a significant proportion of the population is protected.

6.4.2 Incidence of disease

Pot surveys conducted inside and outside Te Tapuwae o Rongokako Marine Reserve showed that up to 29% of the male lobsters captured at sites outside the reserve in any one month were affected to some degree by tail fan necrosis. The average percentage affected outside the reserve (over all surveys completed) was 17%, at sites north and south of the reserve. Within the reserve, the highest percentage of males affected during any one month was 3% and the average over all surveys was 1.8%. Female lobsters, both within and outside the reserve, rarely showed signs of tail fan necrosis – overall, 0.4% of females within the reserve showed signs of necrosis; between 1.9 and 2.6% of females at sites outside the reserve showed signs of necrosis.

It has previously been suggested that handling and holding of lobsters (Jasus edwardsii), in association with elevated water temperature, could predispose lobsters to infection of damaged tissue by bacteria (Reuter et al., 1999). Physical damage to tail fans during normal post-harvest handling of lobsters coincides with high incidence of tail fan necrosis (Musgrove et al., 2005) and it has been recommended that to reduce the prevalence of necrosis and blisters in lobsters, water quality and holding conditions should be improved and potential sources of injury eliminated (Diggles et al., 2002). Although a number of factors have been demonstrated to affect the incidence and severity of disease in lobsters (including water temperature, crowded conditions, diet, habitat, exposure to sewage; Castro & Angell, 2000), it seems likely that the higher incidence of tail fan necrosis outside Te Tapuwae o Rongokako Marine Reserve, compared with inside the reserve, is a result of increased handling of lobsters outside the reserve through normal fishing activity. Previously, it was unknown whether tail fan necrosis was related to fishing (Breen, 2005), but my study strongly suggests that it is. The incidence of tail fan necrosis in males outside the reserve increased up to the minimum legal size and lobsters nearer the
minimum legal size are likely to have been handled more frequently than smaller lobsters (simply because they have been in water longer as sublegal-sized lobsters). Therefore, there exists a correlation between the incidence of necrosis and probable history of handling. Similarly, Breen (2005) noted that the prevalence of tail fan necrosis was highest in lobsters just below the minimum legal size.

The incidence of necrosis in male lobsters tended to decline around the time of the main moulting period in August-September, then increase again after the moul. Castro & Angell (2000) and Glenn & Pugh (2006) also noted a higher incidence of lobster shell disease in pre-ecdysis than in post-ecdysis lobsters. Tail fan necrosis was present in lobsters from throughout the size range within the marine reserve. However, the incidence in large lobsters may have been overestimated, as they moult less frequently and so probably show signs of necrosis for longer periods. A similar situation was described for Homarus americanus from a no fishing area by Castro & Angell (2000). Laufer et al. (2005) found that the presence of lobster shell disease in American lobsters increased the incidence of moulting, possibly as a defensive mechanism, but I recorded no such increase.

Using pots to estimate disease prevalence in lobsters can lead to under- or overestimates (e.g. Castro & Angell, 2000). For example, if the proportion of lobsters affected is low at the time of highest catchability, the infected estimate may be too low. In this study, the highest catches of lobsters were immediately after the male moulting period, which also coincided with the lowest necrosis incidence. This could have resulted in an underestimation of the incidence of necrosis. Conversely, the presence of larger lobsters in the marine reserve, which tend to be more catchable (Miller, 1989) and which may show signs of necrosis for longer periods (see above) may have led to an overestimation of tail fan necrosis in lobsters within the reserve. Stentiford et al. (2001) suggested that infection by the parasite Hematodinium, which is more common in small lobsters (Nephrops norvegicus), could be more prevalent in populations under fishing pressure, due to the effect of fishing on lobster population structure. In addition, infected lobsters were more catchable in trawls, due to their reduced swimming ability and increased out-of-burrow activity. It remains unknown whether lobsters affected by tail fan necrosis in my study were more catchable as a result of their condition, than those without necrosis.

Because tail fan necrosis appears to be increased by handling, there exists the possibility that the sampling effort involved in researching within the reserve may have increased the incidence of tail fan necrosis compared with what could be expected if no fishing was undertaken. However, tail fan necrosis was present in the reserve during the first survey in November 2003. The reserve
had been in place for four years prior to this first survey and no fishing activity (including for research purposes) had taken place during that period. In addition, there was little change in the incidence of tail fan necrosis within the reserve over the 3-year study period, suggesting that the low level of research sampling had no measurable effect on the health of the lobsters. Therefore, the level of necrosis observed during that first survey is likely to reflect either a natural level in an unfished environment, or the movement of diseased animals into the reserve. As shown in Chapter 4, there is movement of lobsters across the boundary of the reserve, and so the possibility of diseased animals, particularly small animals, moving into the reserve cannot be discounted. A disproportionate number of sublegal-sized lobsters within the reserve were recorded to have tail fan necrosis, which may be the result of small lobsters moving into the reserve from the surrounding fishery. In addition, lobsters near the boundary of the reserve had a higher incidence of necrosis, suggesting some movement across the boundary.

There are many potential effects of tail fan necrosis on *Jasus edwardsii* populations and the fishery for this species. The economic implications are considerable, particularly as legal-sized lobsters showing signs of tail fan necrosis are not readily marketable and therefore tend not to be landed in the fishery. In terms of the lobster populations themselves, it remains unknown whether tail fan necrosis is a cause of indirect fishing mortality (Breen, 2005). However, the severity of infection in some lobsters sampled during the present study certainly suggests that infection-related mortality is likely. Infection would probably also affect the lobster’s growth rates. It is known that injured lobsters have a reduced growth rate (Davis, 1981) and it is likely that lobsters severely affected by tail fan necrosis divert their energy resources into replacement of infected or lost tissue during the moulting period. As mentioned above, infected lobsters may also have a different moulting cycle than healthy lobsters. I could not establish such effects on growth and mortality, but they are worthy of further research. The presence of tail fan necrosis in a lobster population may also have implications for the distribution of lobsters. For example, Factor *et al.* (2006) found that large juvenile *Panulirus argus* can detect and avoid diseased conspecifics. Such effects on lobster distribution could have implications for aspects of life history that rely on the interaction among individuals, such as reproduction.

6.4.3 Reproduction

Because of the significant difference in the relationship between tail width and carapace length for females within and outside the marine reserve, clutch size was assessed in relation to both tail width and carapace length. Using just carapace length would have biased the results outside the
reserve, given that these females tended to have narrower tail widths, which would likely affect their clutch size. Given that there was a difference in the relationships between both tail width and clutch size, and carapace length and clutch size, between reserve and fished populations, this discounts the possibility that females of a particular carapace length outside the reserve had smaller clutches simply because they tended to have smaller tail widths.

Although some females within the reserve produced smaller clutches than similar-sized animals outside the reserve, it was established that on average female lobsters within Te Tapuwae o Rongokakako Marine Reserve were producing larger egg clutches than similar-sized females outside the reserve. For example, a female of 100 mm carapace length outside the reserve was predicted to be producing on average only \( \frac{3}{4} \) of the number of eggs as the same-sized female within the reserve; a female of 150 mm carapace length outside the reserve was predicted to produce on average half of the number of eggs as the same-sized female in the reserve. There are several potential explanations for this.

Beyers & Goosen (1987) found that in areas where food availability was high, fecundity of females was higher. Similarly, Annala & Bycroft (1987) suggested that differences in the relationship between carapace length and egg production among localities could be explained by localised variation in factors such as food availability and quality, or morphometrics. However, if food availability was a causative factor in this instance, it could be expected that fecundity would be reduced within the reserve (the opposite of what was observed), due to the increased lobster abundance and concurrent increased competition for food within the reserve.

It has been demonstrated that handling of ovigerous female *Jasus edwardsii* reduces their clutch size, the size of their eggs and also larval competency (Smith & Ritar, 2005). Because the female lobsters within the marine reserve in this study were handled so infrequently compared with lobsters outside the reserve, this could partially explain the increased egg production.

Another explanation for the increased fecundity within the marine reserve relates to the mating dynamics of *Jasus edwardsii*. Female lobsters will actively seek the largest available male to mate with, and large males will generally seek the largest female (MacDiarmid *et al.*, 2000). There is considerable aggression between males during the mating season, and in general larger males will successfully displace smaller males from their dens. Consequently, small males may not get to mate at all. Most importantly, female lobsters mated by large males have larger clutches than those mated by smaller males due to the increased availability of sperm (MacDiarmid & Butler, 1999; MacDiarmid *et al.*, 1999). Because Te Tapuwae o Rongokakako
Marine Reserve supports more large male lobsters compared with the surrounding fishery (Chapter 2), there are more large males available for the females to mate with, which may explain their larger clutch sizes.

In addition to factors relating to the structure of the lobster population outside the reserve, the high incidence of tail fan necrosis in males outside the reserve may also affect egg production because of potential impacts on reproductive ability. The incidence and severity of diseases such as tail fan necrosis may affect the ability of a lobster to reproduce, perhaps through reduced sperm production, or reduced physical ability to mate. Although no evidence had been presented relating to this, it is a possibility that could be explored.

Because there was a significant difference in the relationship between tail width and carapace length for females within and outside the reserve, analysis of the size at onset of maturity based on tail width was unreliable. This analysis suggested that the size at onset of maturity (SOM) may be larger within the reserve than outside, but these results were likely to be influenced by the selective removal of large females outside the reserve, regardless of their maturity. Analysis based on carapace length, which is unaffected by fisheries selection, suggested no such decline in SOM in the fished population.

A decline in the size at onset of maturity (SOM) has been recorded in a number of heavily fished spiny lobster populations (Wahle, 1997), as have increases in spawning frequency (Chittleborough 1976, 1979, cited in Pollock, 1995a). Density-dependent compensatory increases in egg production, due to the limitation of the lobsters’ reproductive potential by food availability, have been suggested for some lobster species (DeMartini et al., 2003; DeMartini et al., 1993; Polovina, 1989). Rothschild (1986, cited in Polovina, 1989) suggested that when a population experiences a reduction in density, the increase in available food for each individual will result in an increase in the rate of sexual development and hence an attainment of the onset of sexual maturity at a small size. Beyers & Goosen (1987) hypothesised that differences in SOM resulted from differences in growth, such that faster growing lobsters are larger when they reach the age of SOM, with SOM being determined exclusively by age. However, this would suggest that if growth increases when lobster density is reduced, then the SOM should increase. This contrasts with the findings of Polovina (1989) for Panulirus marginatus. Bertelsen & Matthews (2001) suggested that the smaller clutch sizes and smaller SOM in spiny lobsters (Panulirus argus) in a fished compared with an unfished area were the result of sublethal fishery practices (e.g. loss of appendages through handling), which accounted for slower growth and smaller but older reproductively active lobsters. Polovina (1989) suggested that it was possible
that behavioural interactions were important in determining the size at onset of maturity in female lobsters and that smaller females in a fished area may be responding not just to a reduction in density but also a reduction in the number of larger females.

A number of the above factors, such as increased handling and reduced density in the fished population, were suggested to potentially have resulted in a reduced SOM outside Te Tapuwae o Rongokako Marine Reserve in comparison with the unfished population. However, no difference in SOM between the fished and unfished population was detected, although sample sizes were small and based upon lobsters caught in pots. Smith et al. (2004) demonstrated how there was a potential bias in using data from pots / traps to estimate the size at onset of sexual maturity of female crustaceans. It was found that compared with other fishing methods, catches obtained from traps contained disproportionately greater numbers of large animals. In addition, most of the females caught using traps were mature, leading to a bias towards mature females, which in turn could result in an underestimate of the SOM. This was also reported to be a problem for the spotted spiny lobster, *Panulirus guttatus* (Robertson & Butler, 2003) and European lobster, *Homarus gammarus* (Lizarraga-Cubedo et al., 2003). The former authors found that diver-sampled lobsters provided a better estimate of SOM than trap-caught samples. The lack of very small females in the catch in the present study precluded the accurate estimation of SOM. Instead, the size frequency distributions of immature females within and surrounding the reserve were used to infer the overall reproductive composition of the population.

There are implications of these findings for not only fisheries management, but also marine protected areas. Given that the landed catch of *Jasus edwardsii* in New Zealand could be 80% or more males in some areas (Breen & Kendrick, 1997), the fishery could be driving the population structure towards more small males and more females. This could reduce the availability of preferred larger males and drive the females to mate with smaller males. MacDiarmid & Butler (1999) and MacDiarmid et al. (2000) suggested that all of these factors had significant implications for egg production and therefore fisheries management, and this is true for the fished locations in my study.

A number of studies have demonstrated increased egg production in marine protected areas relative to fished areas. Edgar & Barrett (1999) suggested that increased reproductive output is a general feature of protected populations in marine reserves of adequate size because higher population densities often occur inside reserves; the population inside reserves include a greater proportion of large animals that are sexually mature; and the large mature animals inside reserves produce more eggs and larvae than the relatively small mature animals outside.
Increased egg production in spiny lobster populations in unfished areas compared with fished areas has been shown for *Panulirus cygnus* (Babcock *et al.*, 2007) and *Palinurus elephas* (Goni *et al.*, 2003b). It has been predicted that New Zealand marine reserves would also have enhanced egg production by *Jasus edwardsii*, through the increased abundance of large females (MacDiarmid & Breen, 1992) and the current study has confirmed this potential. Cole (2000) estimated that a 5 km marine reserve would have egg production equivalent to an unprotected coastline of 50 km length. Comparing the female size – fecundity curve from Te Tapuwae o Rongokako Marine Reserve with that from Cape Rodney to Okakari Point Marine Reserve (MacDiarmid, 1989b) showed that larger females within the older reserve (Cape Rodney to Okakari Point) have the potential to produce more eggs than the same-sized females within Te Tapuwae o Rongokako, and that larger females in both reserves could potentially produce more eggs than the same-sized females in the fishery surrounding Te Tapuwae o Rongokako. This agrees with the results of Kelly *et al.* (2000b), who demonstrated that egg production from four northeastern New Zealand marine reserves increased with reserve age.

Walker & Bentley (2000) suggested that the implementation of marine protected areas was a possible strategy for guaranteeing lobster egg production. However, understanding the fate of the larvae produced by marine protected areas is imperative for understanding their role in managing lobster fisheries (Goni *et al.*, 2003b) and all of the above authors have acknowledged that egg production from marine protected areas would only play a significant role in maintaining or enhancing recruitment when the stocks are severely depleted and also depends on the size and location of the reserve. Recent research has shown that lobster larvae that settle on the North Island’s east coast are mostly produced by lobsters in that region (NIWA, 2006). Therefore, any contribution made by Te Tapuwae o Rongokako Marine Reserve is more likely to benefit local populations. However, the effects of fishing effort displacement on egg production of the lobster population surrounding the reserve also needs to be considered (Gardner *et al.*, 2000).

### 6.4.4 Conclusions

The potential direct and indirect effects of fishing on lobster populations have been described through the study of a fished and an unfished population. Lobsters within Te Tapuwae o Rongokako Marine Reserve were demonstrated to have a different morphology than those outside the reserve, were less affected by a handling-related bacterial infection and produced larger clutches than females in the adjacent fished population. All these factors have implications for
not only the dynamics of the lobster populations themselves, but also for the management of the fishery, and highlights the role of marine protected areas in providing a baseline against which such direct and indirect effects of fishing can be assessed.
Table 6-1  Sample sizes for lobsters from within and surrounding Te Tapuwae o Rongokako Marine Reserve, for which carapace length and tail width were recorded.

<table>
<thead>
<tr>
<th>Location</th>
<th>Sex</th>
<th>Sample Size</th>
<th>Carapace Length Range (mm)</th>
<th>Tail Width Range (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Marine Reserve</td>
<td>Male</td>
<td>5289</td>
<td>67.3-176.4</td>
<td>37.6-77.1</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>1582</td>
<td>55.3-114.4</td>
<td>33.8-69.6</td>
</tr>
<tr>
<td>Fished</td>
<td>Male</td>
<td>2012</td>
<td>65.5-135.1</td>
<td>35.4-69.1</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>581</td>
<td>68.7-117</td>
<td>42.4-69.3</td>
</tr>
</tbody>
</table>

Table 6-2  The qualitative scale used to record the severity of tail fan necrosis in lobsters.

<table>
<thead>
<tr>
<th>Severity of Tail Fan Necrosis</th>
<th>Description</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Necrosis absent. No obvious sign of blistering or blackened areas on any part of the lobster.</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Necrosis present. Small (less than 2x2 cm) area of blistering or blackening on telson or uropod.</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Necrosis present. Area greater than 2x2 cm affected by blistering or blackening. Generally more than one uropod and/or telson affected. Uropod or telson occasionally missing.</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Necrosis present. All uropods and telson affected to considerable extent by blistering and/or blackening.</td>
<td></td>
</tr>
</tbody>
</table>
Table 6-3  Linear regressions relating carapace length (CL) to tail width (TW) for male and female lobsters within and outside Te Tapuwae o Rongokako Marine Reserve.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Location</th>
<th>Regression</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>Reserve</td>
<td>$TW = 10.11 + 0.42 \times CL, r^2 = 0.89, n = 5289$</td>
</tr>
<tr>
<td></td>
<td>Fished</td>
<td>$TW = 11.90 + 0.40 \times CL, r^2 = 0.77, n = 2012$</td>
</tr>
<tr>
<td>Female</td>
<td>Reserve</td>
<td>$TW = 3.11 + 0.58 \times CL, r^2 = 0.83, n = 1582$</td>
</tr>
<tr>
<td></td>
<td>Fished</td>
<td>$TW = 5.54 + 0.55 \times CL, r^2 = 0.80, n = 581$</td>
</tr>
</tbody>
</table>

Table 6-4  Sample sizes for male lobsters for which the presence or absence of tail fan necrosis was recorded, by size class.

<table>
<thead>
<tr>
<th>Tail Width (mm)</th>
<th>Reserve</th>
<th>Fished</th>
</tr>
</thead>
<tbody>
<tr>
<td>34-35.9</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>36-37.9</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>38-39.9</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>40-41.9</td>
<td>10</td>
<td>22</td>
</tr>
<tr>
<td>42-43.9</td>
<td>31</td>
<td>59</td>
</tr>
<tr>
<td>44-45.9</td>
<td>76</td>
<td>150</td>
</tr>
<tr>
<td>46-47.9</td>
<td>231</td>
<td>443</td>
</tr>
<tr>
<td>48-49.9</td>
<td>831</td>
<td>1614</td>
</tr>
<tr>
<td>50-51.9</td>
<td>2120</td>
<td>3102</td>
</tr>
<tr>
<td>52-53.9</td>
<td>3346</td>
<td>2435</td>
</tr>
<tr>
<td>54-55.9</td>
<td>4035</td>
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<td>58-59.9</td>
<td>6961</td>
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</tr>
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<td>60-61.9</td>
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</tr>
<tr>
<td>62-63.9</td>
<td>5097</td>
<td>21</td>
</tr>
<tr>
<td>64-65.9</td>
<td>3010</td>
<td>25</td>
</tr>
<tr>
<td>66-67.9</td>
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<tr>
<td>68-69.9</td>
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<td>70-71.9</td>
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</tr>
<tr>
<td>72-73.9</td>
<td>67</td>
<td></td>
</tr>
<tr>
<td>74-75.9</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>76-77.9</td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>
Figure 6-1 Distribution of pot sampling effort within and surrounding Te Tapuwae o Rongokako Marine Reserve, by season.
Figure 6-2  Plots of carapace length versus tail width for male and female lobsters within and outside Te Tapuwae o Rongokako Marine Reserve.

female

male

n=581

n=2012

fished

n=1582

n=5289

reserve

carapace length (mm)
carapace length (mm)
Figure 6-3  Linear regressions for the relationship between carapace length and tail width (raw data in Figure 6-2; equations in Table 6-3), for male and female lobsters within and outside Te Tapuwae o Rongokako Marine Reserve.
Figure 6-4  Incidence of tail fan necrosis (TFN) in pot-caught male lobsters, within Te Tapuwaef a Rongokako Marine Reserve and at fished locations north (Whangara) and south (Turihaua) of the reserve, between November 2003 and November 2006.

Figure 6-5  Incidence of tail fan necrosis (TFN) in pot-caught female lobsters, within Te Tapuwaef a Rongokako Marine Reserve and at fished locations north (Whangara) and south (Turihaua) of the reserve, between November 2003 and November 2006.  Note different scale from Figure 6-4.
Figure 6-6  Proportion of males affected by tail fan necrosis outside Te Tapuwae o Rongokako Marine Reserve, by tail width. Sample sizes are in Table 6-4.

Figure 6-7  Proportion of male lobsters affected by tail fan necrosis within Te Tapuwae o Rongokako Marine Reserve, by tail width. Sample sizes are in Table 6-4 (note n=2 for the largest size class).
Figure 6-8  Size frequency distributions for male lobsters caught in pots within Te Tapuwae o Rongokako Marine Reserve or south (Turihaua) or north (Whangara) of the reserve, that either showed no sign of tail fan necrosis (TFN absent) or had tail fan necrosis (TFN present).
Figure 6-9  Severity of tail fan necrosis in pot-caught male lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve between November 2003 and November 2006. (Mild = severity 1; moderate = severity 2; severe = severity 3 from Table 6-2).
Figure 6-10  Map showing the locations of the four main reefs within the survey area.
**Figure 6-11** Mean percentage of lobsters affected by tail fan necrosis (TFN) on the four reefs surveyed. Data are from 52 mm pots only.
Figure 6-12  Mean percentage of lobsters affected by tail fan necrosis (TFN) per pot, as a function of distance (in 100 m increments) from the reserve boundary. Bars on and to the right of the vertical line are outside the reserve.
Figure 6-13  Mean percentage of lobsters affected by tail fan necrosis (TFN) per pot, as a function of distance (in 100 m increments) from either the northern or southern marine reserve boundaries. Bars on and to the right of the vertical line are outside the reserve.
Figure 6-14 Plot of female carapace length and clutch weight, for lobsters within and outside Te Tapuwae o Rongokako Marine Reserve.

Figure 6-15 Plot of female tail width and clutch weight, for lobsters within and outside Te Tapuwae o Rongokako Marine Reserve.
Figure 6-16 Plot of female carapace length and weight of clutch / body weight (%), for lobsters within and outside Te Tapuwae o Rongokako Marine Reserve.

Figure 6-17 Plot of female tail width and weight of clutch / body weight (%) for lobsters within and outside Te Tapuwae o Rongokako Marine Reserve.
Figure 6-18  Fecundity of female lobsters as a function of size, for lobsters within and surrounding Te Tapuwae o Rongokako Marine Reserve and for lobsters within Cape Rodney to Okakari Point (Leigh) Marine Reserve (MacDiarmid 1989).
Chapter 7  General Discussion

This thesis describes, through the study of fished and unfished populations of a target species, some potential direct and indirect effects of fishing, how fished and unfished populations compare, and also how they interact. The findings have implications not only for the management of harvested species such as lobsters, but also for the establishment of marine protected areas in terms of their design and consequent ability to fulfil their objectives.

Basic biological data on *Jasus edwardsii* was obtained from Te Tapuwae o Rongokako Marine Reserve, without the confounding effect of fisheries selection or other effects of fishing. Information on aspects of lobster biology and ecology such as distributional patterns, population structure, seasonal movement patterns, growth and fecundity was able to be gathered, increasing our knowledge of a species which is not only important in a fisheries context, but is also an important component of New Zealand rocky reef communities.

Lobsters within Te Tapuwae o Rongokako and Te Angiangi Marine Reserves were more abundant than in the surrounding fisheries and the populations within the reserves were also comprised of a larger proportion of legal-sized animals. Both populations demonstrated an initial rapid rate of recovery, higher than has previously been reported for other New Zealand marine protected areas (Kelly *et al.*, 2000b), probably as a result of higher settlement of pueruli and better placement of the offshore boundary of the reserves. It was expected that given the high abundance and biomass of lobsters, density-dependent effects on population characteristics may have been exhibited within Te Tapuwae o Rongokako Marine Reserve. Such anticipated effects included a reduced growth rate (e.g. Chittleborough, 1976; Pollock, 1991), increased movement rates (e.g. Prescott *et al.*, 1997) and changes in diet or feeding ecology due to competition for food (e.g. Pollock, 1979). It was also anticipated that the large increase in lobster density and biomass within the reserve could be having a significant effect on their prey species (e.g. Shears & Babcock, 2002).

Although significant differences in these factors were described, the mechanisms potentially operating to create these differences and indeed the differences themselves, were not always as expected. Two key areas for discussion are the effects of fishing and marine protected area design and management.
7.1 The effects of fishing and protection on lobsters

A significant decline in the growth rates of tagged male lobsters within Te Tapuwae o Rongokako Marine Reserve was recorded between 2004 and 2006, which coincided with an increase in catch per unit effort. No such changes over time were recorded outside the reserve, which suggested that density-dependent factors could be operating within the reserve. However, it was also shown that over the 3-year study period, the growth rate of sublegal-sized male lobsters within Te Tapuwae o Rongokako Marine Reserve was higher than outside the reserve. This is the opposite of what would be expected if density-dependent factors alone were operating. One suggested cause of the observed difference was negative effects on growth due to handling of lobsters through normal fishing activity outside the reserve. Support for this explanation was given not only by the growth rate of sublegal male lobsters within the reserve being similar to what was reported for that area over 20 years ago (McKoy & Esterman, 1981, Chapter 3) but that the incidence of a bacterial infection known to be associated with handling was significantly higher in the fishery than in the reserve (Chapter 6). The incidence of tail fan necrosis itself may not be the cause of reduced growth, but it provided an “index of handling”.

A further suggested cause of the reduced growth rate of sublegal males was persistent removal of faster-growing individuals from the fished population through the activity of fishing. Faster-growing individuals (including tagged individuals) were suggested to reach minimum legal size more quickly than slower-growing individuals and were removed from the population by fishers. Their removal reduced the number of faster-growing animals available for capture during the research sampling and therefore their inclusion in the analysis of growth rates.

In addition to the effect on the growth of sublegal males, fishing was also implicated in the difference in lobster morphology between the reserve and adjacent fishery (through the removal of legal-sized animals) and also in the difference in female fecundity between the reserve and fishery. There were significant differences in the relationship between carapace length and tail width for lobsters from the reserve and those from outside the reserve, and these differences were demonstrated for both sexes. Female lobsters were shown to produce larger clutches in the reserve, probably as a result of the higher abundance of large males available to mate with (MacDiarmid et al., 1999). There was no evidence for any difference in the size at onset of maturity for females within or outside the reserve.

It was anticipated that lobsters within the reserve could be competing for food resources and that a change in feeding ecology or diet relative to fished areas could have taken place. Within the
reserve, lobsters were actively foraging during the day on intertidal reef platforms at high tide (Figure 7-1) – behaviour not previously reported for this species, and one not recorded outside the reserve in this study. It was also suggested through stable isotope and gut contents analysis that lobsters within the reserve were obtaining a significant dietary contribution from cannibalistic behaviour, whereas outside the reserve, fish bait used in the lobster fishery provided an alternative protein source. Blood sampling revealed no significant difference in protein levels between lobsters inside and outside the reserve (with the exception of sublegal-sized females), but higher weights relative to carapace length as well as higher weights relative to tail width suggested that both male and female lobsters within the reserve were in better nutritional condition than those outside the reserve.

From these results it appears that lobsters within and outside the reserve have adapted their behaviour in order to maintain their nutritional condition. Lobsters are adaptable animals, able to modify their behaviour to take advantage of available resources, and such opportunism has been previously described for other lobster species. At a site of very high biomass of *Jasus lalandii* off the South African coast, planktonic mysids were shown to provide an unexpected source of food, fulfilling the lobsters’ energetic requirements during periods when their usual prey sources were not so abundant (Barkai & Branch, 1988). In addition, an increased incidence of cannibalism was reported at that site, particularly in large lobsters. Off southern California, lobsters (*Panulirus interruptus*) move up on to the intertidal reef platforms during night-time high tides, to feed on the abundant mussel population (Robles *et al.*, 2001). Again, those lobsters have adapted their foraging behaviour to take advantage of available food sources.

It is likely that the cannibalism and daytime foraging observed in the present study are natural behaviours in *Jasus edwardsii* where this species occurs in high abundance and / or in the absence of fishing. Certainly, daytime foraging in shallow water would make lobsters highly vulnerable to removal by fishermen outside protected areas. Neither the cannibalistic or daytime foraging behaviour appear to be negatively affecting the ability of the population within the reserve to increase in abundance. However, it could be expected that the consumption of fish bait by lobsters outside the reserve would increase their growth rate, given that a high protein diet is correlated with higher growth in lobsters (Smith *et al.*, 2005). Other studies of the effect of lobster bait on marine systems have shown that bait can make a substantial contribution to lobster production (Grabowski, 2005; Saila *et al.*, 2002). In this case, the effects of the supplementation of diet outside the reserve with fish bait, in terms of growth, may be counteracted by the negative effects of handling.
Shears & Babcock (2004) suggested that due to environmental stresses such as high sedimentation, turbidity and freshwater input, bottom-up processes such as recruitment and productivity were likely to be weak and therefore habitat-level changes or trophic cascades were unlikely to occur as a result of protection in the Gisborne region. In my study, the effects of lobster predation within a protected area in the Gisborne region were suggested at a habitat level, through the reduction in the cover of coralline turf on an intertidal reef platform within the reserve. However, no “trophic cascades” were recorded – the effect on habitats was a direct, rather than an indirect effect of lobster predation. The foraging activities of lobsters within the reserve not only appeared to be having an effect on intertidal coralline algal communities, but lobsters were also regularly observed digging large holes in the cobble areas adjacent to the intertidal reef platform within the reserve - again, a behaviour not recorded outside the reserve (Figure 7-2). This foraging was observed to occur at quite a large scale, with displacement of cobbles and associated organisms, and disturbance of fine sediment into the water column. Often, several lobsters could be observed foraging in this manner in a relatively small area, resulting in significant disturbance to the benthic habitat. Therefore, the lobsters were not only having a direct impact on their prey species, but were also having a physical effect on the habitats in which they were foraging. Such impacts may affect the ability of some species and communities to recover within protected areas such as Te Tapuwae o Rongokako Marine Reserve and highlights the fact that changes that occur within marine protected areas may not always be positive in terms of biodiversity recovery.

Despite the high sedimentation, turbidity and freshwater input at the locations surveyed, no evidence for a low level of sea urchin recruitment was found in this study. In fact, large numbers of juvenile urchins were recorded in channels on the intertidal reefs, particularly outside the marine reserve. Juvenile urchins were found buried in cobble areas and fine sediment within the channels, as well as beneath the margins of beds of seagrass, *Zostera capricorni*. Within the reserve, juvenile urchins were less abundant, potentially as a result of predation by lobsters, but it is not known whether the removal of this size class of urchins has had any indirect effects on the intertidal reef community.

### 7.2 Experimental design

Comparisons between fished and unfished communities can often be confounded by inherent differences in those areas. In fact, in many cases, a particular management regime may be instated in an area because of the differences between that area and adjacent fished areas. This
can make the assessment of protection or management effects difficult, if not impossible. For example, the subtropical Kermadec Islands Marine Reserve, north of mainland New Zealand, was established because the area was so unique, and so a comparable fished location for detecting a protection effect may be impossible to find. In addition, factors such as wave exposure, geology, habitat quality and impacts of terrestrial processes all vary considerably within particular regions, potentially affecting comparisons among communities. If one protected area is compared with one unprotected area, it is impossible to unambiguously infer that any differences are due to protection or to the natural intrinsic variability characterising the two locations (Guidetti, 2002). In addition, unprotected areas adjacent to protected areas may be influenced by the protected area through processes such as spillover and fishing effort redistribution (Cole, 2003b). Ideally, spatial replication of protected and unprotected areas should occur in the detection of protection effects, but this is not always possible.

In the present study, the response of lobsters to protection was monitored in two marine reserves, with nearby fished areas comprising controls. Although Te Angiangi and Te Tapuwae o Rongokako Marine Reserves are similar in their biogeography (Walls, 2006), there are some differences due primarily to their differences in latitude. However, as they are the only marine reserves on the east coast of the North Island between East Cape and Wellington, they provided the only opportunity for replicate protected areas. Comparison of the two reserves (and control sites), as well as the availability of pre-reserve data for Te Angiangi, enhanced my ability to detect protection effects on the lobster populations.

Both Te Angiangi and Te Tapuwae o Rongokako Marine Reserves are representative of the regions within which they are located. Te Angiangi Marine Reserve contains habitats and communities that are representative of the central Hawke’s Bay coast (Department of Conservation, 1994) and Te Tapuwae o Rongokako protects habitats and communities that are representative of the coast between East Cape and Mahia Peninsula (Department of Conservation & Ngati Konohi, 1998). Therefore, neither reserve is particularly different from the broader regions they represent in terms of biodiversity. This makes comparison with nearby fished areas more robust.

Control locations for both marine reserves in this study were chosen for their required proximity to the reserves, which depended on the objective of the research (for example, sites within 3 km of Te Tapuwae o Rongokako were chosen for the detection of edge effects and spillover through pot surveys) and their similarity in terms of geology, exposure and biodiversity to the reserves. Although there were some differences between reserve and fished locations (for example, the
subtidal reef within Te Tapuwae o Rongokako was slightly wider than those in adjacent fished locations), these differences were unavoidable but unlikely to significantly affect my ability to detect the response of species such as lobsters to protection. The effects of these differences appeared to be on a finer scale than the broad protection effects. For example, the greater width of the subtidal reef within Te Tapuwae o Rongokako resulted in longer inshore-offshore migrations by lobsters, compared with fished areas where the reefs were narrower.

Where sampling occurred in just one protected and one unprotected area (for example, the study of growth), the possibility of some factor other than fishing (and associated differences in density, size structure etc) influencing the observed results cannot be completely discounted. However, the details of the observed responses often strengthened the conclusions. In the case of the occurrence of tail fan necrosis for example, the incidence in males increased up to the minimum legal size outside the reserve and was comparatively low within the marine reserve, correlating with probable history of handling in the fishery. This strengthened the conclusion that the bacterial infection was associated with the activity of fishing.

7.3 Implications for fisheries management

There are implications of these findings in terms of fisheries management. This study has demonstrated the susceptibility of harvested species such as lobsters to not only the direct effects of fishing (such as biomass removal and fisheries selection), but also the indirect effects of fishing, which can influence factors such as growth, mortality and reproduction – all of which are fundamental components of fisheries stock modelling and therefore management. These indirect effects and the scale of these effects only became apparent through the study of an unfished population. In the absence of this, factors such as environmental perturbations may not have been distinguishable from the effects of fishing and therefore the need for any management change may not be recognised, or any management changes may be implemented too late.

The possibility that removal of faster growing sublegal-sized lobsters affects the calculation of average growth rate has implications for fisheries management. The potential for slower growing lobsters to more likely be included in research surveys and faster-growing lobsters to more likely be retained by fishermen and possibly not be reported, may create a bias in growth data, including the data presented in this thesis. In addition, as was the case in this study, there may be a lack of data from the whole size range of lobsters in fished areas. Data from a range of lobster sizes was obtained from Te Tapuwae o Rongokako Marine Reserve, which provided higher \( L_\infty \) values
compared with data from the surrounding fishery i.e. growth estimates were different when data from large lobsters was included in the analysis. Therefore, management decisions based on growth data obtained only from populations that are truncated in their size distribution may be erroneous.

A further finding in this study was that natural mortality through cannibalism may be higher within more abundant populations. In marine protected areas, such mortality may affect the extent to which the area can contribute to the surrounding fishery, in terms of factors such as egg production and emigration. A high level of mortality could also affect the ability of the MPA to achieve its conservation benefits, in terms of the recovery of species within the boundaries of the MPA. In terms of fisheries management, estimates of mortality may need to be density-sensitive.

The incidence of tail fan necrosis within the fished population has obvious implications in terms of fisheries management. With the incidence of infection being associated with probable history of handling, an appropriate management strategy may be to reduce handling, perhaps through tools such as effort restrictions, or spatial or temporal closures.

The variation in lobster morphology near the minimum legal size may have implications for fisheries where the exploitation rate is high or where the size at onset of maturity is above the minimum legal size. In such cases, lobsters with smaller tail widths relative to carapace length may contribute more to subsequent generations than they would in a population where the full range of morphologies are represented. This may in turn affect aspects such as future lobster catches.

In terms of increasing the fisheries yield of *Jasus edwardsii*, rolling closures have been suggested as being a potential alternative to marine protected areas (Edgar & Barrett, 1999; Gardner et al., 2000). The recovery rate of lobsters within Te Tapuwae o Rongokako Marine Reserve, as well as the increased condition of lobsters relative to fished areas, suggests that such rolling closures may be a potential management tool in this region. Prior to the establishment of this reserve, commercial fishermen reportedly caught 10% of the total CRA3 TACC from the reserve area, which equated to 32 tonnes per year (Haist et al., 2005). The biomass of lobsters taken by recreational and customary fishermen is not known. In 2005, dive surveys of the reserve showed that there were approximately 211,484 legal-sized lobsters in the reserve (based on the mean from diver transects, scaled up to 1162 hectares of reef habitat in the reserve). Based on the mean weight of legal-sized lobsters in the reserve at that time (from diver surveys), this equates to 224.4 tonnes of legal-sized biomass in the reserve, or 37.4 tonnes per year of protection. Edgar &
Barrett (1999) found that closing areas to lobster fishing and re-opening them after several years would result in increases in the overall biomass of lobsters caught. Without knowing the total recreational and customary catch taken from the Te Tapuwae o Rongokako Marine Reserve area prior to protection, it is not clear whether a similar strategy could result in increases in overall biomass caught here.

After just 4 years of protection, catches up to 50 times the CPUE of pots set outside the reserve were obtained within the reserve, and individual lobsters within the reserve were heavier than the same-sized animals outside the reserve. During surveys conducted over 5 days in November 2005 the average CPUE in the reserve was 15.4 kg of legal-sized lobsters per pot. Outside the reserve, it was 0.5 kg per pot. Theoretically, if the reserve was opened to harvest at that time (after 6 years of protection), 770 kg of legal-sized lobsters (based on 54 mm tail width for males) could be caught in 50 pots set within the reserve in one day. To catch the same weight of lobsters if the area had not been closed (and assuming that catches in that area were similar to catches surrounding the reserve in November 2005), over 30 times more pots would need to be fished. In addition, lobsters within the reserve would have a much reduced incidence of tail fan necrosis, which would theoretically make a larger proportion of the catch able to be landed if such an area was a rolling closure. The concept of rolling closures may also be successful from a marketing perspective. The cost of fishing within an area newly opened to harvest would be reduced, due to the reduction in distance required to be covered to obtain a day’s catch, and the catch would be comprised of fewer but larger lobsters, which would reduce handling effort for fishing crews and leave more lobsters in the water. The economics and feasibility of implementing rolling closures could be further explored for some New Zealand regions.

7.4 Implications for the design and management of marine protected areas

Not only does this study have implications for the management of fisheries, it has also highlighted some important implications for the design and management of marine protected areas.

It was anticipated that lobsters within Te Tapuwae o Rongokako Marine Reserve may exhibit faster movement rates than those outside the reserve due to the increased density of lobsters. Such an increase in lobster movement rate, in particular an increase in movement away from high densities of lobsters, could contribute to a net emigration of lobsters from the reserve (e.g. Prescott et al., 1997). However, the movement patterns of lobsters in my study were shown to be
potentially more affected by the distribution of habitats, rather than protection status or potential density-dependent effects. Distinct inshore-offshore movements occurred in male lobsters, and these movements were sometimes longer within the reserve, probably a result of the subtidal reefs within the reserve being wider. A key finding though, was that the vast majority of lobster movements took place within reefs, with very little movement between reefs. The location of the marine reserve boundaries, with respect to the distribution of reef habitat, had clear implications for the movement of lobsters across the reserve boundaries and therefore for the ability of the reserve to provide protection to those lobsters. The reef totally enclosed within the reserve boundaries (Pariokonohi Reef) had the highest catches of lobsters and the lowest incidence of tail fan necrosis (an indication of fishing pressure). On Turihaua Reef, which was located across the southern boundary of the reserve, catches from the area of the reef within the reserve differed little from fished reefs. In addition, catches outside the reserve on Turihaua Reef, as well as the incidence of tail fan necrosis, were no different than on a reef that did not have a protected section (B5 Reef). However, catches on Whanga reef, which was bisected by the northern boundary of the marine reserve, were higher on the fished section and the incidence of tail fan necrosis was lower than on the two other fished reefs surveyed. There was an increased rate of movement away from Pariokonohi Reef (the reef with the highest catches), which suggested that a high density of lobsters could encourage greater inter-reef movement.

These results suggest that due to the opportunity for cross-boundary movement of reef-dwelling species such as lobsters, small protected areas, in particular those where the boundaries bisect reefs, are likely to be ineffective in protecting such species. However, when natural boundaries to movement, such as sand channels, are incorporated into the design of an MPA, the ability of reef-dwelling species to increase in abundance is heightened. Where the MPA is large enough to provide both, then there may exist an opportunity not only for species recovery but also for incidental supplementation of catches through spillover.

The higher initial recovery rate of lobsters within Te Tapuwae o Rongokako Marine Reserve compared with northeastern New Zealand marine protected areas, such as the Cape Rodney to Okakari Point Marine Reserve, may be partially attributable to the contrasting design of the reserves. Significant movement of lobsters across the seaward boundary of Cape Rodney to Okakari Point Marine Reserve (which is only 800 m from shore) has been reported, and may be responsible for a reduction in the overall mean size and number of very large individuals in the marine reserve population (Kelly & MacDiarmid, 2003; Kelly et al., 2002). The seaward boundary of Te Tapuwae o Rongokako Marine Reserve is up to 5000 m offshore and from the tagging undertaken here appears to be sufficient to completely contain the majority of the
lobsters’ seasonal inshore-offshore migrations. This may allow the population in this reserve to increase at a higher rate than in reserves that are more susceptible, through their design, to the effects of fishing activity near their boundaries.

7.5 Objectives of marine protected areas

It has been suggested that establishing well-defined and explicitly-stated objectives is probably the most critical step when selecting a marine protected area and that often the goals of marine protected areas are implicit, rather than explicit (Vanderklift & Ward, 2000). Marine reserves often have a number of objectives, usually relating to science, economics, culture and ethics (Hockey & Branch, 1997; Jones, 1994). However, most existing reserves worldwide do not have explicit goals and expectations (Gerber et al., 2005).

A key objective of Te Tapuwae o Rongokako Marine Reserve, and most other New Zealand marine protected areas, is the protection and recovery of biodiversity. However, it is clear from this study that “protection” in marine reserves does not always entail an increase in species size and abundance. The interactions among species need to be considered. For example, the increase in lobster biomass within Te Tapuwae o Rongokako Marine Reserve corresponded with a decline in the abundance of prey species such as coralline turf and potentially an increase in cannibalism in the lobster population. In addition, differences in the population structure of sea urchins between fished and unfished reefs were recorded, which may be attributable to increased predation by lobsters (Pederson & Johnson, 2006; Shears & Babcock, 2002). Jones et al. (1992) noted that while changes in the abundance of species in MPAs have been observed, changes in biodiversity have very rarely been reported (but see Worm et al., 2006). In addition, as discussed above, natural fluctuations in factors such as recruitment influence biodiversity, which can make detection of change attributable to protection difficult (Gardner et al., 2000).

In addition to the issues surrounding the design of marine reserves and the effect of design features such as size on the ability of species to recover fully, there are also issues relating to the concept of what is natural in the ocean and the so-called “shifting baseline syndrome” (Dayton et al., 1998; Pauly et al., 2002). This refers to the sliding and continually reduced expectation or concept of what the natural system is or should be. Restoration of the marine environment to the “way it used to be” is often stated as a goal of marine protected areas, including Te Tapuwae o Rongokako Marine Reserve (Department of Conservation et al., 2005). Is this goal achievable in
New Zealand through the implementation of marine protected areas, in particular marine reserves?

Although the human occupancy of New Zealand and the use of marine resources has been relatively recent compared with other countries, many stocks have been significantly reduced through fishing (Department of Conservation & Ministry for the Environment, 2000), and it may be that some of the changes that have taken place in the New Zealand marine environment are either irreversible or have been such that recovery will take place on a different trajectory. In addition, as is the case for Tasmania (Edgar et al., 2005), there is an almost complete absence of baseline population data for marine species other than those commercially exploited or visible at the sea surface. As Dayton et al. (1998) and Jackson (2001) described, the baseline may have shifted before the ecological roles of many species could be studied and even before fishery-dependent data were collected. Although it is possible in New Zealand to obtain more specific paleoecological, archaeological and historical data on marine ecosystems (as recommended by Jackson et al., 2001), it must be recognised that it may not always be possible to recreate the ecosystems inferred by such data.

In terms of lobsters and the communities of which they are a component in New Zealand, the current community structure may be very different to what it was historically, even in marine protected areas. For example, Kensler (1969) described the early days in the Chatham Islands lobster fishery, when during the first year over 2 million pounds of lobsters were caught. The next year, over 7 million pounds were caught. At that time, the catch was comprised of animals of a size and maturity representative of a virgin stock. The ecological role of lobsters of that size and abundance can now only be inferred through the study of unfished populations, which may or may not represent the historical situation. From Pike’s (1969) descriptions of an unfished population of lobsters from the Bay of Plenty in 1962, where most males caught were between 140 and 180 mm carapace length, and females between 100 and 130 mm carapace length, it appears that both marine reserves I have studied are not yet near what could be considered a “natural state”. In Te Tapuwae o Rongokako Marine Reserve in 2005, most male lobsters surveyed by divers were between 90 and 120 mm carapace length, and females between 60 and 80 mm carapace length. Cole (2003a) suggested that because important ecological changes have taken place over 20 years after the establishment of some New Zealand marine reserves, and many species expected to recover within reserves are long-lived, monitoring to detect protection effects should continue for decades.
In order to take into account issues such as the “shifting baseline syndrome”, the concept of “ecological integrity” (Lee et al., 2005), proposed for the terrestrial environment, could be considered for the marine environment, particularly in terms of assessing the ability of marine protected areas to fulfil their objectives. An ecosystem has ecological integrity when all the indigenous plants and animals typical of a region are present, together with the key major ecosystem processes that sustain functional relationships between all those components, and is the product of an enormous number of interactions. The elements that have been suggested to provide the best guarantee that integrity is being maintained are: indigenous dominance; species occupancy; and environmental representation (Lee et al., 2005). These elements provide the basis of ecological integrity which has been summarised as “the dominance of indigenous biomes, with a full suite of species able to survive in an area, across all the environments represented at the site”. The most important feature is that there is no “fossilisation” of the current or past state of the biota, but recognition that following human modification and environmental change, the configuration of indigenous communities at a location may be quite different from that of the past. The elements allow for natural successional change and trophic cascades, and acknowledge that compositional shifts could occur in environments modified by human activities.

It has been recognised (Shears & Babcock, 2004) that there are four ways in which species in marine reserves may be affected by protection: recovery of previously exploited species; declines in prey or competitor populations; habitat changes resulting from trophic cascades; and changes in faunal distribution and diversity associated with habitat change. However, accurate prediction of the outcome of protecting the marine environment is difficult because of the lack of baseline information on what constitutes natural state and the complexities of trophic interactions and population dynamics (Langlois & Ballantine, 2005). Changes that occur in response to protection are specific to habitats and bioregions and cannot be used to accurately predict likely changes in other habitats and bioregions.

In New Zealand marine environments, one of the essential elements of ecological integrity, species occupancy, has been significantly altered by anthropogenic activity, including fishing. Under the Quota Management System, fish stocks may be reduced to 20-40% of their virgin biomass in order to boost productivity (Ministry for the Environment, 1998). Consequently, the occupancy of some species may be reduced by 60-80%. This may have serious implications for trophic interactions and maintenance of community structure. Fishing may also alter the population structure of species, for example, by removing large adults. This may have repercussions for reproductive output (Birkeland & Dayton, 2005) and may also alter the
functional role of a particular species in a community. For example, large lobsters have higher feeding rates and consume larger sea urchins than do smaller lobsters (Tegner & Levin, 1983). If species are reduced to a very low level, there is the risk of ecological extinction, where populations have been reduced to such a level that they cannot exert former ecological roles (Dayton et al., 1998; Jackson et al., 2001). Marine species may also be at risk of biological extinction, as a result of anthropogenic impacts such as habitat fragmentation interacting with species life history characteristics (Roberts & Hawkins, 1999). However, Jackson (2001) suggested that because few of the large apex predators and herbivores are biologically extinct, restoration of coastal resources for ecosystem services and managed harvest should be possible.

Changes in food webs as a result of altered community structure may affect the ability of marine species to recover from harvesting pressure (Hutchings, 2000). Therefore, the changes in species occupancy in the environment surrounding a marine protected area may affect the recovery trajectory within the marine protected area, such that some populations may never recover to a “natural state”. For example, in New Zealand, some of the historical predators of lobsters, including groper / hapuka (Pike, 1969) and marine mammals (Yaldwyn 1958, cited in Kensler, 1967) have been significantly reduced in their distribution and abundance through anthropogenic activity (e.g. Lalas & Bradshaw, 2001) and because of this are certainly not significant predators of lobsters within Te Tapuwae o Rongokako Marine Reserve or the wider East Coast marine environment today. The absence of species such as these from the wider ecosystem will surely have implications for the ability of communities to recover to a “natural state” within any type of marine protected area.

Ecological extinctions may make ecosystems more vulnerable to other natural and anthropogenic disturbances such as nutrient loading and eutrophication, disease, storms and climate change (Jackson et al., 2001). The establishment of marine protected areas can do little to prevent such disturbances. For example, turbulence and shifting sand during a cyclone was suggested to have caused significant mortality of lobsters in the area of Te Tapuwae o Rongokako Marine Reserve (prior to its establishment) in April 1982 (Kilner & Goodwin, 1982).

In light of all these factors then, perhaps the objective of protection should simply be to minimise human disturbance and allow the recovery of as natural a situation as possible.
7.6 Effect of marine protected areas on fisheries

Although this study has highlighted the ability of MPAs such as Te Tapuwae o Rongokako Marine Reserve to inform fisheries management, the effects of MPA establishment on the surrounding fishery, and the implications and significance of these effects, are also important and largely depend on the objectives of the MPA and the management regime in place surrounding the MPA.

The potential effects of Te Tapuwae o Rongokako Marine Reserve on the surrounding fishery have been estimated by various individuals and organisations. The establishment of this reserve has been suggested to have contributed to increased competition for fishing space in other parts of the CRA3 fisheries management area (National Rock Lobster Management Group, 2005b) and it has been considered that the reserve has no stock-recruit effect and no yield-per-recruit effect, but that the removal of part of the original stock (assumed to be 10%) has had a negative effect on the available stock and subsequent recruitment (Breen et al., 2005a; Haist et al., 2005). Their analysis assumed that there was no increased recruitment through increased egg production within the reserve, no growth-overfishing, and no interchange between reserve and fished lobster populations (Sullivan, 2004). This study has demonstrated that there is some interchange between reserve and fished populations, particularly across the northern boundary of the reserve, which is able to supplement the catches of individual fishermen in that area. Although egg production within Te Tapuwae o Rongokako Marine Reserve is higher than the surrounding fishery (through increased abundance of large lobsters and increased fecundity of females), the corresponding contribution to recruitment remains unclear.

Although approximations of the relative interchange between reserve and fished populations could be obtained (through the comparison of tag recapture rates, which suggested a net export of lobster biomass), the estimation of actual spillover from the reserve proved difficult. However, some crude estimates can be provided, based on population estimates in the reserve from diver and pot surveys (using tag / recapture data from the latter), and on the proportion of tagged lobsters that moved out of the reserve. In 2005, the total population estimate from diver surveys was 613,536 lobsters in the reserve. Of the 5225 lobsters tagged in the reserve, 49 were caught outside the reserve. This provides a minimum estimate of spillover of 0.938%. Based on the population estimate, the number of lobsters that moved out of the reserve in 2005 was 5754. The mean weight of lobsters in the reserve (from diver surveys) in 2005 was 0.536 kg. Therefore, a total of about 3.1 tonnes of lobsters moved out of the reserve in 2005. This is a very crude
estimate, as not only does it not account for sampling or fishing effort, it also assumes that both sexes and all sizes of lobster moved across the reserve boundary at the same rate.

Using the tag / recapture data, an estimate of the “catchable population size” could be obtained. In 2005, based on the total number of animals tagged in the reserve and the number of tagged and untagged animals recaptured, a “catchable population” estimate of 106,168 was obtained. Using the same spillover rate as above indicates that 996 “catchable” animals moved out of the reserve in 2005. Based on the mean weight of tagged lobsters that moved out of the reserve and were caught (0.668 kg), an estimated 665 kg of lobsters moved out of the reserve in 2005 and were available to be caught. Again, this is a crude estimate, but all of these estimates could be further refined as data becomes available to account for factors such as fishing effort, catchability, tag non-reporting and mortality, for both reserve and fished locations.

An important consideration in the assessment of the effects of marine protected areas on fisheries, particularly where fisheries catch is managed by TAC such as in New Zealand and Australia, is the effect of effort displacement. Although this study suggested a net export of lobster biomass from Te Tapuwae o Rongokako Marine Reserve, the reserve’s establishment resulted in displacement of fishing effort, increasing the catch required to be taken from the remaining CRA3 area. Measurement of such effort displacement has not been included in this study, but should be in any analysis of the effect of MPAs on the wider marine environment or fisheries stocks. The impacts of marine protected area establishment on other fisheries for Jasus edwardsii have been assessed in response to proposed implementation of MPA networks in Australia (Buxton et al., 2006; Gardner et al., 2000; Hobday et al., 2005; McGarvey, 2003). The effect on organisms both inside and outside MPAs must be considered when assessing the impacts of MPAs on fisheries (Gardner et al., 2000). Around Tasmania, the potential effect of MPAs on the lobster fishery depends on the size and location of the MPA, primarily because aspects of the biology of lobsters, such as fecundity and growth, vary so dramatically around Tasmania. For example, modelling suggested that MPAs placed in southern Tasmania would reduce the statewide biomass of lobsters (Gardner et al., 2000). Around Victoria, Australia, modelling showed that the displaced effort as a result of MPA establishment would increase the time required for the surrounding stocks to recover to specified targets (Hobday et al., 2005). In South Australia, modelled effects of MPA establishment on the lobster fishery have been used to assist in developing a compensation package for affected fishers, involving the government purchase of harvesting rights (McGarvey, 2003).
In New Zealand, the Government’s strategy for the implementation of marine protected areas (Department of Conservation & Ministry of Fisheries, 2005), states that MPAs should be implemented in areas where the impact on existing users is least. As in Tasmania, the New Zealand government has no policy of fishery buy-back to remove displaced effort and so the location and design of marine protected areas such as marine reserves is going to become increasingly important. Once again, the key is to consider the purpose of MPAs such as marine reserves (which is not always to provide for fisheries benefits) and the existing and proposed management regimes in the area surrounding the MPAs. Marine protected area proposals based on perceived benefits to both fisheries and biodiversity risk failing in both objectives, as they can be contrary goals (Gardner et al., 2000). Buxton et al. (2006) suggested that where MPAs were established as fisheries management tools, they would be inferior to existing management options. In addition, they noted that if a fishery was being managed in accordance with ecologically sustainable development (ESD) principles, which by definition means that the ecosystem in which the fishing occurs is not threatened by the fishery or fishing practices, then fishing should not be a key threatening process. The implication was that in terms of biodiversity conservation, true ESD fisheries management would offer a potentially better outcome than no-take MPAs. The same may be argued in New Zealand. An aim of New Zealand’s MPA Policy and Implementation Plan (Department of Conservation and Ministry of Fisheries, 2005) is that marine habitats and ecosystems will be maintained in a healthy functioning state, and degraded areas will be allowed to recover. An MPA is defined as “An area of the marine environment especially dedicated to, or achieving, through adequate protection, the maintenance and/or recovery of biological diversity at the habitat and ecosystem level in a healthy functioning state”. However, the environmental principles contained in the Fisheries Act (1996) are: associated or dependent species should be maintained above a level that ensures their long term viability; biological diversity of the aquatic environment should be maintained; and habitat of particular significance for fisheries management should be protected. Therefore, if these environmental principles are being fulfilled, then the outcome should theoretically be the same as implementation of a marine protected area, under the given definitions. These overlaps need to be considered for not only successful fisheries management, but successful implementation of an MPA and marine reserve network in New Zealand.

In order for marine protected areas to help fulfil biodiversity protection and / or fisheries objectives, there must be a balance or tradeoff between those objectives that is expressed through the appropriate design and management of the MPAs. Such design and management must be supported by other fishery management tools and coastal zone planning to achieve overall protection and sustainability of marine resources (Babcock, 2003; Hilborn et al., 2004; Sumaila
et al., 2000). In the absence of such planning, there is a risk that implementation of particular tools such as MPAs, while potentially fulfilling their objectives within their boundaries, will have negative effects on the wider marine environment, including its fisheries. The key is to have clearly defined objectives for the marine environment and use the appropriate tool or combination of tools to achieve those objectives. This is particularly important in New Zealand given that under the Government’s MPA Policy and Implementation Plan, the effectiveness of individual MPAs at achieving their own specific biodiversity objectives is to be monitored. Regardless, the goals for marine protected areas must be realistic, achievable and in terms of no take marine reserves, recognise that although restoration of ecological integrity may be possible, restoration to the “way it used to be” may no longer be achievable.

Although marine protected areas may not always provide direct or incidental fisheries benefits, they can contribute to fisheries management by providing the ability to detect indirect and ecosystem effects of fishing, or by providing an opportunity to obtain basic biological data on species in the absence of fisheries selection. This study of Te Tapuwae o Rongokako Marine Reserve has demonstrated the usefulness of marine protected areas in this role, as well as fulfilling its objective of providing an opportunity for protection and restoration of species and communities within its boundaries.

7.7 Conclusions

Changes that have taken place within Te Tapuwae o Rongokako Marine Reserve indicate that not only is the reserve fulfilling its conservation objectives, but that fishing has had a significant effect on the population structure and dynamics of lobsters in the East Coast region.

Basic biological data on lobsters was gathered from the marine reserve, without the confounding effect of fisheries selection. For example, growth rates and fecundity estimates for a range of sizes of lobsters were obtained.

Density-dependent effects on lobster growth were proposed to explain the reduction in male growth rate over time within the marine reserve. Potential indirect effects of fishing were detected outside the reserve, including reduced average growth rate in sublegal males and increased incidence of a bacterial infection associated with handling. This study highlighted the adaptability of Jasus edwardsii, with some novel behaviours being recorded, including
cannibalism and daytime foraging, potentially as a response to increased biomass within the marine reserve.

The design of Te Tapuwae o Rongokako Marine Reserve, in conjunction with the reef-associated movement patterns of lobsters, provided for some movement of lobsters across the marine reserve boundaries. Where the reserve boundaries crossed reef habitat, lobsters moved between fished and unfished areas, which has implications for the design of marine protected areas and fisheries management areas, in terms of their ability to fulfil their objectives.
Figure 7-1 A lobster, foraging during the daytime on the intertidal reef platform within Te Tapuwae o Rongokako Marine Reserve.

Figure 7-2 A large male lobster foraging (during the daytime) in a cobble area adjacent to the intertidal reef platform within Te Tapuwae o Rongokako Marine Reserve.
List of References


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