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Survival and behaviour of juvenile red rock lobster, *Jasus edwardsii*, on rocky reefs with varying predation pressure and habitat complexity

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Abstract. The role of large predatory fish in coastal communities is generally unknown because of overfishing. In order to understand the direct and indirect impacts of these increased population sizes on coastal food chains, the effect of areas with more fish predators on the survival and behaviour of potential prey was assessed. Juvenile lobsters, *Jasus edwardsii* (10–20 mm carapace length), were tethered on rocky reefs inside and outside marine reserves in northeastern New Zealand to assess survival under differing predator densities. Since rocky reef habitats in northeastern New Zealand include zones of kelp forest and barren reef, a two-way factorial design was used to determine the effects of predators, habitat, and the interaction of these two factors on juvenile lobster survival. Overall, the results indicated that neither varying large fish density nor varying kelp density had direct impacts on the survival rate of juvenile lobsters. Laboratory manipulations demonstrated behavioural changes by juvenile lobsters such that when a large predatory fish was present, juvenile lobsters spent significantly less time moving, even when separated from the predator by a porous barrier. Thus areas with more fish predators may increase juvenile lobster survival but potentially at the cost of reduced feeding opportunities.

Additional keywords: Blue Cod, Leigh, marine park, Snapper, Tawharanui.

Introduction

Predation is an important post-settlement process affecting the abundance and distribution of benthic marine invertebrates (Stoner 1990; Hunt and Scheibling 1997; McArthur 1998; Ray-Culp *et al.* 1999; Osman and Whitlatch 2004). The first benthic stages of lobsters are particularly susceptible to predation since they are small and dependent on protective habitat (Heck *et al.* 2003). Settlement into suitable habitat may facilitate the ability of juveniles to seek shelters and use cryptic or aggregation behaviour to increase survival (Eggleston and Lipcius 1992; Palma and Steneck 2001). Shelters are mostly associated with topographically complex habitats such as reefs, macroalgae, or large sessile marine invertebrates. However, many of these complex habitats may also attract predators that are foraging or seeking protection from even larger predators (Choat and Ayling 1987). For these reasons, predation on juvenile marine invertebrates may be an important link in the marine food chain.

The present study focuses on predation on recently settled juvenile lobsters because the adult lobsters are both important predators and a commercial species. Most predation studies on juvenile lobsters have been conducted in areas that have food webs altered by overfishing (Hughes 1994; Steneck 1997; Jackson *et al.* 2001) and where large predatory fish are rare (Steneck 1997; Mai and Hovel 2007). The establishment of marine reserves has allowed populations of large predators to recover in coastal zones, thereby creating areas with increased sizes and densities of predators that may be more representative of natural food chains (Russ and Alcala 1996; Babcock *et al.* 1999; Edgar and Barrett 1999; La Mesa and Vacchi 1999; McClanahan *et al.* 1999; Willis *et al.* 2003; Lafferty 2004). The presence of large predators has caused changes within protected areas. For example, adult lobsters and predatory fish have the potential to indirectly alter habitat structure by consuming urchins and preventing them from overgrazing large macroalgae (Shears and Babcock 2002; Hereu *et al.* 2005). In temperate reef areas protected from fishing, a notable transition from urchin barrens habitat to macroalgal habitat has occurred (Babcock *et al.* 1999; Shears and Babcock 2002, 2003; Lafferty 2004; Parsons *et al.* 2004).

Predation among species at higher trophic levels may modify the response of protected populations in reserves, thus the extent to which predatory fish are impacting other marine invertebrates including juvenile lobsters in protected coastal areas is still unclear, especially in areas where fish populations may recover rapidly (Denny *et al.* 2004). Predators, even in overfished areas, already appear to have a strong effect on the distribution and behaviour of juvenile lobsters. Larvae of most lobster species tend to settle into topographically complex habitats (reviewed by Booth and Phillips 1994), including cobbles in Maine (Wahle

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Table 1. Summary of ratios of fish densities in protected *v.* unprotected areas in north-eastern New Zealand (Cole *et al.* 1990; Willis and Anderson 2003; Willis *et al.* 2003)

'NA' means data not available. Fish species with the size defined as 'large' are target species for fishers in north-eastern New Zealand in accordance with local fishery management rules

Fish species (common name)	Size	Leigh Reserve:non-reserve	Tawharanui Reserve:non-reserve
Pagrus auratus (Snapper)	Large (>270 mm)	16:1	16.5:1.0
Parapercis colias (Blue Cod)	Large	4.8:1.0	NA
Pagrus auratus (Snapper)	Small (<270 mm)	1.0:1.5	1:1
Notolabrus celidotus (Spotty)	Small	1:1	NA
Upenichthys lineatus (Goatfish)	Small	1.0:2.7	NA

and Steneck 1992), macroalgae and sponges in Florida (Herrnkind and Butler 1986; Smith and Herrnkind 1992; Childress and Herrnkind 1994), and crevices in New Zealand (Booth and Phillips 1994). In most of these regions, lobster mortality owing to predation is lower in complex habitats compared with adjacent exposed areas (Herrnkind and Butler 1986; Smith and Herrnkind 1992; Wahle and Steneck 1992; Childress and Herrnkind 1994). Fish predators may also impact the behaviour of some juvenile lobster species by increasing the time individuals spend in shelters and limiting the quantity of food they consume (Lawton 1987; Wahle 1992; Spanier *et al.* 1998). Therefore, an influx of large fish predators may cause rapid changes in lobster populations through direct predation or indirect behavioural changes.

Marine reserves in north-eastern New Zealand provide excellent field sites for determining the impact of large predatory fish on recently settled juvenile lobsters, *Jasus edwardsii* (Babcock *et al.* 1999; Shears and Babcock 2002; Willis and Anderson 2003; Willis *et al.* 2003). Babcock *et al.* (1999) and Willis *et al.* (2003) recorded significantly increased abundances of the Snapper, *Pagrus auratus*, in marine reserves (Table 1). Increased size and abundances of other large fish species, including Blue Cod, *Parapercis colias*, have also been found (Cole *et al.* 1990; Willis and Anderson 2003). Another marine reserve-induced change is the recovery of an *Ecklonia radiata* kelp forest in intermediate depth strata (Babcock *et al.* 1999; Shears and Babcock 2002, 2003; Parsons *et al.* 2004). The increase in kelp forest provides additional complex habitat, which may serve as shelter for settling juvenile *J. edwardsii*. Increased abundances of predatory fish may also influence the behaviour of juvenile lobsters by causing more cautious behaviour, limiting their foraging time and range.

The present study addressed three questions: (*1*) Are decreases in the survival of juvenile *J. edwardsii* associated with areas that contain large fish predators? (*2*) Does the increase in complex kelp forest habitat enhance the survival of juvenile *J. edwardsii*? (*3*) Is the behaviour of juvenile *J. edwardsii* changed by the presence of large fish predators?

Materials and methods

Field survival

Two marine reserves in north-eastern New Zealand were used in the present study (Fig. 1). The Cape Rodney to Okakari Point Marine Reserve (CROP), also known as the Leigh Marine Reserve, was established in 1976, and the Tawharanui Marine Park was established in 1982. Both are completely protected from all forms of fishing. Temperate rocky reefs in north-eastern New Zealand support the brown alga, *Carpophyllum* spp., in the shallowest depths <3 m, mixed fucoid and laminarian algae or urchin barrens between ~3–9 m, and kelp forest dominated by *Ecklonia radiata* in depths 9–18 m (Parsons *et al.* 2004).

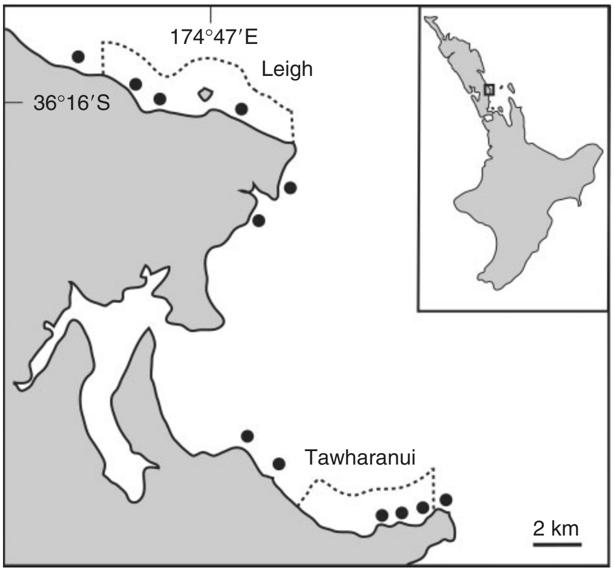

Fig. 1. Study sites around Leigh and Tawharanui in north-eastern New Zealand. The dotted line indicates the boundaries of the no-take marine reserves. Circles specify the study sites. The inset shows the study area location on the North Island of New Zealand.

Tethering experiments were used to determine the survival rates of juvenile *Jasus edwardsii* in reserves relative to surrounding areas. The experiments were conducted in the summer of 2002–2003. Three sites were selected inside and outside both the Leigh and Tawharanui reserves for a total of 12 sites (Fig. 1). Sites were situated at ~8–10 m depth on rocky reef covered with *Ecklonia radiata* forest. At each site, 5 × 5 m plots were cleared of all macroalgae in order to simulate urchin barrens because few such areas remain within marine reserves. Adjacent to the urchin barrens plot, a 5 × 5 m plot with macroalgae was also designated.

Artificial shelters were used to avoid variation inherent in natural crevices. Shelters were constructed using PVC pipes (32 mm diameter × 75 mm length) similar in size to natural holes that typically house settled juvenile *Jasus edwardsii* in this region (Butler *et al.* 1999). Because most natural holes have only one opening, each pipe was closed at one end by inserting a plastic barrier (Norman and Yamakawa 1994; Butler *et al.* 1999). Then each pipe was attached to two 1-kg lead weights with cable ties. The whole assembly was covered in non-toxic black sealant and placed in an outdoor tank with flow-through seawater for a month to be colonised by algae and leach out unnatural chemicals. Shelters were transferred to field sites where five shelters were placed haphazardly in barren plots, and five more were placed in adjacent kelp forest plots at least one week before the start of the tethering experiment. Thus, the experiment included five lobsters per treatment with two treatments per site and three sites per area, equalling 30 lobsters exposed to abundant predators within each of the reserves, and 30 lobsters exposed to less abundant predators outside each of the reserves.

Juvenile *Jasus edwardsii* (10–20 mm carapace length (CL)) were collected from the wild. This size class of recently settled juvenile lobsters is categorised as 'early benthic juvenile' based on ontogenetic differences when compared with older, larger juveniles (see Butler *et al.* 1999). Since only one size class of juvenile lobsters is used in the present study, 'early benthic juveniles' (10–20 mm CL) are hereafter referred to as 'juvenile.' The juvenile lobsters were kept in large flow-through seawater tanks and fed mussels *ad libitum* at the Leigh Marine Laboratory. Tethers were attached to the lobsters using a slight modification of Herrnkind and Butler's (1986) method. A 15-cm long piece of 3-kg monofilament nylon line was tied around the carapace of each juvenile *J. edwardsii* between the 4th and 5th pair of walking legs. The knot was attached to the carapace using a small drop of cyanoacrylate glue. The other end of the line was attached to a clasp with a fishing swivel for quick attachment to shelters. Lobsters were held for 12 h overnight in the laboratory after line attachment. During this period of time no lobsters escaped their tethers and only one mortality potentially associated with the tethering process was observed.

Lobsters were transported to the field in individual containers aerated by battery-operated pumps. A diver swam these containers down to the sites. Tether clasps were attached, and lobsters were gently introduced to the shelters. Observations one day later showed that lobsters behaved naturally, remaining near the shelter entrance with their antennae exposed except when disturbance provoked their withdrawal into the shelter. Because tethers may restrict lobster movement somewhat, they may reduce the effectiveness of natural escape behaviours. Accordingly, the present study focussed not on absolute survival rates but rather on relative survival under contrasting conditions (Barshaw and Able 1990; Peterson and Black 1994). Lobster survival was monitored once every 24 h for 4 to 5 days after initial tethering by which time 100% of the lobsters had been eaten at some of the sites.

Survival data follow a binomial distribution, which violates the normal distribution assumption of ANOVA. Consequently, a generalised linear mixed model was used to analyse the data (McCullagh and Nelder 1989). The data were modelled using SAS statistical software with the GLIMMIX macro. A pooling procedure (i.e. backfitting procedure) was used to combine non-significant factors with the residual to increase statistical power. Covariance parameter estimates included a first-order autoregressive because the time series of observations of lobster survival on consecutive days were not independent (Chatfield 1985). Area (Leigh and Tawharanui), Status (reserve and non-reserve), Day (1, 2, 3, 4), and Habitat (Kelp and Urchin Barrens) were treated as fixed effects. Day 5 was not tested in the model because it was observed only at Leigh. Site was treated as a random block.

Laboratory behaviour

Behaviour experiments conducted in laboratory tanks examined effects of large predatory fish on juvenile *Jasus edwardsii* foraging time. The experimental set-up resembled that of Spanier *et al.* (1998). Two large flow-through seawater tanks were each divided into two sections by a clear perforated piece of plastic. Water flowed through the tank from a hose in the first compartment to the drain in the second compartment. The first compartment contained either a large predatory fish, the Blue Cod, *Parapercis colias* (>300 mm) or was empty (control) and the second compartment contained an individual juvenile lobster (10–20 mm CL). During the experiment, the lobster could receive both visual and chemical cues from the predator in the first tank without being eaten. The tanks were exposed to a 12-h light-dark cycle with the tanks illuminated by an overhead fluorescent light during the day and infrared bulbs at night. A time-lapse video recorder directly above the tanks recorded the movements of the lobsters over 24 h.

When not used in experiments, juveniles were kept in large flow-through seawater tanks at the Leigh Marine Laboratory. They were fed mussels *ad libitum*. At the start of each experimental run, one haphazardly selected and recently fed juvenile *J. edwardsii* was introduced to a small shelter made of half a PVC pipe (16 mm height and 75 mm length) in each tank and allowed to acclimate for 24 h. The shelter was located near the centre of the lobster compartment with the opening directed towards the predator compartment. One tank was then randomly selected as the predator treatment and the other tank was left empty as the control treatment. A Blue Cod was placed in the first compartment of the predator tank, and the tanks were videotaped for the next 24 h.

Videos were examined to quantify the amount of time during the 24-h period that the lobster was active. Activity was measured because movement provided the best evidence of foraging behaviour. Lobsters were considered inactive if they remained stationary for more than 5 min. There were five replicates of each treatment ($n = 5$), and lobsters were used only once throughout the experiment to maintain independence. A t-test for paired data was used to compare the number of minutes in 24 h the juveniles remained active in predator treatments and controls.

Results

Field survival

Survival of juvenile lobsters was not influenced by Area, Habitat, or Predator Presence (Fig. 2). However, there was a significant first-order autocorrelation estimate in the covariance parameters ($Z = 17.93$, $P < 0.0001$, $d.f. = 23$) which indicates that sites

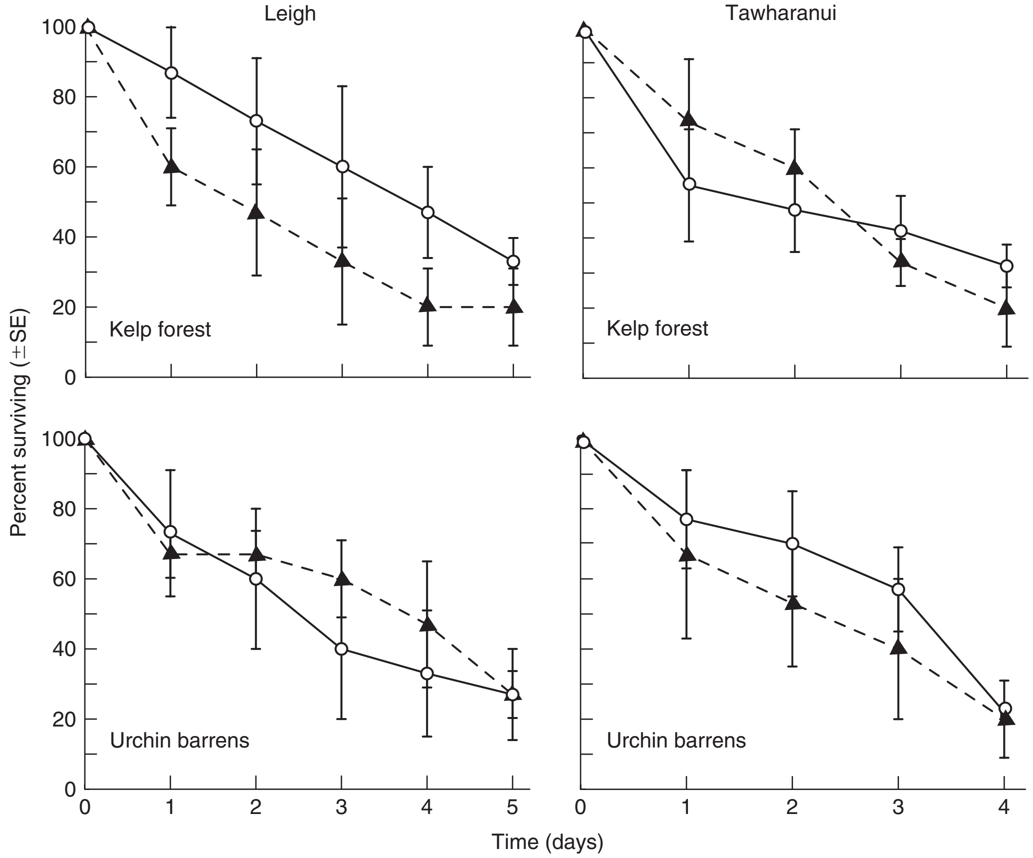

Fig. 2. Survival of juvenile lobsters tethered in different habitats. –▲– indicates the mean percentage surviving at sites where large predators are abundant. –○– indicates the mean percentage surviving at sites where large predators are rare. Each point represents the average percentage of a maximum of five lobsters that remain present each day at three sites. The error bars represent standard error.

with lobster predation on one day would tend to have lobster predation on the following day. There also was a significant effect of Day ($F_{3,67} = 19.27$, $P < 0.0001$) which means that lobsters were consumed daily during the present study. The autocorrelation and the Day effects means were consistent within the factors of Area, Status, and Habitat. Figure 2 shows that over a period of 4 days, the number of surviving lobsters fell to less than 30 percent of the 60 lobsters initially present. A comparison between the number of lobsters eaten per capita per day in reserves and non-reserve areas was non-significant ($F_{1,20} = 0.75$, $P = 0.39$) (Fig. 3).

The identity of the lobster predator(s) remains unclear because in most cases only a small piece of carapace remained attached to the tether by the cyanoacrylate glue. However, small octopuses were sometimes unexpectedly found in the shelters after the lobsters had been eaten. It seems likely that they consumed the former inhabitants of the shelters, but this suspicion could not be confirmed.

Laboratory behaviour

In the laboratory, predator presence greatly reduced juvenile lobster activity ($t_4 = 8.58$, $P = 0.0010$) (Fig. 4*a*). Most of the time,

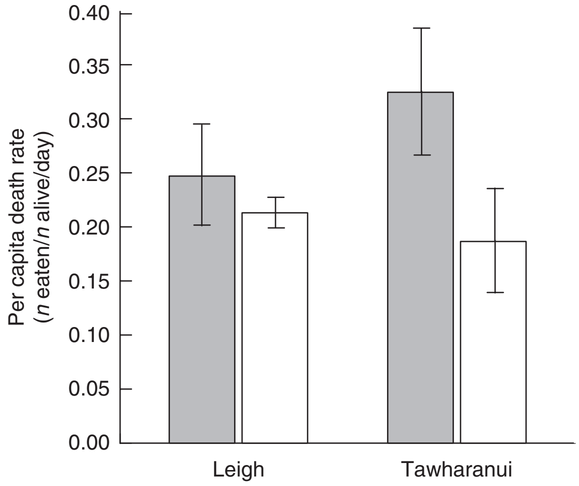

Fig. 3. The predation rate of juvenile lobsters tethered in areas with different predator densities. Solid bars: large fish predators abundant. Open bars: large fish predators rare. Data are the mean number of lobsters that disappeared on each day divided by the number that had been alive on the previous day, ± standard error, $n = 30$.

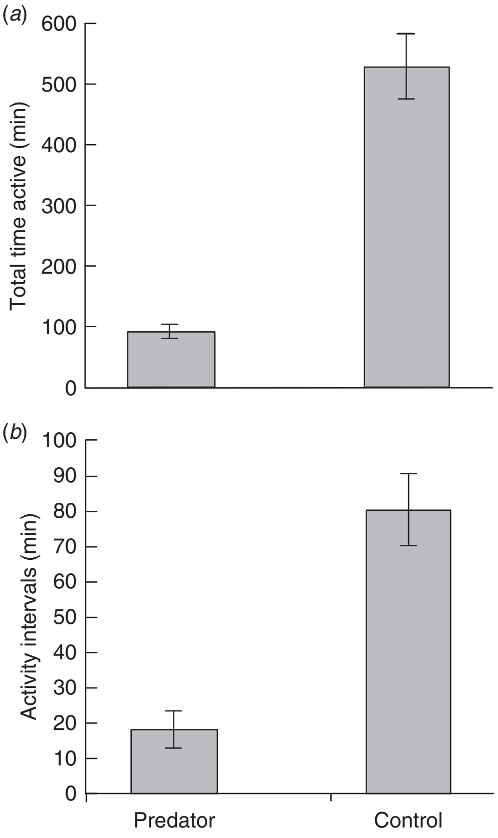

Fig. 4. The effects of predators on juvenile lobster behaviour during 24-h observation periods. The error bars represent standard error and $n = 5$. (*a*) Data are the mean total minutes that the lobsters were active. (*b*) Data are the mean minutes that the lobsters were continuously active at a time.

inactive lobsters retreated into shelters or corners of the tank when startled by predator movement. Juvenile lobster activity occurred mainly at night. In the predator treatment tanks, juvenile lobster activity followed a pattern of short, quick movements divided by long periods of inactivity (Fig. 4*b*). In contrast, the juvenile lobsters in control treatments remained constantly active for periods up to 464 min.

Discussion

Recovery of large predatory fish populations in marine reserves in north-eastern New Zealand led to the discovery of top-down controls on the trophic structure there (Cole and Keuskamp 1998; Babcock *et al.* 1999; Shears and Babcock 2002). Large predatory fishes, including Snapper and Blue Cod, are both more abundant and greater in size inside marine reserves than in physically similar areas less than 2 km away (Cole *et al.* 1990; Babcock *et al.* 1999; Willis and Anderson 2003). In the present study, the first question addressed whether there was a decrease in the survival of juvenile *Jasus edwardsii* in areas with large predators. The present study found that survival of small lobsters, 10–20 mm carapace length, in the field appears not to be associated with the abundance of large fishes. Many studies have shown that the Leigh and Tawharanui marine reserves have greater densities of large predatory fish compared with unprotected areas (Table 1). It is possible that abundance of large fish did not affect juvenile lobster survival because large predatory fish may not be major juvenile lobster predators. Recently recruited lobsters of 10–20 mm carapace length are quite small and may provide little or no net energetic benefit to a large fish. Instead, small predatory fish and juveniles of larger fish, which are found in all areas, may be the most important juvenile lobster predators (Table 1). In a similar study in Maine, Steneck (1997) found that juvenile *Homarus americanus*, 30–38 mm carapace length, were more heavily predated upon at sites where large predatory fish were rare, a pattern consistent with this conclusion. In addition, removal of the large fish may release predatory invertebrates and smaller fish from predation, allowing their populations to expand (Steneck 1997; Graham *et al.* 2003).

Predation by invertebrates such as octopus also may be a factor (Berger and Butler 2001). Octopuses have similar habitat preferences to juvenile lobsters and occupy crevice shelters in rocky reefs. Shelters are not believed to be limiting for octopuses in rocky reef areas, and octopuses frequently move to new shelters (Ambrose 1982). Thus, the octopuses found in the lobster shelters may have just been looking for a new shelter rather than a meal when they found the shelters during the present study. However, it is also possible that the octopuses were actively searching for food and discovered the tethered lobsters. *Octopus bimaculatus* preferred crustaceans in laboratory choice experiments in California (Ambrose 1984), and *Octopus maorum* are considered a pest that consumes lobsters in traps by the commercial lobster industry in Australia and New Zealand (Ambrose 1988; Harrington *et al.* 2006). Historically, octopuses may have been subjected to predation pressure from large fish (Ambrose 1988). In marine reserves in north-eastern New Zealand, octopus remains have been found in the guts of fishes, but the impact of increased densities of fish predators on octopus distribution and survival has not been measured (Anderson 1997). Therefore, if mid-sized predatory fish and octopuses are major predators on lobster recruits, there may actually be lower predation on small lobsters in protected areas that have abundant large fish. Unfortunately, the present study was not able to resolve this matter.

The second question addressed whether an increase in complex kelp forest habitat enhanced the survival of juvenile lobsters. It was found that kelp forest cover did not appear to enhance the survival rate of juvenile lobsters using artificial shelters. However, additional topographical complexity may not have been necessary because lobsters were already provided with protective artificial shelters that could completely conceal them. In a study at the Medes Islands Marine Protected Area, there was no difference in survival of juvenile lobsters, *Palinurus elephas*, in fished *v.* unfished areas when the lobsters were able to access natural rock shelters (Díaz *et al.* 2005) which is consistent with the findings of the present study. However, Díaz *et al.* (2005) did find lower survival in unfished *v.* fished areas when lobsters had no shelter access. Although this is consistent with expectations, the ecological significance of this pattern is unresolved as juvenile lobsters are rarely found outside shelters except at night when visual predators such as fish are inactive or disadvantaged.

The shelter design used in the present study was selected based on a similarity to small natural holes where juvenile *J. edwardsii* are most often found (Norman and Yamakawa 1994; Butler *et al*. 1999). Although many settling lobsters use small holes, it is possible that some lobsters settle in areas with fewer or lower quality shelters. In these shelter-poor areas, topographical complexity from kelp canopy may increase lobster survival. Alternatively, topographical complexity from the kelp canopy may provide cover for some of the small fish and invertebrates that are potential juvenile lobster predators. In this case, kelp cover would not be advantageous for the lobsters, and it is unlikely that there would be a difference in survival between the kelp forest and barren areas. However, in order for this to be determined, it would be necessary to identify the lobster predators and observe the predators' habitat preferences.

The third question addressed whether the behaviour of juvenile lobsters changed in the presence of fish predators. It was found that when presented with a large predatory fish in a confined area in the laboratory, juvenile lobsters greatly reduced the kind of activity (i.e. movement outside shelters) that in nature is required for foraging. Large predatory fish may cause changes in juvenile lobster behaviour even if they do not directly feed on them. During laboratory trials, the reduction in *Jasus edwardsii* activity in response to the Blue Cod, *Parapercis colias*, may indicate that higher densities of fish reduce foraging time, food consumption, and growth rate.

This response is similar to that of many other organisms that assess predation risk and modify their behaviour accordingly (reviewed by Lima and Dill (1990)). Evidence for this ability in other crustaceans including juvenile American lobsters, *Homarus americanus*, and small freshwater crayfish, *Orconectes propinquus*, consists of observed decreases in activity and food consumption in response to predator presence (Stein and Magnuson 1976; Lawton 1987; Wahle 1992; Spanier *et al*. 1998). Behavioural adaptations of prey have also successfully decreased predation by some fish predators (Main 1985). During the field experiment, lobster behaviour may also have been an influencing factor on survival. Sheltering behaviour may have compensated for the increased risk of predation from fish in reserves or the presence or absence of kelp cover, which may explain the similarity in survivorship between the treatments. Whether this level of compensation could be maintained throughout the entire juvenile stage as the need to forage became progressively greater is not clear. This is a question that needs to be addressed if the implications of variation in predator density on lobster recruitment are to be fully understood.

Marine reserves continue to provide opportunities to demonstrate potential interactions between large predators and their prey species in north-eastern New Zealand (Babcock *et al*. 1999; Shears and Babcock 2002; Willis and Anderson 2003). In any case, an increase in large fish predator abundance appears not to have exerted much direct impact on juvenile *Jasus edwardsii* in the present study, but a more indirect influence remains a possibility. It is important to note that abundances of commercial size *J. edwardsii* have continued to increase in fully-protected marine reserves since their establishment and consistently higher abundances of lobsters have been found inside reserves compared with surrounding areas (Shears *et al*. 2006). Results to date are encouraging in that they suggest the existence of few if any feedbacks in the interactions between major commercially fished predatory species such as lobster and large finfish on reefs in north-east New Zealand. If true, it will simplify efforts to implement ecosystem-based fisheries management in this region, but our results need to be extended by larger, longer-term studies of lobster survival.

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