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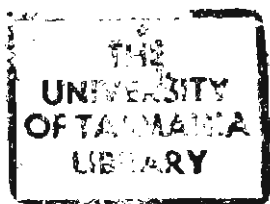
**The Ecology of the Juvenile Southern Rock Lobster,  
*Jasus edwardsii* (Hutton 1875) (Palinuridae).**

by

Matthew Edmunds B.Sc. Hons

Submitted in fulfilment of the requirements for the degree of  
Doctor of Philosophy

University of Tasmania, August 1995



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A handwritten signature in blue ink, appearing to read 'Matthew Edmunds'.

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## Abstract

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This study examined the life history of juvenile *Jasus edwardsii*, with a particular emphasis on ontogenetic shifts in ecology, and how these shifts and other ecological factors may influence recruitment rates to maturity and the fishery. The aspects examined included settlement, density and distribution, shelter utilisation and availability, diet, morphology, as well as growth, survival and movement.

Shifts in ecology, particularly in dispersion patterns, shelter utilisation and diet were found throughout the juvenile size range. However, a distinct early benthic phase was recognised, with a rapid transition from this phase occurring at approximately 35 mm carapace length (CL). More gradual shifts in ecology occurred after this size. Early benthic phase lobsters were solitary dwellers, randomly to evenly dispersed over the reef and consumed predominantly ophiuroids, isopods and bivalves. In contrast, larger juveniles were gregarious, cohabiting in shelters with conspecifics and having clumped shelter distributions. They also consumed predominantly bivalves, crabs and urchins. These changes corresponded with allometric changes in morphology.

Early benthic lobsters had specific shelter requirements compared to the broader range of shelters used by larger lobsters, and were more likely to be affected by limitations in shelter availability. Shelter availability was dependent on the substrate type and structure, but was not found to be limiting during this study. However, settlement rates during this study were low, and shelter may be limiting at higher settlement rates.

Internal microtagging techniques were developed to examine the population dynamics of newly settled lobsters (from 10 mm CL or 0.6 g). The growth of microtagged lobsters released in the wild was seasonal, ranging from a mean of 2.5 mm CL per month in summer to a mean of 1.1 mm CL per month in the winter. The loss rates of tagged lobsters from the study area, due to mortality and emigration, were high and varied between release batches, the probability of survival ranging from a maximum of 51% to less than 1%. Lobsters remaining in the study area had a high fidelity to particular shelters.

The results of this study suggest that the early benthic phase is a critical phase in determining recruitment rates to maturity and the fishery, particularly due to the influences of specific shelter requirements, increased susceptibility to predation and variations in growth and survival.

## Acknowledgments

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This project was first conceived while I was counting thousands of eggs for Bob Kennedy, at the Division of Sea Fisheries laboratories at Taroona. Bob filled my head with ideas about lobster ecology and microtagging, and things just escalated from there. Many thanks go to Bob for introducing me to the world of lobsters.

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Substantial support was also provided by the staff of the Zoology Department at the University of Tasmania. I wish to thank Ron Mawbey for making sure I brought my assistants (and myself) back in one piece. I would like to thank Richard Holmes for fixing everything that broke, and particularly for keeping both *SS Chuck* and *Uni Research* afloat. I would also like to thank Barry Rumbold, Wayne Kelly, Sherrin Bowden and Sam Thalman for their help. I am grateful to Leon Barmuta and Alistair Richardson for help with statistical problems, and also to Simon (Spooner) Wotherspoon (Department of Mathematics).

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## Introduction

### 1.1 General Biology and the Fishery

The southern rock lobster *Jasus edwardsii* (Hutton 1875) (Palinuridae) inhabits rocky reefs, between 1 m and 200 m depth, along the coastlines of southern mainland Australia, Tasmania and New Zealand. The range of *J. edwardsii* in Australia extends from as far west as Geraldton in Western Australia (29° S, 114° E) to Coffs Harbour in northern New South Wales (30° S, 172° E; Brown & Phillips 1994). In New Zealand, the range extends from Three Kings Islands in the north (34° S, 172° E) to the Auckland Islands in the south (51° S, 166° E), and to the Chatham Islands in the east (44° S, 176° W; Kensler 1967). Most of the Australian population is present in South Australia, Victoria and Tasmania, supporting a substantial fishery in these areas (Fig. 1.1). There are also small fisheries near Esperance in Western Australia and in New South Wales. The main fishing areas in New Zealand are the east coast of the North Island, the east, south and southwestern coasts of the South Island, Stewart Island and the Chatham Islands. The Australian population was formerly described as *Jasus novaehollandiae* (Holthius 1963), but recent studies found the Australian and New Zealand populations to be a single species and possibly the same stock (Booth *et al.* 1990; Ovenden *et al.* 1992).

*Jasus edwardsii* populations were originally fished by the indigenous people of Australia and New Zealand. A small scale fishery also emerged with the arrival of Europeans in the late 1700's, and lobsters were often the primary sustenance of shipwrecked sailors, being easily caught from rock pools and shallow waters (O'May 1985; Brettingham-Moore 1988; Booth & Breen 1994; Brown & Phillips 1994). Prior to the rapid expansion of the fishery in the late 1940's, the population stocks were high. During the late 1800's and early 1900's, fishermen on the east coast of Tasmania reported huge catches of lobsters with minimal effort. Record catches include a hundred score (24 to the Tasmanian fisherman's score) of lobsters in one day using cray rings (a baited hoop net) by James Rattenbury (between 1899 and 1918; Kerr 1985). James Rattenbury's son, Harold, also reported exceptional catches of 61 score from 48 potlifts in 1925 and 127 score in 14 hours in 1934

(Kerr 1985). At that time, it was considered common for a boat with 20-30 pots to catch 36 score a day (Bridge 1993). Dense aggregations of lobsters were also directly observed in the 1920's by Jack Norling, an eastern Bass Strait fisherman:

*I found the ground there at Patriarchs [Flinders Island]. I saw crays [lobsters] so thick there once that there was crays with their horns out of the water all along the beach. Just shoot the pots and haul them and they were full, and crays all over the top of them too. (Kerr, Of Men, Boats and Crayfish, undated).*

The *J. edwardsii* fishery in New Zealand and Australia expanded dramatically after World War II with the development of a large market in the United States for frozen tails (Booth & Breen 1994; Brown & Phillips 1994). Catches increased to a maximum level in the late 1950's to early 1960's, with peak catches of 12000 t in New Zealand and 6000 t in South Australia (Booth & Breen 1994; Brown & Phillips 1994). Catches were generally stable between the 1960's and 1980's, but the effort steadily increased as populations declined. *Jasus edwardsii* is currently fully exploited in both countries with catch rates still declining in many areas. There is currently a concerted effort by industry and governments to limit the exploitation rate and increase the egg production (Booth & Breen 1994; Brown & Phillips 1994).

The *Jasus edwardsii* fishery is currently one of the most economically valuable fisheries for both New Zealand and Australia. The current markets are primarily Japan, Hong Kong and Taiwan for live lobsters and the United States for frozen tails. The Australian catch for the 1992/93 season was 5184 t (for Victoria, South Australia and Tasmania) with a landed value of approximately \$A 110 million (Southern Rock Lobster Research Group Meeting, Adelaide, 30 June 1994). The New Zealand catch in 1991 was limited to a total allowable catch of 3000 t from the North and South Islands and 503 t from the Chatham Islands, with the 1991 exports worth \$US 56 million (Booth & Breen 1994).

The biology of *Jasus edwardsii* has been well studied compared to many other coastal reef animals. Much of the current knowledge was determined from fishery-related investigations, and mostly pertains to the commercially caught sub-adult and adult stages. However, the knowledge of other life history stages has expanded rapidly in recent years from diving research and the development of larval sampling techniques.

*Jasus edwardsii* usually shelters by day within holes and crevices on the reef. The larger juveniles and adults are gregarious, with occasionally up to 105 individuals cohabiting in

the same shelter (MacDiarmid 1994). Peers of the same size and sex tend to cohabit, although mature males are usually more widely dispersed between the shelters, particularly during the mating period (MacDiarmid 1994).

The lobsters emerge from their shelters soon after sunset to forage on the reef. Although the lobsters will scavenge dead material, and hence enter baited traps, they are primarily a predator of urchins, crabs and other crustaceans, as well as gastropods, chitons and bivalves (Hickman 1945; Fielder 1965). Individual lobsters do not move far from their shelters while foraging, with a median range of 24 m, and usually return to the same shelter, or one nearby, before sunrise (MacDiarmid *et al.* 1991).

Seasonal movements (of 100s of metres) occur between shallow and deep areas of coastal reefs (less than 30 m): moving inshore to moult (females in May, males in October to November); females aggregating at the deeper reef edges during the egg-bearing period; and large males foraging off the deeper reef edges in summer (December to January; McKoy & Leachman 1982; MacDiarmid 1991). Larger scale dispersal also occurs, particularly onto deeper reefs, but most lobsters do not move further than a few kilometres each year (Annala 1981; J. Prescott, pers. comm., South Australian Research and Development Institute; R. Kennedy, pers. comm., Tasmanian Division of Marine Living Resources). A small proportion of lobsters move long distances (10s to 100s of kilometres), but mass migrations have only been observed on the South Island of New Zealand, moving south from the east coast, around the bottom of the island and up the west coast (McKoy 1983; Annala & Bycroft 1993).

Growth rates vary considerably between locations, and between sexes after maturation. Subadults moult one to two times a year, in spring and autumn to early winter, with mature females only moulting in autumn to winter and mature males generally only moulting in spring (Hickman 1945; Annala & Bycroft 1988). The increase in carapace length at moulting ranges from 2 to 14 mm for subadult and adult lobsters (McKoy 1985; Annala & Bycroft 1988; Kennedy & Tarbath 1991). *Jasus edwardsii* can attain large sizes, especially around the islands of Bass Strait, the northwestern coast of South Australia and on the northeastern coast of New Zealand. Lobsters in the Cape Rodney to Okakari Point marine reserve, New Zealand, attain a size of over 160 mm carapace length (CL) for females and 200 mm CL for males (approximately 1.5 kg and 3.0 kg respectively; MacDiarmid 1989a, 1991).

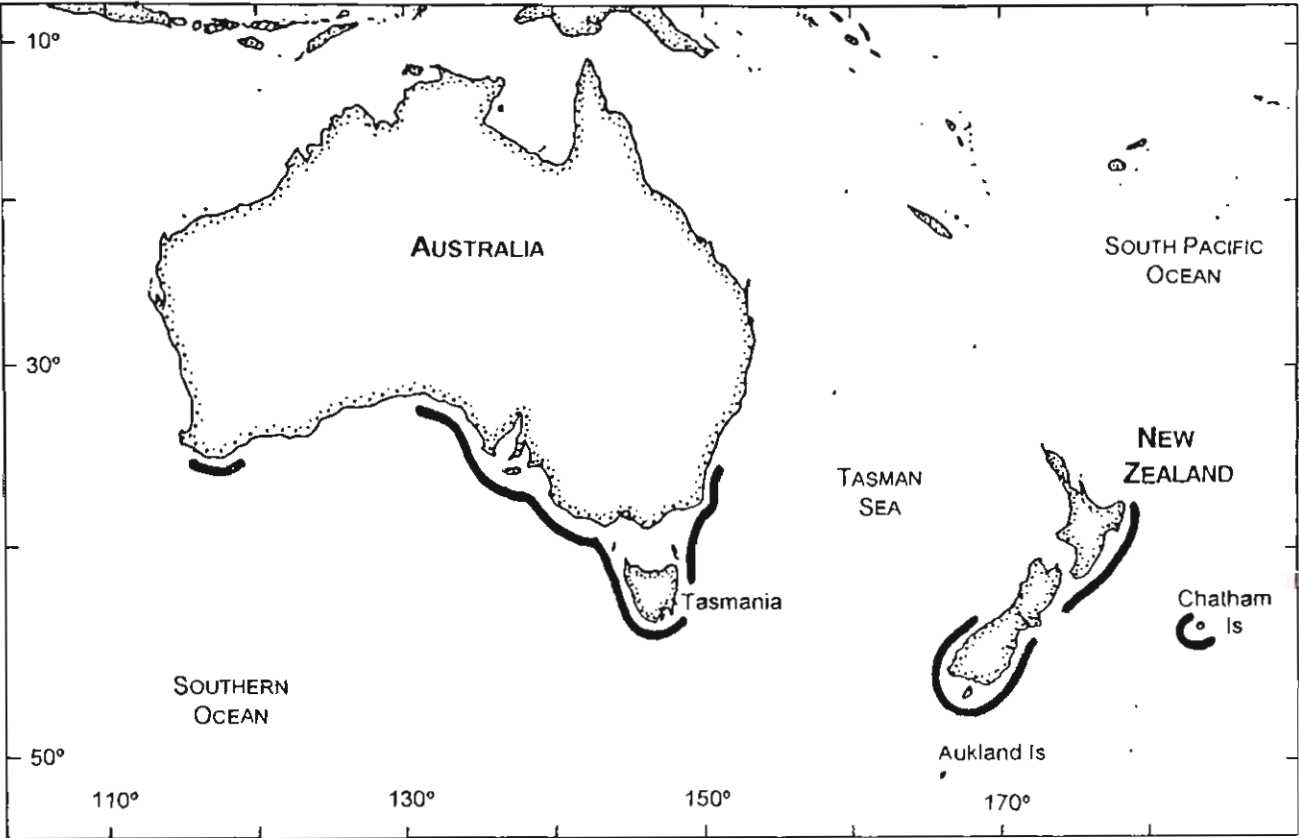


Fig. 1.1. Distribution of the main fishing areas for *Jasus edwardsii*.

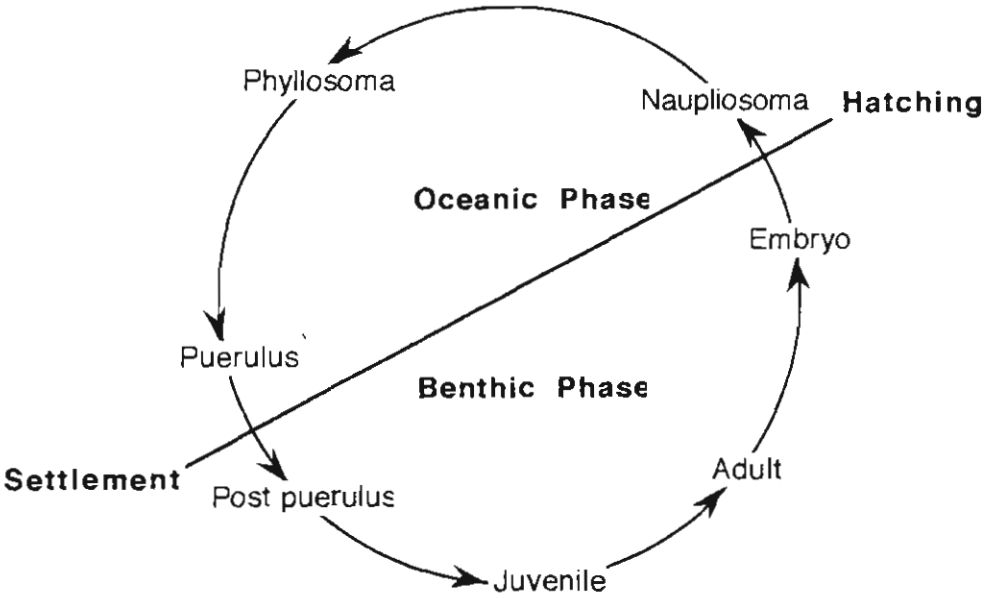


Fig. 1.2. Summary of the life cycle for *Jasus edwardsii*.

The size at onset of maturity is also highly variable between locations, ranging from 72 to 171 mm CL (Annala *et al.* 1980), but lobsters at higher latitudes generally mature at smaller sizes (Kennedy 1989). The age at maturity ranges from 3 to 12 years and the age at legal fishing size (90 to 110 mm CL) is approximately 7-11 years for females and 5-6 years for males (Annala *et al.* 1980; McKoy 1985; Breen & Booth 1994; Brown & Phillips 1994)

## 1.2 The Life Cycle

Mating occurs in autumn (April to July), with the male depositing a spermatophore on the sternal plates of the female (MacDiarmid 1988). The eggs are fertilised externally, and carried by the female on the underside of the abdomen, attached to setae on the pleopods. The number of eggs held is dependent on the lobster size, ranging from 69 000 for a 74 mm CL lobster to over 600 000 for a 155 mm CL lobster (Hickman 1945; Annala & Bycroft 1987; R. Kennedy, pers. comm.). The eggs develop over a period of approximately 100 days (depending on temperature) and usually hatch in spring (September to November; Hickman 1945; MacDiarmid 1989b).

The eggs hatch into a planktonic naupliosoma larval stage, which lasts approximately 12 hours, before moulting into the thin, leaf-like phyllosoma form (2 mm long). The phyllosoma develops through eleven stages, for between 8 to 24 months (Kennedy 1990; Booth 1994). During this time, the phyllosoma are dispersed long distances offshore. At the end of the phyllosoma phase (30-50 mm long), the phyllosoma metamorphoses into the puerulus stage, when near the continental shelf (Booth 1994).

The puerulus (25 mm long) resembles the adult form, but is completely clear and has enlarged pleopods for active swimming. Pueruli cross the continental shelf and settle onto reefs near the coastline, up to depths of 50 m (Booth *et al.* 1991). Pigmentation and moulting occurs within two weeks after settling. The first moult post-puerulus is very similar to the adult form, but has a brown colouration with pale bands, which changes to the distinctive red colour of the adult over subsequent moults.

## 1.3 Ecology of Juveniles

Little is known of the ecology of *Jasus edwardsii* during the first few years after settlement. Post-puerulus lobsters are small, cryptic in colouration and often sparsely distributed, making them difficult to examine in the field. Puerulus regularly settle in high

densities at Castlepoint (north east New Zealand) and at Blackfellows Caves (South Australia) and these sites have been used for examining settlement dynamics and growth rates (Lewis 1977; Booth. 1979). Growth has also been investigated at other areas of high juvenile density, namely Gisborne (northeast New Zealand), Stewart Island (southern New Zealand) and Crayfish Point (Tasmania) (Winstanley 1971; McKoy & Esterman 1981; Annala & Bycroft 1985; Breen & Booth 1989). However, few lobsters below 40 mm CL were observed during these studies.

The development of *J. edwardsii* involves comparatively large changes in body size. Newly settled lobsters weigh approximately 0.4-0.8 g (10-15 mm CL) and attain a weight of approximately 500 g at the legal fishing size (105-110 mm CL in Tasmania). Body size has a predominant influence on energetic requirements, resource exploitation abilities and susceptibility to predation (McMahon 1973; Schoener 1974; Werner & Gilliam 1984). Differences in body size often serve to partition resources, and hence niche requirements, of closely competing species, with a difference in body weight of a factor of two usually required for coexistence (Schoener 1974; Werner & Gilliam 1984). Size changes within species are also often associated with changes in niche and resource use (review by Werner & Gilliam 1984). On this basis, it is likely that there are significant ontogenetic shifts in ecology of juvenile *J. edwardsii*, especially given size changes of nearly three orders of magnitude. Distinct ontogenetic shifts in ecology occur in all other juvenile lobster species that have been examined (reviewed by Cobb & Wahle 1994 and Herrnkind *et al.* 1994).

The ecology of juvenile *J. edwardsii* has important implications for understanding ecological processes of temperate reef communities. Anecdotal evidence of high catch rates of pre-fished stocks, as described above, suggest *J. edwardsii* was an important component of the reef ecosystem, the large numbers probably exerting a considerable predation pressure on the abundance of urchins and other grazers. Other lobster species are also considered important regulators of community structure (*e.g.* Tegner & Levin 1983; Witman 1985). Although stocks have been reduced considerably, *J. edwardsii* may still have a substantial role in community structure and function. However, this cannot be determined accurately without an understanding of the ecology and interactions of both juveniles and adults, as ontogenetic niche shifts can increase the complexity of community interactions. In some instances, the nature of interactions may be reversed at larger sizes (Werner & Gilliam 1984).

The ecology of juvenile lobsters also has an important bearing on the management of the fishery. Density dependent and environmental processes may occur which have a significant impact on the recruitment to maturity and the fishery. This is particularly true



where there are juvenile stages which have specific ecological requirements, or increased susceptibility to predation and environmental influences, than later stages (Childress & Herrnkind 1994; Forcucci *et al.* 1994). Habitat and predator-mediated bottlenecks to recruitment have been found for the American clawed lobster *Homarus americanus* (Wahle & Steneck 1991), the Caribbean spiny lobster *Panulirus argus* (Smith & Herrnkind 1992; Herrnkind & Butler 1994) and the Hawaiian lobster *P. marginatus* (Parrish & Polovina 1994).

## 1.4 Aims and Structure of the Thesis

The aim of this study was to examine and describe the ecology of juvenile *Jasus edwardsii*, particularly from the newly settled post-juvenile stage. Specific aims were to examine:

- a. the nature of ontogenetic changes in habitat and resource use, particularly with respect to distribution, shelter utilisation and diet; and
- b. factors which may influence recruitment, including shelter availability and the dynamics of settlement, growth, survival and movement.

Changes in morphology were also examined to further assess ontogenetic shifts in ecology.

These ecological aspects were studied using direct observations and measurements in the field. Because of the small size of early benthic lobsters, it was necessary to develop and test new tagging methods for studying growth, survival and movement.

The methods and results of these investigations are presented here in separate chapters, relating to settlement, density and distribution, shelter utilisation and availability, diet, morphology, tagging methods and population dynamics. Specific information relating to each of these topics is introduced and discussed within each chapter. An overview of the results, and their implications, is given in the final chapter (Chapter 9). Most of the investigations were carried out at the same sites and, to avoid repetition, these sites are described below.

## 1.5 Description of Study Sites

The geographical range of *Jasus edwardsii* encompasses several biogeographical provinces. These include the western (Flindersian), southern (Maugean) and eastern (Peronian) provinces in Australia (Edgar 1984), and the warm and cool temperate provinces of New Zealand. In addition, *J. edwardsii* occupies a wide range of reef habitats within each region from shallow to deep, and sheltered to exposed, reefs. The reef

communities change significantly between these different habitats (Choat & Schiel 1982; Edgar 1984).

This study was restricted to several locations on the southeast coast of Tasmania (Fig. 1.3), in the cool temperate Maugean province. All study sites were in depths of less than 10 m, were moderately to highly exposed and characterised by a thick canopy of kelps. The principle study sites were mudstone and dolerite habitats in Watsons Bay (Marion Bay, Figs. 1.3, 1.4), and the dolerite reef at Crayfish Point (Hobart, Fig. 1.3).

The mudstone habitat of Watsons Bay was highly diverse with areas of flat reef, eroded gutters, large (> 2 m) rock slabs, boulders and irregular bedrock. Many of the vertical rock faces were highly eroded, providing a high density of small and large crevices, and larger caverns were present beneath the rock slabs. The dolerite habitat of Watsons Bay generally consisted of medium to large boulders (0.5-1.5 m diameter) sloping steeply to flat and irregular bedrock at 8 m depth. Both the Watsons Bay habitats had a thick canopy of *Ecklonia radiata* and *Phyllospora comosa*, with *Carpoglossum confluens* also present. There was a variety of small rhodophyte and phaeophyte algae present beneath the canopy, including *Zonaria* spp, *Sonderopelta coriacea*, *Plocamium* spp and *Lenormandia marginata*. Many of the flat areas beneath the *Phyllospora* were covered in encrusting coralline algae. Large colonies of the bushy bryozoan *Amathia wilsoni* were present, and a diverse range of sessile invertebrates covered the sides of rocks and caverns.

The substrate at Crayfish Point was predominantly dolerite boulders and irregular bedrock structures, sloping gently from the shore to sand at approximately 10 m depth (300 m offshore). The study sites was located at a depth of 6 m. The kelp canopy consisted of *Ecklonia radiata* and *Laminaria corrugata*, and a diverse range of small rhodophytes was present beneath the canopy.

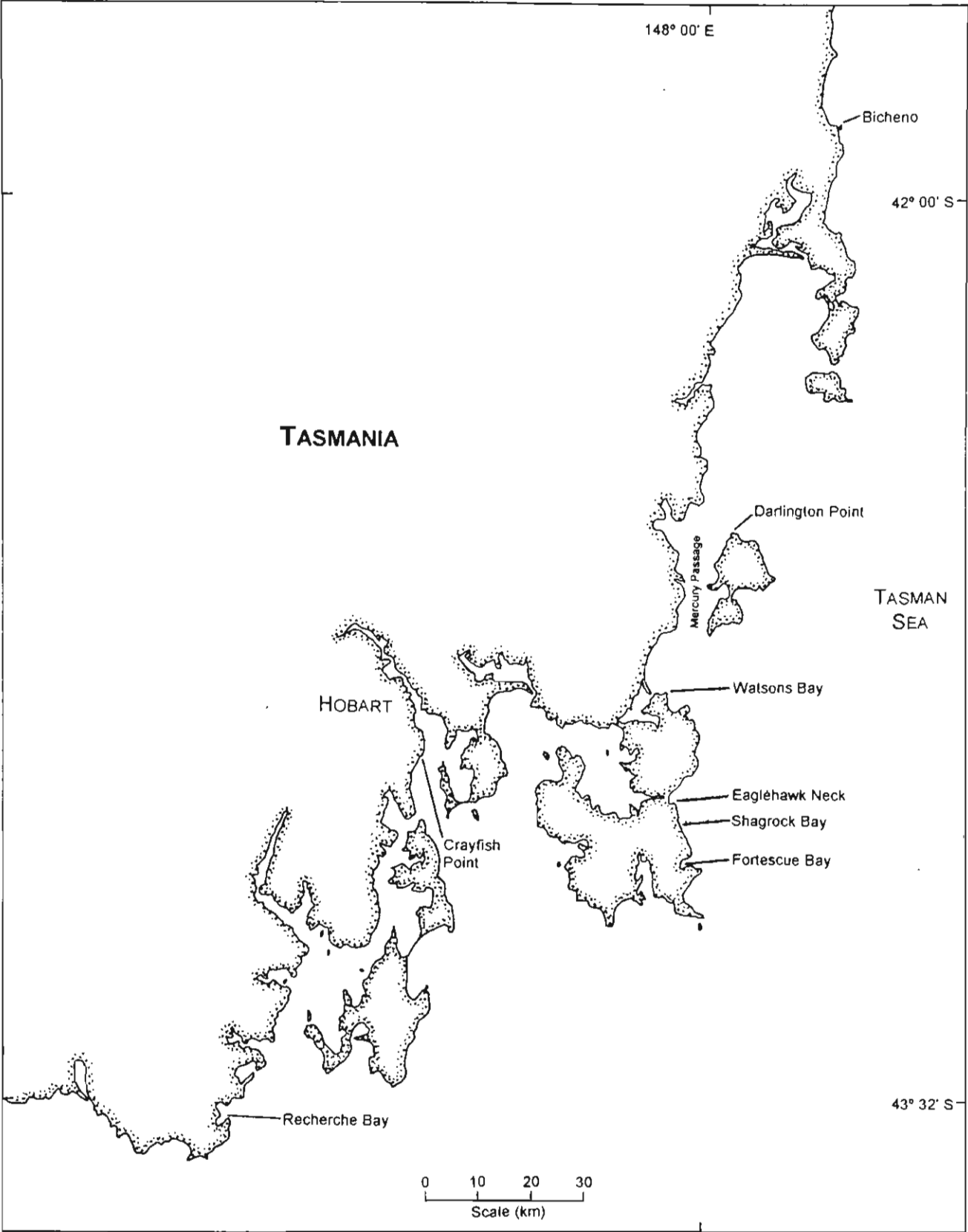


Fig. 1.3. Location of study sites, southeastern Tasmania. The location of government puerulus collector monitoring sites at Bicheno and Recherche Bay are also shown.

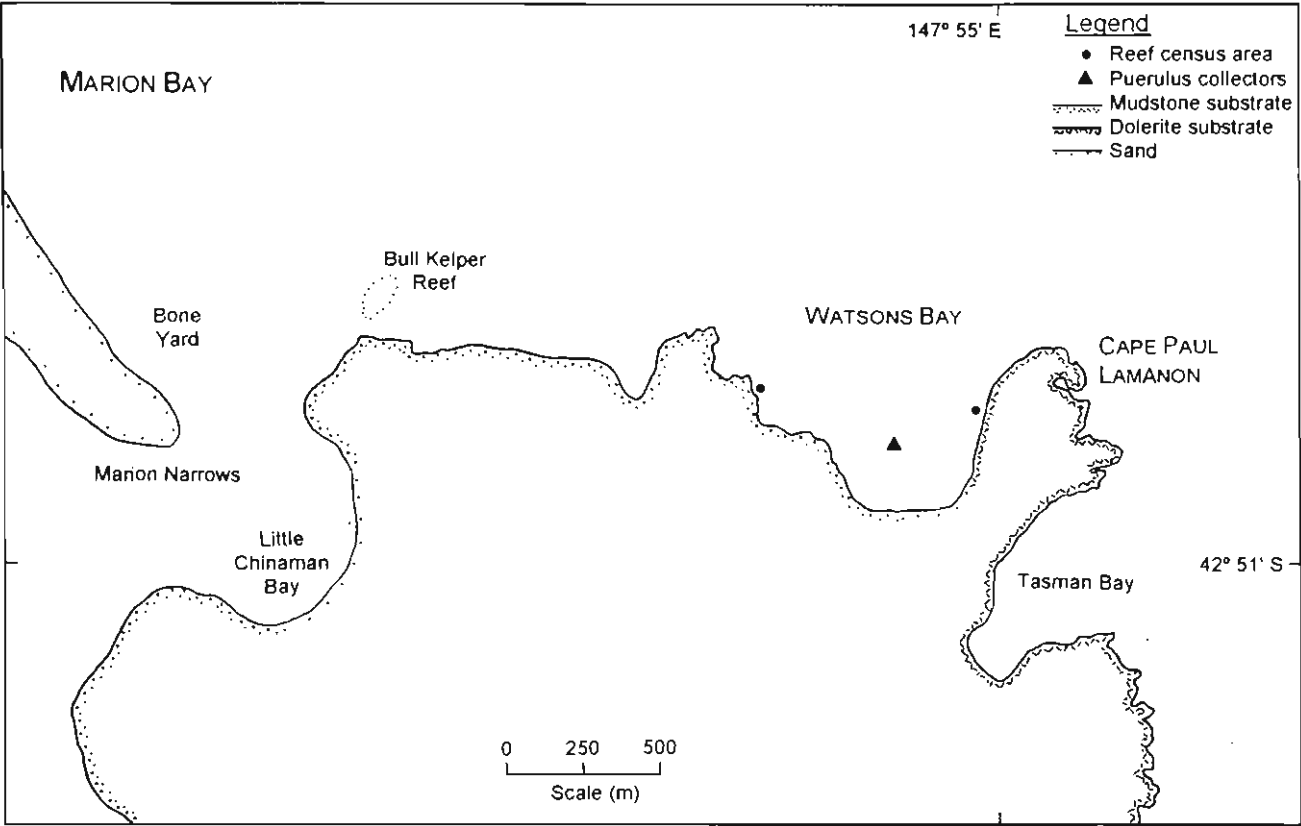


Fig. 1.4. Location of the census areas and puerulus collectors in Watsons Bay.

# Settlement

## 2.1 Introduction

The postlarval settlement of lobsters is potentially a major determinant of abundance and distribution of subsequent year classes. The influx and settlement of lobster postlarvae may vary, both temporally and spatially, due to egg production, fertilisation success, hydrodynamic conditions, larval distribution, larval development and habitat selection at settlement (reviewed by Booth and Phillips 1994). This variation in settlement may then be reflected in the abundance of cohorts recruiting to the adult population. However, post-settlement mortality and movements, such as those caused by demographic bottlenecks, may reduce the influence of settlement patterns on subsequent recruitment of lobsters to maturity and/or the fishery (Caddy 1986; Pollock 1986; Wahle & Steneck 1991; Parish & Polovina 1994).

The settlement patterns of many palinurid species have been examined using artificial collectors, usually of a floating 'seaweed' type (*e.g.* Phillips 1972) or a benthic 'crevice' type (*e.g.* Booth 1979). Such collectors have shown that, for most palinurids, settlement is usually confined to a series of pulses, either seasonal or irregularly throughout the year, and there can be considerable inter-annual and spatial variation in the magnitude of settlement (Booth 1994; Booth & Phillips 1994).

These artificial collectors have proven to be useful for investigating larval lobster ecology and determining and monitoring stock–recruitment relationships. The *Panulirus cygnus* fishery is an exemplary case, where the long-term monitoring of settlement has enabled relationships to be determined for predicting future recruitment to the fishery from settlement indices (Phillips 1986). Such long-term monitoring has also been useful for examining causes of inter-annual and spatial variability in settlement, such as by El Niño–Southern Oscillation climatic events and other hydrological factors (MacDonald 1986; Pearce & Phillips 1988; Booth 1994; Briones-Fourzán 1994). However, larvae collectors monitor relative settlement rates only and reveal little about the ecology and habitat

requirements of lobsters recently settled on natural substrates.

Many studies have examined larval settlement habitats of palinurid lobsters (*e.g.* Engle 1979; Marx & Herrnkind 1985a; Yoshimura & Yamakawa 1988; Jernakoff 1990), but few have monitored settlement patterns on natural substrates for extended periods of time. Such studies have found that discrepancies can occur in settlement between artificial collectors and natural substrates, as found with *Panulirus argus* in Florida Bay (Herrnkind & Butler 1994). Studies of *Jasus edwardsii* have found density dependent processes occurring in post-settlement juveniles (Lewis 1977; Breen & Booth 1989). These studies highlight the necessity for information on settlement to obtain an understanding of density dependent processes and the relationships between larval influx, settlement and future recruitment to maturity or the fishery.

This study examined the settlement of *J. edwardsii* on a mudstone reef at Watsons Bay using a direct census of recently settled lobsters, over a 22 month period. Artificial collectors were monitored concurrently to compare settlement rates at Watsons Bay with settlement on collectors at other sites monitored by the Tasmanian Division of Marine Resources (then Division of Sea Fisheries), and to examine the performance of the collector settlement index as a measure of actual settlement on the reef.

## 2.2 Materials and Methods

Indices of lobster settlement in Watsons Bay were determined from the abundance of post-*pueruli*,  $\leq 20$  mm CL, on a 768 m<sup>2</sup> area of reef, and from the abundance of *pueruli* and post-*pueruli* on artificial crevice collectors.

### 2.2.1 Reef Census

The reef surveys were confined to a permanently marked 32 x 24 m area on the mudstone substrate on the western side of Watsons Bay (Fig. 1.4). The site was censused monthly from 17 December 1992 to 29 September 1994, but excluded the months January 1993, August 1993, December 1993, March 1993, April 1994 and August 1994.

The perimeter of the census area was permanently marked by chains and lead weights. Prior to each census, the area was divided into 2 x 24 m lanes using weighted and numbered transect lines running perpendicular to the shore. The census was done by two divers moving slowly side by side within each lane (at approximately 1.5 m min<sup>-1</sup>), and pulling aside the kelp to inspect every crevice for lobsters.

For each lobster encountered, the carapace length was estimated by eye to the nearest 5 mm, usually with a pair of calipers held close to the animal. The position of each lobster within the census area was also noted to the nearest 0.5 m, using the numbered transect lines. During the first three surveys, a number of easily accessible lobsters were captured by hand and the carapace length was measured to assess the accuracy of the estimated lengths. The mean difference between the estimated carapace length and actual carapace length was  $\pm 3.8$  mm ( $n = 54$ ). The capture of lobsters was discontinued after the third survey to minimise disturbance and damage to the lobsters. Each census took 8-15 diver-hours over 2 days, including the laying and retrieval of the temporary lane markers.

Each census was confined to the same area to standardise the search effort and habitat for comparisons of lobster densities over time. Because of the dense algal cover, a feature common to most Tasmanian shallow reef habitats (Edgar 1984), the 768 m<sup>2</sup> area was considered the largest area that could be safely surveyed over a reasonably discrete period of time. A single area was censused, rather than a series of smaller samples, to obtain information on the spatial relationships between lobsters and the habitat. The density and spatial data are analysed further in Chapter 3.

### 2.2.2 Collector Census

Twelve crevice collectors were positioned in the middle of Watsons Bay (Fig. 1.4). These were of the type described by Booth and Tarring (1986) with a modified concrete-filled tyre stand (Kennedy 1990). Booth and Tarring collectors are used to monitor settlement of *J. edwardsii* throughout most of its geographical range (Kennedy 1990; Prescott 1991; Booth 1994). The collectors were placed in a cross pattern with three collectors spaced 3 m apart along each of the north, east, south and west arms. This layout of the collectors is the same pattern used by the Tasmanian Division of Marine Living Resources for their long-term monitoring program (R. B. Kennedy, personal communication, Division of Marine Living Resources, Department of Primary Industry and Fisheries, Tasmania). The collectors had been previously deployed at sites approximately 33 km north of Watsons Bay, for a minimum immersion period of 260 days. The collectors were placed in Watsons Bay on 11 January 1993 and were monitored every month, where possible, until 20 June 1994. The collectors were not checked in August 1993 or March 1994.

Monitoring of the collectors consisted of a diver placing a fine mesh bag over the collector head and securing it with a surface buoy line. The collector was then hauled up to the boat. Once on deck, the collector was scraped lightly over a bin to remove any puerulus and post-puerulus lobsters and the mesh bag was also checked carefully. The lobsters were counted and each puerulus staged according to descriptions by Hayakawa *et al.* (1990):

stage 1 is transparent; stage 2 has a white digestive gland; and stage 3 has exoskeletal pigmentation. First moult post-pueruli were identified as being brown in colour with pale bands on the antennae, carapace, abdominal segments and leg segments (particularly the meropodite). Older juveniles are red, purple or pale in colour and, although banding may be present on the appendages, the carapace is generally uniform in colour. Each collector head was scraped clean of fouling organisms and debris before being returned to its base.

## 2.3 Results

A series of settlement pulses were detected on both the reef and collectors during the 22 month monitoring period (Fig. 2.1). However, the abundances were generally low, with a total of 27 pueruli and post-pueruli observed on the collectors and 32 post-pueruli and juveniles  $\leq 20$  mm CL observed on the reef. The settlement pulses occurred principally during the summer months of January and February and in the winter months of June and July. A settlement peak was also detected in November 1993.

The correlation between settlement of lobsters on the reef and settlement on the collectors was examined using the Spearman rank correlation coefficient, with correction for ties (Zar 1984). The settlement of lobsters on the reef did not correlate well with settlement on the collectors,  $r_s = -0.129$ , and it can be seen from Fig. 2.1 that the settlement pulses on the reef lagged behind those of the collectors. Correlation coefficients with lag times of 10, 20 and 30 days were 0.163, 0.500 and 0.453 respectively. Although the correlation of the settlement indices improved with a lag time of 20 d, this correlation was not significant (critical  $r_{s\ 0.05(2),15} = 0.521$ ).

Most of the lobsters found on the collectors were third stage pueruli. Five second stage pueruli and 2 first moult post-pueruli were collected in June and July of 1993, and 1 first stage puerulus and 3 first moult post-pueruli were collected in June of 1994. No pueruli were detected on the reef during the monitoring period, with 9 of the 32 juveniles detected being first moult post-pueruli. These first moult post-pueruli were present during most of the settlement pulses shown in Fig. 2.1.



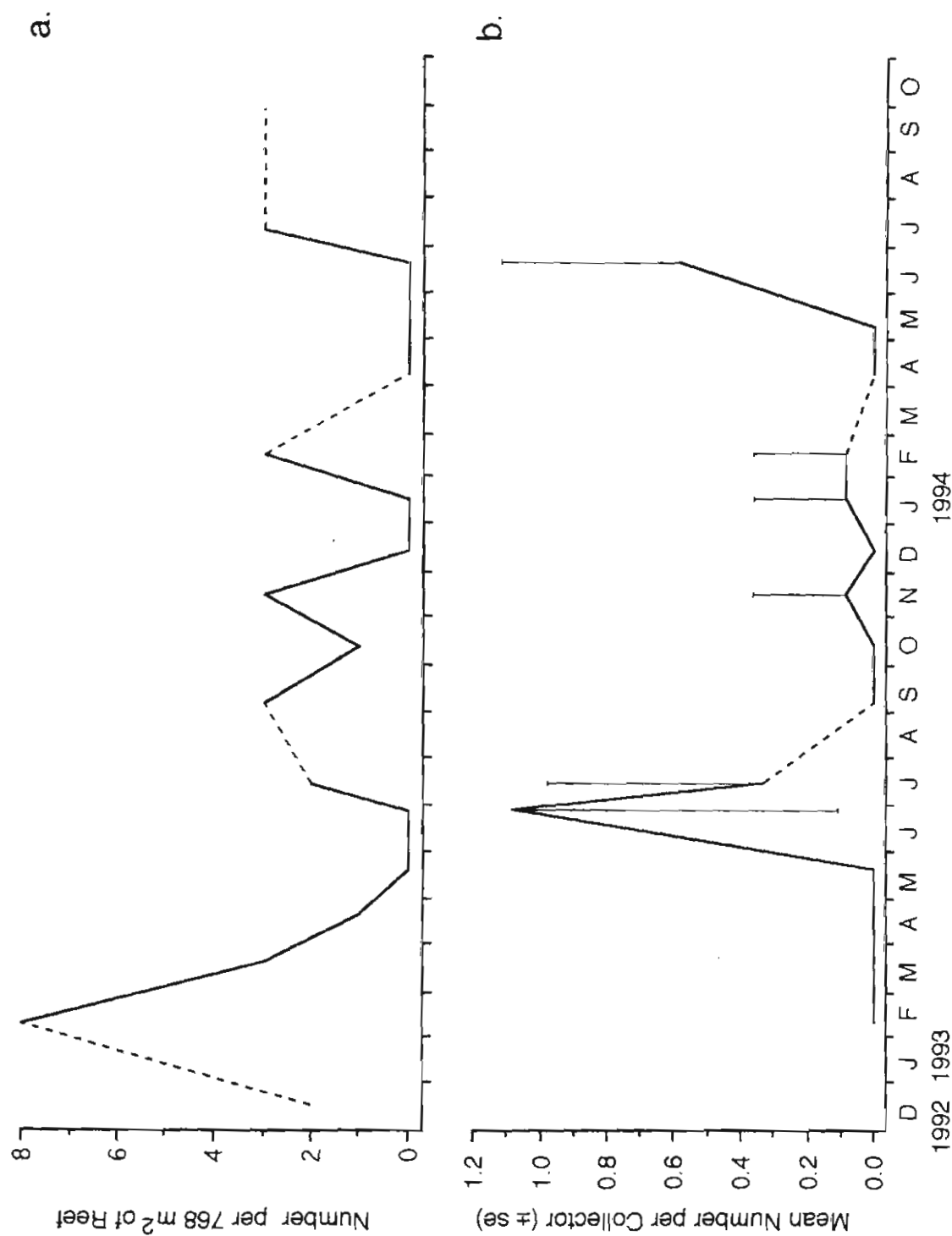


Fig. 2.1. Settlement of puerulus and post-juvenile *Jasus edwardsii* on (a) mudstone reef and (b) crevice collectors at Watsons Bay. Reef. The settlement index includes all lobsters  $\leq 20$  mm CL. Dashed lines indicate months not sampled.

## 2.4 Discussion

The indices of settlement on both the collectors and the reef were low compared to the settlement rates found in other studies. The highest settlement rate on the collectors at Watsons Bay was 1.08 (mean per collector per month), compared to peak rates of over 5 at Bicheno, 110 km to the north, for the same period (R. B. Kennedy, pers. comm.). In other years, average settlement rates of *Jasus edwardsii* have been recorded at over 20 per collector per month, with peaks consistently above 5 per collector per month (Booth 1979; Booth & Tarring 1986; R. B. Kennedy, pers. comm.). Similarly, the highest post-plerulus density observed on the reef, 0.01 m<sup>-2</sup>, was low compared to post-plerulus densities of 0.2 to 1.8 m<sup>-2</sup> recorded for *Panulirus cygnus* (Jernakoff 1990; Jernakoff *et al.* 1994) and 0.09 to 0.32 m<sup>-2</sup> for *P. japonicus* (Norman *et al.* 1994). However, the densities of *J. edwardsii* were only slightly lower than densities of *P. argus*, of approximately 0.03 m<sup>-2</sup> (Marx and Herrnkind 1985a).

The low settlement values obtained in this study may be due to Watsons Bay being a naturally poor area for settlement. Considerable geographic differences in rates of settlement have been observed on the east coast of New Zealand, and are generally associated with differences in offshore abundances of phyllosoma larvae and water flow patterns (Booth 1994). Similar differences in settlement rates have been observed between locations on the east coast of Tasmania (R. B. Kennedy, pers. comm.).

Settlement rates at Watsons Bay may also have been reduced due to sampling in a period adversely affected by oceanographic influences. Inter-annual oceanographic events, such as El Niño-Southern Oscillation (ENSO) events, have a significant influence on ocean circulation processes, affecting the survival and advection of planktonic organisms (Barber & Chavez 1983; Harris *et al.* 1987; Clementson *et al.* 1989). ENSO events have been implicated in affecting settlement levels of *J. edwardsii* (Harris *et al.* 1988; Booth 1994), as well as settlement of *P. cygnus* (Pearce & Phillips 1988) and *P. marginatus* (Polovina & Mitchum 1992). ENSO effects reduces the flow of the warm East Australia Current into the Tasman Sea and increases the West Wind Drift, driving sub-Antarctic waters up the east coast of Tasmania (Harris *et al.* 1987, 1988). Recent ENSO events occurred during this study in 1992, 1993 and 1994 (Bureau of Meteorology, Hobart). At the same time lobster settlement indices at Bicheno showed a significant decline from 1991 values (R. B. Kennedy, pers. comm.), and it is possible that this decline may be due to the ENSO events.

Despite low settlement levels, winter and summer pulses were detected on both the reef and collectors. This seasonal pattern of settlement for *J. edwardsii* also occurs at other locations in Tasmania, South Australia and New Zealand (R. B. Kennedy, pers. comm.; Lewis 1977; Booth 1979; Booth & Tarring 1986). The apparent lag time between the settlement peaks on the collectors and reef is to be expected due to the inclusion of lobsters up to 20 mm CL in the reef settlement index. This was considered necessary as pueruli and first moult post-pueruli (10-12 mm CL) were too scarce to determine settlement rates directly. Studies involving *P. argus* have also included larger early benthic phase lobsters in settlement indices due to the scarceness, small size and crypticity of newly settled lobsters (Herrnkind *et al.* 1988; Forcucci *et al.* 1994; Herrnkind & Butler 1994). This requires the assumption that early benthic phase lobsters do not move far from the point of settlement, which has been supported for *P. argus* (Forcucci *et al.* 1994). Possible sources of sampling bias, including cryptic behaviour, are discussed in Chapter 3.

The settlement values obtained in this study are considered too low to provide useful quantitative information on settlement and post-settlement dynamics of *J. edwardsii*. This problem may be overcome by examining natural settlement in locations and periods of known high settlement rates, as achieved by Lewis (1977) at Blackfellows Caves in South Australia. However, such periods and locations may be exceptional and ecological processes elucidated from these places and times may not be representative of the general population dynamics. It can be concluded from this study that sampling of larger areas, at a variety of locations and for longer periods, is required in future studies of natural settlement dynamics of *J. edwardsii*.

# Density and Distribution

### 3.1 Introduction

For many palinurid lobsters, the habitat requirements of the juvenile benthic stages are different from that of the adults. In extreme cases, such as for the western Australian lobster *Panulirus cygnus* and the Caribbean lobster *P. argus*, the juvenile stages are effectively segregated from the adults, developing on shallow reefs and 'nursery' areas before migrating to preferred adult habitats in deeper water (Chittleborough 1970; Herrnkind & Lipcius 1986). However, many differences in habitat use also occur at smaller scales, with sequential stages occupying different microhabitats within an area. For example, newly settled juvenile *P. argus* ( $\approx 6$  mm CL) initially inhabit clumps of the red algae *Laurencia* spp before aggregating in more widely available crevices and den structures at about 20 mm CL (Marx & Herrnkind 1985a; Childress & Herrnkind 1994). Similarly, both *P. cygnus* and the Japanese lobster *P. japonicus* have initial stages that occupy individual holes, before aggregating in regions with crevices and ledges at increased sizes (Jernakoff 1990; Norman *et al.* 1994).

Changes in the habitat use of spiny lobsters are because of a variety of physical and biological factors. Known factors include size-related changes in foraging behaviour, shelter preferences, predation susceptibility and intraspecific interactions, and are usually manifested by differences in distribution patterns (*e.g.* Marx & Herrnkind 1985b; MacDiarmid 1991; Childress & Herrnkind 1994). Knowledge of habitat use and spatial distribution patterns is important for determining animal-resource relationships (*e.g.* Reaka 1987; Andrew and MacDiarmid 1991) and fishery management (*e.g.* Walters *et al.* 1993). Size-related changes in habitat use are of particular interest, as these changes can affect recruitment processes and increase the complexity of biological interactions in the reef community.

The habitat use and spatial distributions of *Jasus edwardsii* have been studied extensively by MacDiarmid and his colleagues (MacDiarmid 1989, 1991, 1994; Andrew and

MacDiarmid 1991; MacDiarmid *et al.* 1991). They found differences in distribution patterns according to size, sex, depth and season. Although all lobster sizes co-occur on the same reefs, juvenile lobsters (< 85 mm CL) tend to be more abundant in shallower waters (< 10 m depth), with adult male and female lobsters seasonally migrating between shallow and deeper waters (MacDiarmid 1991). The aggregation patterns of *J. edwardsii* are also related to size, sex and season, particularly with regard to cohabitation within shelters (MacDiarmid 1994). Cohabitation rates are the lowest for juvenile lobsters < 30 mm CL and highest for larger juveniles 30–70 mm CL, with moderate to low cohabitation rates occurring in adult lobsters (MacDiarmid 1994). These studies were over a large area in a marine reserve in northeast New Zealand, and involved a large size range of lobsters (15–200 mm CL), mostly over 85 mm CL. As such, the results generally pertained to large scale ecological processes.

The aims of the study reported here were to examine size-related differences in distribution patterns of *J. edwardsii*, with a particular emphasis on the distribution and habitat use of newly settled lobsters. Distributions were examined in terms of dispersion of occupied shelters, from mapped data, and in terms of aggregations within shelters (cohabitation). Because of the small size of early benthic phase lobsters and thick kelp in the study area, only a small area could be adequately censused. Therefore, only small-scale relationships were examined, more at the scale of individuals rather than populations. In addition, the study site was heavily fished, and lobsters above 110 mm CL, the male legal size limit, were uncommon. Specific hypotheses examined include whether the distribution patterns change with lobster size; if so, whether the distribution patterns between sizes are independent; and the nature of temporal and density-related changes in distribution.

### 3.2 Materials and Methods

The investigation of lobster density and spatial distribution was confined mostly to the permanently marked mudstone survey site in Watsons Bay, using the density and distribution data obtained from the monthly surveys described in Chapter 2 (Section 2.2.1). Sites on dolerite substrata in Watsons Bay (Cape Paul Lamanon) and at Darlington Point (Fig. 1.3) were also censused, with densities determined at Cape Paul Lamanon on 11 September 1993, 14 October 1993 and 20 January 1994, and at Darlington Point on 27 August 1993. Distributions were also mapped at Cape Paul Lamanon on 14 October 1993 and 20 January 1994. The same census technique was used at all locations, with the same sites examined each time. Relationships between density, cohabitation, distribution and lobster size were examined using three size classes:  $\leq 35$  mm CL, 36–60 mm CL and  $> 60$  mm CL.

The dispersion of lobsters was examined at scales of both within and between shelters. Within shelter dispersion was examined from patterns of cohabitation. The degree of cohabitation (aggregation within shelters) for each size class was assessed using the proportion of lobster abundances which were cohabiting, and the median aggregation size. Size-related differences in cohabitation behaviour are also addressed in Chapter 4 (Shelter Use and Availability). Changes in the proportion of cohabitation were also compared with time and changes in density.

The dispersion of lobsters between shelters was examined using a nearest-neighbour type of analysis of mapped data (Diggle 1979). The spatial pattern of occupied shelters, rather than individual lobsters, was analysed to separate the influence of aggregations within shelters. In this case, a point-to-nearest-occupied-shelter method was used, where 99 equidistant points (2.5 m apart) were positioned within the maps of shelter positions. The distances from each point to the nearest occupied lobster shelter were then determined for each size class. To correct for edge effects, the census area was treated as a torus, such that opposite boundaries of the area were considered adjacent (Ripley 1981).

The set of point-to-nearest-occupied-shelter distances were used to calculate a dispersion index for comparison of dispersion patterns between the census times and different densities. In this case, Pielou's and Mountford's alpha was used:

$$\alpha = \rho \pi (\sum x^2) m^{-1} \quad (3.1)$$

where  $\rho$  is the density (per unit area),  $x$  is the point-to-nearest-lobster-shelter distance and  $m$  is the number of point-to-shelter measurements (Pielou 1977). Mountford's (1961) correction for density estimation was not used as the total abundance of lobsters within the census area was known. Random dispersion is indicated by alpha values equal to one, regular or segregated dispersion by  $\alpha < 1$  and clumping by  $\alpha > 1$ . The significance of departures of  $\alpha$  from 1 was analysed using a chi-squared test, where  $\chi^2 = 2m\alpha$  with  $2m$  degrees of freedom (Pielou 1977). The magnitude of alpha responds to both the intensity (density within clumps) and grain (density of the clumps themselves) of a pattern (Pielou 1977).

To determine the scales (or grain) at which spatial patterns were occurring, the cumulative distribution of observed point-to-nearest-lobster distances,  $\hat{f}(x)$ , was compared with that expected from a random (Poisson) distribution,  $f(x)$ , where:

$$f(x) = 1 - \exp(-\rho \pi x^2) \quad (3.2)$$

(Diggle 1979). The distributions were compared by plotting the residual difference between

the observed distribution and the expected random distribution:  $f(x) - \hat{f}(x)$  against distance,  $x$ . Segregation or regular dispersion is indicated by the observed distribution exceeding the expected distribution:  $f(x) - \hat{f}(x) < 0$ . Clustering or aggregation is indicated by the expected distribution exceeding the observed distribution:  $f(x) - \hat{f}(x) > 0$ .

In cases where a regular dispersion pattern was evident, the pattern was examined further by plotting  $\rho\pi x^2 - \hat{f}(x)$  against  $x$ . This plot provides information on the nature of the separation between individuals. Where there is complete inhibition inside an area of radius  $r$ , termed a hard-core situation,  $\rho\pi x^2$  is the maximum value attainable by  $f(x)$  for all  $x \leq r$ , with  $f(x) < \rho\pi x^2$  thereafter (Upton and Fingleton 1985). The hard core radius is determined from the point of rapid inflection of the curve from the baseline of  $\rho\pi x^2 - f(x) = 0$ . Hard core situations represent the most severe forms of spatial segregation, with complete occupancy or aggressive territorialism of an area (Cormack 1979).

The point-to-nearest-shelter distances were also used to examine the relationships of shelter dispersion pattern between lobster size classes. Paired distances of point-to-nearest-shelter of one size class and from the same point to the nearest shelter of another size class were compared using Spearman's rank correlation coefficient. Distances from each point to lobsters  $\leq 35$  mm CL and  $> 35$  mm CL; and to lobsters 36-60 mm CL and  $> 60$  mm CL were compared. If two size categories of lobsters are attracted to one another, then the pairs of point-to-lobster distances will be positively correlated. Conversely, a negative correlation indicates repulsion or segregation between groups. No correlation will occur if the groups are distributed independently (Upton and Fingleton 1985).

The distribution of shelters occupied by lobsters within the permanent census area was compared with the reef topography, both qualitatively and quantitatively. Distribution maps were compared visually with prominent reef features and the general topography. The cumulative frequency of shelter positions (total for the 22 month study period) within a grid of 2 x 2 m cells was also compared with the substratum rugosity and density of crevices within each cell. A rugosity index was determined using depth measurements (to the nearest 0.1 m) taken on a 1 x 1 m grid over the study area. The rugosity index, RI, was calculated as the sum of the deviations between the depth in the centre of the cell and the five adjacent depth measurements around the perimeter of the cell:

$$RI = \sum_{i=-1}^{+1} \sum_{j=-1}^{+1} \left| Z_{x,y} - Z_{x+i,y+j} \right| \quad (3.3)$$

where  $Z_{x,y}$  is the depth at position  $x, y$ . The methods used to estimate crevice density are given in Chapter 4 (Shelter Use and Availability). Comparisons involving crevice density were only made for cells that corresponded with the areas sampled for crevice density

estimates (as described in Section 4.2.2).

### 3.3 Results

#### 3.3.1 Density

The density of lobsters in the permanent census area at Watsons Bay was quite variable over the 22 month study period (Fig 3.1). The total density ranged from 2.6 to 7.7 lobsters per 100 m<sup>2</sup>, with those in the 36 - 60 mm CL size group usually being the most abundant. Lobsters  $\leq 35$  mm CL remained relatively low in density ( $< 1.7$  per 100 m<sup>2</sup>). No distinct seasonal trends could be detected for any size group, however, peaks in density were apparent in June 1993 and May 1994, particularly for the 36 - 60 mm CL lobsters.

Density was also highly variable at, and between, other sites, the total density ranging from 1.5 to 20.3 lobsters per 100 m<sup>2</sup> (Table 3.1). The density of lobsters  $\leq 35$  mm was also low at these sites. Only lobsters  $> 60$  mm CL were found at Darlington Pt, with 55% being females bearing eggs.

Table 3.1. Densities of lobsters (per 100 m<sup>2</sup>) at Cape Paul Lamanon and Darlington Pt, on the east coast of Tasmania (see Figs. 3.3 & 3.4 for maps of locations).

Location	Size Class			Total
	≤ 35 mm CL	36 - 60 mm CL	> 60 mm CL	
Cape Paul Lamanon				
11 September 1993	0.8	0.3	0.5	1.5
14 October 1993	1.9	10.6	7.8	20.3
20 January 1994	0.1	5.2	4.1	9.5
Darlington Pt				
27 August 1993	0	0	4.6	4.6
Watsons Bay Mudstone				
minimum	0.3	0.7	0.7	2.6
maximum	1.7	4.4	3.1	7.7



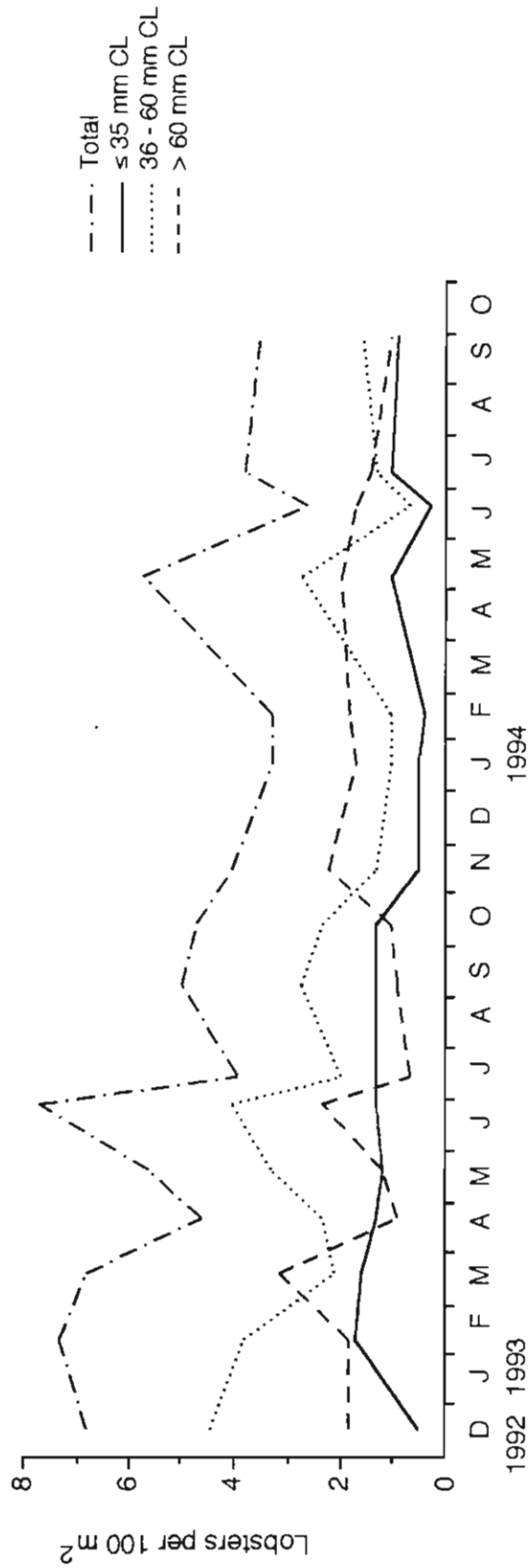


Fig. 3.1. Monthly changes in density of *Jasus edwardsii* in the mudstone census area at Watsons Bay.

### 3.3.2 Cohabitation

Lobsters smaller than 35 mm CL were not observed to cohabit with lobsters of either the same or larger sizes at any time during the censuses. This contrasted with the larger size groups which often had a high proportion of cohabitation. The proportion of cohabitation (with lobsters of any size) was quite variable between months for both the 36 - 60 mm CL and > 60 mm CL size groups, and generally ranged from 35% to 80% (Fig. 3.2). No seasonal trends were evident in this variation, and no differences were apparent between the two larger size groups.

For lobsters 36 - 60 mm CL, the proportion of cohabitation was positively correlated with the abundance of this size group (Fig. 3.3a;  $r = 0.607$ ,  $df = 14$ ,  $p = 0.013$ ). Although the proportion of cohabiting lobsters increased with density, the aggregation sizes were highly variable and not related to density (Fig. 3.3b;  $r = 0.148$ ,  $df = 14$ ,  $p > 0.05$ ).

For lobsters > 60 mm, no relationship was found between either the proportion of cohabiting lobsters, or the median aggregation size, with density (Fig. 3.4; proportion cohabiting:  $r = 0.084$ ,  $df = 14$ ,  $p > 0.05$ ; aggregation size:  $r = 0.237$ ,  $df = 14$ ,  $p > 0.05$ ).

Lobsters of both larger size categories, 36 - 60 mm CL and > 60 mm CL, were often found together in the same shelter. The proportion of lobsters cohabiting with lobsters of another size category generally ranged between 10% and 50%, with a high amount of variation between months (Fig. 3.5). No seasonal trends were evident.

The number of shelters occupied was directly proportional to the density of lobsters (Fig. 3.6). For lobsters 36 - 60 mm CL, the proportion of shelters to lobsters decreases at higher densities (top right of Fig. 3.6). This is consistent with the increases in proportion of cohabitation with increased lobster density for this size group, as shown in Figure 3.3a.

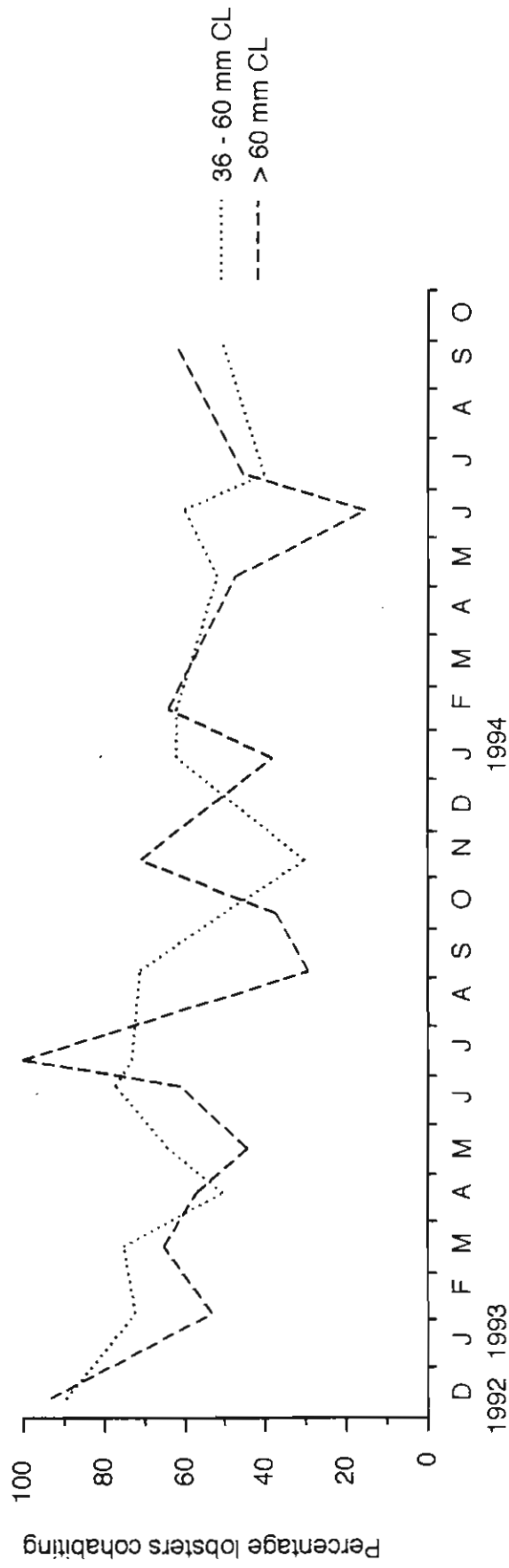


Fig. 3.2. Monthly changes in the proportion of cohabiting *Jasus edwardsii* in the mudstone census area at Watsons Bay.

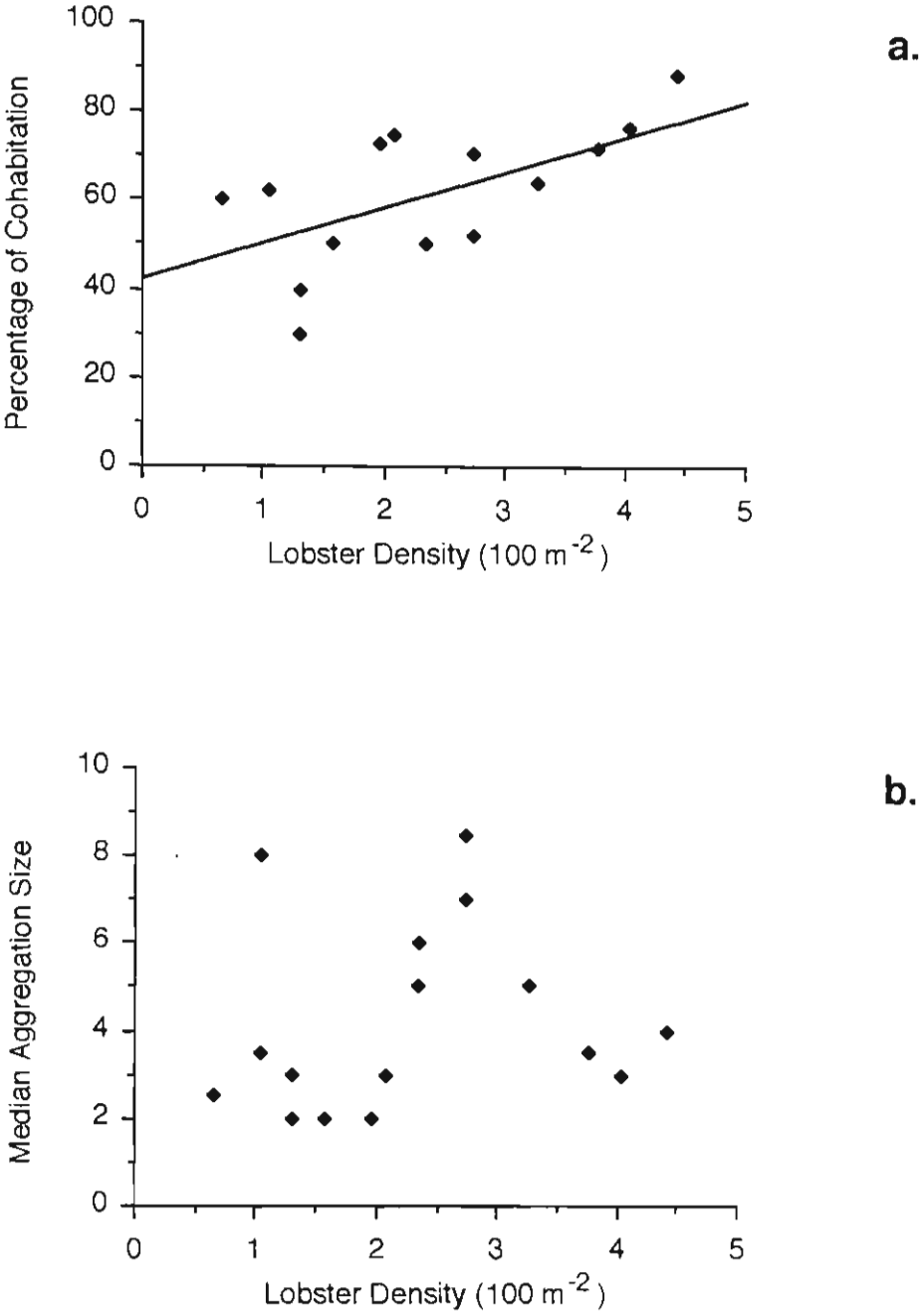


Fig. 3.3. Relationship between the density of *Jasus edwardsii* 30 - 60 mm CL and (a) the percentage of cohabitation and (b) the median aggregation size, at Watsons Bay. Least squares line for (a):  $y = 42.64 + 8.06x$ .

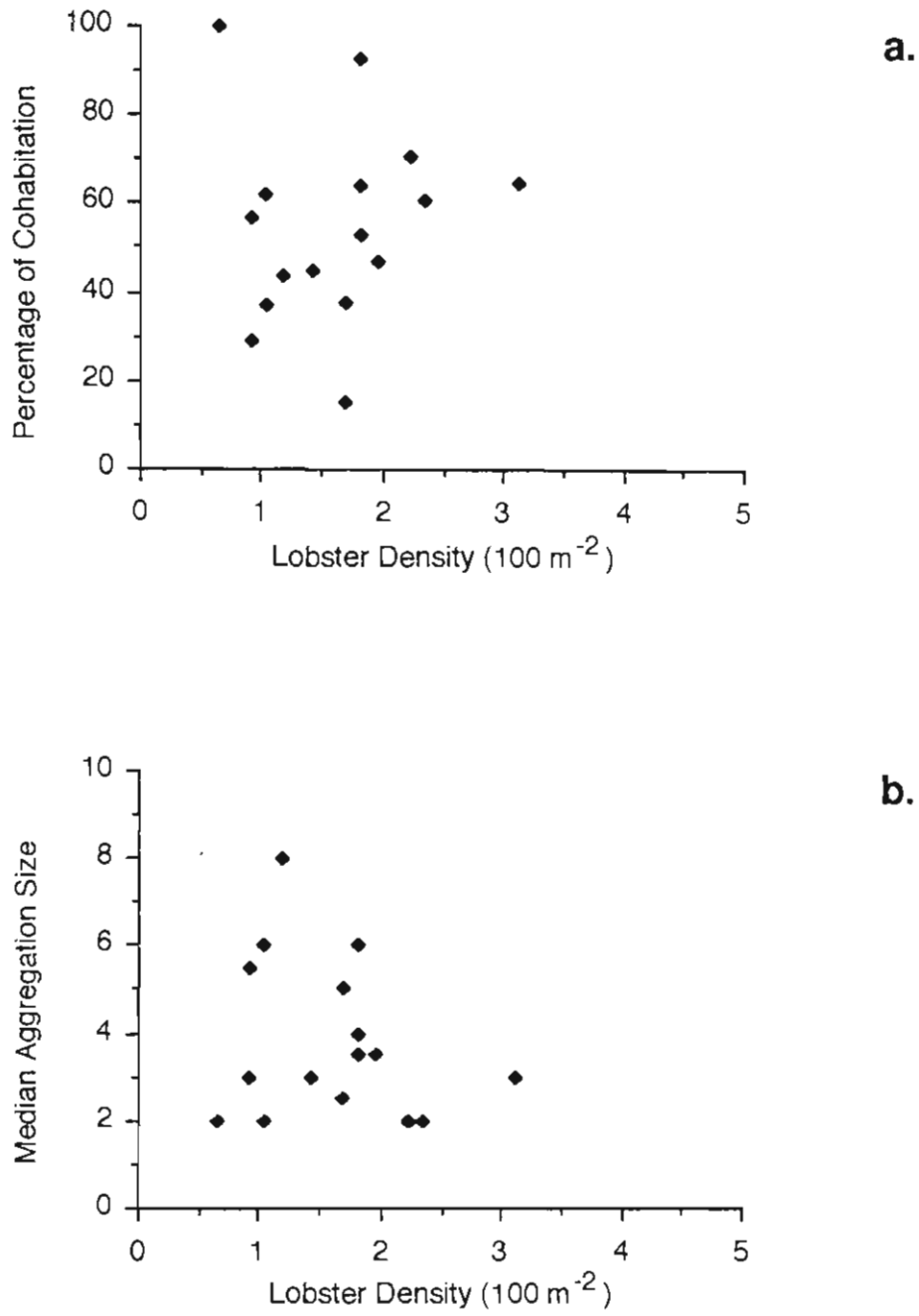


Fig. 3.4. Relationship between the density of *Jasus edwardsii* > 60 mm CL and (a) the percentage of cohabitation and (b) the median aggregation size, at Watsons Bay.

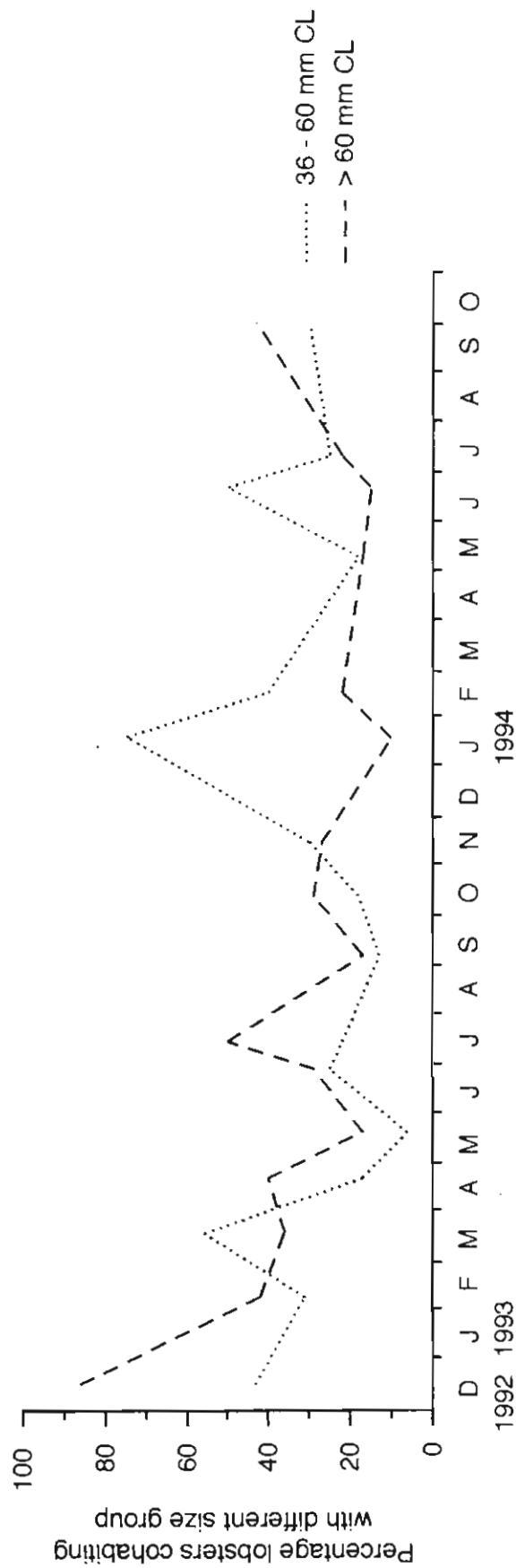


Fig. 3.5. Monthly changes in the proportion of shelters shared between medium (36-60 mm CL) and large (> 60 mm CL) *Jasus edwardsii* , in the mudstone census area at Watsons Bay.

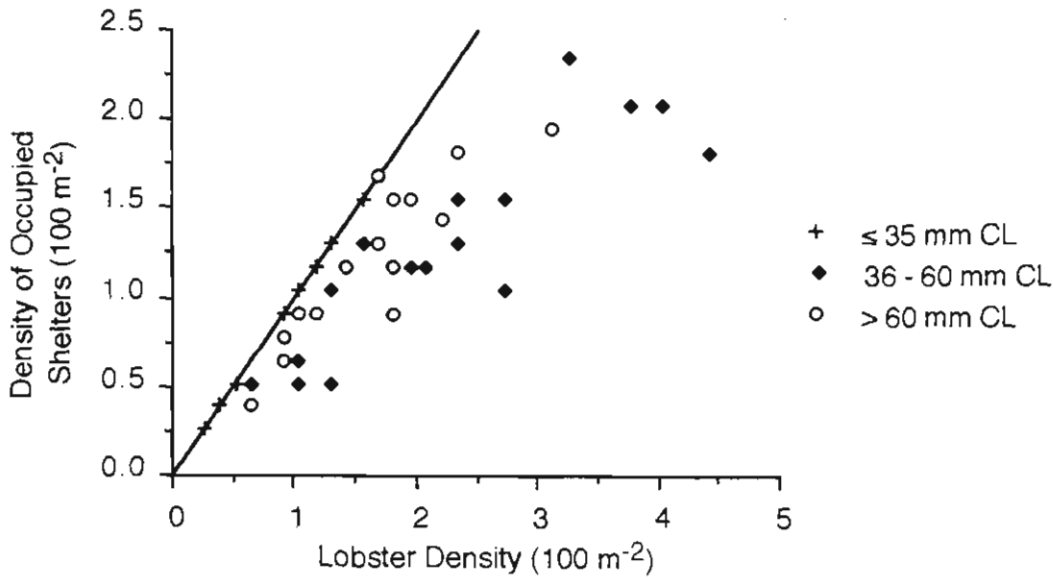


Fig. 3.6. Relationship between the number of shelters occupied and density of *Jasus edwardsii* for different size groups. The line indicates the proportion of no cohabitation, where occupied shelter density equals lobster density (slope = 1).

### 3.3.3 Dispersion Patterns

The distribution pattern of shelters occupied by lobsters varied considerably between times, and without any seasonal trends (Fig. 3.7). From the alpha index, the dispersion pattern of shelters for lobsters  $\leq 35$  mm CL was usually either regular (segregated) or random (Fig. 3.7). Shelters for lobsters 36 - 60 mm CL were usually random to clumped in distribution, while lobsters  $> 60$  mm CL were random to regular in distribution (Fig. 3.7).

The deviations of nearest-neighbour distance cumulative frequency distributions from that expected from a random distribution (plots of  $f(x) - \hat{f}(x)$ ) showed that the clumping and segregation of occupied shelters mostly occurred at scales of 3 to 6 m (e.g. Figs. 3.8 to 3.12). Plots of  $\rho\pi x^2 - \hat{f}(x)$  showed that the spacing between segregated lobster shelters was generally at least 4 m. Although clumped and random distributions were observed statistically, the intensity of these patterns were such that they were not visually distinct from random distributions.

The dispersion index for lobsters  $\leq 35$  mm CL was not related to the density of shelters occupied ( $r = 0.19$ , 15,  $p > 0.05$ ). The dispersion index increased for lobsters 36 - 60 mm CL and decreased for lobsters  $> 60$  mm CL with an increase in the total density of shelters

occupied by lobsters above 35 mm CL ( $r = 0.58$ ,  $df = 15$ ,  $p = 0.018$  and  $r = -0.50$ ,  $df = 15$ ,  $p = 0.048$  respectively). Therefore, with increased shelter density, the dispersion of shelters for lobsters 36 - 60 mm CL tended to be more clumped while the dispersion of shelters for lobsters > 60 mm CL tended to be more uniform (Fig. 3.13).

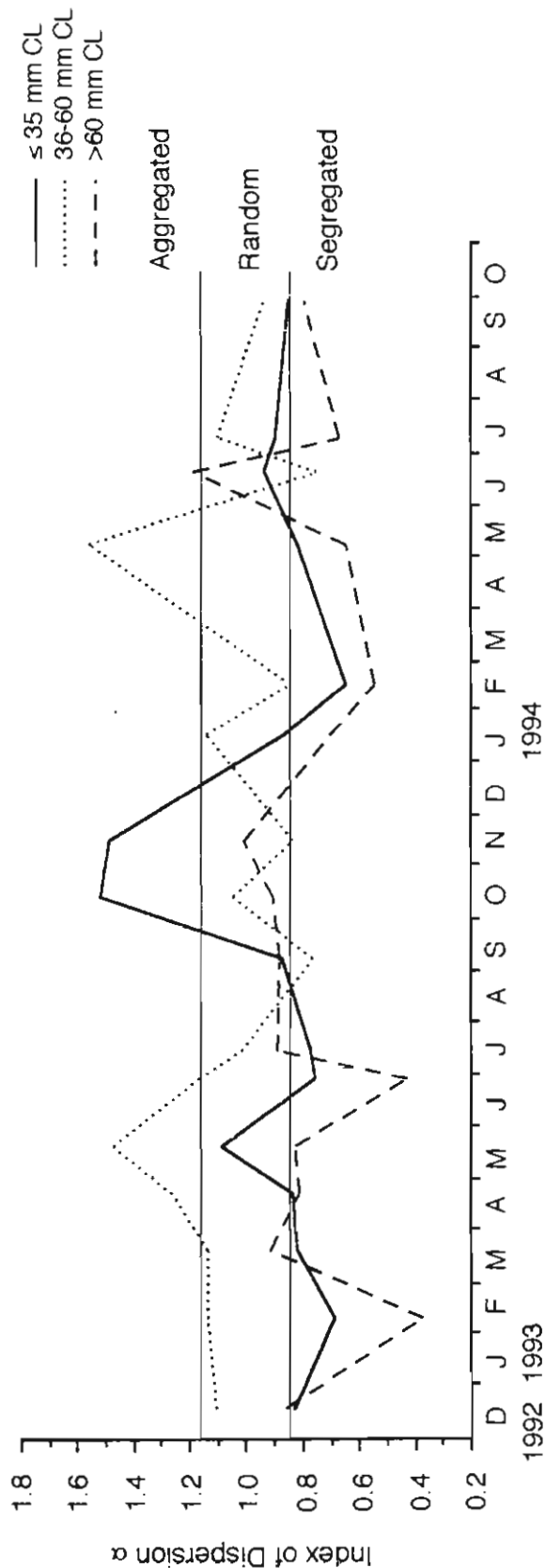
The dispersion of small lobsters  $\leq 35$  mm CL was often positively correlated with the distribution of larger lobsters > 35 mm CL (Table 3.2). However, the relationship between these two size classes was generally weak, with low correlation coefficients, and the distributions were independent approximately 30% of the time. The correlation between small and larger lobster dispersion patterns was proportional to the shelter density of both size groups ( $r_{\text{small}} = 0.49$ ,  $df = 15$ ,  $p = 0.050$ ; and  $r_{\text{large}} = 0.50$ ,  $df = 15$ ,  $p = 0.048$  respectively; Fig. 3.13).

The distributions of occupied shelters for medium-sized lobsters 36-60 mm CL and larger lobsters > 60 mm CL were positively correlated at all times except for September 1993 (Table 3.2). The higher correlation coefficients also indicate that the spatial relationships between these two size classes were stronger than those involving small lobsters  $\leq 35$  mm CL. However, these correlations were not correlated with density (lobsters 36-60 mm CL:  $r = 0.22$ ,  $df = 15$ ,  $p = 0.40$ ; lobsters > 60 mm CL:  $r = 0.14$ ,  $df = 15$ ,  $p = 0.60$  respectively).

Table 3.2. Spearman rank correlation coefficients of distributions between lobsters  $\leq 35$  mm CL and > 35 mm CL, and between lobsters 36-60 mm CL and > 60 mm CL, at the Watsons Bay mudstone site ( $df = 98$ , ns = not significant, \* = significant at  $\alpha = 0.05$ ).

Year	Month	CL $\leq 35$ mm vs CL > 35 mm		CL 36 - 60 mm vs CL > 60 mm	
		$r_s$	Significance	$r_s$	Significance
1992	December	0.21	*	0.72	*
1993	February	0.61	*	0.58	*
	March	0.76	*	0.55	*
	April	0.18	ns	0.75	*
	May	0.44	*	0.39	*
	June	0.46	*	0.49	*
	July	0.22	*	0.32	*
	September	0.34	*	0.04	ns
	October	0.33	*	0.44	*
	November	0.69	*	0.69	*
1994	January	0.17	ns	0.33	*
	February	-0.16	ns	0.38	*
	May	0.51	*	0.45	*
	June	0.19	ns	0.40	*
	July	0.68	*	0.56	*
	September	0.07	ns	0.68	*





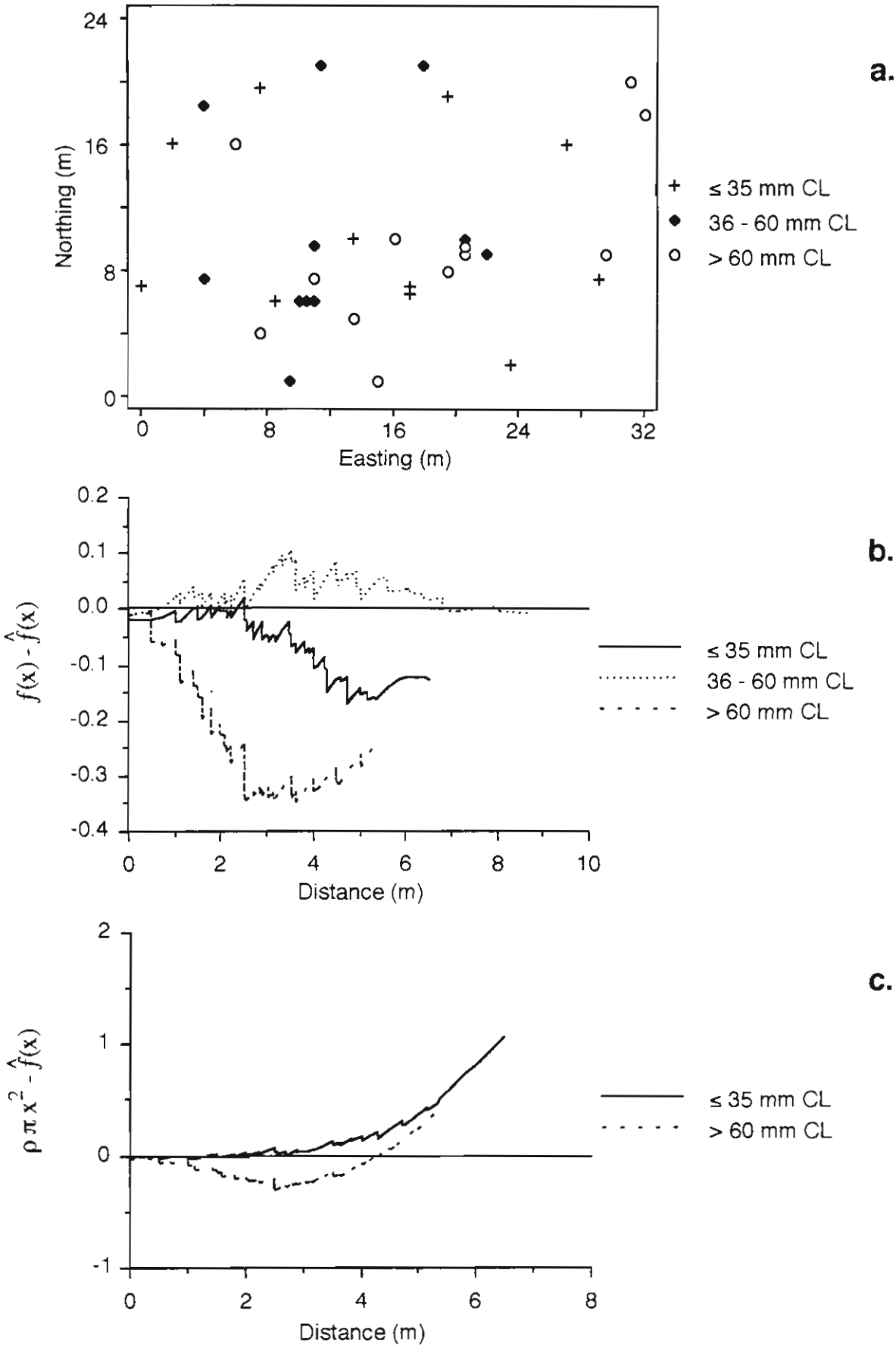


Fig. 3.8. Spatial distribution patterns of *J. edwardsii* at Watsons Bay, February 1993: (a) positions of occupied shelters within the census area; (b) plot of residuals from nearest neighbor analysis; and (c) hard-core plot for groups with regular distributions.

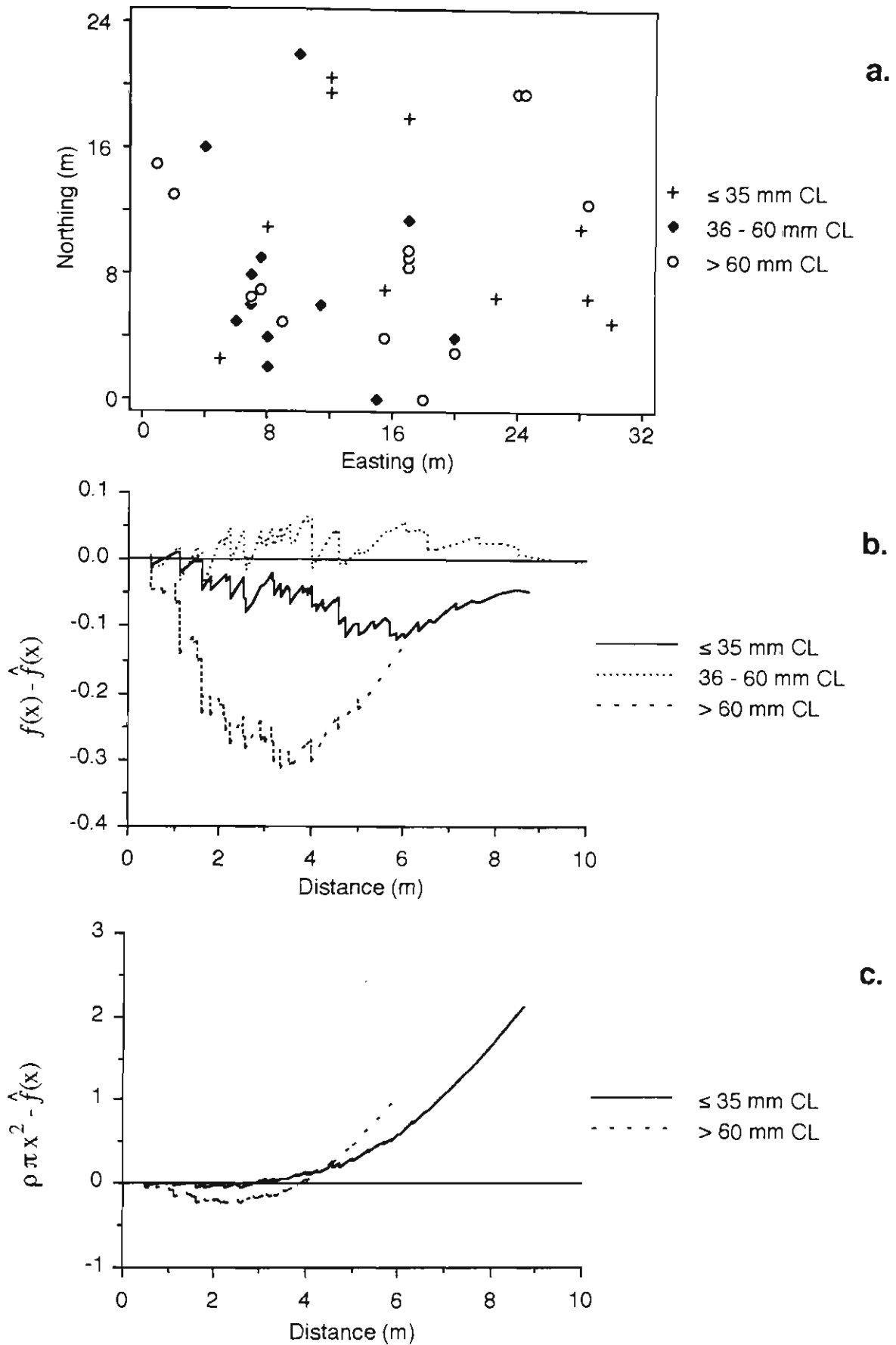


Fig. 3.9. Spatial distribution patterns of *J. edwardsii* at Watsons Bay, June 1993: (a) positions of occupied shelters within the census area; (b) plot of residuals from nearest neighbor analysis; and (c) hard-core plot for groups with regular distributions.

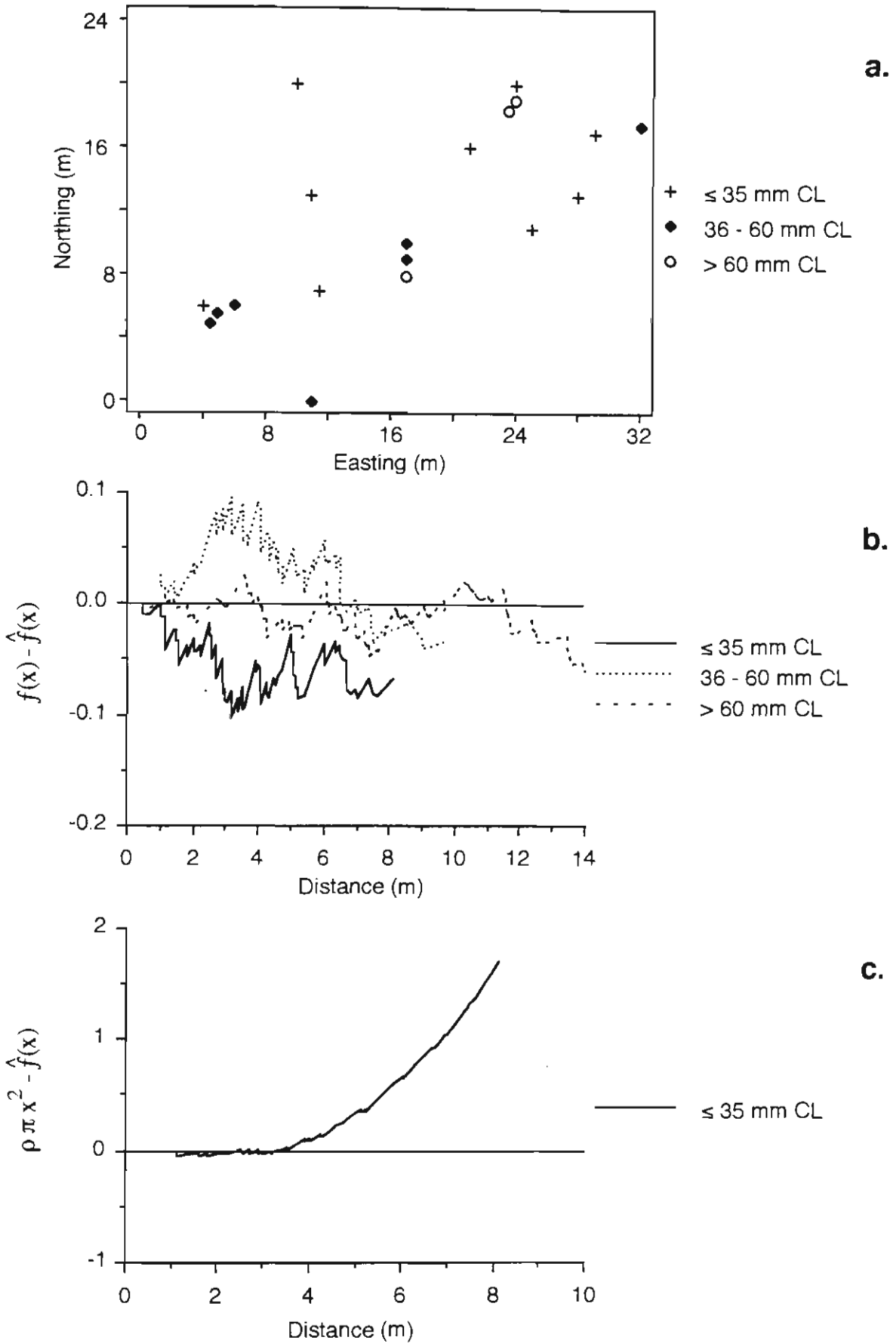


Fig. 3.10. Spatial distribution patterns of *J. edwardsii* at Watsons Bay, July 1993: (a) positions of occupied shelters within the census area; (b) plot of residuals from nearest neighbor analysis; and (c) hard-core plot for groups with regular distributions.

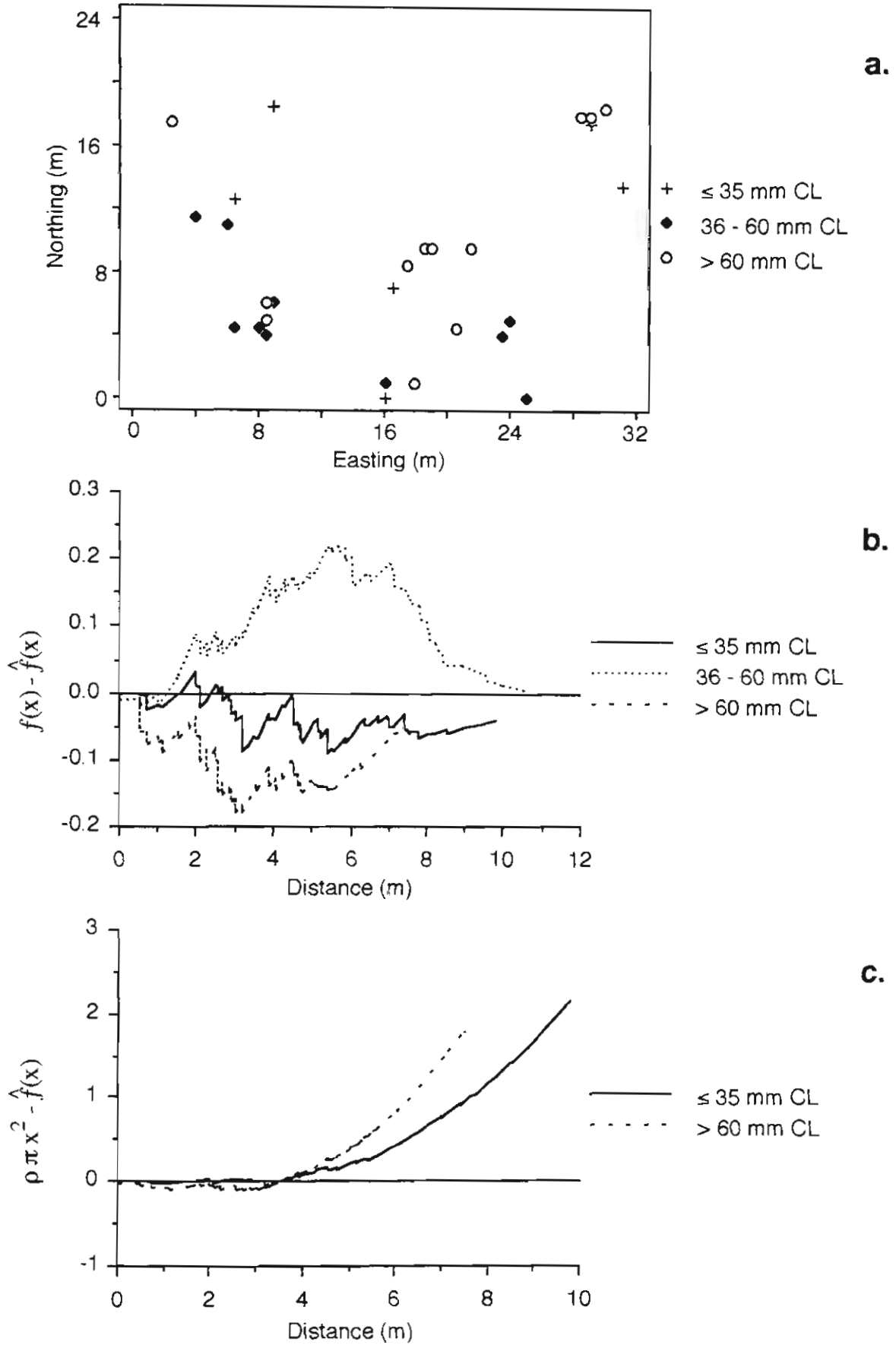


Fig. 3.11. Spatial distribution patterns of *J. edwardsii* at Watsons Bay, May 1994: (a) positions of occupied shelters within the census area; (b) plot of residuals from nearest neighbor analysis; and (c) hard-core plot for groups with regular distributions.

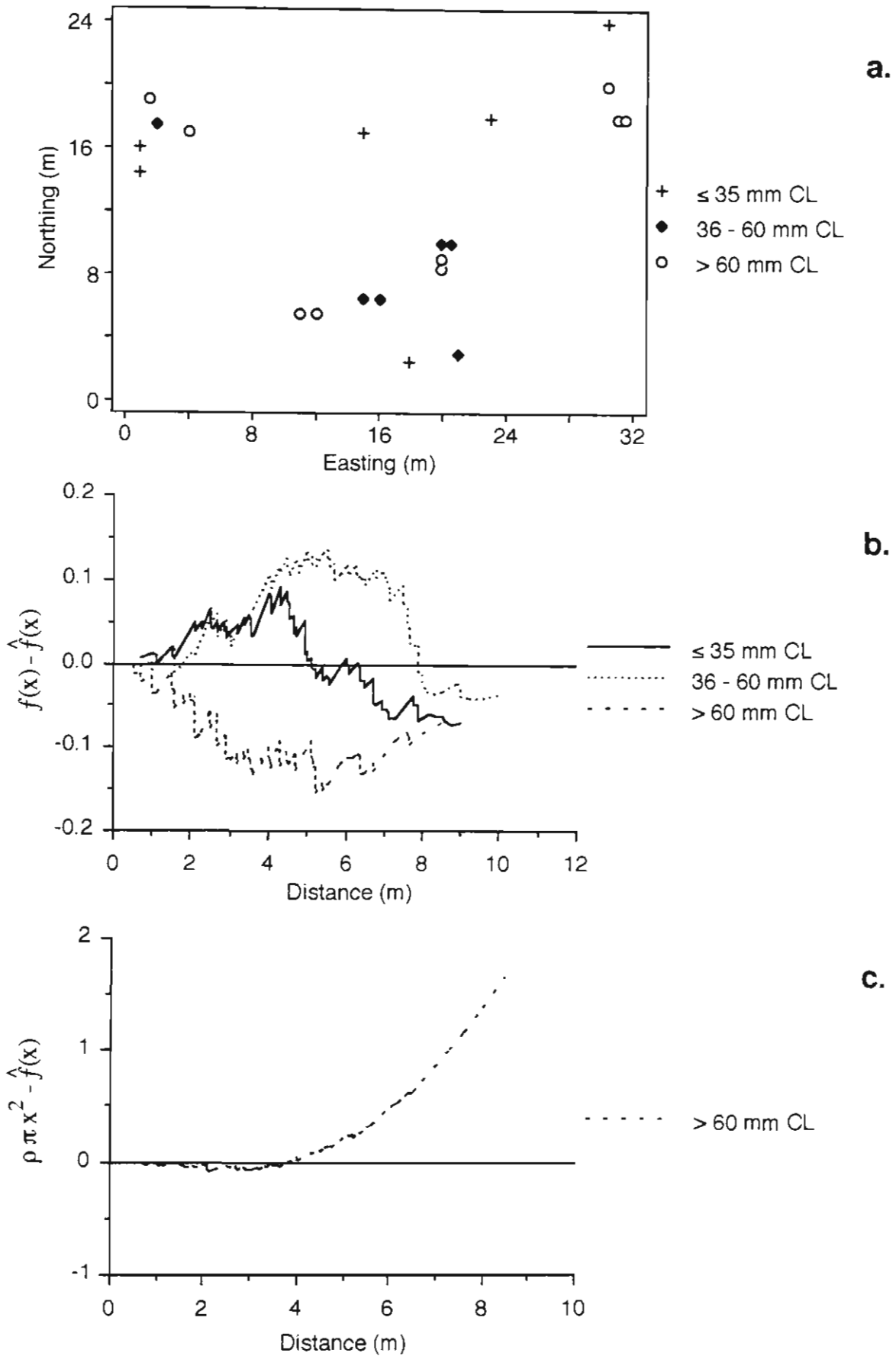


Fig. 3.12. Spatial distribution patterns of *J. edwardsii* at Watsons Bay, July 1994: (a) positions of occupied shelters within the census area; (b) plot of residuals from nearest neighbor analysis; and (c) hard-core plot for groups with regular distributions.

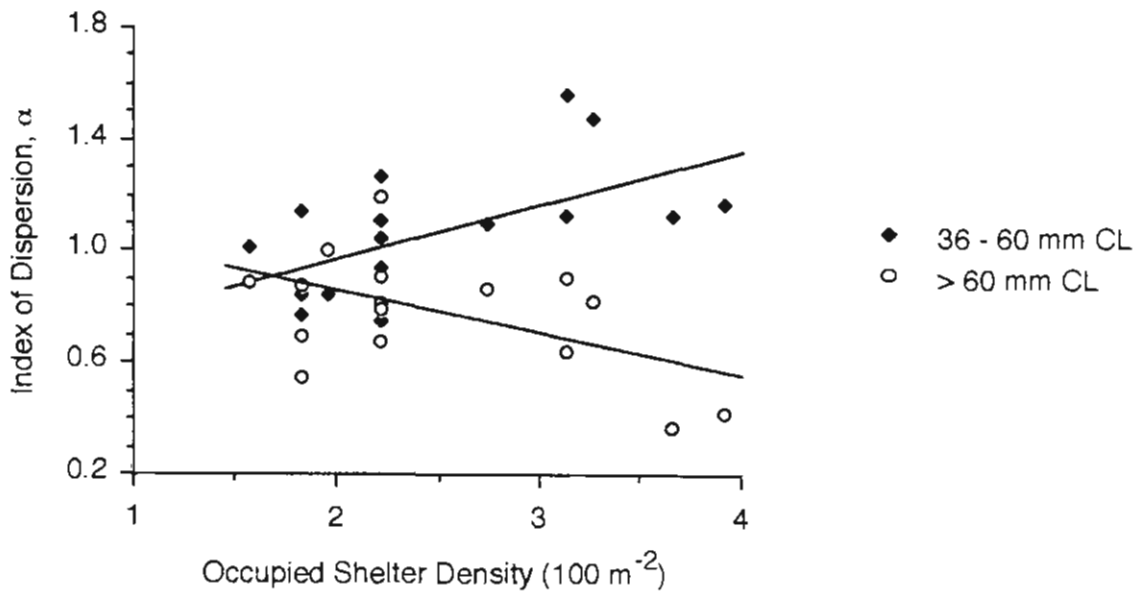


Fig. 3.13. Relationship between dispersion and total occupied shelter density for *Jasus edwardsii* > 35 mm CL. Least squares lines, CL 36 - 60 mm:  $y = 0.62 + 0.19x$ ; CL > 60 mm:  $y = 1.15 - 0.15x$ .

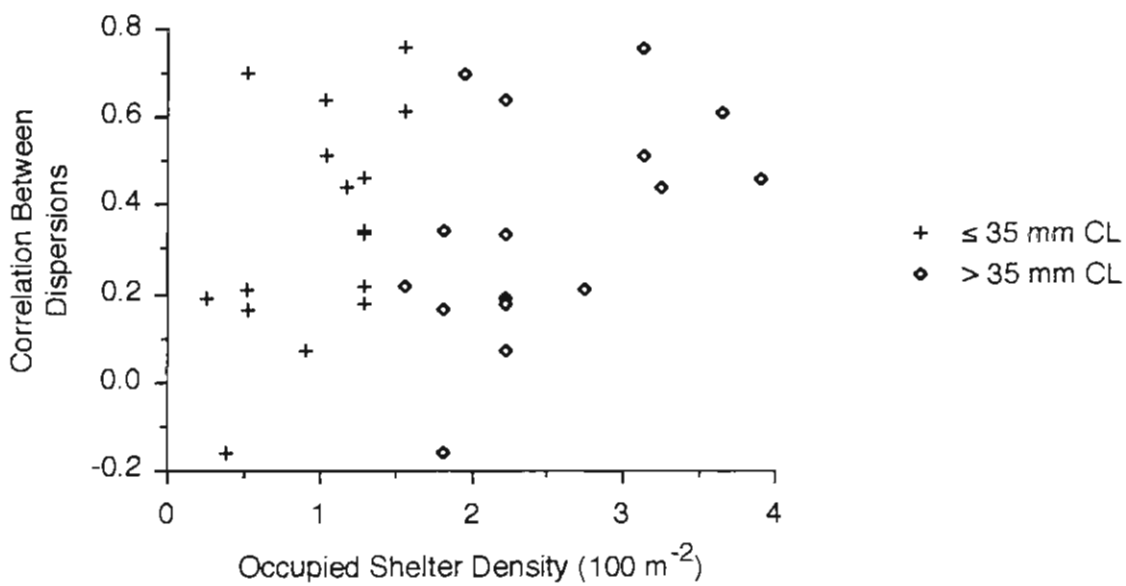


Fig. 3.14. Relationship between occupied shelter density, for small ( $\leq 35$  mm CL) and large ( $> 35$  mm CL) *Jasus edwardsii*, and the correlation of shelter dispersions.

### 3.3.4 Distribution and Topography

Small lobsters,  $\leq 35$  mm CL were generally found throughout the whole study area over the 22 month monitoring period (Fig. 3.15). In contrast, the larger lobsters, 36 - 60 mm CL and  $> 60$  mm CL, were mostly confined to particular areas of the reef, especially the northwest, northeast and mid southern regions (Figs. 3.16, 3.17; note: frequencies of lobsters on these maps may be biased by the repeated sampling of individuals with a fidelity to particular areas). These areas were typified by having increased abundances of interstices, present as crevices between boulders, caverns under large rock slabs or vertical cracks in the bedrock. It was noted that the five largest caverns within the census area were rarely inhabited by lobsters.

Although the dispersion of larger lobsters appeared to be related to the substrate structure, the relationship between distribution and reef structure was not adequately quantified using either the rugosity index or the crevice density estimates (Table 3.3). No correlations were found between these indices and presence of occupied shelters, except for a weak positive correlation between rugosity and occurrence of lobsters  $\leq 35$  mm CL ( $r_s = 0.16$ ,  $df = 163$ ,  $p = 0.03$ ).

Table 3.3. Spearman rank correlation coefficients for reef structure indices and presence of occupied lobster shelters (\* = significant,  $p = 0.03$ ).

substratum Parameter		n	CL $\leq 35$ mm	CL 36 - 60 mm	CL $> 60$ mm
Rugosity		165	0.162*	0.116	0.072
Crevices	- small	63	-0.116		
	- large	63		-0.049	-0.060
	- total	63	-0.103	0.096	0.088



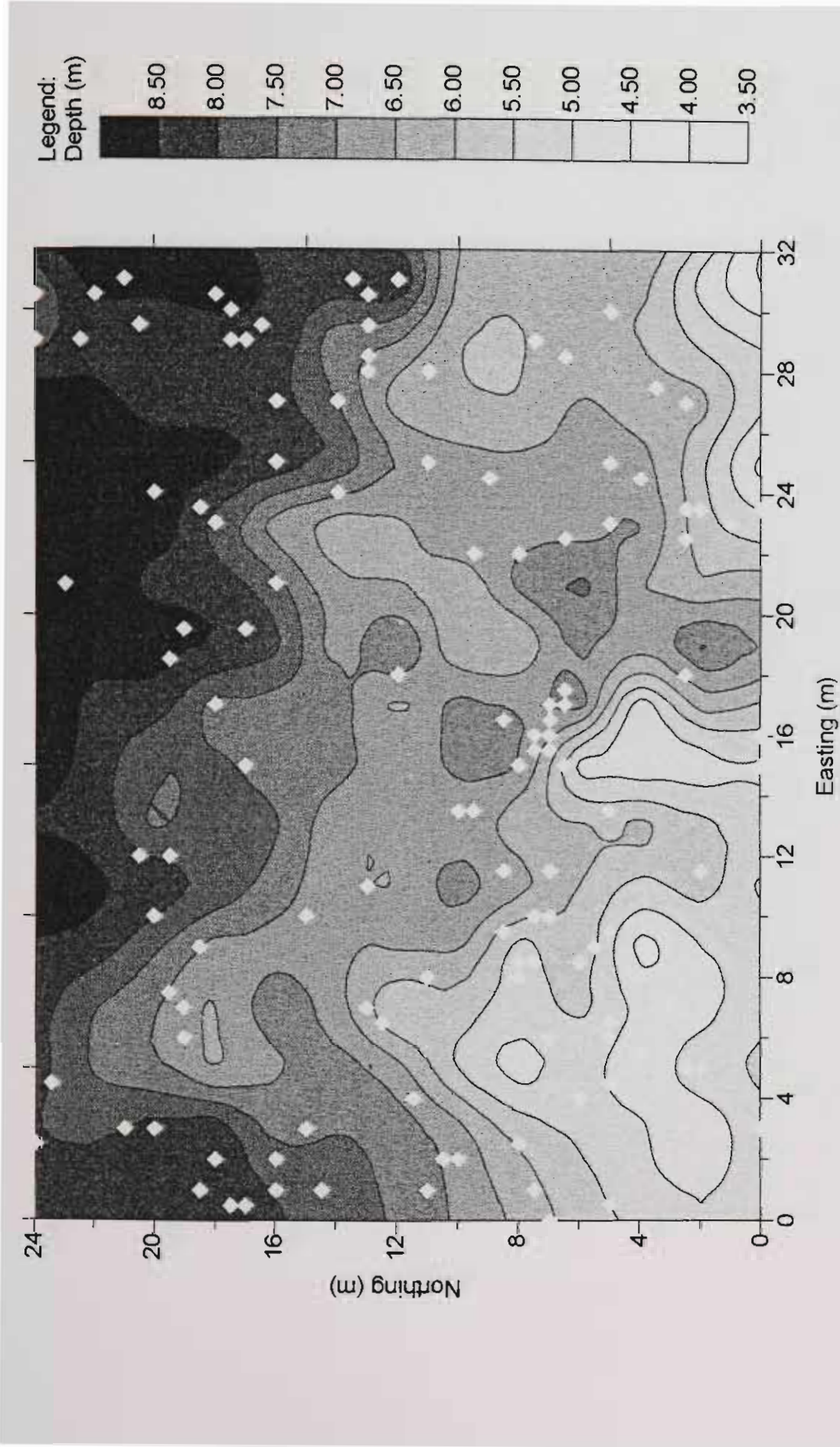


Fig. 3.15. Distribution of *Jasus edwardsii*  $\leq 35$  mm CL over the mudstone census area in Watsons Bay. The white diamonds indicate the position of lobsters for all surveys between 17 December 1992 and 29 September 1994.

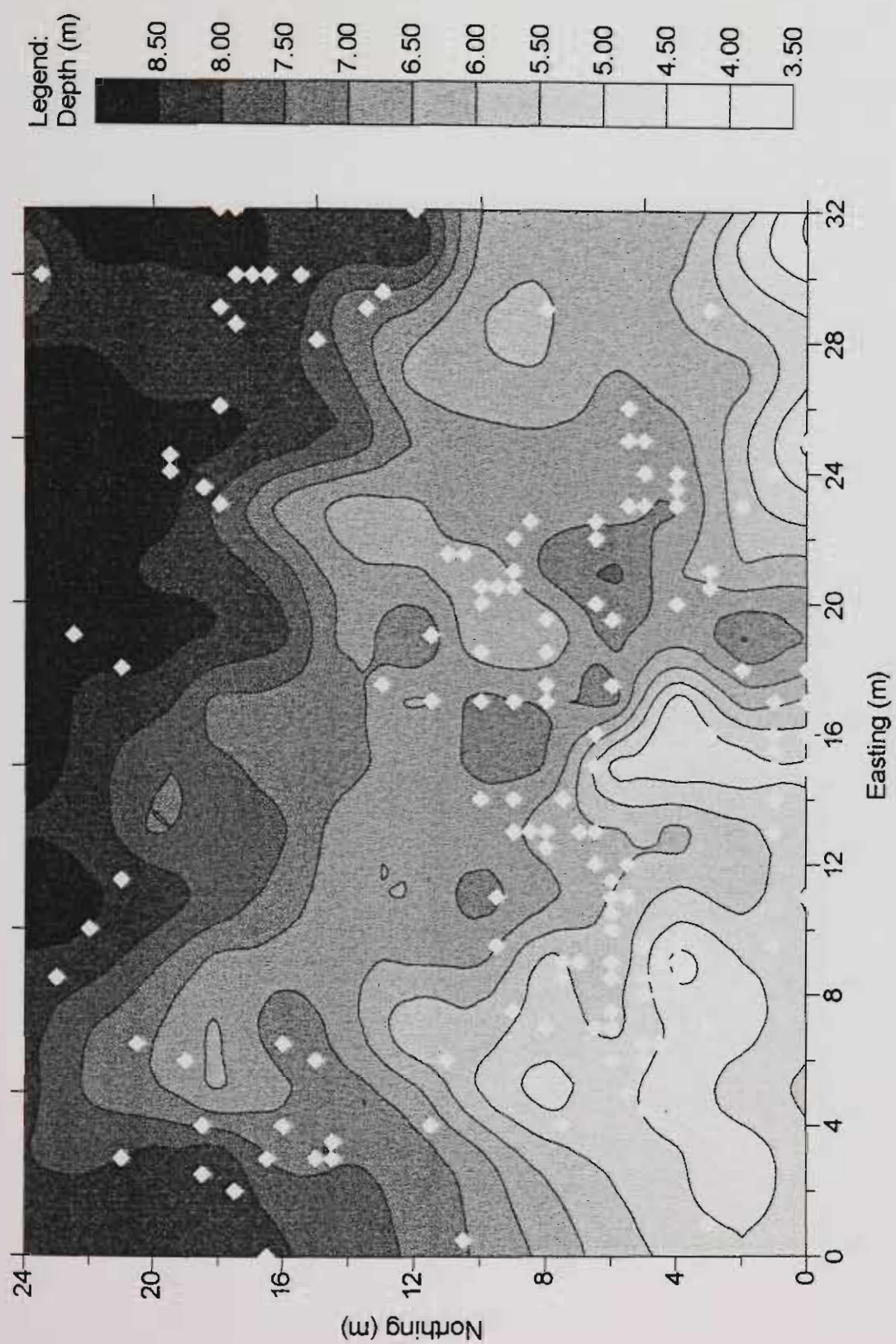


Fig. 3.16. Distribution of *Jasus edwardsii* 35-60 mm CL over the mudstone census area in Watsons Bay. The white diamonds indicate the position of lobsters for all surveys between 17 December 1992 and 29 September 1994.



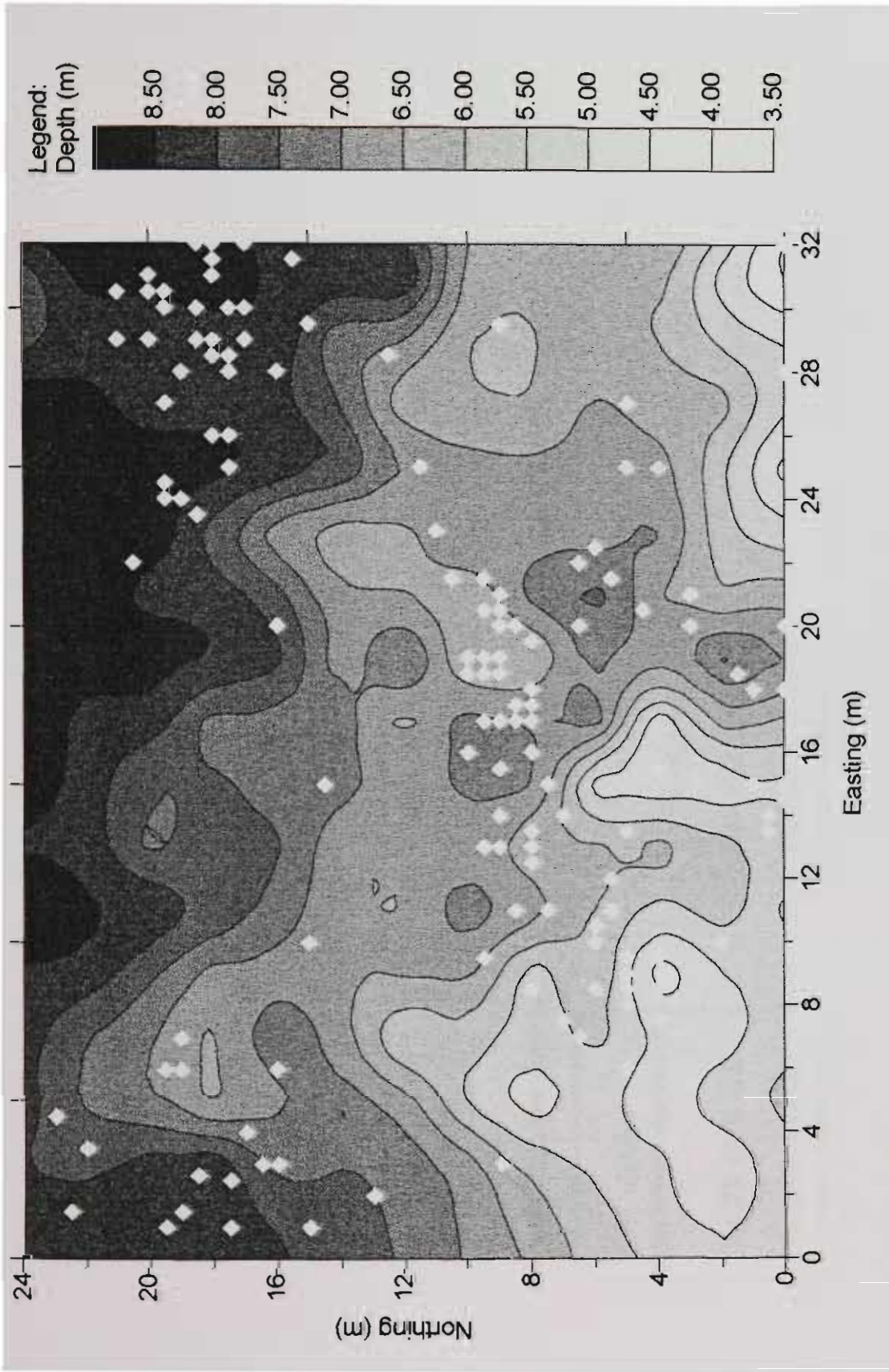


Fig. 3.17. Distribution of *Jasus edwardsii* > 60 mm CL over the mudstone census area in Watsons Bay. The white diamonds indicate the position of lobsters for all surveys between 17 December 1992 and 29 September 1994.

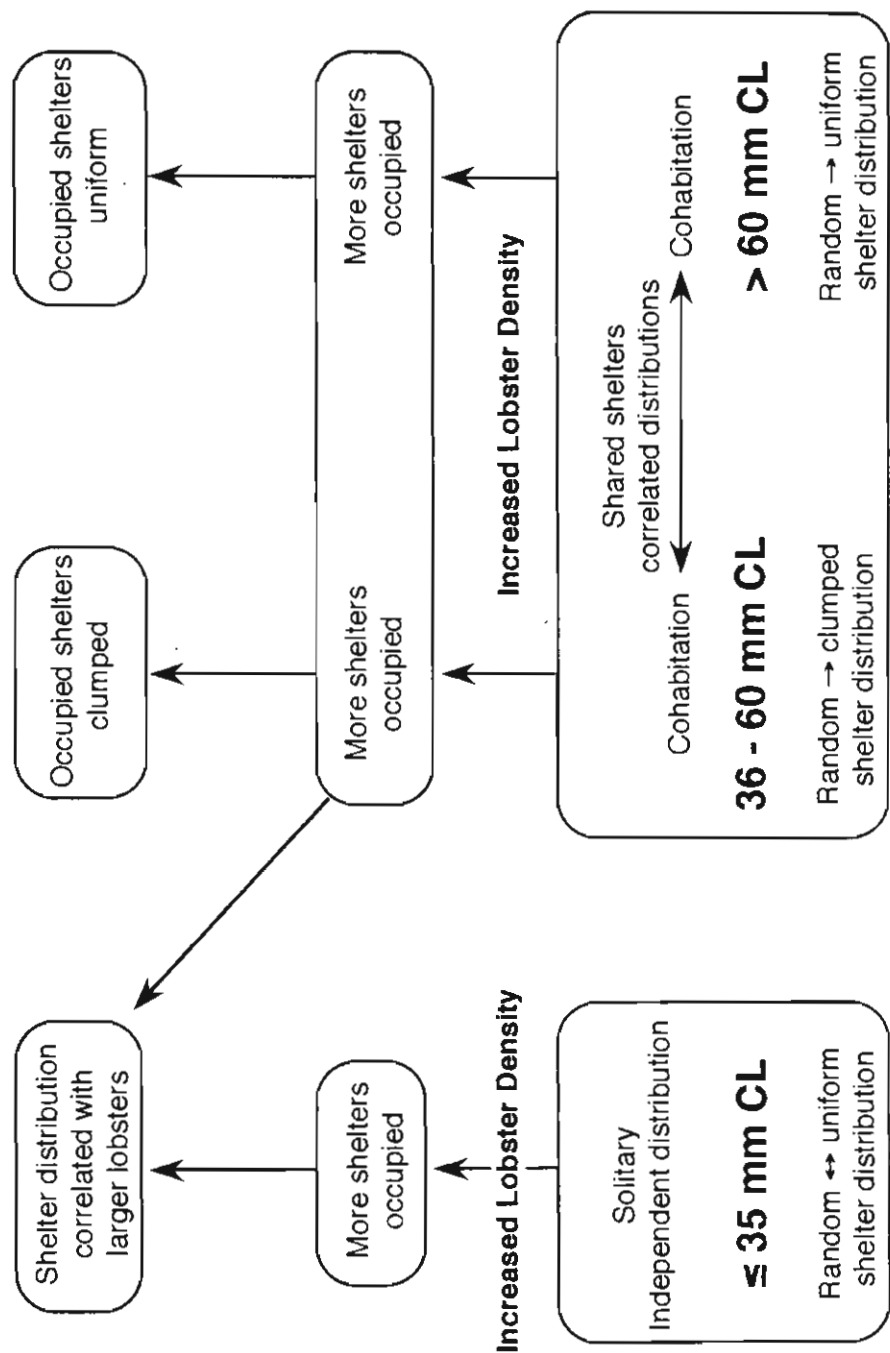


Fig. 3.18. Summary of relationships between size, distribution of occupied shelters and density for *Jasus edwardsii*, identified from field observations.

### 3.4 Discussion

#### 3.4.1 Density

The density of small *Jasus edwardsii*  $\leq 35$  mm CL was consistently low ( $< 1.9$  per 100 m<sup>2</sup>) compared with the estimates for the larger size groups, and with other palinurid species. For example, mean densities of 10 to 170 individuals per 100 m<sup>2</sup> have been observed for *Panulirus cygnus* ( $< 38$  mm CL; Jernakoff 1990; Jernakoff *et al.* 1994), 9 to 32 per 100 m<sup>2</sup> for *P. japonicus* ( $< 30$  mm CL; Norman *et al.* 1994) and 20 to 50 per 100 m<sup>2</sup> for *P. interruptus* ( $< 30$  mm CL; Engle 1979). However, densities of small *P. argus* are relatively low: 1 to 4 per 100 m<sup>2</sup> ( $< 35$  mm CL; Marx & Herrnkind 1985a; Forcucci *et al.* 1994). Comparatively low densities of early benthic *J. edwardsii* also occur at Stewart Island and the Leigh Marine Reserve in New Zealand (Breen & Booth 1989; MacDiarmid 1991; MacDiarmid & Breen 1992).

Because of the intensive search methods used, with the divers averaging 40-50 seconds per square metre, the low density estimates for small *J. edwardsii* are thought to be reasonably accurate. If this is so, the densities at the sites examined may be normally low, or unusually reduced by low settlement or high mortality during the sampling period. However, the sampling may have been biased because of lobsters residing in cryptic microhabitats, the lobsters being less detectable by the divers. Alternatively, the early benthic lobsters may be restricted to highly localised 'nursery areas', these being loci for subsequent recruitment to the rest of the coastline. If this is the case, then the low densities may have been because of the sites being remote from such nursery areas.

Important nursery areas occur for *Jasus verreauxi* in northern New Zealand (Booth 1979). Regions of consistently high densities of juvenile *J. edwardsii* have also been observed in New Zealand, at Castlepoint in the north (Booth 1979) and Stewart Island in the south (Annala & Bycroft 1985; Breen & Booth 1989), and at Blackfellows Caves in South Australia (Lewis 1977; J. Prescott 1994, South Australian Fisheries, *pers. comm.*). However, from personal observations and discussions with many recreational, fishery and scientific divers, there appears to be no anecdotal evidence of *J. edwardsii* being restricted to large scale nursery regions on the Tasmanian coastline (although high densities do occur). Similarly, no evidence for distinct nursery areas was found by Bradbury (1974) or in this study (Chapter 4).

Although all microhabitats within the census area were searched as thoroughly as possible, several microhabitat types were identified where post-puerulus lobsters could reside and not be seen by the divers. These were: the thalli of small bushy algae, such as *Plocamium*,

*Jeannerettia* and *Zonaria*; the similarly structured bushy bryozoan *Amathia wilsoni*; and the rear of long narrow crevices and the interstices of boulder and rubble substrata.

*Jasus edwardsii* will settle into artificial 'seaweed' type collectors (Booth 1979), and several palinurid lobsters reside in algae as small juveniles, including *P. argus*, *P. japonicus* and *P. interruptus* (Engle 1979; Marx & Hermkind 1985a; Yoshimura *et al.* 1994). Therefore, it is possible that the small *J. edwardsii* also utilise algae for shelter. However, the common algal species suitable for shelter, particularly the small fucoid and rhodophyte species, would give little protection from wave turbulence. Hence, it is unlikely that algae are the principle microhabitat of *J. edwardsii*. The nature of any cryptic behaviour can be conclusively determined only by destructive sampling. This would involve the removal of boulders and algae within net-enclosed corrals, as done by Hudon (1987) and Jernakoff (1990). An alternative may be to use a surgical endoscope to investigate smaller holes (P. Breen, pers. comm., NIWA New Zealand).

The densities of larger *J. edwardsii* (> 35 mm CL), were within the range of values found in New Zealand, except for the markedly higher densities present in marine reserves (Cole *et al.* 1990; MacDiarmid 1991; MacDiarmid & Breen 1992). Although MacDiarmid (1991) found patterns of abundance and movement for lobsters > 85 mm CL, the lack of seasonal patterns in the > 60 mm CL category of this study is probably because of the pooling of male, female and immature lobsters, thus confounding any seasonal patterns. It is interesting to note that a high proportion of ovigerous females were found at Darlington Point on August 1993. This reef projects into Mercury Passage and is relatively exposed to tidal and wind driven currents. This is consistent with observations in New Zealand, where aggregations of ovigerous female *Jasus edwardsii* tend to occur at the reef edges and in areas of high water movement (McKoy & Leachman 1982; MacDiarmid 1991). It is thought that this behaviour facilitates the dispersal of larvae and minimises predation on the larvae by reef planktivores.

### 3.4.2 Distribution

Substantial size-based differences in distribution patterns were observed, with the greatest differences occurring between the smallest lobsters  $\leq 35$  mm CL and larger lobsters > 35 mm CL. The small lobsters were segregated from each other with no cohabitation within shelters (Fig. 3.6) and occupied shelters often being uniformly distributed (Fig. 3.7). In contrast, larger lobsters were aggregated with cohabitation occurring within shelters (Figs. 3.3 & 3.4) and random to aggregated distributions of occupied shelters, the tendency for aggregation being stronger in the medium size class, 36 - 60 mm CL (Figs. 3.7 & 3.13; summarised in Fig. 3.18).

These differences in distribution may be because of size-related changes in physical microhabitat requirements (such as shelter) or changes in interspecific and intraspecific interactions (such as predation and sociality). Although there is little evidence to attribute causality to any abiotic or biotic factors, there is some evidence these differences may be associated with changes in shelter requirements (presented in Chapter 4).

Irrespective of causal influences, the solitary, random to regular dispersion of the small juveniles is likely to reduce any agonistic and competitive interactions between peers. Foraging efficiency may also be optimised with the small lobsters not having to move far from shelters to find food.

The distribution patterns of the medium and large size groups were similar, occupying similar areas of the reef and with shelters being shared. However, the changes in aggregation patterns with density suggest that medium-sized lobsters may have a higher degree of sociality (attraction between peers) than larger lobsters. This was indicated by the medium-sized lobsters occurring in more dense aggregations, both within and between shelters, with increased density (Figs 3.3 & 3.13). This would be expected if there is some level of attraction between peers, or if there are favourable microhabitats. The fact that shelters of larger lobsters were not aggregated at higher densities suggests that favourable microhabitats were not as patchy as exhibited by the distribution of medium-sized lobsters at higher densities, suggesting an attraction to peers (36 - 60 mm CL). Attraction to conspecifics has also been found in *P. interruptus* with the attraction being facilitated by chemical substances emanating from the conspecifics (Zimmer-Faust *et al.* 1985; Zimmer-Faust & Spanier 1987). The sociality of *P. interruptus* is generally higher for juveniles than adults (Zimmer-Faust & Spanier 1987). This was found for *J. edwardsii* between juveniles 36 - 60 mm CL and sub-adults and adults of > 60 mm CL. Such gregariousness is thought to be associated with anti-predatory defence and avoidance behaviour (Zimmer-Faust *et al.* 1985).

The early benthic ( $\leq 35$  mm CL) lobsters were solitary shelter dwellers and were therefore segregated from both peers and larger lobsters at the scale of shelters (up to metres). Segregation between peers of early benthic lobsters was also found at larger (reef-wide) scales, with a tendency for a uniform distribution of shelters over the reef. However, no segregation was found between the size groups at the reef-wide scale (10's to 100's of metres), with all sizes found together on the same reefs and the shelter distributions of different sizes not segregated within the reefs.

This presents the possibility that larger juveniles and adults can have a direct influence on the ecology of small juveniles. For example, adult lobsters may provide a stimulus for the settlement of pueruli through odour cues, or adults may adversely affect juvenile populations through agonistic interactions, with cannibalism in the extreme case. If adverse interactions between large and small lobsters were occurring in Watsons Bay, then the relative dispersions of shelters would be expected to be negatively associated. This was not found, with shelter dispersions often positively correlated at a scale of metres (although small juvenile lobsters never occupied the same shelters as larger lobsters). However, this does not preclude the presence of negative interactions as the distribution of shelters suitable for small juvenile lobsters may have been limited to microhabitats near shelters for larger lobsters. This potential for juvenile-adult interactions in *J. edwardsii* does not generally occur in other palinurid species because of migrations of adolescent juveniles into different habitats (*e.g.* Chittleborough 1970; Engle 1979; Herrnkind *et al.* 1994).

### 3.4.3 Conclusions

Considerable differences in spatial patterns were found between different sizes of *Jasus edwardsii*. These changes with size are likely to reflect changes in microhabitat requirements and in interspecific and intraspecific interactions. However, the different size groups were not spatially segregated, occupying similar areas on the reef. This suggests that juvenile habitats are not markedly different from adult habitats, but also has implications for the existence of important juvenile-adult interactions.



# Shelter Use and Availability

## 4.1 Introduction

Most lobsters, including spiny lobsters (Palinuridae), clawed lobsters (Nephropidae) and slipper lobsters (Scyllaridae), are facultative shelter dwellers (Kanciruk 1980; Phillips *et al.* 1980). *Jasus edwardsii* is no exception, and uses rock crevices throughout its benthic life phase (This thesis: Chapter 2; Booth 1979; Lewis 1977; MacDiarmid 1994). Lobsters often exhibit preferences for specific shelter types, such as the narrow holes with dual openings used by *Scyllarides latus* (Spanier & Almog-Shtayer 1992) or the large red macroalgae *Laurencia* spp used by juvenile *Panulirus argus* (Marx & Herrnkind 1985a). The requirement for specific shelter structures can also vary with size, in accordance with large changes in size and shifts in ecology (*e.g.* Marx & Herrnkind 1985a; Wahle & Steneck 1991). The type of shelter structures used is often a function of predation risk, food resources and protection from physical forces (Howard & Nunny 1983; Herrnkind & Butler 1986; Eggleston & Lipcius 1992, Wahle & Steneck 1992).

Obligate shelter requirements have the potential for determining the size structure and dynamics of lobster populations through the influences and limitations of habitat structures. The size composition of available shelters has been shown to control the abundance and size distribution of *Homarus gammarus* (Howard 1980). Habitat limitations for early benthic phase lobsters can also lead to bottlenecks in recruitment, as found for *H. americanus* and *P. argus* (Wahle & Steneck 1991; Smith & Herrnkind 1992; Wahle 1992b). Shelter limitations also affect the population dynamics of other refuge dwelling crustaceans, such as gonodactylid stomatopods (Steger 1987; Moran and Reaka 1988).

The geographic range of *J. edwardsii* (see Chapter 1) encompasses a diverse range of substratum types and structures. These substrata include igneous, sedimentary and metamorphic rocks which vary greatly in form because of differences in lithology, stratigraphy and weathering (Fish & Yaxley 1966; Thom 1984; Davis 1994). Subtidal substratum structures include smooth boulders, broken rubble, smooth reef and highly

eroded or structured reef. These substratum differences are likely to result in differences in shelter quality and quantity. Which, in turn, may affect the population structure and dynamics of *J. edwardsii*.

An objective of this study was to characterise the properties of shelters used by *J. edwardsii*, and to determine how these properties change with lobster size. A second objective was to estimate the abundance of available shelters and examine the influence of substratum structure on shelter quality and abundance. These objectives were addressed through field observations of lobsters and their shelters, and measurements of abundance, size and structure of crevices and interstitial spaces on adjacent Permian mudstone and Jurassic dolerite substrata, at Watsons Bay.

## 4.2 Materials and Methods

### 4.2.1 Shelter Use

The shelter use of *J. edwardsii* was examined primarily at the mudstone and dolerite sites in Watsons Bay (Fig. 1.4), but complementary observations were made at Eagle Hawk Neck (mudstone), Shagrock Bay (granite) and Darlington Pt, Maria Is (dolerite) (Fig. 1.3). At each site, all shelters occupied by lobsters within pre-determined areas, usually between 3 to 9 m depth, were examined by diving.

The properties of each shelter were determined by first removing the lobster and measuring its carapace length, then measuring the shelter entrance width, entrance height and depth from the entrance to the rear of the shelter. The shape of the shelter in the width-height plane (front shape) and in the depth-height plane (side shape) was classified as being rectangular, triangular, circular or irregular. Other observations on shelter structure, such as the presence of additional openings and other animals were also noted. Where more than one lobster was present, the shelter properties were assigned to the smallest lobster. The number of other conspecifics in the shelter was counted, and as many as possible were captured and measured.

### 4.2.2 Shelter Availability

Shelter availability was determined from the number, type and size of holes within 1 m<sup>2</sup> quadrats sampled on the mudstone and dolerite substrata at Watsons Bay. The quadrats were sampled at the intersections of a 4 x 4 m grid within each census area. The permanently marked 32 x 24 m census area on the mudstone substratum was examined (63 quadrats), as well as a 28 x 24 m area (57 quadrats) on the dolerite substratum of Cape Paul Lamanon (Fig. 1.4).

For each quadrat, measurements and observations on hole size and shape, as described above, were made for every cavity that exceeded 10 x 10 x 10 mm in aperture width, aperture height and depth respectively, and with a height less than 400 mm. The 10 x 10 x 10 mm dimensions are considered the smallest that a puerulus could occupy. In addition to the shelter observations, the general substratum structure was described for each quadrat. The suitability of each hole as a shelter for *J. edwardsii* was later assessed using the information gained from the study of lobster-occupied shelters.

## 4.3 Results

### 4.3.1 Characteristics of Shelter Use

A total of 119 lobster shelters were observed in the field, 73 from sedimentary substrata and 46 from igneous substrata. Lobsters between 10 mm CL (post-puerulus) and 35 mm CL displayed a strong relationship between shelter size and body size, occupying shelters which generally conformed to their body dimensions (Fig. 4.1a). However, lobsters above 35 mm CL were more variable in the size of shelters occupied, and were often present in shelters much larger than their body size (Fig. 4.1a). There were no obvious differences in shelter use between the igneous and mudstone substrata and the data were pooled for all further analyses.

Small lobsters,  $\leq 35$  mm CL, were more frequent in holes which were enclosed on all sides and relatively deep compared to the width of the entrance (high depth to width ratio: Table 4.1). Larger lobsters,  $> 35$  mm CL, occupied similar shelters but also occupied those which were less enclosed, such as open ledges and boulder junctions. These larger lobsters were frequently found in shelters with one or more openings to the rear or sides. Larger lobsters also occupied shelters with sides enclosed by sea urchins and, in four cases, were present in shelters with a gravel or sand floor. A higher proportion of lobsters tended to occupy shelters with rectangular openings (parallel top and bottom in the width-height plane) and most occupied shelters were either rectangular or triangular in the height-depth plane (Table 4.1). There were no significant differences in the shelter shapes occupied by small and large lobsters, although significant differences were found in the general shelter structure and the number of openings (Table 4.1).

Conspecifics were rare in the shelters of lobsters smaller than 35 mm CL and only two cases (4%) were found. Cohabitation for lobsters larger than 35 mm CL was common with 18 cases (25%) observed. These differences in cohabitation proportions were significant (G-test of independence:  $G = 10.25$ ,  $df = 1$ ,  $p < 0.05$ ).

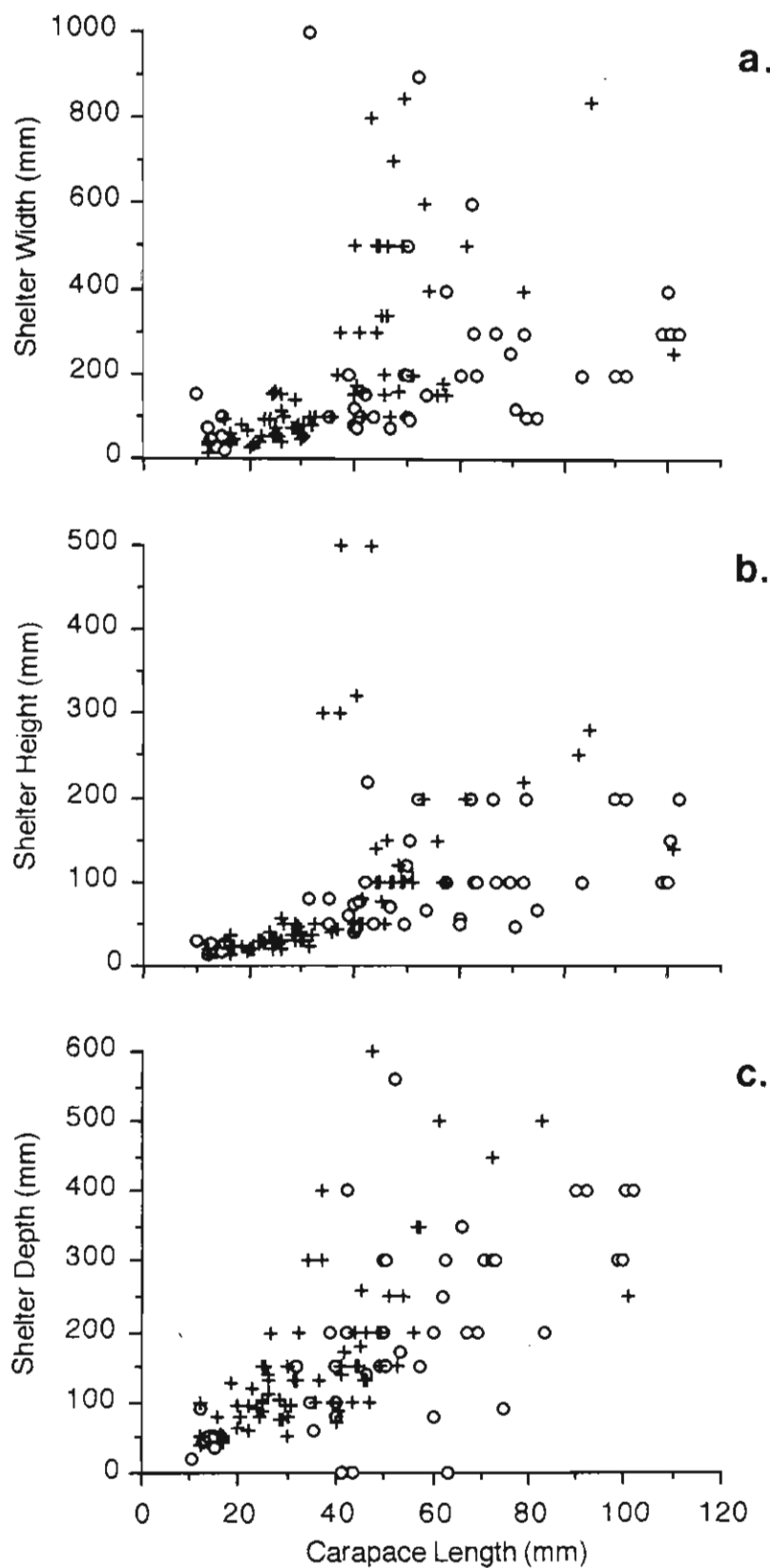


Fig. 4.1a. Relationship between lobster carapace length and shelter (a) width, (b) height and (c) depth. o = igneous substrata; + = mudstone substrata.

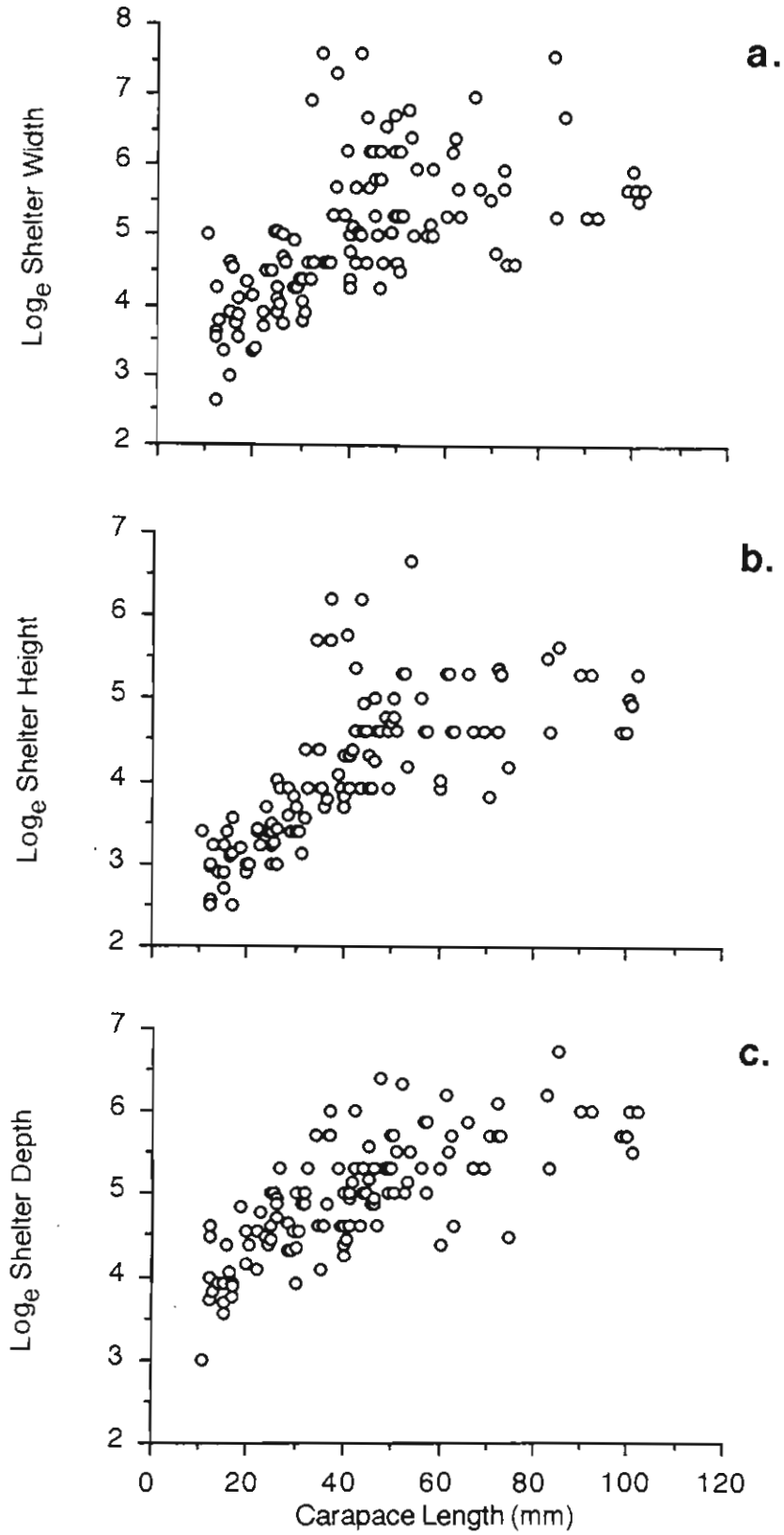


Fig. 4.1b. Relationship between lobster carapace length and natural log of shelter (a) width, (b) height and (c) depth.

Table 4.1. Frequencies (F) of occupation of shelters with different shape and structural characteristics for two size groups of lobsters. Maximum and minimum dimensions exclude 5% of outlying data.

Shelter Characteristic		≤ 35 mm CL		> 35 mm CL		G-test of independence
		F	%	F	%	
Structure	hole	37	84	10	16	G = 53.23, df = 2, p < 0.05
	ledge	5	11	27	44	
	boulder junction	2	5	25	40	
Openings	entrance only	43	91	27	38	G = 33.16, df = 3, p < 0.05
	one side	3	6	22	31	
	both sides	1	2	15	21	
	rear	0	0	4	6	
Width-height shape	rectangular	16	52	31	53	G = 4.69, df = 3, p > 0.05
	triangular	3	10	14	24	
	circular	7	23	6	10	
	irregular	5	16	7	12	
Height-depth shape	rectangular	15	50	17	30	G = 5.93, df = 3, p > 0.05
	triangular	11	37	37	64	
	circular	2	7	2	3	
	irregular	2	7	2	3	
Biotic component	none	45	96	59	81	G = 5.09, df = 2, p > 0.05
	sessile animals	2	4	4	6	
	sea urchins	0	0	9	13	
Depth:width ratio > 1		37	79	37	51	
Shelter dimensions (mm)	width	14 - 160		70 - 2000		
	height	12 - 85		40 - 800		
	depth	35 - 200		70 - 840		

Table 4.2. Pearson’s correlation matrix of regression variables (shelter dimensions  $\log_e$  transformed). All correlations significant at  $p < 0.001$ .

	lnWidth	lnHeight	lnDepth
lnHeight	0.788		
lnDepth	0.747	0.812	
Carapace length	0.737	0.889	0.828

Table 4.3. Assessment for multicollinearity in shelter use data: eigenvalues, condition indices, variance proportions and tolerance values.

Index	1	Component			Tolerance
		2	3	4	
Eigenvalue	3.964	0.023	0.008	0.004	
Condition index	1.000	13.052	21.647	31.441	
Variance proportions					
lnWidth	0.001	0.121	0.860	0.018	0.347
lnHeight	0.001	0.073	0.786	0.440	0.268
lnDepth	0.000	0.002	0.028	0.970	0.310
Constant	0.001	0.455	0.027	0.517	

Table 4.4. Multiple regression of carapace length of lobsters on occupied shelter variables. B = regression coefficient;  $SE_B$  = standard error of coefficient; 95%CI = 95% confidence interval;  $\beta$  = standardised regression coefficient;  $sr^2$  = squared semipartial correlation.

Variable	B	$SE_B$	95% CI	$\beta$	$sr^2$
lnWidth	0.075	1.339	-2.58 – 2.73	0.004	
lnHeight	14.444**	1.907	10.66 – 18.23	0.634	0.107
lnDepth	8.414**	2.114	4.22 – 12.61	0.310	0.030
Constant	-60.614**				

$R = 0.907^{**}$ ,  $R^2 = 0.824$ , Adj  $R^2 = 0.818$ , SE of regression = 7.729

\*\*  $p < 0.01$

### 4.3.2 Relationship between Lobster Size and Shelter Dimensions

The relationship between lobster carapace length and shelter width, height and depth was approximately log-linear (Fig. 4.1a). Using the shelter use data, a multiple linear regression model was developed to estimate lobster carapace length from the natural logs of the three shelter dimensions.

Prior to analysis, univariate outliers were evaluated using standardised scores and six cases were deleted with scores greater than 2.50. Multivariate outliers were screened using Cook's distance, leverage and standardised residuals, and cases with a high influence on the regression were deleted (Tabachnick and Fidell 1989; Wilkinson *et al.* 1992). The analysis was re-run until no further outliers were detected. A total of 21 cases, with carapace lengths ranging from 10 to 102 mm, were deleted as outliers, reducing the sample size to 98. Most of the outliers were lobsters > 35 mm CL, occupying shelters much larger than their body size. An examination of the residuals showed that the assumptions of the analysis were met, having: errors of prediction normally distributed around each dependent variable score; a general linear relationship between the dependent and independent variables; and standard deviations of prediction approximately equal for all predicted dependent variable scores (homoscedasticity; Tabachnick & Fidell 1989).

A potential problem with the multiple regression analysis was multicollinearity, because of the similar nature of the three shelter variables. High correlations were found between the shelter variables (0.74 to 0.88; Table 4.2) but were not considered too high for the analysis (< 0.90; Tabachnick & Fidell 1989). Multicollinearity is also detected by: high condition indices (square root of the ratio of the largest eigenvalue to each successive eigenvalue); the variance proportions (loadings) where a component with a high condition index contributes to the variance of two or more variables; and very low tolerance values among the predictor variables (Wilkinson *et al.* 1992). The fourth component of the regression had a low eigenvalue and high condition index. However, only  $\log_e$  shelter depth loaded highly on this component and tolerance values were not exceptionally low (Table 4.3). On the basis of these statistics, multicollinearity was not considered a problem and all shelter variables were included in the regression.

A significant relationship was determined for predicting carapace length from the three shelter variables ( $F = 146.2$ ,  $df = 3, 94$ ,  $p < 0.001$ ). Unstandardised and standardised regression coefficients are given in Table 4.4. Only height and depth contributed significantly to the regression ( $df = 96$ , width:  $t = 0.056$ ,  $p = 0.95$ , height:  $t = 7.574$ ,  $p < 0.001$ ; depth:  $t = 3.98$ ,  $p < 0.001$ ). The squared semi partial correlations (Table 4.4)



show that height and depth uniquely contributed 11% and 3%, respectively, to the variance in carapace length. The three combined shelter variables further contributed a shared variance of 68%, with a total of 82.4% (81.8% adjusted) of the variability in carapace length being predicted by the three shelter dimensions.

#### **4.3.3 Shelter Related Defence Behaviour**

The removal of lobsters from their shelters for measurements and assessment of shelter properties provided an opportunity to observe behavioural responses to disturbances. Two behaviour patterns were observed which were independent of lobster size, but dependent on the type of shelter that the lobster occupied.

Lobsters occupying comparatively small, enclosed holes with only one opening were usually found towards the entrance of the hole, with the antennae directed forward and just protruding. On approach of a diver, the activity of the antennae and antennules increased, the body was raised slightly by the pereopods and the lobster moved slightly forward. On contact with the antennae, or rapid approach by the diver, the lobster rapidly retreated to the rear of the shelter and remained motionless. If the lobster was further disturbed, it firmly wedged itself across the back or one side of the shelter using the abdomen, pereopods and antennae, and the body was directed anteriorly towards the shelter entrance. This 'wedging' behaviour made it difficult to extract the lobster as the anteriorly directed spines assisted to lock the lobster in the hole. If the abdomen was the first point of contact, the lobster would flee immediately from the shelter.

Lobsters occupying comparatively large shelters and shelters with more than one opening were also usually found towards the front of the shelter, but not with the antennae protruding from the entrance. Where cohabitation occurred, larger lobsters were usually found positioned to the rear of smaller ones. On approach of a diver, increased movements of antennae and antennules would occur and the lobsters would slowly move towards the rear of the shelter and towards other entrances, larger lobsters displacing smaller ones. If disturbed further, the lobsters moved rapidly to the rear of the shelter and, if the disturbance continued, fled the den. Lobsters which could not move past the diver wedged their body in a narrow part of the shelter, in a similar manner to lobsters in small shelters.

#### **4.3.4 Shelter Availability and Effects of Substratum**

Measurements were taken from a total of 270 holes on the mudstone substratum and 91 holes on the dolerite substratum. The suitability of these holes for lobsters  $\leq 35$  mm CL was determined using the criteria: width = 14-160 mm, height = 12-82 mm, depth = 35-200 and no openings to the sides or rear. The suitability of the holes for lobsters  $> 35$  mm

CL was determined using the criteria: width = 70-2000 mm, height = 40-800 mm, depth = 70-840 mm (see Section 4.3.1). The numbers of holes classified as suitable for the two size classes of lobsters are given in Table 4.5. The holes and crevices classified as unsuitable were usually either too shallow, or were the correct dimensions for lobsters  $\leq 35$  mm CL but open at the sides or rear. Because of the broad properties of shelter use by lobsters  $> 35$  mm CL, it is unlikely that all suitable shelters were recognised in the field. In addition, only holes less than 400 mm in height were measured. For these reasons, estimates of shelter availability for larger lobsters were considered minimum values only.

The density of shelters for lobsters  $\leq 35$  mm CL was significantly higher on the mudstone substratum (mean  $\pm$  SE =  $2.14 \pm 0.36$  m<sup>-2</sup>) than on the dolerite substratum ( $0.77 \pm 0.12$  m<sup>-2</sup>; Table 4.6). There was no significant difference in the relative density of shelters for lobsters  $> 35$  mm CL between the two substratum types (Table 4.6).

The mudstone site varied considerably in substratum structure, including highly eroded vertical walls, smooth walls, flat reef, irregular reef and boulders. For lobsters  $\leq 35$  mm CL, wall substratum structures and areas with a mixture of wall and other substratum structures had high densities of available shelters:  $2.96 \pm 0.067$  m<sup>-2</sup> and  $1.69 \pm 0.042$  m<sup>-2</sup> respectively. Other substratum structures, including flat reef, irregular reef and boulders had a significantly lower density of available shelters:  $0.33 \pm 0.016$  m<sup>-2</sup> (Scheffe's F,  $p < 0.05$ ; Table 4.7). No significant difference in the relative densities of shelters for lobsters  $> 35$  mm CL was detected between these different substratum structures.

Table 4.5. Number of potential shelters sampled and numbers classified as suitable for either of two size classes of lobsters, on mudstone and dolerite substrata.

Substratum	Quadrats	Total	CL $\leq 35$ mm	CL $> 35$ mm	Both	Unsuitable
Mudstone	63	270	137	25	2	108
Dolerite	57	91	44	28	4	19

Table 4.6. Mean densities of available shelters ( $\pm$  SE m<sup>-2</sup>) on mudstone and dolerite substrata. Means were compared using the Mann-Whitney U test.

Size Class	Mudstone n = 63	Dolerite n = 57	Significance
$\leq 35$ mm CL	$2.14 \pm 0.36$	$0.77 \pm 0.12$	$p = 0.003$
$> 35$ mm CL	$0.39 \pm 0.11$	$0.49 \pm 0.11$	$p = 0.418$

Table 4.7. Comparison of available shelter densities (mean  $\pm$  SE m<sup>-2</sup>) on different mudstone substratum structures. Data for shelters suitable for lobsters  $\leq 35$  mm CL were square root transformed prior to analysis (test for homogeneity of variances after transformation: Cochran's  $C = 0.460$ ,  $p > 0.05$ ). Densities for lobsters  $\leq 35$  mm CL were compared using Scheffé's  $F$ . Because of non-normal distributions, densities for lobsters  $> 35$  mm CL were compared using the non parametric Kruskal-Wallis method.

Size Class	Walls n=13	Mixed Walls n=26	Other n=24	Significance
$\leq 35$ mm CL	<u>2.96 <math>\pm</math> 0.067</u>	<u>1.69 <math>\pm</math> 0.042</u>	0.33 $\pm$ 0.016	$p < 0.001$
$> 35$ mm CL	1.00 $\pm$ 0.392	0.307 $\pm$ 0.617	0.168 $\pm$ 0.077	$p = 0.081$

\* underline denotes non-significantly different means

Table 4.8. Comparison of available shelter densities (mean  $\pm$  SE m<sup>-2</sup>) on different dolerite substratum structures. Data square root transformed prior to analysis (test for homogeneity of variances after transformation: CL  $\leq 35$  mm, Cochran's  $C = 0.460$ ,  $p > 0.05$ ; CL  $> 35$  mm, Cochran's  $C = 0.5336$ ,  $p > 0.05$ ). Means were compared using t-tests

Size Class	Boulder n = 37	Mixed n = 20	Significance
$\leq 35$ mm CL	0.497 $\pm$ 0.012	0.190 $\pm$ 0.016	$p = 0.130$
$> 35$ mm CL	0.182 $\pm$ 0.009	0.094 $\pm$ 0.016	$p = 0.470$

The dolerite site had heterogeneous substratum structures, including smooth boulders, flat reef, irregular reef and sand patches. There were no differences in shelter availability between boulder substrata and other mixed substrata for either shelter size class (Table 4.8).

The spatial distributions of available shelters were examined by assessing the goodness of fit of the observed frequencies within the quadrats with that expected from a Poisson (random) distribution. An indication of whether the distributions were clumped or regular was obtained from an examination of variance/mean ratios (Zar 1984). The distribution of shelters for lobsters  $\leq 35$  mm CL was strongly clumped on the mudstone substratum ( $G = 31.059$ ,  $df = 4$ ,  $p < 0.01$ ,  $s^2/\bar{X} = 3.702$ ). This clumped distribution reduced the probability of locating a quadrat with at least one suitable shelter from 0.886, expected from the Poisson distribution (and a mean density of 2.14 per quadrat), to the observed probability

of 0.666, a reduction of 22%. There was also evidence of clumping of shelters for lobsters > 35 mm CL on the dolerite substratum ( $G = 5.801$ ,  $df = 1$ ,  $p < 0.05$ ,  $s^2/\bar{X} = 1.390$ ). However, this clumping did not result in a reduction in the probability of locating a suitable shelter: 0.388 for a Poisson distribution and 0.381 for the observed distribution. The distribution of shelters was random for lobsters  $\leq 35$  mm CL on the dolerite substratum ( $G = 2.900$ ,  $df = 2$ ,  $p > 0.05$ ,  $s^2/\bar{X} = 1.111$ ), and lobsters > 35 mm CL on the mudstone substratum ( $G = 3.119$ ,  $df = 1$ ,  $p > 0.05$ ,  $s^2/\bar{X} = 1.751$ ).

The relative proportions of different shelter shapes were also found to vary between the mudstone and dolerite substratum types (Table 4.9). For lobsters  $\leq 35$  mm CL, the proportions of shelter shapes in the width-height plane (entrance shape) was significantly different between the mudstone and dolerite substrata (Log-likelihood Ratio, William's correction:  $df = 2$ ,  $G = 20.018$ ,  $p < 0.01$ ), with a higher proportion of triangular shaped shelters on the dolerite substratum. There was no significant difference in the proportions of shelter shapes in the height-depth plane (side shape) between substratum types ( $df = 2$ ,  $G$  with William's correction = 3.231,  $p > 0.05$ ).

For lobsters > 35 mm CL, the proportions of shapes in the width-height plane was not significantly different between the substratum types ( $df = 1$ ,  $G$  with Yate's correction for continuity = 0.602,  $p > 0.05$ ). A moderately significant difference was detected for shapes in the height-depth plane ( $df = 1$ ,  $G$  with Yate's correction = 5.749,  $0.05 > p > 0.01$ ), with a higher proportion of triangular shelters on the mudstone substratum (Table 4.9). The proportion of shelters with openings to the sides or rear was not significantly different between substrata ( $df = 1$ ,  $G = 0.056$ ,  $p > 0.05$ ).

#### 4.3.5 Lobster Selection of Shelter Structures

The preferences by lobsters for particular shelter shapes was examined by comparing the frequency of shelter-shape occupation (Section 4.3.1) with the frequency of shelter shape availability (Section 4.3.3). Lobsters  $\leq 35$  mm CL showed no preferences for any particular shelter shapes, occupying shelter structures in proportions similar to their availability (Table 4.10). Lobsters > 35 mm CL displayed significant preferences for circular and irregular shapes in the width-height (front) plane and triangular shelters in the height-depth (side) plane (Table 4.10). These larger lobsters also showed a significant selection for shelters which had openings to the sides or rear (Table 4.11).

Table 4.9. Frequencies of available holes with different shape and structural characteristics for two lobster size classes on mudstone and dolerite substrata.

Hole characteristic		CL $\leq$ 35 mm				CL > 35 mm			
		Mudstone		Dolerite		Mudstone		Dolerite	
		F	%	F	%	F	%	F	%
Openings	entrance only	137	100	44	100	16	64	19	68
	one side					3	12	7	25
	both sides					6	24	1	4
	rear					0	0	1	4
Width-height shape	rectangular	89	65	26	59	19	76	19	68
	triangular	9	7	12	27	4	16	9	32
	circular	32	23	6	14	1	4	0	0
	irregular	7	5	0	0	1	4	0	0
Height-depth shape	rectangular	73	53	20	46	10	40	18	64
	triangular	52	38	22	50	15	60	10	36
	circular	10	7	2	4	0	0	0	0
	irregular	2	2	0	0	0	0	0	0
Depth:width ratio > 1		63	46	31	71	0	0	13	46

Table 4.10. Comparison of the frequency of occupation of different shelter shapes by lobsters (observed) and the available frequencies of shelter shapes (expected). Expected frequencies of shelter shape were calculated from suitable shelters pooled from both mudstone and dolerite substrata. Shelter shapes are: (R) rectangular, (T) triangular, (C) circular and (I) irregular. Frequencies were compared using the Log-Likelihood Ratio (G) statistic with William's correction for  $df \geq 2$  and Yate's correction for continuity for  $df = 1$ .

Size Class	Shape Plane		R	T	C	I	Significance
CL $\leq$ 35 mm	width - height	Observed	16	3	7	5	$df = 2$ , $G = 2.837$ , $p > 0.05$
		Expected	19.7	3.6	6.5	1.2	
	height - depth	Observed	15	11	2	2	$df = 2$ , $G = 1.154$ , $p > 0.05$
		Expected	15.4	12.3	2.0	0.3	
CL > 35 mm	width - height	Observed	31	14	6	7	$df = 2$ , $G = 27.244$ , $p < 0.01$
		Expected	41.6	14.2	1.1	1.1	
	height - depth	Observed	17	37	2	2	$df = 1$ , $G = 9.111$ , $p < 0.01$
		Expected	28.5	25.5	-	-	

Table 4.11. Comparison of shelters with different opening arrangements for lobsters > 35 mm CL. The observed occupation frequencies of lobsters in shelters with different opening arrangements was compared with the available (expected) shelter frequencies using a G-test (with William’s correction).

	None	One Side	Both Sides	Rear	Significance
Observed	31	22	15	4	df = 2, G = 15.711, p < 0.01
Expected	47.5	13.6	9.5	1.4	

4.3.6 Shelter Abundance and Lobster Size

The size distribution of available shelters, for both the mudstone and dolerite substrata, was determined in terms of the probable size of lobsters that would occupy them. Carapace lengths for available shelters were estimated using the multiple regression model described in Section 4.3.2. Shelters which did not fit the characteristics described in Section 4.3.1 were excluded. Plots of shelter abundance per lobster size class (Fig. 4.2) show that, for the mudstone site, abundance was relatively high for the smallest lobsters, but there was a rapid decline as the lobsters grew. For the dolerite site, shelter abundance was comparatively low for all lobster size classes.

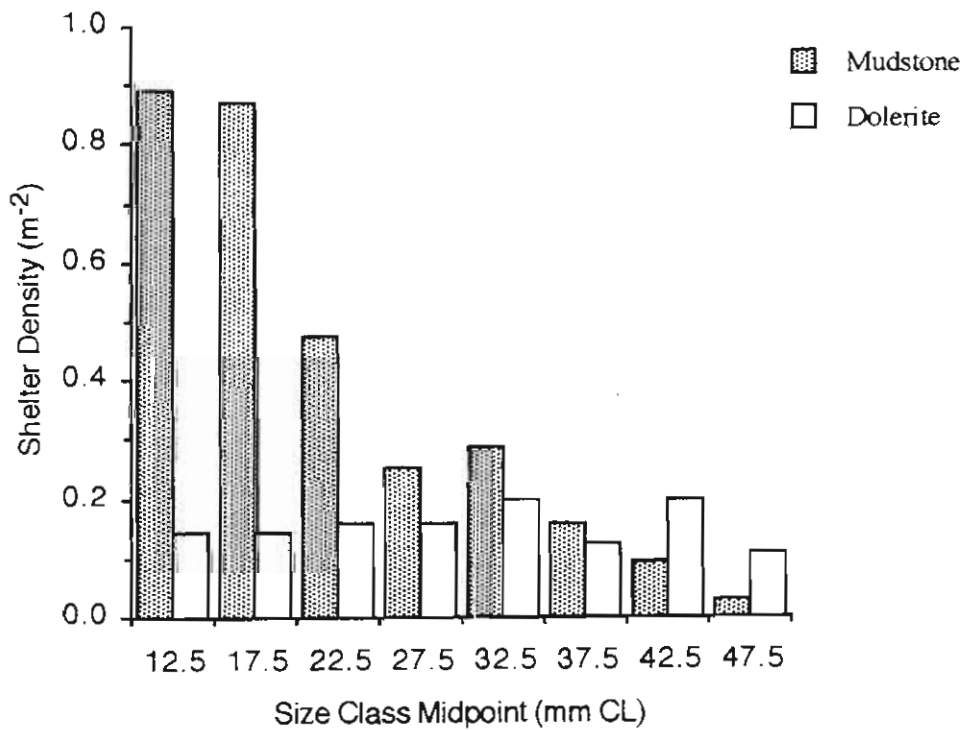


Fig. 4.2. Changes in predicted shelter availability with increases in lobster size for the mudstone and dolerite substrata in Watsons Bay.

## 4.4 Discussion

### 4.4.1 Properties of Shelter Use

A distinct ontogenetic shift was observed in the shelter properties of juvenile *J. edwardsii*. Early stage juveniles ( $\leq 35$  mm CL) were mostly solitary and occupied shelters which were enclosed on all sides and closely related to the size of the lobster (in all three dimensions). In contrast, lobsters above approximately 35 mm CL were more variable in shelter use, occupying shelters much larger than their body size and with more than one opening, as well as cohabiting with conspecifics. Lobsters  $\leq 35$  mm CL showed no preferences for any particular shelter shape, while larger lobsters showed some selection for circular and irregularly shaped shelters. These larger lobsters also displayed a preference for shelters with more than one opening.

The shelter properties of *J. edwardsii* and the ontogenetic shift in these properties are similar to that of the Japanese spiny lobster *Panulirus japonicus*. Early stage *P. japonicus*, from 6 mm CL at settlement to approximately 22 mm CL, are also solitary and occupy holes closely related to their body size (Yoshimura & Yamakawa 1988; Norman *et al.* 1994; Yoshimura *et al.* 1994). This lobster-shelter size relationship is approximately linear (Norman *et al.* 1994; Yoshimura *et al.* 1994), as found in *J. edwardsii*, but exponential relationships have also been fitted (Yoshimura & Yamakawa 1988). Above a size of approximately 22 mm CL, *P. japonicus* occupies a wider range of shelter sizes and cohabits in more open cave/ledge type shelters (Norman *et al.* 1994). The post-juvéniles of *P. cygnus*, 7–31 mm CL, also show similar patterns of shelter use, with the smallest lobsters tending to be more solitary, a linear relationship between lobster size and hole size, and a trend towards aggregating with conspecifics and occupying relatively larger ledges and caves as the lobsters grow larger (Jernakoff 1990). However, for *P. cygnus*, there is no clear distinction in shelter use between smaller and larger lobsters, as seen in *J. edwardsii* (this study) and *P. japonicus* (Norman *et al.* 1994).

*Panulirus argus* and *P. interruptus* also display well-defined shifts in shelter use, but the post-juvéniles initially occupy vegetative microhabitats. *Panulirus argus* inhabits the thalli of rhodophytes, *Laurencia* spp, from settlement at approximately 6 mm CL to approximately 17 mm CL, before moving into shelters formed by the substratum (Marx and Herrnkind 1985a). *P. interruptus* inhabits shallow surfgrass beds, *Phyllospadix*, from approximately 7 mm CL to 30 mm CL, before moving to predominantly deeper, rocky habitats (Engle 1979). The post-juvéniles of both *P. interruptus* and *P. cygnus* are initially solitary before aggregating with conspecifics in larger shelter structures (Engle 1979; Marx & Herrnkind 1985a; Zimmer-Faust & Spanier 1987).

The shelter properties of *J. edwardsii*  $\leq 35$  mm CL appear to provide a high degree of protection from both predators and environmental forces. The close association of lobster size and hole dimensions is likely to restrict the entry of larger predators and enable the lobster to wedge itself in the hole to resist extraction (see Section 4.3.3). In contrast, the relatively spacious shelters frequently inhabited by lobsters  $> 35$  mm CL provide access to larger predators and provide fewer opportunities for ‘wedging’ defence behaviour (see Section 4.3.3). However, these shelters provide more opportunities for escape, through additional openings or the enlarged entrance, and for cohabitation with conspecifics. Cohabitation may facilitate defence through communal defence behaviour, increased prey vigilance and concealment among conspecifics (Atema & Cobb 1980; Spanier & Zimmer-Faust 1988; Eggleston & Lipcius 1992).

The ontogenetic shift of *J. edwardsii* to shelters of reduced apparent protection properties suggests that the ontogenetic shift is mediated by a reduced susceptibility to predation. This is consistent with the principles of “size escape”. Where predators are size selective, and prey species encompass a large size range, prey species can often attain refuge from predation with increased size (Menge & Sutherland 1976; Werner & Gilliam 1984). Such changes in predation risk influence the habitat selection of many species (Werner and Gilliam 1984; Quinn & Janssen 1989; Ojeda and Dearborn 1991; Richards 1992), including the lobsters *Homarus americanus* (Wahle 1992a; Wahle & Steneck 1992) and *P. argus* (Smith & Herrnkind 1992). Possible predation effects are discussed further in Chapter 9.

The ontogenetic shift in shelter use may also be mediated by changes in shelter availability. The availability of suitable shelters required by early benthic lobsters has been shown to decline with increased size for *P. japonicus* (Norman *et al.* 1994), *P. argus* (Marx and Herrnkind 1985a) and *Homarus americanus* (Wahle and Steneck 1991). For these three species, there is evidence to suggest that this decline becomes limiting before the lobsters shift to more abundant shelter forms. This study showed a similar decline in shelter availability for early benthic *J. edwardsii* on the mudstone substratum. This aspect is discussed further in Section 4.4.3.

Nearly all *J. edwardsii*  $\leq 35$  mm CL observed during this study, and during the density and distribution surveys (described in Chapter 3), occurred singly in shelters. This contrasts with observations on the same species at the Leigh Marine Reserve, on the northeast coast of New Zealand (MacDiarmid 1994). MacDiarmid found that only 16% of lobsters  $< 30$  mm CL resided solitarily (although Macdiarmid states this may be an over-



estimate). MacDiarmid's findings are also inconsistent with the solitary nature of many other early benthic palinurid species (see discussion above). The differences between this study and that of MacDiarmid (1994) suggest that shelter selection by *J. edwardsii* is influenced by certain environmental variables. These may include density at settlement and available shelter structures; it is possible that holes for solitary dwelling are not present in the Leigh Marine Reserve. An examination of the processes involved in these observed differences may be useful in elucidating substratum related influences on recruitment.

#### 4.4.2 Substratum Type and Shelter Availability

The density of shelters suitable for lobsters  $\leq 35$  mm CL varied considerably between the mudstone and dolerite substrata, and between mudstone substratum structures. This may be attributed to the different weathering and geomorphological nature of the two substratum types. Jurassic dolerite is comparatively hard and, because of the overall uniformity of composition, erodes in a uniform fashion (Davis 1994), creating relatively smooth boulders and reef surfaces. Shelters suitable for small lobsters are generally structured by the junction of rocks or boulders or by fissures and cracks in the reef. In contrast, Permian mudstone is more prone to erosion (Sunamura 1983; Davis 1994) and, because of heterogeneity between sediment layers, erosion of the vertical faces creates a high density of pockets suitable for small lobsters. This is in addition to the structures formed by boulder junctions or fissures in the reef. Substratum type did not influence the mean density of shelters suitable for larger lobsters,  $> 35$  mm CL. This reduced influence of substratum type and structure on shelter availability possibly reflects the broader properties of shelter use of lobsters  $> 35$  mm CL, and similarities of geomorphological structures at larger scales.

These differences in shelter availability between substratum types and structures may influence the abundance and distribution of lobsters  $\leq 35$  mm CL. This influence may be as a direct limitation of shelter abundance, the mudstone substratum having a carrying capacity far exceeding that of the dolerite substratum:  $2.14 \text{ m}^{-2}$  compared to  $0.77 \text{ m}^{-2}$  respectively. Substratum factors may also affect lobster abundance indirectly by affecting shelter accessibility. The distribution of shelters suitable for lobsters  $\leq 35$  mm CL on the mudstone substratum was clumped, having patches of high and low densities of shelters. The accessibility of shelters on the mudstone substrate is therefore affected by both the density of shelters and the probability of finding a patch of shelters (the intensity and grain of the patchiness). Although the mean density of  $2. \square 4$  shelters per quadrat on the mudstone suggests a high probability of finding at least one shelter in every quadrat (88% if a random distribution), the patchiness resulted in finding shelters in only 42 of the 63 quadrats (66%), effectively lowering the probability of finding a shelter within a unit area by 22%.

Factors which reduce shelter accessibility can result in shelter being a limited resource well before the abundance of animals matches the abundance of their refuges (Andrewartha & Birch 1954; Steger 1987). The clumped nature of shelters on the mudstone substratum is therefore likely to reduce the carrying capacity of lobsters ( $\leq 35$  mm CL) below  $2.14 \text{ m}^{-2}$ . Other factors which may affect shelter accessibility include interspecific competition for refuges, intraspecific interactions, predator distribution and the local abundance of prey (Andrewartha & Birch 1954; Steger 1987). Although these factors can modify the influence of substratum factors, their importance is considered secondary, as shelter accessibility can only be limiting in combination with the numerical abundance of shelters (Steger 1987).

Qualitative differences in the nature of available shelters for both small and large lobsters were also detected between the substratum types. These qualitative differences are not likely to affect the distribution of small lobsters,  $\leq 35$  mm CL, as no preferences were apparent: they occupied different shelter shapes in proportion to their environmental availability. However, lobsters  $> 35$  mm CL displayed preferences for more open, triangular or wedge shaped shelters. These preferences possibly influence their distribution, both within and between substratum types.

#### 4.4.3 Lobster Size and Shelter Availability

The close relationship between lobster size and shelter size of early benthic *J. edwardsii* indicates that larger shelters are required with growth. This conforms with patterns in *H. americanus* and other palinurid species (Jernakoff 1990; Wahle 1992b; Norman *et al.* 1994). The implications of these size changes for *J. edwardsii* are likely to be dependent on substratum type. Shelter availability changed little with size on the dolerite substratum, whereas shelter availability dramatically declined with size on the mudstone substratum.

As lobsters grow, the decline in shelter abundance with size on the mudstone substratum may increase constraints on abundance and recruitment, possibly inducing migration, mortality or reduced growth (Caddy 1986). However, these constraints are expected to be relaxed with changes in shelter use at a size of approximately 35 mm CL. Because larger lobsters occupy a variety of shelter sizes and cohabit within shelters, they are less likely to be limited by shelter availability. Therefore, a bottleneck in recruitment could occur at a size just prior to the shift in shelter use. On the dolerite substratum, the constant abundance of shelters with lobster size means shelter related bottlenecks would only occur at the time of settlement.

It is conceivable that the rate of decline in shelter abundance could mediate the size at which the ontogenetic shift in properties of shelter use occurs. Ontogenetic shifts would be

advantageous when shelter limitations exceed those imposed by factors confining the lobsters to specific shelters, such as the effects of predation.

#### 4.4.4 Fractal Properties of Substrata and Shelter Availability

Caddy (1986) postulated that hard substrata inhabited by lobsters have fractal properties, and that these properties could be useful for modelling shelter availability and recruitment processes. Fractals were first described by Mandelbrot (1977) as continuous but non-differentiable functions, with texture present at all scales:

*a fine-grained lumpiness or wigliness that remains inherent in its texture no matter how thin you slice it. (Dyson 1978).*

Fractals often have the properties of statistical self-similarity, the same pattern being repeated at smaller and smaller scales. Because of the inherent texture, fractals effectively exceed their topological dimension. For example, a one dimensional curve can be so convoluted as to fill a plan, or approach a dimension of 2. This intermediate dimension is known as the fractal dimension,  $D$ .

An important property of a fractal curve is that its length becomes disproportionately large as the unit of measurement is decreased, according to the relationship:

$$l(r) \propto r^{(1-D)} \quad (4.1)$$

where  $l(r)$  is the perceived length of a line using a step-length of  $r$  (Mandelbrot 1983). This principle also applies to a fractal surface and implies that small animals occupying such a surface have proportionately more usable space than larger animals (Morse *et al.* 1985).

Various vegetation structures have been found to be fractal in structure, influencing the body size distribution of associated animal assemblages (Morse *et al.* 1985; Gunnarsson 1992; Gee & Warwick 1994). Landforms, coastlines and coral reefs also have fractal properties (Mandelbrot 1983; Bradbury *et al.* 1984; Mark 1984; Pennycuick & Kline 1986), and Caddy (1986) postulates that subtidal surfaces occupied by lobsters are fractals, influencing shelter availability.

If a subtidal surface is a fractal, then, because of self-similarity, the appearance of a cross section of the substratum should be the same regardless of the magnification it is viewed at (Mark 1984). Therefore, holes and crevices in the substratum will be repeated in a similar form at larger scales, but there will be proportionally fewer of them. Substrata with higher values of fractal dimension,  $D$ , result in the number of holes being reduced more rapidly

with increased lobster size. Lobsters will experience a decline in shelter availability as they grow, according to the relationship:

$$N(L) \propto L^{(1-D)} \quad (4.2)$$

where  $N(L)$  is the number of holes suitable for lobsters of size  $L$  in a given cross-section of surface. Thus, for a fractal surface, the log abundance of shelters will decline linearly with log lobster size, the slope being negatively proportional to the fractal dimension. From log transformations of the shelter availability results (see Fig. 4.2, Section 4.3.6), a significant linear relationship was detected for the mudstone substratum, indicating it has fractal properties (Fig. 4.3,  $r^2 = 0.82$ ,  $df = 1, 6$ ,  $F = 33.73$ ,  $p = 0.001$ ). However, no significant relationship was found for the dolerite substratum (Fig. 4.3,  $r^2 = 0.002$ ,  $df = 1, 6$ ,  $F = 0.013$ ,  $p = 0.912$ ).

The non-fractal nature of the dolerite substratum is likely to be because of the smooth, rounded nature of the boulders and reef at the scale of lobsters (10-100 mm CL). It is conceivable that substrata of smooth boulders could produce surfaces with fractal properties, depending on the size distribution and aggregation pattern of the boulders (*e.g.* the Apollonian gasket of Mandelbrot 1977). However, in this case, the size distribution of holes and crevices indicates a regular structure to the substratum. The fractal dimension of this surface is the same as its topological dimension:  $D = 2$ , contrasting with the more rugose mudstone surface with a fractal dimension of  $2 < D \leq 3$ .

The fractal dimension is a direct index of the decline in shelter availability. As stated by Caddy (1986), this index may be of value for comparing substratum structures and incorporating substratum related processes into recruitment models. Caddy postulated that as the lobsters grow on a fractal surface, the number of appropriate sized holes will always be less than the potential number of occupants and result in mortality and/or migration. This theory is based on the assumptions that crevice dwelling is an obligate requirement; growth rate is not influenced by the availability of suitable shelters; and that all available shelters of dimension  $L$  are filled with organisms of the same linear dimensions. Assuming growth approximates a von Bertalanffy function, Caddy (1986) showed that this mortality could be expressed as a function of the fractal dimension:

$$M_L = \frac{K \cdot \log_e \left( L_2^{D+1} / L_1^{D+1} \right)}{\log_e \left( L_\infty - L_1 \right) / \left( L_\infty - L_2 \right)} \quad (4.3)$$

where  $K$  and  $L_\infty$  are the Brody coefficient and maximum size respectively.  $L_1$  and  $L_2$  are the lobster size at time 1 and 2 respectively.

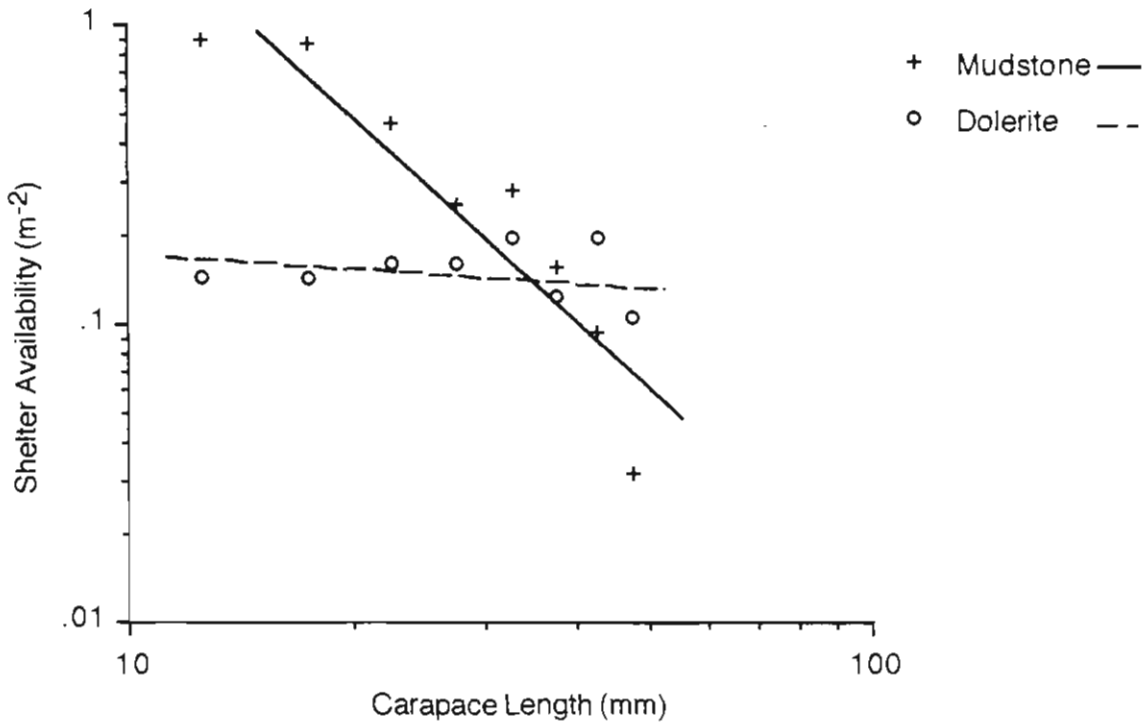


Fig. 4.3. Log relationship between shelter availability and lobster size for mudstone and dolerite substrata at Watsons Bay.

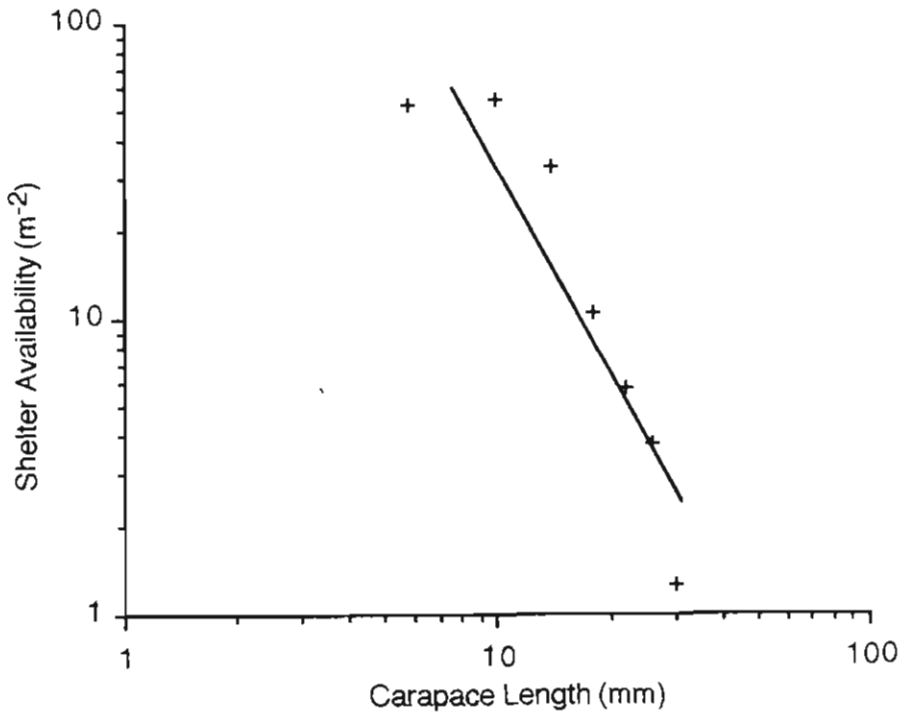


Fig. 4.4. Log relationship between shelter availability and size of *Panulirus japonicus* for sandstone substratum at Banda, Chiba Prefecture, Japan ( $r^2 = 0.84$ ,  $df = 1, 5$ ,  $F = 26.17$ ,  $p = 0.003$ ). Data from Norman *et al.* (1994).

The fractal dimensions of objects can be determined empirically using the 'dividers relationship', where lengths of different scales are stepped across the object and using equation (4.1) (Bradbury & Reichelt 1983; Mandelbrot 1983; Pennycuick & Kline 1986; Williamson & Lawton 1991). A similar method could be used to estimate the fractal dimensions of substrata where the number of shelters, of linear dimension  $L$  (using the same terminology as in equations 4.2 and 4.3), is determined by stepping length  $L$  across the substratum (*i.e.* along a transect) and, from equation (4.2), use the relationship:

$$N(L) = \frac{k'}{L^D} \quad (4.4)$$

for a given cross section of substratum and where  $k'$  is a constant.

This relationship can be modified to apply to shelter availability data collected from quadrats, as in this study. After Caddy (1986), for all holes of dimension  $L$  to be identified by parallel transects across the surface, the transects would be placed  $L$  units apart. For a flat rectangle of width  $x$  and length  $y$ , there will be  $x/L$  transects of length  $y$ . Therefore, the total transect length surveyed will be effectively  $xy/L$ , or  $k''/L$  where  $k''$  is the area of the rectangle. Hence, the number of holes of dimension  $L$  is given by:

$$N(L) = \left( \frac{k'}{L^D} \right) \cdot \left( \frac{k''}{L} \right) \quad (4.5)$$

Therefore the fractal dimension,  $D$ , can be determined from the relationship:

$$\frac{N(L) \cdot L}{k''} = \frac{k'}{L^D} \quad (4.6)$$

or

$$\log \left( \frac{N(L) \cdot L}{k''} \right) = D \cdot \log \left( \frac{1}{L} \right) + \log k' \quad (4.7)$$

Using equation (4.7), with lobster carapace length as an index of shelter size ( $L$ ), the fractal dimension of the mudstone substratum at Watsons Bay was estimated as 1.27 ( $k' = 4.6 \times 10^{-4}$ ;  $r^2 = 0.64$ ,  $df = 1, 6$ ,  $F = 10.58$ ,  $p = 0.017$ ) for a line across the surface, or 2.27 for the surface. The same method was used with shelter availability data obtained by Norman *et al.* (1994), for *P. japonicus* on sandstone substratum at Banda, Chiba Prefecture, Japan. This substratum also showed fractal properties with a fractal dimension of 1.25 (Fig. 4.4,  $k' = 5825$ ;  $r^2 = 0.62$ ,  $df = 1, 5$ ,  $F = 8.08$ ,  $p = 0.036$ ).

The similar fractal dimension for both sites indicate similarities in the rate of decline of shelter availability with size, and overall complexity of the surface structure. This is despite

the Banda site having a higher density of shelters (as reflected in the constant  $k'$ ). However, these results are unreplicated and more work is required in determining the precision of these methods of estimation. This is necessary before fractal dimension can be used for reliable comparison of substratum structures, or as an index of substratum related effects in population dynamics models.

Modelling by Caddy and Stamatopoulos (1990) demonstrate that substrata with fractal properties can have a number of important implications for recruitment processes. Salient points emerging from these models are that stunting and density dependent growth could be a response to physical niche availability; highly dissected surfaces (high fractal dimensions) are good for initial recruitment, but are not good for 'grow-on' (i.e. nursery areas may be a function of the fractal nature of surfaces); and bottlenecks in recruitment are likely to occur with changes in fractal dimension, or with slow initial growth on surfaces of high fractal dimension. Such processes can be reasonably well incorporated into population dynamics models using the fractal dimension as index of substratum character (e.g. Equation 4.3; Caddy 1986; Caddy & Stamatopoulos).

However, Caddy and Stamatopoulos' (1990) models are theoretical and remain untested as to their applicability. A basic assumption for applicability to lobsters and many other crevice dwellers is that reefs have fractal properties and that the fractal dimension is an index of size-related changes in shelter availability. In this study, I have shown empirically that reefs have fractal properties, and that the fractal dimension can be derived from the size distribution of available shelters.

Although the results are encouraging in terms of incorporating substratum effects in population dynamics models, two complicating factors are evident. The first is that the substratum characteristics (and hence fractal dimension) can change remarkably over short distances (hundreds of metres). This may not be a problem if it can be shown that particular structures (e.g. dolerite boulders or weathered mudstone) have consistent fractal properties. Secondly, further information is required on the generality of the lobster-shelter relationships found in this study, as it is possible these relationships change at higher densities.

As yet, there is little conclusive evidence as to whether substratum is an influential factor in the recruitment of juvenile *Jasus edwardsii*. Until this information is available, substratum-incorporated models may be useful in (at least) determining the carrying capacity of habitats, and developing hypotheses on recruitment processes.

#### 4.4.5 Conclusions

The distinct ontogenetic shift in shelter use of *J. edwardsii*, from specific shelter requirements to broader properties of shelter use, implies that newly settled lobsters are more susceptible to shelter limitations than larger lobsters ( $> 35$  mm CL). No evidence was found for shelter to be limiting. However, shelter availability was highly influenced by substratum structure which may, in turn, affect recruitment to maturity or the fishery.



# Diet

### 5.1 Introduction

Studies on the natural diet of *Jasus edwardsii* populations by Hickman (1945) and Fielder (1965) demonstrated that adult lobsters feed on a wide variety of taxa, including chitons, bivalves, gastropods, sea urchins, algae, crabs and other crustaceans. However, the relative importance of the various dietary taxa and the effects of habitat, season, moult stage and lobster size on diet have received little attention.

Size is likely to have a significant effect on diet and ontogenetic shifts have been documented for the western rock lobster, *Panulirus cygnus* (Edgar 1990; Jernakoff *et al.* 1993), the American lobster, *Homarus americanus* (Scarratt 1980; Carter & Steele 1982b) and the Cape lobster, *Jasus lalandii* (Barkai & Branch 1988). For all three species, there is evidence to suggest that the dietary shifts are caused by differences in foraging habitats, nutritional requirements or changes in feeding abilities because of differences in morphology and scale.

Diet and food availability influences the growth and ecology of juvenile *P. cygnus* and *J. lalandii* (Chittleborough 1976; Pollock & Seyers 1981; Joll & Phillips 1984; Edgar 1990). This suggests that, if certain size classes have ecological limitations imposed by specific nutritional requirements or foraging behaviours, ontogenetic shifts in diet could result in differences in growth and survival. Ontogenetic shifts in diet may also function to minimise competition through reduced overlap in resource use, both within and between species (Schoener 1974; Werner & Gilliam 1984). In addition, ontogenetic shifts increase the complexity of interactions within communities and have implications for determining the nature of energy flow, nutrient cycling and structuring processes within a community (Werner & Gilliam 1984). A variety of studies have shown that predation by adult lobsters can have a considerable influence on prey populations and the structure and organisation of benthic communities (*e.g.* *H. americanus*: Witman 1985, Ojeda & Dearborn 1991). Predation by juvenile lobsters may also have important roles in community structure, but

on a scale different from that of larger lobsters.

The objectives of this study were to examine the natural diet of juvenile *J. edwardsii* and determine if there were changes with size. The selectiveness of the diet and possible foraging strategies were also examined by comparing the diet with the abundance and distribution of the benthic macrofauna.

## 5.2 Materials and Methods

Lobsters were collected from Watsons Bay ( $n = 129$ , size range 10.9–117.5 mm CL), Crayfish Pt ( $n = 30$ , 10.8–77.1 mm CL), and five miscellaneous sites ( $n = 34$ , 10.2–137.1): Bull Bay (5), Ile du Nord (2), Shagrock Bay (3), Eaglehawk Neck (11) and Conical Rocks (13). All lobsters were collected by diving, between the depths of 2 to 10 m, and were preserved in 70% ethanol within 90 min of collection. All lobsters were collected during the warmer months between October and March, between 1992 and 1994.

The foreguts were dissected from the lobster and the percentage fullness was estimated by eye, before being opened and the contents flushed into a Petri dish. The gut contents were sorted and identified into the lowest possible taxon and counted. The volume of each taxon, as a percentage of the total volume for each animal, was estimated by eye using a dissecting microscope (Carter & Steele 1982a; Joll & Phillips 1984; Edgar 1990; Jernakoff *et al.* 1993). Although the estimation by eye was open to subjectivity, the fragmented nature of the gut contents, and the large number of samples, precluded direct volumetric measurements. To standardise the estimates, only 1 analysed the gut contents, the the relative volume estimations were made easier by spreading the sorted taxa to an even thickness over the Petri dish and estimating the relative area of cover by each taxon. No studies were found in the literature pertaining to the reliability of visual estimates compared with direct volume measurements of gut contents in spiny lobsters, but relative visual estimates are considered acceptable for the analysis of fish diets (Hyslop 1980). The lobsters were classified into post, inter and premoult stages from the examination of setal development within the pleopods and carapace flexibility (Aiken 1973, 1980; Aiken & Waddy 1992).

The lobsters were divided into five size groups:  $\leq 30$  mm, 31–40 mm, 41–50 mm, 51–60 mm and  $> 60$  mm carapace length. Sample sizes for each group are given in Table 5.1. The adequacy of the sample sizes for characterising the diet of each size group were assessed using ‘rarefaction’ curves of cumulative numbers of taxa types consumed and an intragroup diet overlap index. The cumulative mean number of dietary taxa was plotted against sample

size for each size group, with reliable sample sizes being indicated by the point of asymptotic stabilisation of the curves (Williams 1981). The cumulative means were determined from 30 randomisations of the order of inclusion of lobsters. Intragroup overlap indices were determined by random allocation of each sample into two subsets and calculating Schoener's index of overlap (Schoener 1970). The index was calculated for 30 randomisations and the 95% upper confidence limits of intragroup overlap was determined. Sample sizes were considered sufficient if the 95% upper confidence limit of intragroup overlap was greater than 60% (Wallace & Ramsey 1983).

The relative dietary importance of each prey taxon ( $i$ ) within each size group was evaluated using percentage total volume (sum of volumes for prey taxon  $i$  divided by the sum of volumes for all prey taxa, multiplied by 100), and percentage frequency of occurrence (the proportion of lobsters with prey taxon  $i$  in the gut, multiplied by 100: Williams 1981; Elner & Campbell 1987). Differences in dietary composition between the size groups were also compared using a one-way multivariate analysis of variance (MANOVA) and linear discriminant functions analysis (LDFA). The number of dependent variables (dietary taxa in this case) that can be analysed by MANOVA and LDFA is restricted to much less than the number of cases per level (size category) to ensure adequate power, and to meet the assumptions of the analysis (Tabachnick & Fidell 1989). On this basis, the number of dependent variables were reduced by aggregating the dietary taxa into 7 dietary groups. These groups included hiatellid bivalves, ophiuroids, echinoids, isopods, brachyuran crabs and other molluscs, which were selected as the most dominant groups according to frequencies of occurrence and percentage volume for each size class. The remaining taxa were aggregated into a seventh group, the 'remainder'.

The dietary data are compositional, with the relative volumes of each dietary component summing to unity, or 100%. This compositional nature means there is co-dependence between the components and leads to biases in the covariance matrix (Aitchison 1986). These problems can be removed by using log ratios of the components with one of the components selected as a common denominator, the choice of the divisor component not affecting subsequent analyses. This additive log ratio transformation generally produces data with a logistic normal distribution, and hypotheses can be tested using parametric tests involving the covariance structure, including statistical procedures based on multivariate normality (Aitchison 1986). The volumes for each diet group for each lobster were transformed using the additive log ratio transformation:

$$y_i = \log_e \left( \frac{x_i}{x_D} \right) \quad (5.1)$$

where  $y_i$  is the transformed volume quantity for dietary group  $i$  (the dietary groups being hiatellids, ophiuroids, echinoids, isopods, crabs or other molluscs),  $x_i$  is the estimated volume of food group  $i$  and  $x_D$  is volume of the selected divisor category: the ‘remainder’ category in this case. Zeros were replaced by a trace value of 0.1% and a compensatory 0.1% was subtracted from the ‘remainder’ group prior to the transformation (Aitchison 1986). To reduce possible biases, only the diets of lobsters in the intermoult stage and with a stomach fullness > 10% were analysed in all tests and comparisons. This was to avoid an increased weighting of small food volumes, and reduce dietary variation because of moult stage, as found in *P. cygnus* (Joll & Phillips; Edgar 1990; Jernakoff *et al.* 1993). Most post-moult lobsters had empty stomachs. Numbers of each moult and stomach fullness category are given in Table 5.1.

The overall MANOVA was performed using Pillai’s Trace criterion ( $V$ ) as the test statistic. This statistic is relatively robust to departures from the assumptions of the MANOVA model, especially with an unbalanced design and some heterogeneity of variances, as was the case here (Tabachnick & Fidell 1989; Johnson & Field 1993). Specific contrasts between the size groups were performed with a simultaneous test procedure (STP) based on Roy’s gcr for the overall test (Bird & Hadzi-Pavlovic 1983; Harris 1985). Simultaneous test procedures based on Roy’s gcr have the advantage of being consonant. If the overall test is statistically significant, there exists at least one contrast on some linear combination of the dependent variables (Harris 1985). The power of a Roy’s gcr-based contrast is also higher than any other STP (Bird & Hadzi-Pavlovic 1983). Contrasts were considered significant if the contrast statistic  $\theta_1/(1-\theta_1)$  exceeded the critical value of  $R_{0.05}/(1-R_{0.05})$ , where  $\theta_1$  is Roy’s gcr for the contrast and  $R_{0.05}$  is the critical gcr for the over-all test (Bird and Hadzi-Pavlovic 1983). The critical value of Roy’s gcr was obtained by interpolation from Harris’ (1985) tables.

Differences in diet between the size groups were further examined using linear discriminant functions analysis. The relative contribution of each dietary category was assessed using both standardised canonical coefficients and canonical correlations. Canonical coefficients represent the unique contribution of a dietary variable to the discriminant functions, while canonical correlations represent the amount of variance a dietary variable shares with the functions. Canonical coefficients are considered more informative but less stable because of influences by intercorrelations among dependent variables (Bray & Maxwell 1985; Scheiner 1993).

The density and size frequency of potential prey species were determined at Watsons Bay, the main collecting site, using 0.25 m<sup>2</sup> quadrats. Ten quadrats were sampled at 2 m intervals along a transect running from 3 to 10 m depth, placed immediately to the east of the census area. The lamina of large kelps (*Ecklonia radiata* and *Phyllospora comosa*) were cut off and placed in 5 mm mesh bags. Holdfasts, smaller algae and all other benthic organisms were scraped off the substratum and placed in sealable plastic bags. The samples were then preserved in 70% alcohol and later sorted, identified to the lowest possible taxon, counted and measured.

Prey preferences were estimated using Pearre's prey selection index,  $C$  (Pearre 1982; Ojeda & Dearborn 1991). For each size category and prey item (A), the abundance of prey in the diet (the number of individuals in the foreguts of all lobsters in that size class) was compared with the abundance of prey in the environment (the number of individuals in all ten quadrats) using a 2 x 2 contingency table:

	Frequency of Prey Items		
	A	All other	Total
In the diet	$a_d$	$b_d$	$d = a_d + b_d$
In the environment	$a_e$	$b_e$	$e = a_e + b_e$
Total	$a = a_d + a_e$	$b = b_d + b_e$	$n = a_d + a_e + b_d + b_e$

A chi-square statistic with Yates' correction for continuity was calculated:

$$\chi^2 = \frac{n \left( \left| a_d b_e - b_d a_e \right| - \frac{n}{2} \right)^2}{abde} \quad (5.2)$$

and this was used to determine Pearre's index,  $C$ :

$$C = \pm \left( \frac{\chi^2}{n} \right)^{1/2} \quad (5.3)$$

The significance of this index was evaluated from the  $\chi^2$  value with one degree of freedom. The index  $C$  ranges between -1 and +1. A significantly negative value indicates that a given prey item was avoided, a zero value indicates that a prey item was taken in proportion to its abundance in the environment and a significantly positive value indicates preference or selection for that prey item (Pearre 1982; Ojeda & Dearborn 1991).

### 5.3 Results

Upper 95% confidence limits for intragroup overlap were all above 0.60 (Table 5.1), indicating that the sample sizes were sufficient for reliable characterisation of the diet for each size group (Wallace and Ramsey 1983). The cumulative rarefaction curves stabilised after the inclusion of at least 20 lobsters in each size group (Fig. 5.1), also indicating that sample sizes were sufficient.

The ingested material of the lobsters consisted mostly of highly fragmented remains of animals with hard parts: shells of bivalves, gastropods and chitons; spines and ossicles of ophiuroids and sea urchins; segments and appendages of isopods, crabs and other crustaceans; and calcareous tubes of serpulid worms. Calcareous remains of byozoans and the spicules and keratin fibres of sponges were also present (Table 5.2).

For the smallest lobsters ( $\leq 30$  mm CL), isopods, ophiuroids, hiatellid bivalves and unidentified crustacean remains appeared important in terms of both percentage total volume and percentage frequency of occurrence (Fig. 5.2). Small gastropods, bivalves and sponges were also consumed frequently but in reduced volumes.

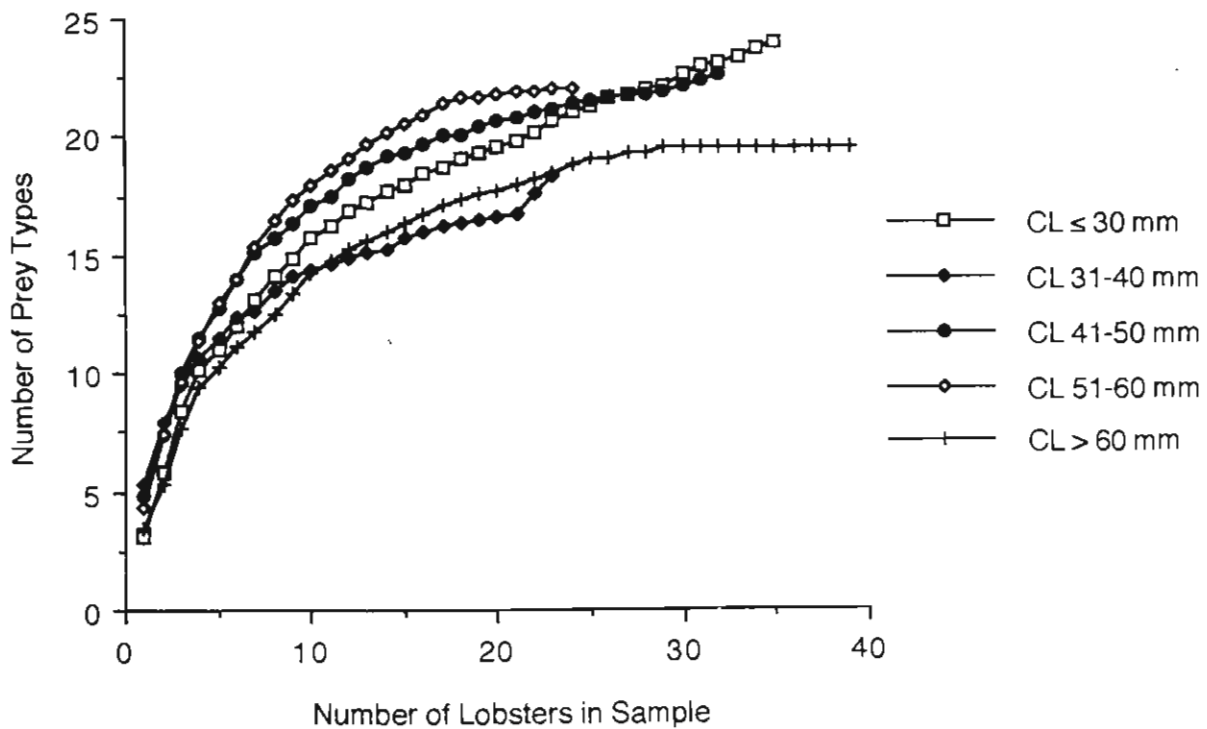


Fig. 5.1. Cumulative numbers of dietary taxa with sample size for each size category. Cumulative numbers are means of thirty randomisations.

Table 5.1. Sample sizes, mean gut fullness and intragroup overlap index means and upper 95% confidence limits. Mean gut fullness was calculated for all lobsters. Note: many postmoult stage lobsters had a stomach fullness of less than 10%.

	Size (mm CL)					Total
	≤ 30	31–40	41–50	51–60	> 60	
Sample size						
Total	44	30	36	29	54	193
Postmoult stage	3	6	1	1	8	19
Foregut < 10% full	8	7	3	5	13	36
Intermoult and ≥ 10% full	35	22	33	24	41	155
Mean gut fullness	61.2	69.4	73.6	64.7	55.9	
Mean intragroup overlap	0.614	0.751	0.731	0.665	0.698	
Upper 95% confidence limit	0.638	0.772	0.756	0.682	0.719	

Hiatellid bivalves, crabs, sea urchins and sponges were dominant in the diet of three size groups: 31–40 mm, 41–50 mm and 51–60 mm CL. However, hiatellids were successively less predominant in the larger size classes, with sea urchins and crabs being more important. Gastropods, fleshy algae and other bivalves were also frequently consumed by these three size groups, but in low volumes. The diet of the largest size class (> 60 mm CL) was dominated by chitons, crabs and sea urchins. Hiatellids, other bivalves, gastropods and fleshy algae were also consumed, but in low volumes and less frequently than smaller size classes.

Porifera was a common, and often predominant, component of the diet, particularly for the 31 to 60 mm CL size range, and was often seen associated with or attached to fragments of crabs and small cryptic bivalves. A significant association was found between crabs and cryptic bivalves and the occurrence of poriferan material in the foregut ( $df = 2$ ,  $\chi^2 = 6.0987$ ,  $p = 0.047$ ). This suggests that the ingestion of poriferan material was mostly incidental with the consumption of camouflaged and cryptic organisms. Although Porifera was a common dietary component, it was not included as a separate variable in the multivariate tests of size effects on diet. The attachment of poriferan material to other dietary items means much of the variation in this dependent variable (Porifera) would not be independent of other dependent variables (a high degree of non-orthogonality). Because of a limitation on the number of dependent variables that could be used, preference was given to other variables that were more likely to measure separate aspects of the influence of lobster size on diet.

Table 5.2. Diet composition of the five size groups. %F: percentage frequency of occurrence (proportion of lobsters with each prey taxon in the gut, multiplied by 100); %V: percentage total volume (sum of volumes for each prey taxon divided by the sum of volumes for all prey taxa, multiplied by 100). Values are given for the common taxa encountered as well as cumulative values for higher taxonomic levels. Lobsters with foreguts < 10% full and post-moult lobsters were excluded from the calculations.

Sample size	≤30 mm 35		31–40 mm 22		41–50 mm 33		51–60 mm 24		>60 mm 41	
Diet	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V
PORIFERA	25.7	7.4	73.9	17.3	59.4	10.6	75.0	19.2	30.8	3.9
BRYOZOA	2.9	0.1	17.4	0.2	9.4	0.1	20.8	0.7	10.3	1.6
ANNELIDA	2.9	1.7	-	-	15.6	0.4	4.2	-	5.1	0.1
SIPUNCULIDA	-	-	-	-	3.1	0.1	4.2	0.4	-	-
MOLLUSCA	68.6	26.2	100.0	37.4	100.0	32.6	87.5	18.5	82.1	39.0
Bivalvia	48.6	18.6	100.0	29.2	90.6	25.4	83.3	14.4	56.4	8.9
<i>Hiatella australis</i>	31.4	11.2	100.0	25.1	81.3	17.3	79.2	8.1	35.9	2.5
Bivalve A	14.3	1.7	52.2	2.3	62.5	5.4	45.8	3.0	23.1	1.0
Mytilids	5.7	0.6	17.4	0.4	18.8	1.3	20.8	1.3	15.4	3.6
Unidentified	28.6	5.2	30.4	1.5	28.1	1.5	20.8	2.1	41.0	1.7
Amphineura	2.9	0.1	13.0	1.0	12.5	1.2	33.3	1.6	51.3	25.3
Gastropoda	48.6	7.5	87.0	7.2	78.1	6.0	75.0	2.6	51.3	4.8
<i>Haliotis</i> sp	2.9	0.3	4.3	0.0	18.8	1.3	8.3	0.5	-	-
Limpets	-	-	8.7	1.1	9.4	1.5	12.5	0.2	-	-
Trochids	8.6	1.3	30.4	1.1	21.9	0.4	45.8	1.0	20.5	1.1
Turbinids	8.6	1.7	26.1	0.5	15.6	0.1	16.7	0.2	2.6	0.0
Unidentified	37.1	4.1	43.5	4.4	53.1	2.7	29.2	0.7	30.8	3.7
ECHINODERMATA	48.6	14.3	87.0	18.8	81.3	22.2	83.3	25.3	69.2	24.2
Ophiuroidea	45.7	14.1	65.2	6.4	34.4	3.2	20.8	2.3	15.4	1.2
Echinoidea	-	-	56.5	12.4	56.3	18.2	70.8	20.8	61.5	19.8
Asteroidea	-	-	-	-	6.3	0.4	8.3	1.2	5.1	2.8
Unidentified	2.9	0.2	4.3	0.0	9.4	0.3	8.3	0.9	7.7	0.5
CRUSTACEA	82.9	40.6	82.6	22.8	84.4	24.0	83.3	25.6	69.2	24.6
Amphipoda	8.6	3.5	4.3	0.1	-	-	-	-	2.6	0.6
Isopoda	37.1	16.9	13.0	0.7	21.9	2.6	8.3	0.3	2.6	1.0
Natantia	5.7	4.1	8.7	1.6	-	-	-	-	-	-
Brachyura	11.4	6.3	52.2	18.6	56.3	19.2	50.0	19.2	56.4	18.0
<i>J. edwardsii</i>	-	-	-	-	-	-	8.3	4.5	7.7	4.4
Unidentified	34.3	9.8	21.7	1.8	28.1	2.2	33.3	1.6	12.8	0.5
ALGAE	25.7	0.6	52.2	0.5	40.6	1.9	45.8	1.1	33.3	0.9
Coralline	2.9	0.0	-	-	3.1	0.0	8.3	0.1	-	-
Fleshy	22.9	0.6	52.2	0.5	46.9	1.8	41.7	1.0	33.3	0.9
UNIDENTIFIED										
Unidentified soft	8.6	8.6	4.3	2.8	15.6	6.4	37.5	9.1	15.4	5.7
Unidentified hard	8.6	0.4	4.3	0.0	21.9	1.6	12.5	0.1	-	-



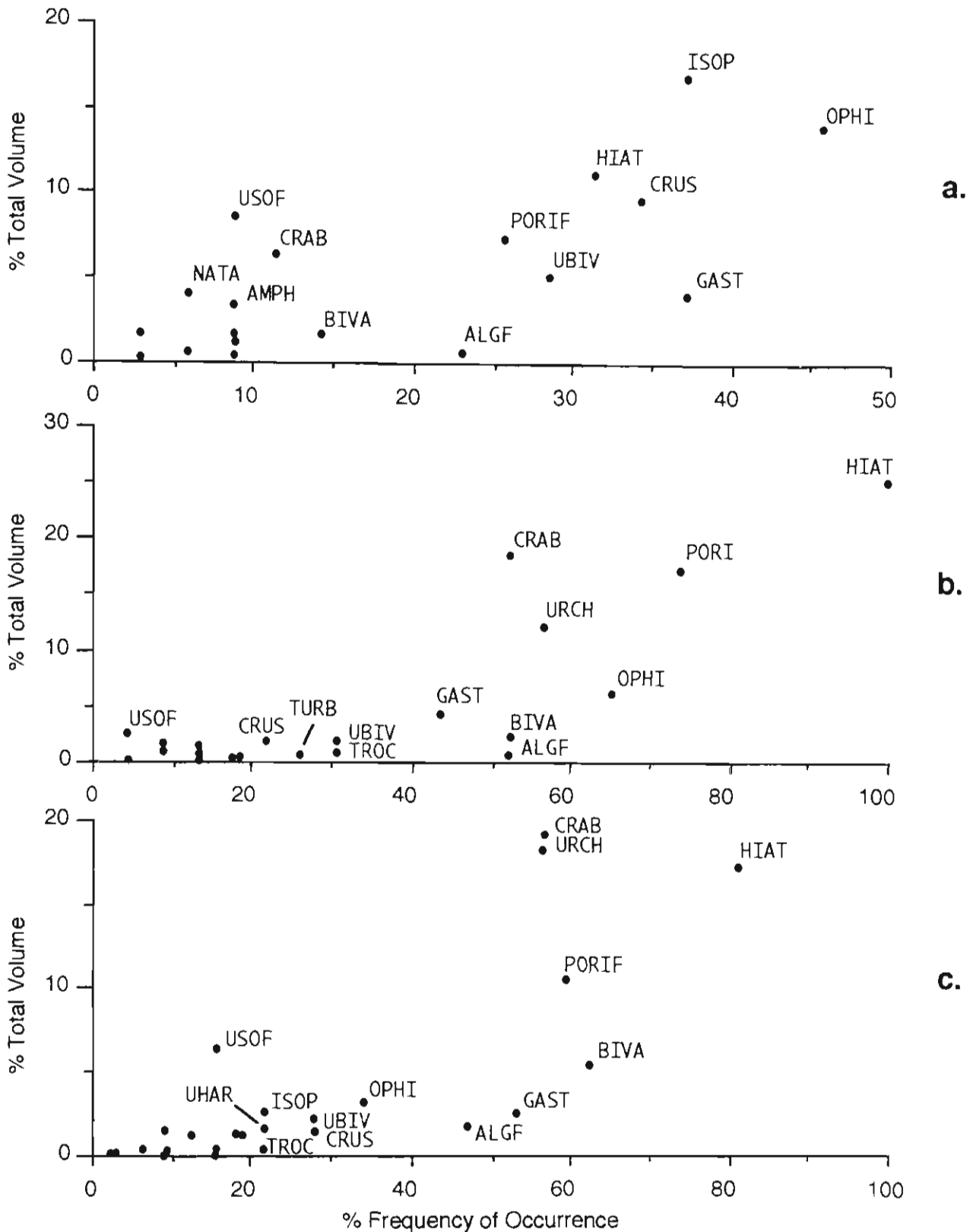


Fig. 5.2. Relative contribution of dominant dietary taxa in lobster foreguts, in terms of frequency of occurrence and volume, for the size groups (a)  $\leq 30$  mm CL, (b) 31–40 mm CL, (c) 41–50 mm CL, (d) 51–60 mm CL and (e)  $> 60$  mm CL. Abbreviations of taxa are: ALGF, fleshy algae; AMPH, amphipods; ASTE, asteroids; BIVA, unidentified bivalve A; BRYO, bryozoans; CHIT, amphineurans; CRAB, brachyuran crabs; CRUS, unidentified crustaceans; GAST, gastropods; HIAT, hiatellid bivalves; ISOP, isopods; JASU, *Jasus edwardsii*; MYTI, *Mytilus*; bivalves NATA, natantian shrimps; OPHI, ophiuroids; PORI, Porifera; TROC, trochids; TURB, turbinids; UBIV, unidentified bivalves; URCH, echinoids; UHAR, unidentified hard material; USOF, unidentified soft material. Taxa with volume contributions less than 2.5% and frequencies less than 20% are too numerous to label here and their relative contributions are given in Table 5.2.

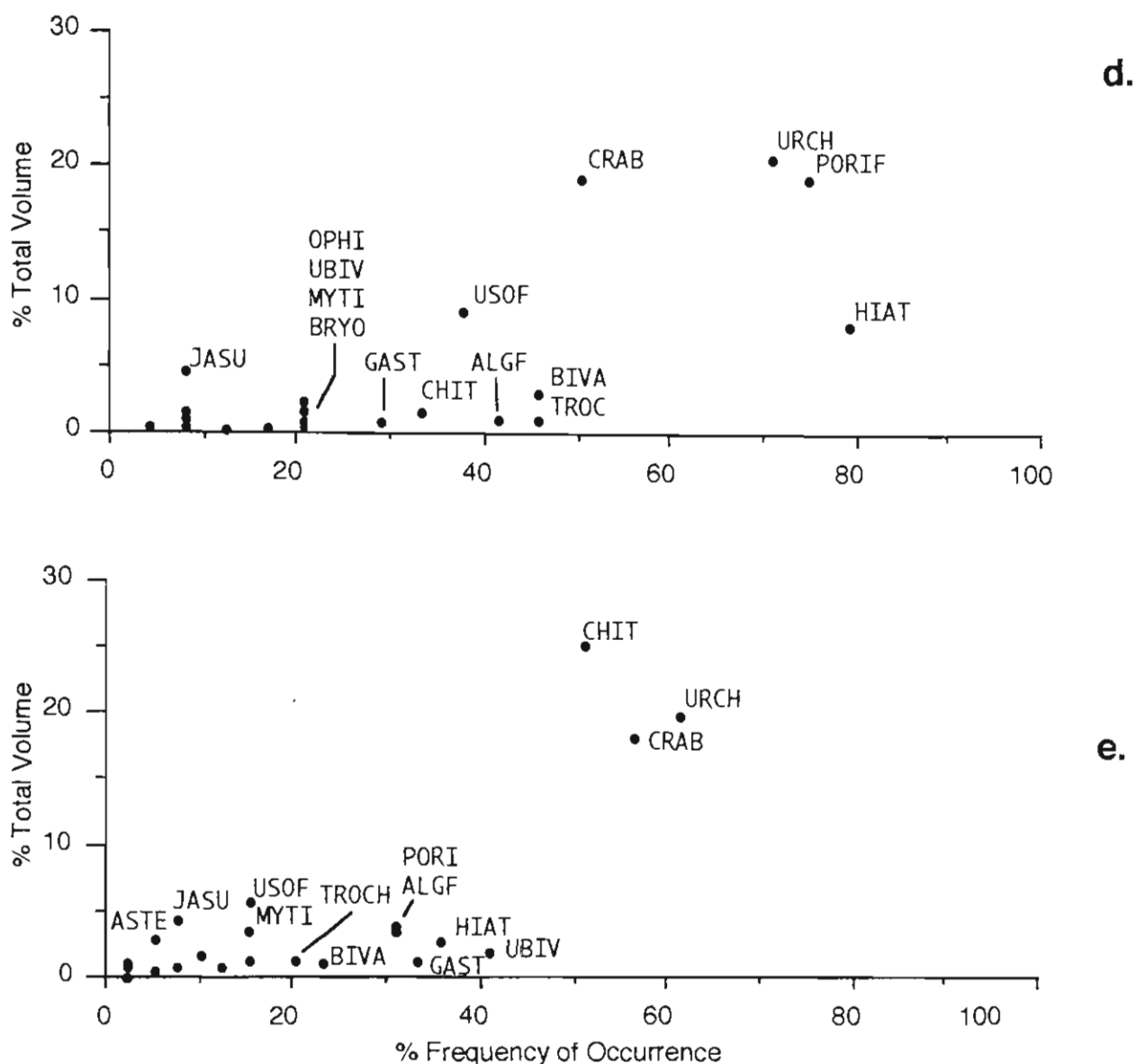


Fig. 5.2 (continued). Relative contribution of dominant dietary taxa in lobster foreguts, in terms of frequency of occurrence and volume, for the size groups (a)  $\leq 30$  mm CL, (b) 31–40 mm CL, (c) 41–50 mm CL, (d) 51–60 mm CL and (e)  $> 60$  mm CL. Abbreviations of taxa are: ALGF, fleshy algae; AMPH, amphipods; ASTE, asteroids; BIVA, unidentified bivalve A; BRYO, bryozoans; CHIT, amphineurans; CRAB, brachyuran crabs; CRUS, unidentified crustaceans; GAST, gastropods; HIAT, hiatellid bivalves; ISOP, isopods; JASU, *Jasus edwardsii*; MYTI, *Mytilus*; bivalves NATA, natantian shrimps; OPHI, ophiuroids; PORI, Porifera; TROCH, trochids; TURB, turbinids; UBIV, unidentified bivalves; URCH, echinoids; UHAR, unidentified hard material; USOF, unidentified soft material. Taxa with volume contributions less than 2.5% and frequencies less than 20% are too numerous to label here and their relative contributions are given in Table 5.2.

Prior to multivariate analysis, the data were screened for univariate and multivariate outliers, multivariate normality, homogeneity of variance-covariance matrices and multicollinearity, using the methods of Tabachnick and Fidell (1989). Multivariate outliers were determined using Mahalanobis' distances, evaluated as  $\chi^2$  with degrees of freedom equal to the number of dependent variables and  $\alpha=0.001$ . Seven multivariate outliers were identified, all in the  $\leq 30$  mm size group, and were because of a high dominance of isopods and/or ophiuroids in the diet. MANOVA and discriminant functions analysis are sensitive to multivariate outliers so these outliers were deleted from the analysis. No multivariate outliers were present after the deletions. Final sample sizes for analyses were 28, 22, 33, 24 and 41 for the  $\leq 30$  mm, 31–40 mm, 41–50 mm, 51–60 mm and  $> 60$  mm size groups respectively. Multivariate normality was assumed, with more than 20 cases per cell. Homogeneity of variance-covariance matrices was also assumed with the ratio of largest to smallest sample sizes not exceeding 2:1 and the largest to smallest variance not exceeding 5.7:1 for any dependent variable. There was no evidence for multicollinearity as there were no high correlations between the dependent variables and squared multiple correlations did not exceed 0.179.

The six dietary variables (hiatellid bivalves, other molluscs, ophiuroids, echinoids, isopods and brachyurans) were significantly affected by size (Pillai's Trace  $V = 0.695$ ,  $F = 0.695$ ,  $df = 24, 564$ ,  $p < 0.001$ ), and there was a reasonably strong association between the size scores and the combined dietary variables ( $\eta^2 = 0.56$ ). The diet of the  $\leq 30$  mm CL size group was significantly different from all of the larger size groups (Table 5.3). The diet for the 31–40 mm size group was not significantly different from the 41–50 mm and 51–60 mm groups but was significantly different from the  $> 60$  mm group. No significant differences in diet were found between the 41–50 mm, 51–60 mm and  $> 60$  mm size groups (Table 5.3).

The discriminant analysis also indicated differences between the five size groups (Fig. 5.3, Table 5.4). A test of residual roots showed there was a reliable relationship between groups and predictors ( $\chi^2(24) = 115.99$ ,  $p < 0.001$ ). This association was still strong after the removal of the first function ( $\chi^2(15) = 53.75$ ,  $p < 0.001$ ) but subsequent tests of residual roots were not significant, indicating that only the first two discriminant functions were reliable. The first and second discriminant functions accounted for 51% and 37%, respectively, of the between-group variability. Both discriminant functions distinctly separated the  $\leq 30$  mm size group from the larger size groups, but the second discriminant function maximally separated the  $\leq 30$  mm size group from the subsequent, 31–40 mm, size group. The four larger size groups, 31 to  $> 60$  mm, were close together, but linearly

arranged in order of size along both discriminant functions (Fig. 5.3).

Echinoids and brachyuran crabs had highest canonical correlations ( $> 0.3$ ) with the first discriminant function, both variables being negatively correlated. Hiatellid bivalves and echinoids were correlated with the second discriminant function (Table 5.4). The canonical coefficients indicated that ophiuroids and other molluscs on the first function, and isopods on the second function, were also important in discriminating between the groups, but these variables were not correlated with the discriminant functions.

The canonical correlations and group means (Table 5.5) indicate that the change in diet from the  $\leq 30$  mm size group to the 31–40 mm size group is because of an increase in the volume of hiatellid bivalves, a slight increase in echinoids and a decrease in isopods. The more gradual shift in diet between the 31–40, 41–50, 51–60 and  $> 60$  mm size groups is because of an increase in the proportion of echinoids and brachyuran crabs and a decrease in hiatellid bivalves and ophiuroids in the diet.

Table 5.3. Pairwise comparisons between size groups using Roy's gcr simultaneous test procedure.  $\theta_1$  = Roy's gcr. Critical gcr:  $R_{0.05}/(1-R_{0.05}) = 0.1823$ .

Comparison		$\theta_1$	$\theta_1/(1-\theta_1)$	Significance
$\leq 30$ mm vs	31–40 mm	0.2153	0.2744	*
	41–50 mm	0.2209	0.2835	*
	51–60 mm	0.2421	0.3194	*
	$> 60$ mm	0.3069	0.4428	*
31–40 mm vs	41–50 mm	0.1332	0.1537	ns
	51–60 mm	0.1505	0.1772	ns
	$> 60$ mm	0.3136	0.4569	*
41–50 mm vs	51–60 mm	0.0502	0.0529	ns
	$> 60$ mm	0.1232	0.1405	ns
51–60 mm vs	$> 60$ mm	0.1136	0.1282	ns

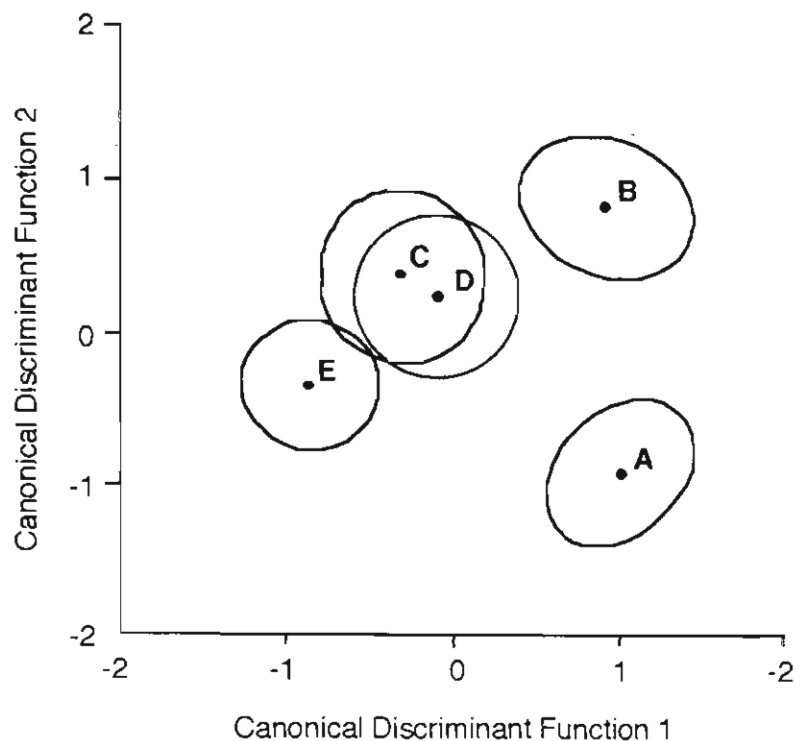


Fig 5.3. Discriminant functions plot of centroids (dots) and 95% confidence ellipses for six diet categories for the five size groups: A,  $\leq 30$  mm CL; B, 31–40 mm CL; C, 41–50 mm CL; D, 51–60 mm CL; E  $> 60$  mm CL. Foreguts  $\geq 10$  % full; intermoult and premoult stages.

Table 5.4. Results of discriminant functions analysis using six diet categories. Canonical coefficients and canonical correlations are given for the first two discriminant functions.

Diet category	Canonical coefficients		Canonical correlations		Pooled within-group correlations among predictors				
	1	2	1	2	Ophi	Echi	Isop	Brac	Moll
Hiatellids	0.725	1.189	0.026	0.522	0.57	0.58	0.66	0.54	0.69
Ophiuroids	0.916	-0.034	0.141	-0.035		0.52	0.69	0.61	0.68
Echinoids	-0.815	0.377	-0.566	0.328			0.58	0.53	0.55
Isopods	0.097	-0.976	-0.119	-0.216				0.59	0.72
Brachyurans	-0.534	0.158	-0.369	0.166					0.54
Molluscs	-0.750	-0.440	-0.285	-0.040					
Eigenvalue	0.356	0.255							
Canonical Correlation	0.597	0.505							
Percent Variance	51.2	36.7							

Table 5.5. Mean relative volumes of diet categories for each size group, from additive log ratio transformed data.

Diet Category	Size Group				
	$\leq 30$	31–40	41–50	51–60	$> 60$
Hiatellid bivalves	0.032	0.363	0.095	0.073	0.027
Ophiuroids	0.049	0.049	0.008	0.007	0.012
Echinoids	0.005	0.035	0.050	0.132	0.149
Isopods	0.016	0.004	0.006	0.004	0.008
Brachyuran crabs	0.012	0.039	0.048	0.049	0.112
Other molluscs	0.164	0.145	0.622	0.116	0.485

A total of 4091 benthic invertebrates, of over 74 taxa, were collected from the 10 quadrats ( $2.5 \text{ m}^2$ ) at Watsons Bay. The most abundant animals were gammaridean amphipods, polychaetes, hiatellid bivalves and holothurians, with densities of 831, 191, 174 and 66  $\text{m}^{-2}$  respectively. Other common animals included other bivalves, ophiuroids, gastropods, isopods and brachyuran crabs (Table 5.6). The abundance of the benthic fauna varied greatly between the ten quadrats, ranging from 1 to 170 per quadrat ( $0.25 \text{ m}^2$ ) for hiatellid bivalves, 1 to 52 for ophiuroids, 1 to 50 for isopods and 2 to 20 for brachyuran crabs. The benthic animals were small, mostly ranging from 1 to 6 mm in size with a size frequency mode between 1 and 3 mm (Fig. 5.4).

Table 5.6. Composition, abundance and size of benthic fauna at Watsons Bay.

Taxon		Mean Abundance (m <sup>-2</sup> ± se)		Mean Size (mm)	Size Range (mm)	Measurement
ANTHOZOA		0.4	1.26	8.6	8.6	Base diameter
POLYCHAETA	Polychaeta	190.8	130.12	6.0	2.0 - 30.0	Length
	Serpulid colony	1.2	1.93	-	-	
MOLLUSCA						
Bivalvia	<i>Hiatella australis</i>	174.4	258.01	4.2	0.7 - 10.1	Shell length
	Pectinidae	6.0	8.89	2.2	1.1 - 2.9	Shell length
	Unidentified A	31.6	41.37	3.1	1.4 - 9.1	Shell length
	Unidentified B	3.6	6.38	12.3	4.8 - 20.0	Shell length
	Unidentified C	3.6	7.41	2.4	1.2 - 3.7	Shell length
	Unidentified D	14.0	27.41	2.1	1.0 - 3.9	Shell length
	Unidentified Other	17.2	24.73	2.0	0.9 - 9.5	Shell length
Amphineura						
	Callochitonidae	0.8	2.53	3.3	2.9 - 3.7	Length
	Acanthochitonidae	2.8	4.24	8.2	2.9 - 10.1	Length
	Unidentified	0.4	1.26	1.5	1.5	Length
Gastropoda	Epitoniidae	3.2	5.27	3.1	1.8 - 6.8	Shell length
	Ranellidae	1.6	2.80	11.9	3.4 - 20.0	Shell length
	Xenophoridae	0.8	2.53	3.4	3.0 - 3.8	Shell length
	Cerithiidae	9.2	12.08	4.9	2.4 - 11.2	Shell length
	Columbellidae	2.4	5.06	6.2	3.4 - 8.6	Shell length
	Muricidae	27.2	29.80	3.2	1.3 - 9.0	Shell length
	Phasianellidae	0.8	2.53	1.7	1.5 - 1.8	Shell length
	Trochidae	10.8	17.49	3.2	1.0 - 31.6	Shell length
	Turbinidae	9.2	12.93	6.5	0.8 - 18.0	Shell length
	Marginella	0.8	2.53	1.7	1.7	Shell length
	Fissurellidae	0.4	1.26	2.0	2	Shell length
	Volutidae	0.8	1.69	1.7	1.6 - 1.8	Shell length
	Littorinidae	0.8	2.53	2.6	1.6 - 3.5	Shell length
	Cassidae	0.4	1.26	3.0	3	Shell length
	<i>Haliotis</i> sp	0.4	1.26	1.4	1.4	Shell length
ECHINODERMATA						
Crinoidea	<i>Antedon incommoda</i>	2.0	3.89	26.8	15.0 - 40.0	Arm length
	<i>Comatulella brachiolata</i>	8.0	12.51	17.3	8.0 - 44.0	Arm length
Ophiuroidea	<i>Amphipholis squamata</i>	34.8	25.23	1.5	0.8 - 3.1	Disc diameter
	<i>Amphiura trisacantha</i>	30.8	23.25	2.6	1.2 - 5.3	Disc diameter
	<i>Ophiacantha alternata</i>	8.0	9.24	2.3	1.0 - 3.7	Disc diameter
	<i>Ophiothrix caspitosa</i>	25.6	26.14	3.5	1.6 - 7.3	Disc diameter
	<i>Ophioceres bispinosus</i>	0.4	1.26	5.4	5.4	Disc diameter
	<i>Ophiomyxa australis</i>	0.4	1.26	3.1	3.1	Disc diameter
Echinoidea	Unidentified	1.2	1.93	2.6	2.0 - 3.6	Test diameter
Holothuroidea	Unidentified	66.4	92.57	4.3	1.7 - 10.5	Length

Table 5.6 (continued). Composition, abundance and size of benthic fauna at Watsons Bay.

Taxon		Mean Abundance (m <sup>-2</sup> ± se)		Mean Size (mm)	Size Range (mm)	Measurement	
ECHINODERMATA (Continued)							
Asteroidea	<i>Coscinasterias calamaria</i>	0.8	1.69	5.0	4.0 - 6.0	Arm-disc length	
	<i>Tosia australis</i>	1.6	2.07	7.7	4.4 - 14.7	Arm-disc length	
	<i>Patiriella exigua</i>	0.8	2.53	5.8	7.0 - 4.6	Arm-disc length	
PYCNOGONIDA <i>Stylopallene</i> sp		3.2	7.50	-	-		
CRUSTACEA							
Cirripeda		1.2	1.93	18.7	7.0 - 30.6	Base diameter	
Amphipoda							
Gammaridea		830.8	720.48	3.1	1.0 - 10.0	Length	
Cyamidea	<i>Caprella danilevskii</i>	2.0	3.40	8.6	6.0 - 11.0	Length	
	<i>Caprellascaura</i>	0.4	1.26	11.0	11	Length	
	<i>Paraprota spinosa</i>	2.0	6.32	8.3	6.0 - 11.0	Length	
Isopoda							
Flabellifera	Unidentified	1.6	2.07	3.8	2.7 - 4.9	Length	
Anthuridae	Unidentified	0.8	1.69	4.2	3.0 - 5.3	Length	
Sphaeromidae	Unidentified	0.8	1.69	5.0	4.0 - 5.9	Length	
	<i>Exosphaeroma</i> sp	1.2	1.93	5.2	3.5 - 7.8	Length	
	<i>Ciliceaea</i> sp	0.8	2.53	6.6	5.6 - 7.6	Length	
Eubranchiatae	Unidentified	1.2	3.79	3.6	2.9 - 4.3	Length	
	<i>Amphoroidella elliptica</i>	10.0	17.61	2.5	1.5 - 3.2	Length	
	<i>Cerceis</i> sp	2.8	4.24	4.3	3.3 - 5.3	Length	
	<i>Haswellia emarginata</i>	16.4	23.05	5.6	1.5 - 12.4	Length	
	<i>Accalathura gigas</i>	0.4	1.26	8.0	8	Length	
	<i>Cranchii australiense</i>	0.4	1.26	4.3	4.3	Length	
	<i>Limnoria lignorum</i>	0.4	1.26	4.4	4.4	Length	
	Asellota	Stenetridae	3.6	3.98	5.3	2.6 - 8.0	Length
		Janiridae	1.0	0.10	2.7	2.7	Length
	Tanaidacea	Apseudidae	6.8	5.67	3.8	2.0 - 8.4	Length
Tanaidae		8.4	9.70	5.0	2.2 - 8.6	Length	
Decapoda							
Caridea	<i>Crangon socialis</i>	2.4	4.30	3.9	2.2 - 6.3	Carapace length	
	<i>Athanus granti</i>	2.0	6.32	2.4	2.2 - 2.5	Carapace length	
	<i>Hyppolyte australiensis</i>	3.2	5.90	3.2	2.3 - 4.0	Carapace length	
	<i>Alope australis</i>	0.8	2.53	4.9	4.1 - 5.6	Carapace length	
	<i>Latreutes</i> sp	0.4	1.26	3.9	3.9	Carapace length	
Anomura	Paguridae	6.8	9.25	4.5	2.0 - 7.0	Shell length	
Brachyura	<i>Naxia aurita</i>	0.4	1.26	5.5	5.5	Carapace width	
	<i>Halicarcinus ovatus</i>	21.2	14.49	2.6	1.0 - 5.7	Carapace width	
	<i>Doclea profunda</i>	0.4	1.26	5.4	5.4	Carapace width	
	<i>Pilumnus fissifrons</i>	6.4	10.70	3.3	1.2 - 5.6	Carapace width	
	<i>Eriocheir spinosus</i>	0.4	1.26	4.2	4.2	Carapace width	
	Dromiidae	0.4	1.26	2.7	2.7	Carapace width	



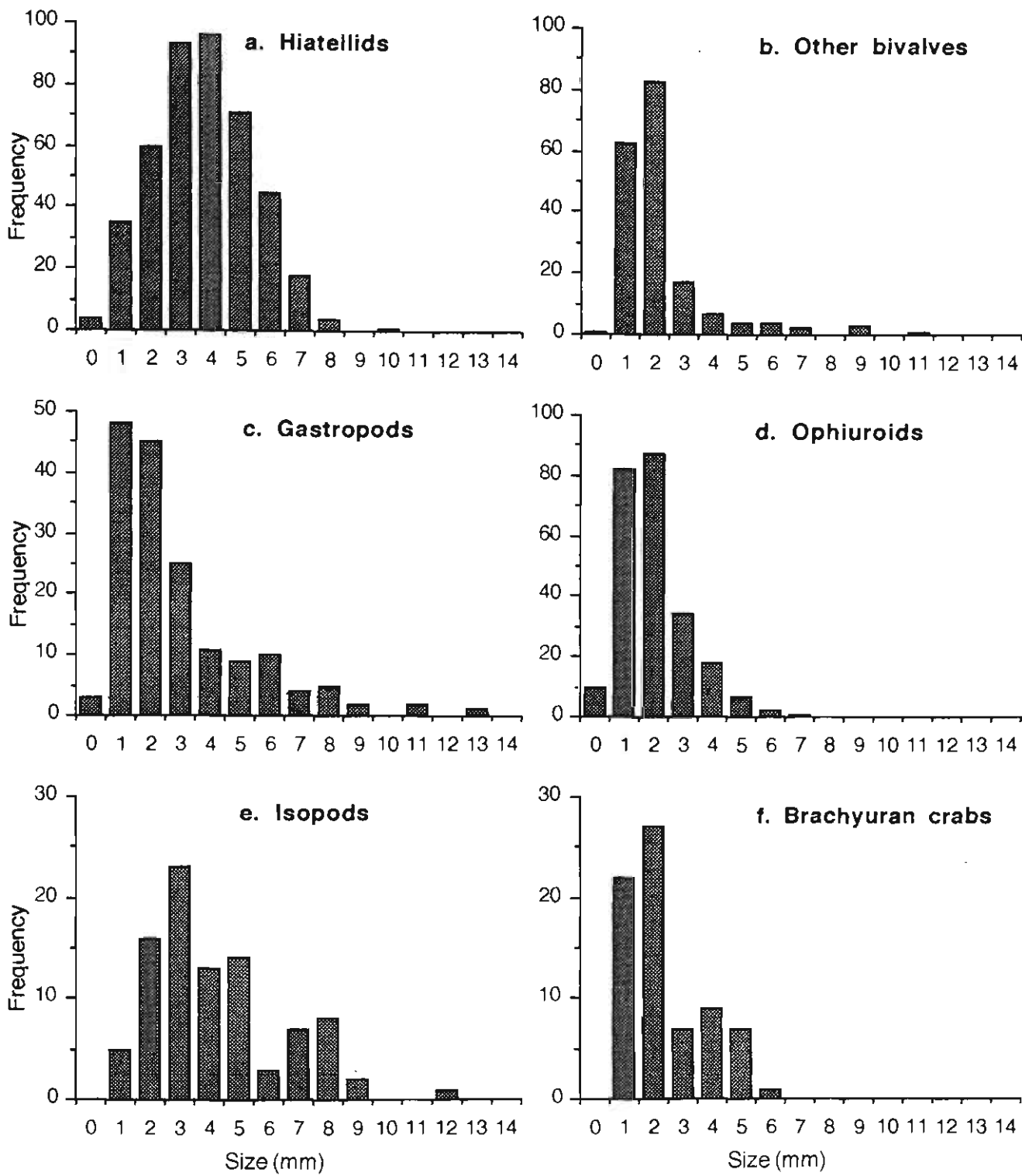


Fig. 5.4. Size frequency distributions (per 2.5 m<sup>2</sup>) of (a) hiatellid bivalves, (b) other bivalves, (c) gastropods, (d) ophiuroids, (e) isopods and (f) brachyuran crabs at Watsons Bay.

The majority of the animals collected were cryptic, usually inhabiting the sponge, algal and bryozoan matrix present within the holdfasts of the large kelp *Ecklonia radiata*. Most animals were also found within the thalli of small algae and bryozoans, and beneath the flat lamina of the rhodophyte, *Sonderpelta*. Other observed microhabitats include the underside of coralline algal plates, sponges and on kelp lamina, but fewer taxa were observed in these microhabitats (Table 5.7). Most animals were also present in rock crevices, but generally in association with sessile invertebrates such as sponges and bryozoans.

For all lobster sizes, Pearre's prey selection index ( $C$ ) indicated that bivalves and gastropods were selected in proportions higher than their relative abundances in the environment, while amphipods were avoided (Table 5.8). Ophiuroids were consumed by lobsters in the  $\leq 30$  mm and 31–40 mm size groups in proportions similar to their environmental abundance, but were avoided by larger lobsters. Isopods and miscellaneous crustacea were a selected prey item of  $\leq 30$  mm lobsters, but isopods were avoided by larger lobsters. Brachyurans were a preferred prey item for larger lobsters,  $> 30$  mm CL. Amphineurans and echinoids were also selected for by the larger lobsters.

Table 5.7. Microhabitat specific distribution of benthic fauna at Watsons Bay, from qualitative observations in the field. Key: (++) high abundance; (+) present; and (o) absent.

Taxon	Algal thalli/ bryozoa	Holdfast ( <i>E. radiata</i> )	<i>Sonderopelta</i>	Coralline Algae	Rock Crevice	Sponges
Polychaeta	++	++	+	+	o	+
Hiatellid bivalves	o	++	++	o	+	o
Other bivalves	++	+	+	+	+	+
Amphineura		+	o	o	+	o
Gastropods	++	++	+	o	o	o
Crinoidea	+	+	+	+	+	o
Ophiuroidea	+	++	+	+	+	o
Echinoidea	+	+	o	o	+	o
Asteroidea	o	+	o	o	+	o
Holothuroidea	++	++	++	+	+	o
Gammaridean amphipods	++	+	+	+	o	+
Amphoroid isopods		++	++	o	o	o
Other isopods	+	+	+	+	o	o
Tanaidacea	+	+	+	+	o	o
Caridea	++	+	o	o	o	o
Anomura	+	+	+	o	+	o
Brachyura	+	++	+	o	+	o

Table 5.8. Prey selection values (C) based on Pearre's (1982) selection index and chi-square values ( $\chi^2$ ) for each size group.

Prey Item	$\leq 30$ mm		31-40 mm		41-50 mm		51-60 mm		> 60 mm	
	C	$\chi^2$	C	$\chi^2$	C	$\chi^2$	C	$\chi^2$	C	$\chi^2$
<i>Hiattella australis</i>	0.03	4.09 *	0.27	348.42 **	0.22	223.08 **	0.13	78.58 **	0.06	18.34 **
Other bivalves	0.05	12.56 **	0.04	8.18 **	0.10	44.73 **	0.07	20.64 **	0.09	32.66 **
Amphineura	0.01	0.56	0.05	9.81 **	0.05	11.02 **	0.13	72.28 **	0.27	296.76 **
Gastropoda	0.18	142.39 **	0.13	74.74 **	0.15	91.05 **	0.10	41.37 **	0.10	39.40 **
Ophiuroidea	0.02	2.32	-0.01	0.81	-0.05	10.47 **	-0.04	8.33 **	-0.04	7.23 *
Echinoidea	-0.03	3.09	0.17	112.94 **	0.17	114.33 **	0.23	214.85 **	0.27	296.76 **
Asteroidea	-0.02	2.15	-0.02	2.19	0.01	0.17	0.02	1.31	0.02	1.24
Amphipoda	-0.13	100.60 **	-0.16	166.55 **	-0.20	246.43 **	-0.15	137.25 **	-0.15	134.43 **
Isopoda	0.05	11.42 **	-0.03	3.98 *	-0.02	2.50	-0.03	3.98 *	-0.04	5.92 *
Natantia	0.01	0.15	0.00	0.07	-0.03	3.94 *	-0.03	2.74	-0.03	2.77
Brachyura	0.00	0.00	0.04	8.17 **	0.05	8.74 **	0.04	8.24 **	0.10	44.38 **
Other Crustacea	0.20	168.79 **	-0.01	0.43	0.00	0.03	0.03	3.83	0.02	2.15

\* Significant,  $p < 0.05$ ; \*\* highly significant,  $p < 0.01$ .

## 5.4 Discussion

The natural diet of *Jasus edwardsii* comprised a diverse spectrum of benthic prey which was largely dominated by molluscs, echinoderms and crustaceans, as found by Hickman (1945) and Fielder (1965). However, significant size-related differences were detected (Table 5.3, 4.4; Fig. 5.3). The diet for juveniles  $\leq 30$  mm CL was distinct from larger lobsters and was dominated by ophiuroids, isopods and, to a lesser extent, hiatellid bivalves and small unidentified crustaceans. Hiatellid bivalves, crabs and sea urchins were important for lobsters  $> 30$  mm CL, but there was a gradual shift of decreased volumes of hiatellid bivalves and increased volumes of sea urchins, crabs and chitons with an increase in size. For lobsters 30–60 mm CL, poriferan material was also frequently consumed, and in considerable volumes. However, the high association with other prey, particularly cryptic crabs and bivalves, suggests that the ingestion of porifera is coincidental.

Ontogenetic shifts in diet have also been observed in other lobster species but are different in nature to that of *J. edwardsii*. The diet of *Homarus americanus* shifts from a predominance of sea stars, sea urchins, ophiuroids and mussels in small lobsters,  $< 40$  mm CL, to tunicates, sea urchins and molluscs in intermediate sized lobsters, 40–50 mm CL, to mussels, crabs, fish and polychaetes in larger lobsters,  $> 50$  mm CL (Scarratt 1980; Carter & Steele 1982b). Sea urchins, in addition to small crustaceans, were also important for small *J. lalandii*, with a shift towards mussels in larger lobsters,  $> 50$  mm CL (Barkai & Branch 1988). Shifts in the diet of *Panulirus cygnus* were confounded by season with small lobsters,  $< 40$  mm CL, consuming more molluscs and crustaceans than larger lobsters in the summer, and consuming more coralline algae in the winter (Edgar 1990; Jernakoff *et al.* 1993).

The prey selection indices (Table 5.8) show that the dietary shifts of *J. edwardsii* were associated with changes in preferences for particular prey types. Bivalves, gastropods, isopods and other crustaceans were taken by small juveniles,  $\leq 30$  mm CL, in proportions higher than their environmental abundances. Sea urchins, crabs, bivalves, chitons and gastropods were preferred prey items of larger lobsters,  $> 30$  mm CL. These preferences for particular prey items may be a function of differences in feeding behaviour and abilities, and because of differences in calorific and nutritive values of the various prey types.

The broad dietary spectrum of *J. edwardsii* indicates that this species is opportunistic and may capitalise on unusual food sources, as found with *J. lalandii* (Barkai & Branch 1988), *H. americanus* (Scarratt 1980; Hudon & Lamarche 1989) and *P. cygnus* (Edgar 1990). However, the homogeneity of dominant prey items within each size group (Fig 4.1;

Costello 1990) and the selectivity for particular prey types (Table 5.8) show that *J. edwardsii* is a discriminate feeder rather than a random scavenger, as proposed by Fielder (1965). Discriminate, or selective feeding has also been reported for *H. americanus* (Ennis 1973; Scarratt 1980; Carter & Steele 1982b; Elner & Campbell 1987; Hudon & Lamarche 1989) and *J. lalandii* (Barkai & Branch 1988).

The prey of smaller *J. edwardsii*, particularly isopods, other small crustaceans, ophiuroids and small bivalves, were highly cryptic and generally inhabited the thalli of bushy rhodophytes and bryozoans, or were embedded in the sponge-algal-bryozoan matrix found between the haptera of kelp holdfasts (Table 5.7). This suggests that the smaller juveniles were probing in amongst these complex microhabitats to extract their prey from the benthos. In contrast, the prey of larger lobsters, particularly sea urchins, chitons and larger crabs were less cryptic and with a more general distribution. This indicates that larger lobsters may forage more widely and in more open areas. The ontogenetic shifts in diet of *H. americanus* and *P. cygnus* also appear to be associated with a more open and wider ranging foraging mode in larger lobsters (*H. americanus*: Lawton 1987, Elner & Campbell 1988 ; *P. cygnus*: Edgar 1990, Jernakoff *et al.* 1993).

There is little overlap in the dietary requirements between lobsters of different sizes (Fig. 5.3), and this may be a significant factor in reducing both inter- and intra-specific competition (Schoener 1974; Werner & Gilliam 1984). This also implies that each size class could be limited by different resources, but this is unlikely given each size group appears to be an opportunistic generalist. The benthic fauna showed little evidence of any limitations to lobster feeding; most animals were of a suitable size range and abundances were relatively high, except for sea urchins and chitons.

The ontogenetic shift in diet of *J. edwardsii* implies that lobsters of different sizes may have different roles in community structure and function. The consumption of detritivores by small lobsters and the consumption of herbivorous grazers by larger lobsters suggests that energy transfer and material flow through the community is partitioned between the different sizes. Ontogenetic shifts in feeding also imply differences in the structuring of prey populations and the overall community. Lobsters may exert an influence on prey population structure, abundance and distribution (*e.g.* *H. americanus*: Witman 1985, Ojeda & Dearborn 1991; *J. lalandii*: Pollock 1979; Griffiths & Seiderer 1980, Barkai & Branch 1988; *P. interruptus*: Tegner & Levin 1983). Lobsters may also maintain community structures through the control of herbivore populations such as sea urchins (Mann & Breen 1972; Breen & Mann 1976; Wharton & Mann 1981; Tegner & Levin 1983), but this is the subject of some debate (Wharton & Mann 1981; Elner & Campbell

1987; Andrew & Macdiarmid 1991). In the case of *J. edwardsii*, small lobsters may influence the distribution of small prey items, such as ophiuroids, small crustaceans and bivalves, by restricting them to cryptic refuges. However, given the relatively high abundances of juvenile lobster prey (Table 5.6), this is only likely to occur if there is intensive feeding pressure over small areas. Larger lobsters may be more influential in herbivore/kelp relationships through the consumption of sea urchins and chitons.

In conclusion, there is a significant ontogenetic shift in the diet of *J. edwardsii* and this has implications for understanding the population dynamics of this species, and in determining the role of lobsters in community patterns and processes. However, further knowledge of size differences in feeding and dietary limitations is required for a greater understanding of the implications of this ontogenetic shift in diet.

# Morphology

### 6.1 Introduction

Palinurid lobsters develop through distinct morphological stages, from newly hatched naupliosoma larvae, through phyllosoma and puerulus stages, to the benthic stage (as described in Chapter 1). The post-pueruli are similar to the adult form, but morphological changes continue to occur with growth after settlement. An obvious change in the benthic form occurs with maturation. In most palinurids, these changes include the relative lengthening of the anterior legs of males and, in females, the legs becoming comparatively shorter, pleopods enlarging and becoming setose and the abdomen widening (Gordon 1960; George & Morgan 1979; Grey 1979; Breen *et al.* 1988; Skewes *et al.* 1994).

In other crustaceans, more subtle changes in morphology can occur that are not necessarily related to maturation and the development of secondary sexual characteristics. Ontogenetic changes in morphology of the fiddler crab *Uca* spp has been well documented, with complex changes in the relative shape and size of eyestalks, legs, chaelae and pleopods occurring through the whole benthic size range (Huxley 1924; Miller 1971; Williams *et al.* 1980).

Morphological changes with size may result in differences in resource utilisation abilities and predation risk, mediating ontogenetic shifts in ecology (Werner & Gilliam 1984). This has been found in the crayfish *Oronectes propinquus*, where relative size changes in the chelae of males reduce predation risk, allowing it to occupy less protective substrates (Stein 1977).

This study describes the general morphology of juvenile *Jasus edwardsii* and examines allometric changes in morphology that may have ecological implications.

6.2 Materials and Methods

Measurements were taken from 112 lobsters, which were collected and preserved as part of the diet and growth studies (Chapters 5 & 8). The lobsters ranged in size from 10 to 57 mm CL and included puerulus and first moult post-puerulus stages; few lobsters between 22 and 30 mm CL were obtained.

Eleven variables (characyers) were measured, relating to size of the carapace, abdomen, tail fan and appendages, and are listed in Table 6.1. Carapace width and thorax thickness (depth) were not measured as the carapace had been removed for the diet study. However, carapace length was measured prior to removal. Median values for paired appendages were used for the analysis.

All measurements were compared against the carapace length as a reference dimension. Carapace length was used as it is a relatively large dimension with comparatively small measurement errors, and is a standard index of lobster size. The relationship between carapace length and the size of each variable was examined using bivariate plots, and by fitting empirical mathematical models to the data.

Table 6.1. Variables measured for juvenile *Jasus edwardsii*.

Variable	Description
carapace length	frontal tubercle to posterior edge of carapace
abdomen length	anterior edge of squamae on first tergum to posterior edge of sixth tergum
abdomen width	inter-pleuron distance of second abdominal segment
abdomen thickness	dorso-ventral height of second abdominal segment
telson length	posterior edge of sixth abdominal tergum to distal edge of telson
tail fan spread	lateral-distal edges of uropods at maximum lateral extension
antenna length	distal edge of antennal peduncle to distal end of flagellum
first leg length	proximal-ventral tip of first coxopodite to distal tip of dactylopodite
third leg length	proximal-ventral tip of third coxopodite to distal tip of dactylopodite
fifth leg length	proximal-ventral tip of fifth coxopodite to distal tip of dactylopodite
first leg thickness	dorso-ventral distance of proximal end of first propodite.



The relationship between the size of one variable,  $y$ , and another,  $x$ , can be described by the power function:

$$y = \alpha x^\beta \quad (6.1)$$

where  $\alpha$  and  $\beta$  are coefficients (Huxley 1924). Here,  $\beta$  represents the proportional change in variable  $y$  with a unit change in variable  $x$ . If  $\beta$  is equal to one, then  $y$  changes in size at the same rate as  $x$  (isometry). Where  $\beta$  is greater than one, then  $y$  increases at a faster rate than  $x$  (positive allometry), and where  $\beta$  is less than one,  $y$  grows more slowly than  $x$  (negative allometry). The index of allometry,  $\beta$ , can be easily determined from the logarithmic form of Equation 6.1:

$$\log y = \log \alpha + \beta \log x \quad (6.2)$$

This equation is classically termed the equation of simple allometry (Teissier 1960).

A limitation of this relationship is that it assumes the relative growth rate of variable  $y$  is constant with changes in  $x$ , *i.e.*  $\beta$  is the same for all  $x$ . This is not always the case, as found in fiddler crabs *Uca* spp, with the  $\beta$  for chela size changing with increased body size (Huxley 1924; Miller 1971; Williams 1980). Such complex allometric relationships can be described by expanding the function (6.1) to a polynomial function:

$$\log y = \sum_{k=0}^P (\log x)^k \beta_k \quad (6.3)$$

where  $P$  is the order of the polynomial.

This function (6.3) was used to assess the relative growth of each of the variables for *Jasus edwardsii*. In each case, three was chosen as the upper limit for  $P$  (due to substantially increased error terms at higher orders: Williams 1980), giving the cubic function (using logarithms to the base 10):

$$\log y = \beta_0 + (\log x) \beta_1 + (\log x)^2 \beta_2 + (\log x)^3 \beta_3 \quad (6.4)$$

Following the methods of Williams (1980), a step-down polynomial regression analysis was used to estimate the  $\beta_k$  coefficients ( $b_k$ ) and determine their significance. The sequence of tests were: if  $b_3$  was not significantly different from zero, set  $\beta_3$  to zero and test if  $b_2$  significantly different to zero; if not, set  $\beta_2$  to zero and test if  $b_1$  significantly different from one; if not, accept  $\beta_1 = 1$ . Based on these tests, the proportional changes in the size of a variable can be determined as either isometric ( $\beta_3 = \beta_2 = 0$ ,  $\beta_1 = 1$ ), simple allometric ( $\beta_3 = \beta_2 = 0$ ,  $\beta_1 \neq 1$ ), complex allometric with a linear trend in size ( $\beta_3 = 0$ ,  $\beta_2 \neq 0$ ) and complex allometric with a quadratic trend ( $\beta_3 \neq 0$ ). All tests were examined at a

significance level of  $\alpha = 0.05$ .

### 6.3 Results

The plots of body variable against carapace length (Figs 6.1 a-k) show that all variables increase with lobster size in an approximately linear trend. No major discontinuities in variable size are evident at any size stage and no differences can be detected between males and females.

However, subtle changes occur in the relative size of each variable (as a proportion of carapace length), as seen in Figs. 6.2 a to k. These allometric changes are statistically significant for all variables (Table 6.2).

Positive, simple allometric relationships exist for the length of the abdomen, antennae, third leg, fifth leg and width of the first leg; the relative size of these variables increase linearly with carapace length (Table 6.2; Figs. 6.2 a, f, h, i, j).

More complex allometric relationships occurred for abdomen width and depth, tail fan spread and first leg length. The relative size of the abdomen width and depth and tail fan spread increased rapidly at small sizes, but changed little at sizes above approximately 30 mm CL (negative parabola: Table 6.2; Figs. 6.2 b, c, e) This contrasted with changes in relative first leg length, which increased more rapidly at sizes above 30 mm CL (positive parabola: Fig. 6.2g).

Using the coefficients in Table 6.2, estimates of relative size of each variable were calculated for lobsters with carapace lengths of 15 mm, 35 mm and 55 mm. The magnitude of changes in size proportions of abdomen width, abdomen depth, telson length, tail fan spread and first leg width were quite small ( $\leq 6\%$ ) between 15 mm CL and 55 mm CL (Table 6.3). However, a moderate change of 9% was estimated in relative first leg length and large changes occurred in abdomen length, antenna length and third and fifth leg length (Table 6.3).

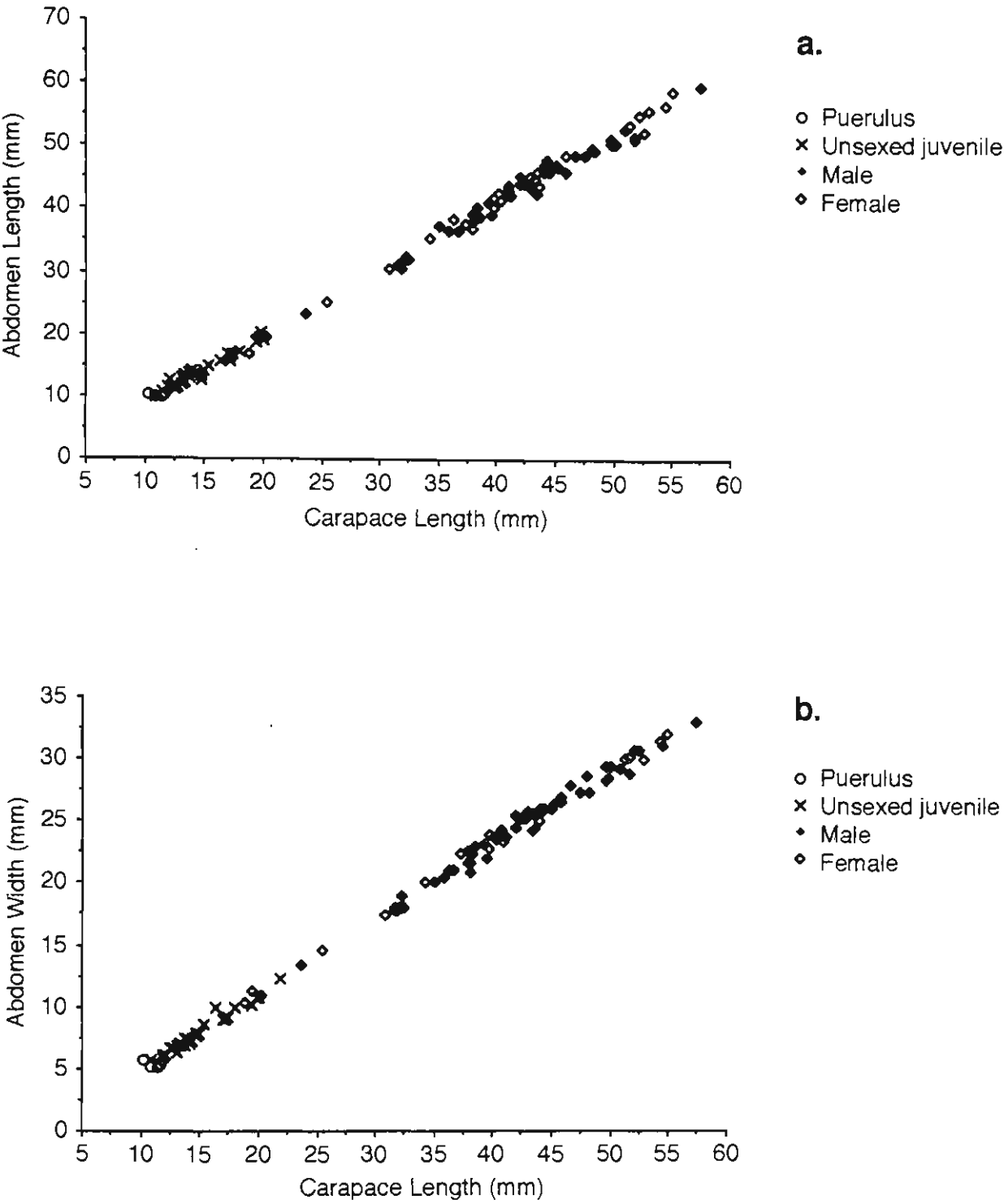


Fig. 6.1. Relationship between (a) abdomen length and (b) abdomen width with carapace length in juvenile *Jasus edwardsii*.

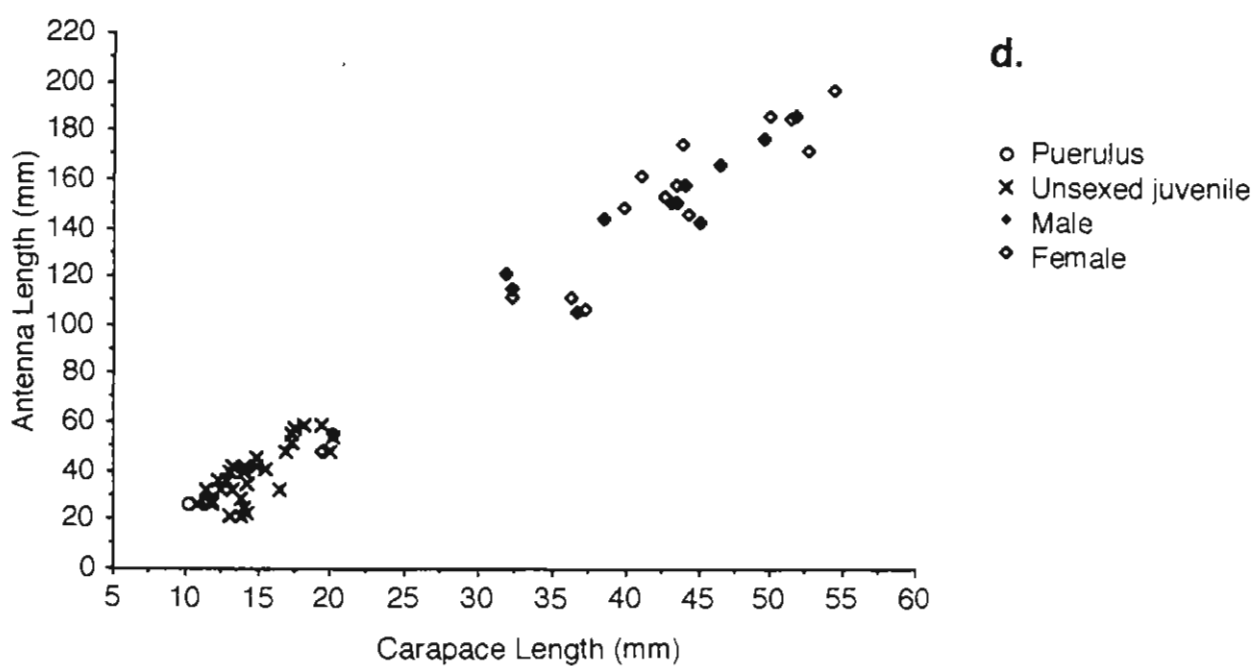
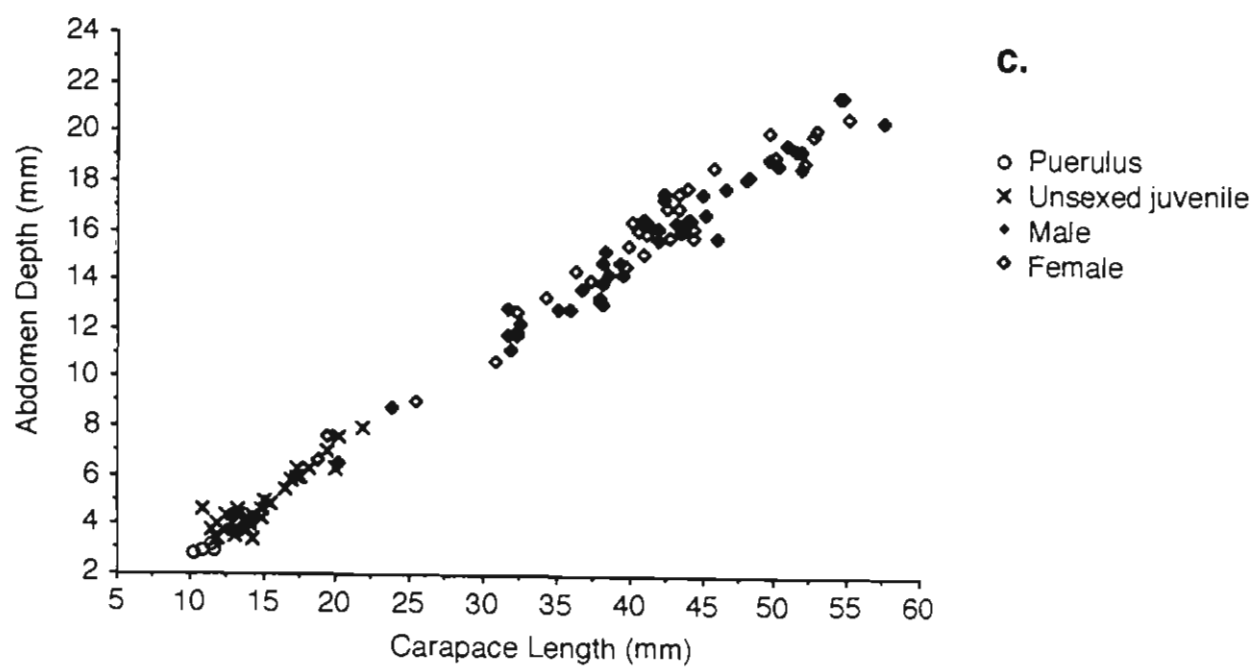


Fig. 6.1. Relationship between (c) abdomen depth and (d) antenna length with carapace length in juvenile *Jasus edwardsii*.

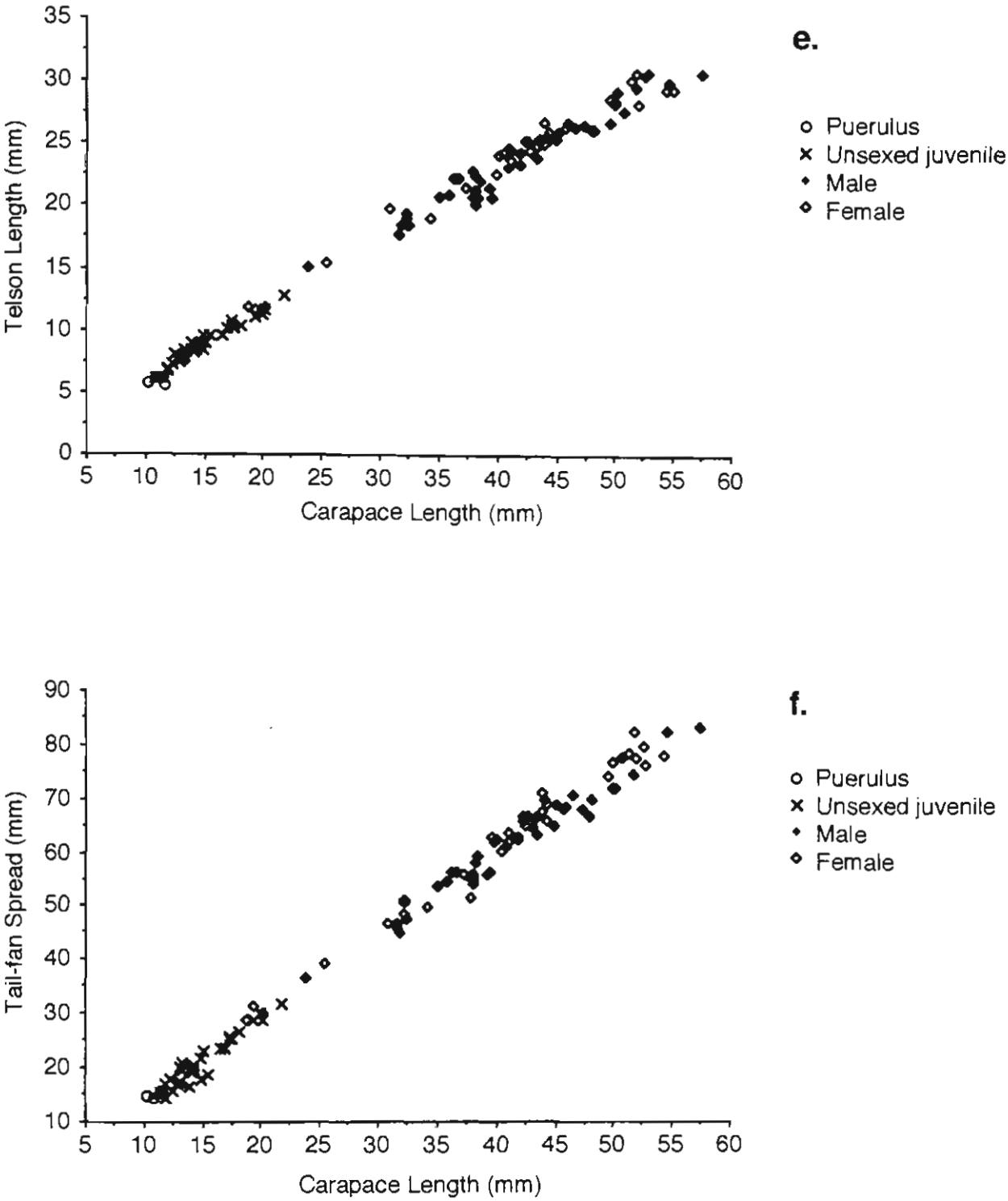


Fig. 6.1. Relationship between (e) telson length and (f) tail fan spread with carapace length in juvenile *Jasus edwardsii*.

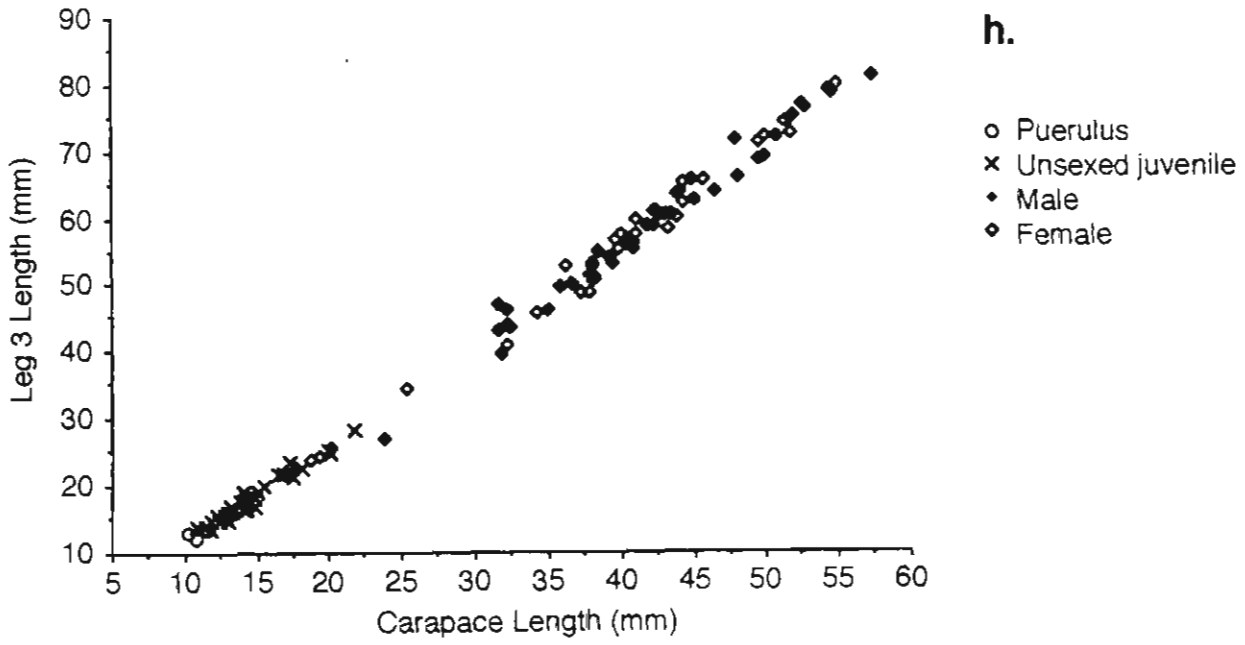
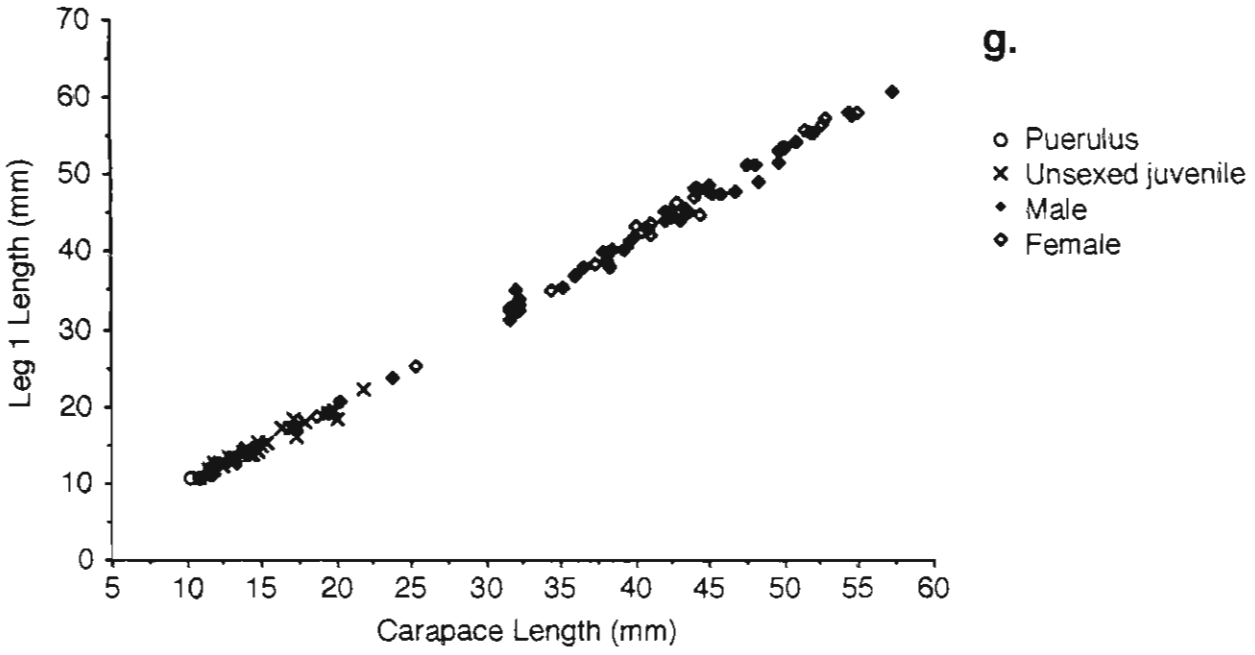


Fig. 6.1. Relationship between (g) first leg length and (h) third leg length with carapace length in juvenile *Jasus edwardsii*.

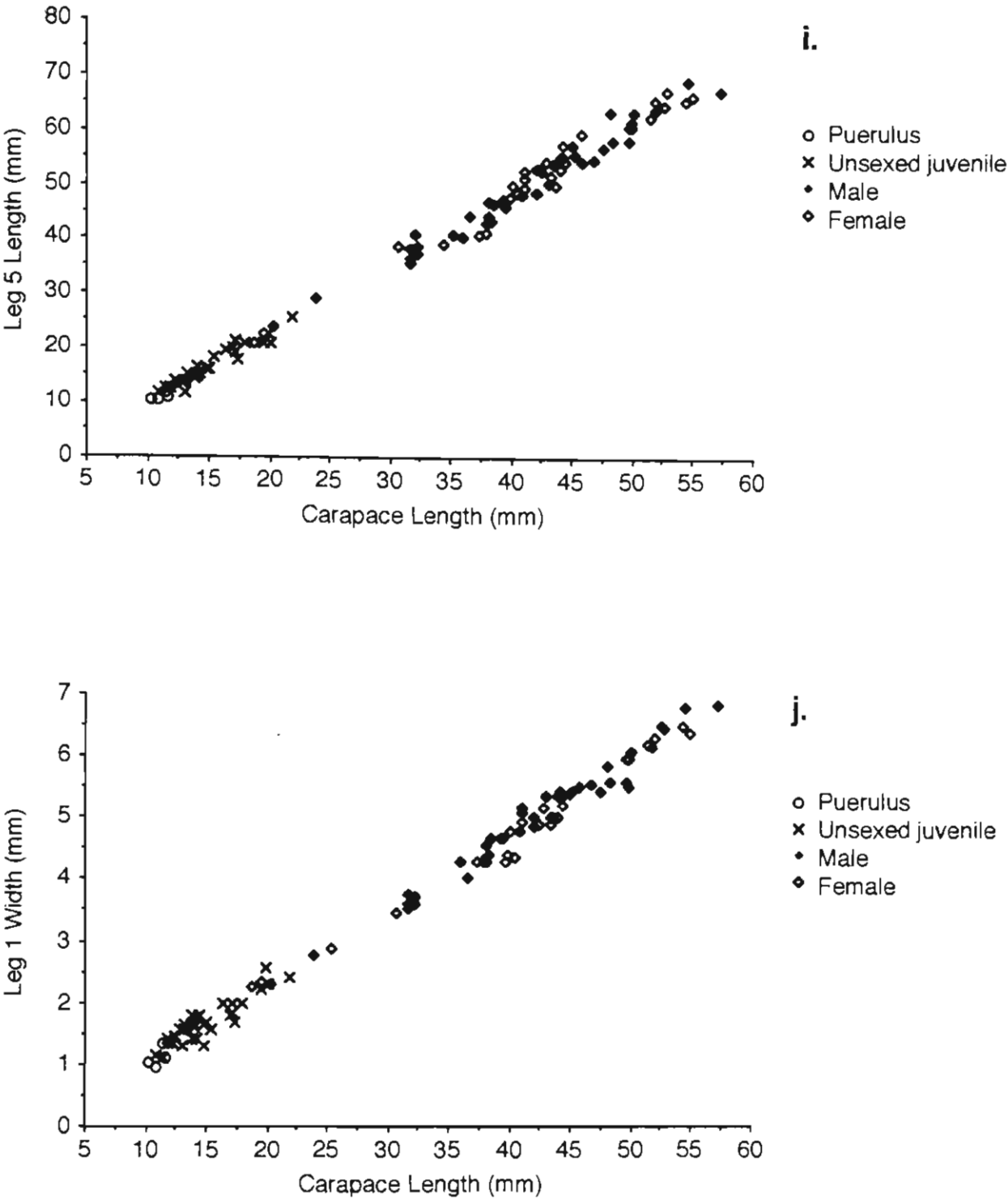


Fig. 6.1. Relationship between (i) fifth leg length and (j) first leg width with carapace length in juvenile *Jasus edwardsii*.

Table 6.2. Estimates of allometry coefficients  $\beta_k$  from Equation (5.4) using step-down polynomial regression ( $\pm$  se). Sequential tests of significance were: third order  $b_3 = 0$ ; second order  $b_2 = 0$ ; and first order  $b_1 = 1$  ( $n$  = number individuals analysed; \*  $p < 0.05$ )

Variable	n	$b_0$	$b_1$	$b_2$	$b_3$
Abdomen length	95	-0.114 $\pm 0.009$	1.079 * $\pm 0.006$	0	0
Abdomen width	98	-0.671 $\pm 0.074$	1.500 $\pm 0.106$	-0.143 * $\pm 0.038$	0
Abdomen depth	101	-1.376 $\pm 0.156$	2.168 $\pm 0.225$	-0.355 * $\pm 0.080$	0
Telson length	104	-0.177 $\pm 0.012$	0.962 * $\pm 0.008$	0	0
tail fan spread	98	-0.287 $\pm 0.112$	1.617 $\pm 0.161$	-0.203 * $\pm 0.057$	0
Antenna length	53	0.151 $\pm 0.040$	1.242 * $\pm 0.029$	0	0
leg 1 length	97	0.152 $\pm 0.066$	0.741 $\pm 0.096$	0.111 * $\pm 0.034$	0
leg 3 length	94	-0.045 $\pm 0.011$	1.118 * $\pm 0.007$	0	0
leg 5 length	96	-0.062 $\pm 0.013$	1.091 * $\pm 0.009$	0	0
leg 1 width	91	-0.987 $\pm 0.016$	1.035 * $\pm 0.010$	0	0



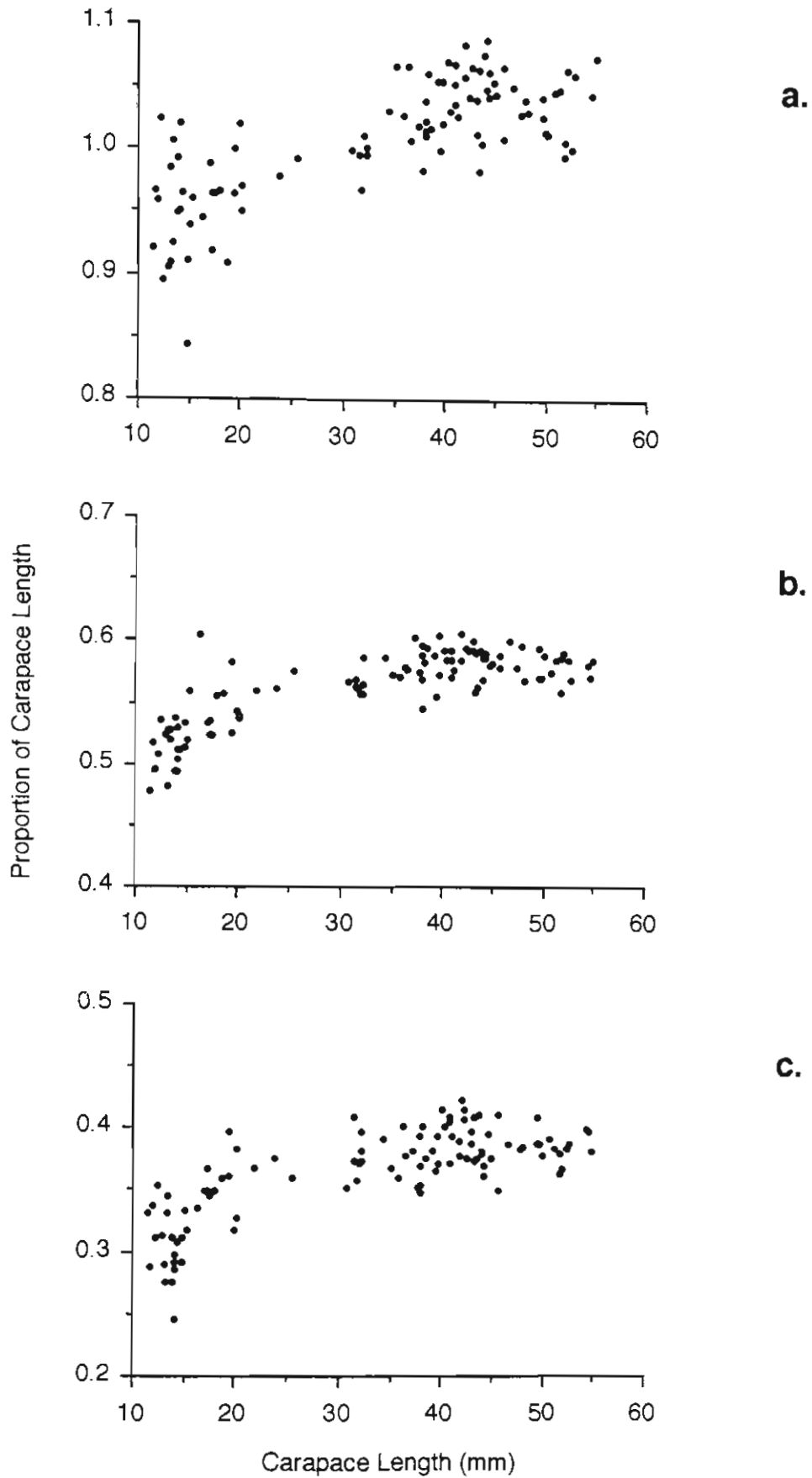


Fig. 6.2. Changes in relative size of (a) abdomen length, (b) abdomen width and (c) abdomen depth in juvenile *Jasus edwardsii*.

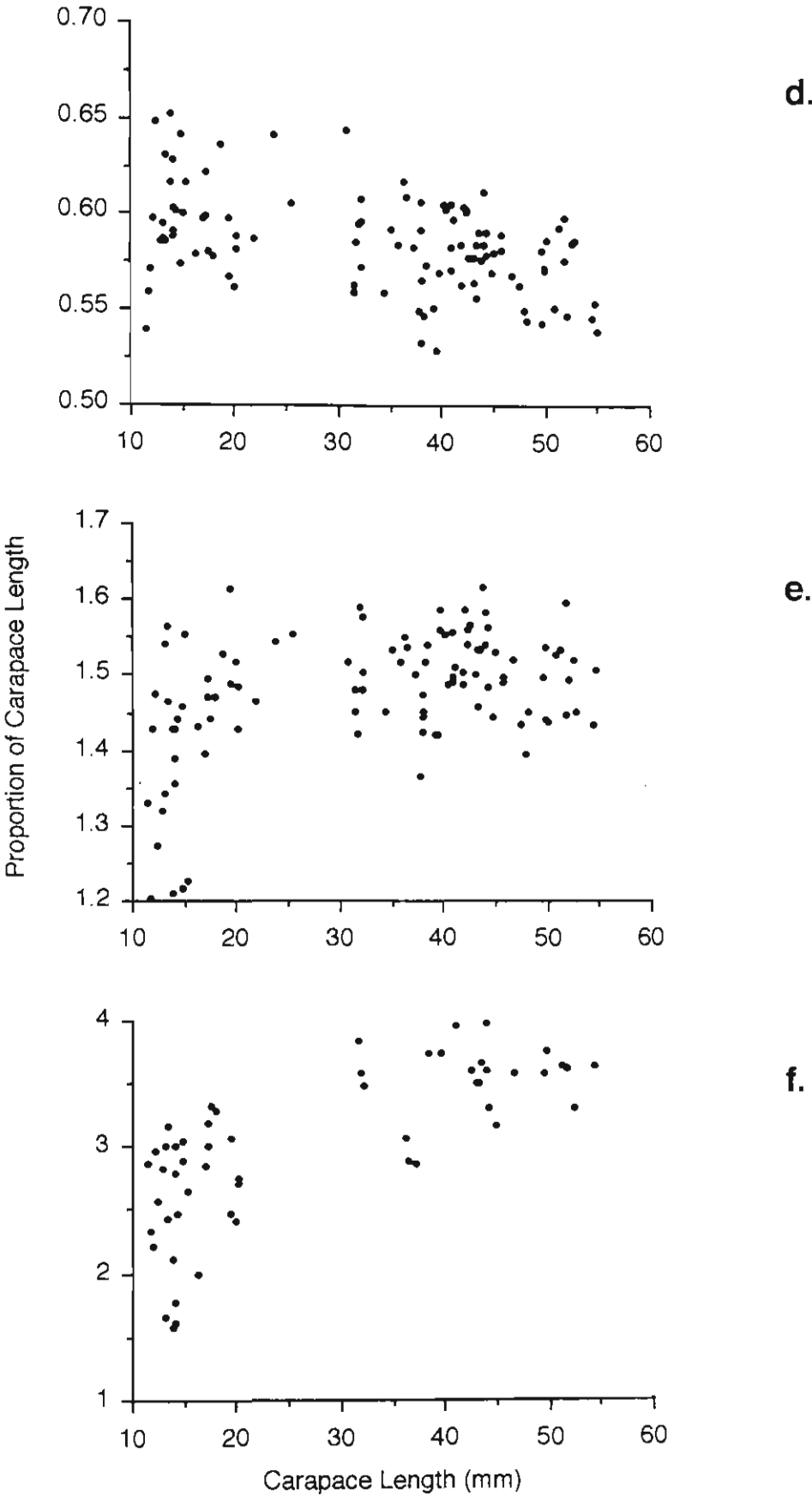


Fig. 6.2. Changes in relative size of (d) telson length, (e) tail fan spread and (f) antennae length in juvenile *Jasus edwardsii*.

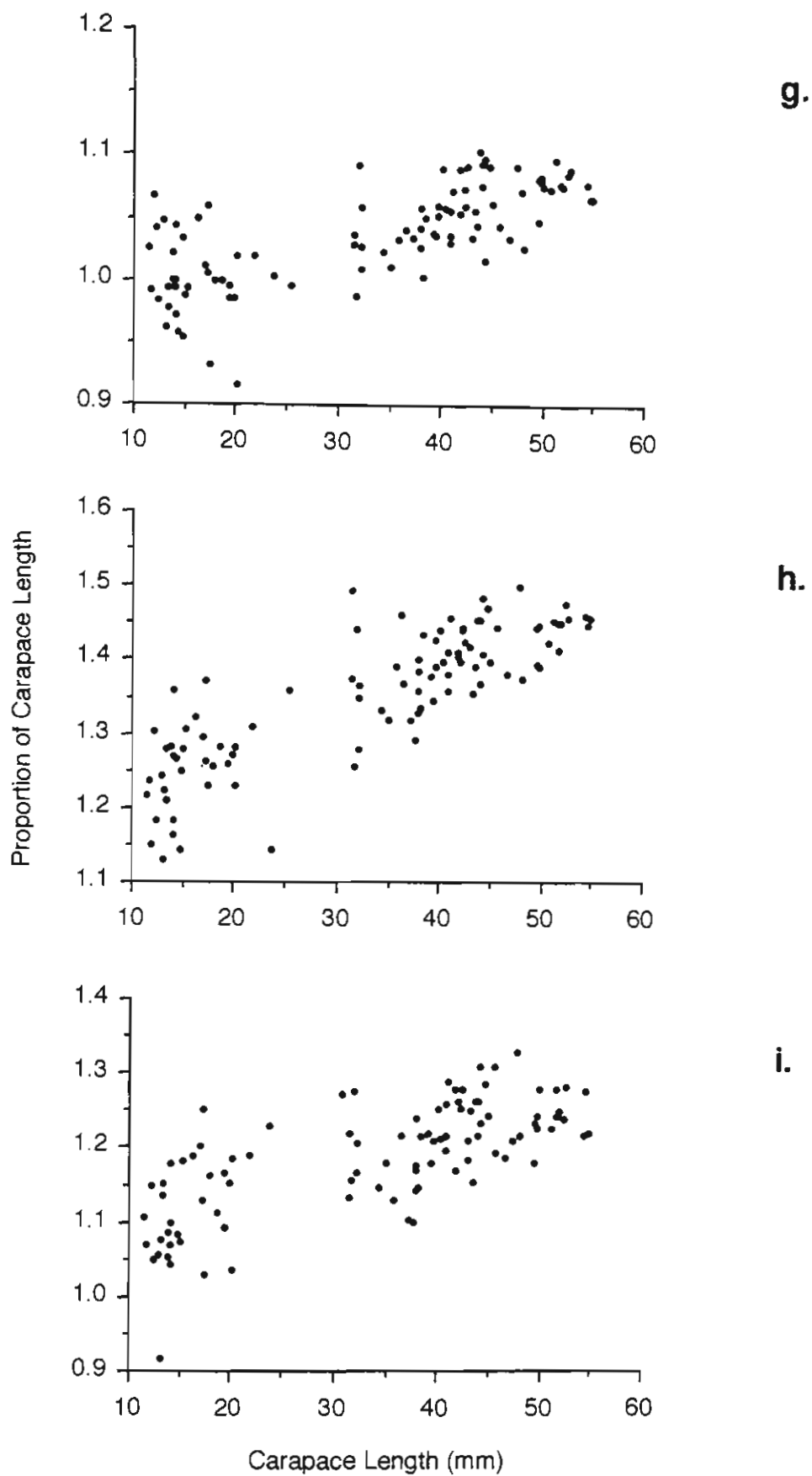


Fig. 6.2. Changes in relative size of (g) first leg length, (h) third leg length and (i) fifth leg length in juvenile *Jasus edwardsii*.

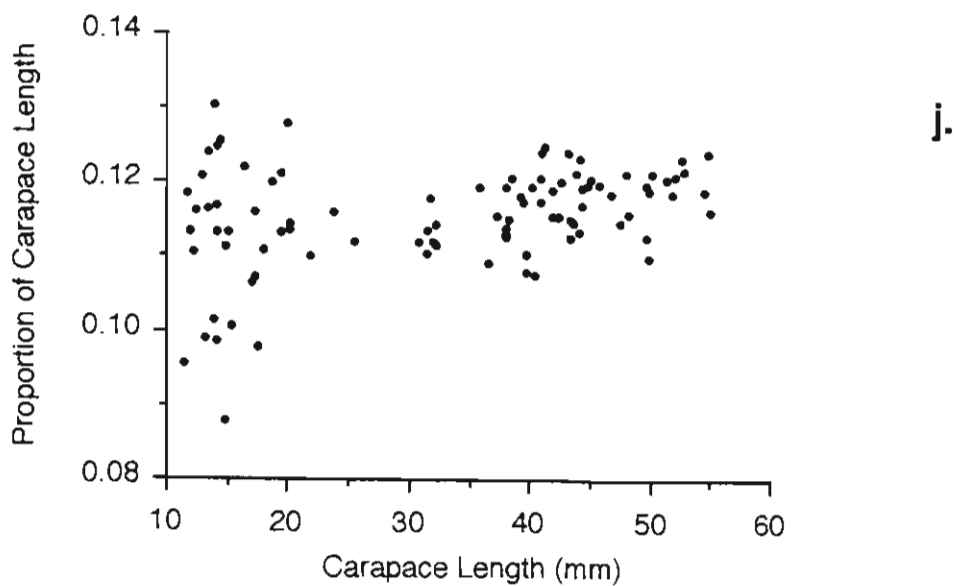


Fig. 6.2. Changes in relative size of (j) first leg width in juvenile *Jasus edwardsii*.

Table 6.3. Relative size of measures (as a proportion of carapace length) estimated from regression models in Table 6.2.

Variable	Carapace Length			Deviation (15 to 55 mm CL)
	15 mm	35 mm	55 mm	
a. Abdomen length	0.953	1.019	1.056	0.103
b. Abdomen width	0.524	0.576	0.584	0.060
c. Abdomen depth	0.312	0.381	0.382	0.060
d. Telson length	0.600	0.581	0.571	-0.029
e. Tail fan spread	1.438	1.520	1.486	0.047
f. Antenna length	2.727	3.347	3.734	1.007
g. Leg 1 length	1.002	1.039	1.090	0.088
h. Leg 3 length	1.241	1.372	1.447	0.206
i. Leg 5 length	1.109	1.198	1.248	0.139
j. Leg 1 width	0.113	0.117	0.119	0.005

## 6.4 Discussion

Changes in resource use and survivorship with size, such as in feeding ability and susceptibility to predation and physical factors, are likely to occur due to increases in size alone, as a function of simple scaling laws (McMahon 1973). Such ecological shifts may occur in a gradual, continuous manner as individuals increase in size. However, morphological changes such as those found for juvenile *Jasus edwardsii* may act to make niche and habitat changes more discrete (reviewed by Werner & Gilliam 1984). This is particularly the case where the morphological changes strongly affect functional capabilities, such as feeding and predator avoidance. For example, the increases in antenna length of *Jasus edwardsii* may reduce susceptibility to predation through increased predator detection. Given that significant allometric changes were observed for all variables measured in juvenile *Jasus edwardsii*, size-related changes in morphology may play a role in ontogenetic shifts in ecology.

The discreteness of ecological changes may be exacerbated by the complexity of the allometry. In this case, abdomen width, abdomen depth, tail fan spread and first leg length did not change at a constant rate with increased lobster size. Abdomen width and depth and tail fan spread increased in relative size most rapidly at sizes below approximately 35 mm CL, with little change in relative size in larger lobsters (to  $\approx 60$  mm CL). Conversely, first leg length changed little in relative size in lobsters below 35 mm CL, but increased with growth in larger lobsters. These complex allometric changes in body shape make morphological changes more discrete and, hence, may mediate distinct niche shifts with ontogenetic development.

# Development of Tagging Methods

## 7.1 Introduction

Tagging is an important tool for examining population dynamics, including aspects of growth, survival, abundance and movement. Tagging methods are particularly important for studying lobsters and other crustaceans as all hard parts are shed at ecdysis, precluding the use of information such as growth rings. The regular moulting of crustaceans also increases the difficulty of marking these animals.

A diverse range of methods have been developed for tagging lobsters, and can be divided into several types: temporary marks and tags, permanent external tags and permanent internal tags. In order to select a suitable tagging technique to examine the population dynamics of early benthic *Jasus edwardsii* (< 30 mm CL), these techniques were reviewed with respect to their effectiveness in small lobsters.

### 7.1.1 Temporary Markings

Many studies of small scale processes, such as local movements, shelter fidelity and short-term density and distribution patterns, have successfully used temporary markings and mutilations. These methods usually involve either an attachment of a tag to the carapace or appendages, or mutilation such as branding, hole punching and spine clipping.

Although tags attached to the exocuticle are shed with the exuviae at moulting, tags such as coloured or numbered antennal tags (*e.g.* Trendall & Bell 1989; MacDiarmid *et al.* 1991) and claw bands (*e.g.* Karnoffsky *et al.* 1989) allow researchers to visually identify individuals *in situ* with minimal disturbance. More elaborate temporary tags include flashing light tags (Karnoffsky *et al.* 1989) and electromagnetic transmitters (Ramm 1980; Jernakoff 1987). Miniature antennal tags have been used for small (18–42 mm CL) *Panulirus japonicus* (Norman *et al.* 1994); however, it was found that tagged lobsters had an elevated movement rate from the study area. Norman *et al.* (1994) discontinued the use of antennal tags in favour of individual recognition from colour and shape characteristics,

and from antennal lengths measured *in situ*. Yoshimura and Yamakawa (1988) also used individual characteristics to monitor the shelter use of twelve puerulus *P. japonicus*. In contrast, Jernakoff (1990) found that individual post-puerulus *P. cygnus* (< 15 mm CL) could not be recognised with certainty, although higher numbers were monitored (approximately 20 - 50).

Mutilation marks have been widely used in lobster research (*e.g.* Wilder 1963; Chittleborough 1976; Winstanley 1976), particularly before the development of smaller, more effective permanent tags. The most commonly used methods involve clipping pleopods and abdominal spines, as well as hole punching the telson and uropods, in various combinations to code for size and date of marking. Mutilation has the advantages of being simple to implement, and usually lasts for several moults before the marks and scars disappear (Winstanley 1976). Disadvantages include limitations in the number of locations that can be mutilated, and therefore the amount of information that can be coded, and a direct effect on growth and survival (where internal resources are diverted from growth to healing, and wounds increase the susceptibility to disease). Hole punching of the tail fan is considered particularly severe as the wound seals together the upper and lower surfaces such that the lobster must tear the tail fan to extract it from the exuviae during moulting.

Mutilation by antennal clipping was useful for batch marking small (< 25 mm CL) *P. cygnus* for a single capture-mark-recapture estimate of density (Jernakoff *et al.* 1994). Winstanley (1976) also used hole punching to assess growth in juvenile *J. edwardsii* > 30 mm CL. However, mutilation marks have a limited application for early benthic lobsters as small sizes have higher moulting frequencies (*e.g.* *P. interruptus*: Engle 1979), resulting in a rapid loss of the markings. Mutilations may also have a relatively greater biological effects at smaller sizes.

### 7.1.2 Permanent External Tags

External tags for lobsters are similar to those used for fish research, consisting of a visible external leader attached, *via* a percutaneous filament, to an anchor embedded into tissue or muscle of the animal. External tags are widely used for lobster fishery research because they are easily injected, detectable and readable at sea by both scientists and fishers. Many variations occur in the form of the anchor, filament and leader, with the effectiveness of each type dependent on the lobster species (Chittleborough 1974).

The three most widely used tag types are the Sphyrion, T-bar and western rock lobster tags. The Sphyrion tag was developed by Scarratt, Elson and Cooper (Scarratt & Elson 1965; Cooper 1970; Scarratt 1970) and consists of a stainless steel wire anchor attached to

a polyethylene filament and labelled piece of polyvinyl chloride 'spaghetti' tubing (*e.g.* the Floy FTL6, Floy Tag & Manufacturing, Washington). The T-bar tag is similar, except the filament terminates in a 'T' as the anchor (*e.g.* the Floy FD67; and the Hallprint T-bar, Hallprint, South Australia). The western rock lobster tag also has a spaghetti leader, but has a much larger anchoring toggle of sheet plastic. This toggle is labelled in addition to the external leader in case of tag breakage, or chewing by other lobsters (Chittleborough 1974). The utility of each of these tags is largely species specific, with problems including wound reopening, poor healing, secondary infections and tag shedding (*e.g.* Scarratt & Elson 1965; Chittleborough 1974; Winstanley 1974).

External 'spaghetti' tags have proven to be useful for a wide size range of lobsters. For fisheries research, the smallest size is usually limited by the capability of the trapping gear used. Standard Sphyrion tags have been used in *Homarus americanus* as small as 52 mm CL (Scarratt 1970; Ennis 1972); T-bar tags in 60 mm CL *Jasus edwardsii* (R.B. Kennedy, pers. comm., Department of Primary Industry & Fisheries, Tasmania) and western rock lobster tags in  $\approx$  40 mm CL *Panulirus cygnus*, *P. argus* and *H. americanus* (Chittleborough 1974; Lozano-Alvarez *et al.* 1991; and Krouse and Nutting 1990a respectively). However, western rock lobster tags are not suitable for *J. edwardsii* below 70 mm CL (McKoy & Esterman 1981).

Smaller versions of the external spaghetti tags have been used in *P. argus* from 34 mm CL with a T-bar tag (Davis 1978) and in *H. americanus* from 39 mm CL with a western rock lobster tag (Krouse & Nutting 1990a). Sphyrion tags with only one hook on the anchor have also been used in *P. argus* from 20 mm CL (Forcucci *et al.* 1994).

Although miniature external tags are being developed (Michael Hall, pers. comm., Hallprint, South Australia), several factors may reduce their effectiveness at smaller sizes. Firstly, standard sized tags are often broken or chewed by other lobsters (Chittleborough 1974) and a finely constructed tag may not be durable with growth. Secondly, and perhaps more importantly, newly settled lobsters have high moulting frequencies and, because the tag must be pulled through the old exuviae each time, such tags are likely to have an increased biological effect. Krouse and Nutting (1990b) reported that anchors of external tags did not implant firmly in *H. americanus* less than 30 mm CL.

### 7.1.3 Internal Tags

Internal microtags may be a more appropriate method for marking early benthic lobsters. Advantages of internal tags are that they are small and do not penetrate the cuticle, so are less likely to affect moulting, growth and survival, and retention rates be higher also. A



disadvantage of internal tagging systems is that they are often harder to detect, and tag insertion can be a complex and involved process.

A milestone in the development of internal tags was the production of coded wire tags by Jefferts *et al.* (1963). These tags, usually 1.03 mm long by 0.25 mm in diameter, consist of cold-worked Type 302 stainless steel. Consequently, this material holds a permanent magnetic moment, and is therefore easily detectable by external means, while being biologically non-reactive. Information is usually conferred by a binary code stamped on the wire, but binary magnetism and colour coating of the wire are possible alternatives (Jefferts *et al.* 1963).

Coded wire tags, remote tag detectors and semi-automatic injectors were further developed by Northwest Marine Technology (Shaw Island, Washington, USA), primarily for the rapid tagging and detection of large numbers ( $10^5$  to  $10^8$ ) of fish (*e.g.* Blankenship & Hanratty 1990; Kaill *et al.* 1990). Tag loss is usually less than 5% in fish from 0.25 g to 2 kg in size (*e.g.* Ingram 1993). This technology has been used successfully in small juvenile *H. gammarus* from 12 mm CL (Wickens & Beard 1984; Walker 1986; Beard & Wickens 1992; Bannister *et al.* 1994), in *H. americanus* from 12 mm CL (Krouse & Nutting 1990b), in 15 - 20 mm CL *Panulirus argus* (reported in Herrnkind & Butler 1994 and Herrnkind *et al.* 1994) and in 10 mm CL *P. cygnus* (Phillips *et al.* 1992).

Coded wire tags implanted in small animals have reasonable retention rates (usually above 80%) and few observable biological effects in lobsters (Ennis 1972; Wickens & Beard 1984; Krouse & Nutting 1990b; Beard & Wickins 1992; Phillips *et al.* 1992). Some initial mortality occurred in *P. argus*, 25% for first moult stage post-*puerulus* and less than 10% in second stage post-*puerulus*, in addition to slightly retarded growth (Herrnkind *et al.* 1994). Coded wire tagged *H. gammarus* have survived up to 8 years after release in the wild (Bannister *et al.* 1994). Coded wire tags are less effective in crabs with low tag retention and increased biological effects, probably because of the necessity to implant in leg segments, as opposed to the more suitable abdominal musculature of lobsters (van Mountfans *et al.* 1986; Bailey & Dufour 1987; Hurley *et al.* 1990).

A major disadvantage of coded wire tags is that they must be excised from the animal for the binary code to be read. This can limit their use to single capture-mark-release experiments where tag removal will affect the parameters being measured. In some cases, this problem was overcome by inserting the tag into appendages such as the chelate propodus of *H. americanus* (Krouse & Nutting 1990b) or the dactylus of the crab *Chionoecetes opilio* (Bailey & Dufour 1987), allowing non-lethal removal. Bailey and

Dufour (1987) also placed tags in particular according to the initial size class, allowing information transfer when recaptured by detecting the position of tag.

An alternative to coded micro wire tags for small lobster research may be visible implant tags. Visible implant tags consist of thin material etched with alphanumeric descriptors, and are implanted in transparent tissues of the animal such that the code is externally readable.

Visible implant tags were first used by Butler (1957) in the rainbow trout *Salmo gairdneri*. Butler's tag was made of vinyl, 3 mm wide by 20 mm long by 0.5 mm thick, and was implanted beneath the relatively clear belly skin of the trout. The concepts and technology of visible implant tags were developed further by Haw *et al.* (1990, in association with Northwest Marine Technology). After experimenting with a variety of materials, a miniature, commercially available tag was designed in a range of sizes: 0.5 -1.5 mm wide by 1.5 - 4.0 mm long and 0.05 to 0.08 mm thick. These tags consist of a mylar wafer with a photographically imprinted alphanumeric code, and are effective for tagging in the clear, post-orbital adipose tissue of many fishes (Haw *et al.* 1990; Kincaid & Calkins 1992).

Although untried, the Northwest Marine Technology visible implant tags are of a size suitable for use in juvenile lobsters. These tags could be placed beneath the clear intersternal membranes on the underside of the abdomen. If successful, visible implant tags would have the dual advantages of the benign biological properties of coded wire tags, and the easily accessible information properties of external tags.

A considerable problem with lobster tagging studies is the effect of capture and handling. For adult *J. edwardsii*, the effects of capture and handling alone can be as great as the effects of tagging (MacDiarmid *et al.* 1991). In the case of juvenile *P. cygnus*, legs are rapidly autotomised if not handled correctly (David Wright, pers. comm., CSIRO Division of Fisheries, Western Australia). Exposure to air can also affect the growth of *P. cygnus* and *P. argus* (Brown & Caputi 1985; Hunt *et al.* 1986). Therefore, tags that can be read *in situ* and remote from the lobster have a distinct advantage.

A hand held detector is available for coded wire tags (*e.g.* the Northwest Marine Technology Wand Detector). However, although this enables remote detection, little information can be transferred by this means.

Tags which enable remote information transfer are passive integrated transponder tags. These tags consist of a tightly coiled antenna bonded to an integrated circuit chip, and sealed in a glass tube. The smallest commercially available transponder tag measures 11 mm long by 2.2 mm diameter and are internally implanted. A remote hand held reader energises the tag with a 400 kHz magnetic field and the tag subsequently transmits its individual code back to the reading device (Prentice *et al.* 1990a, 1990b). These tags, such as the 'trovan' ID100 (TROVAN) and the D-IDI (Destron-Identification Devices), are widely used to identify agricultural, domestic and zoo animals, as well as experimental, rare and endangered animals in the wild (Rick Walduck, pers. comm., Central Animal Records, Australia).

Passive integrated transponders have been tested in a range of salmonids as small as 55 mm fork length (Prentice *et al.* 1990a). No detectable effects on growth and survival were found and tag retention was above 99.0%. On this basis, the use of these tags is considered technically feasible in *Jasus edwardsii*, but probably only from a size of 40–50 mm CL. It is postulated that these tags could be implanted under the rear of the carapace, to one side of the digestive tract. Passive integrated transponder tags have been recently miniaturised to approximately 2 mm long, and this size may be suitable for post-*puerulus* lobsters. However, the cost of these smaller tags is approximately \$100 each, which is prohibitively high for a large scale field program (C. Walters, pers. comm., University of British Colombia).

#### 7.1.4 Tagging Small Juvenile *Jasus edwardsii*

Coded wire tags and visible implant tags were selected as the most appropriate methods to examine growth, survival and movement patterns of juvenile *J. edwardsii*, from settlement onwards. To date, coded wire tags have only been used in a few lobster species: *P. cygnus*, *P. argus*, *H. americanus* and *H. gammarus* (as referred to above), and tagging effects and tag retention rates have only been reported for *H. gammarus* and *H. americanus* (Wickins & Beard 1984; Krouse & Nutting 1990b). No record was found for the use of visible implant tags in lobsters, although these tags are currently being tested in the freshwater crayfish *Cherax quadricarinatus* (Clive Jones, pers. comm., Freshwater Fisheries and Aquaculture Centre, Department of Primary Industries, Queensland). Because these tagging methods are relatively new and untried, laboratory tests were used to assess their technical and biological feasibility for small *J. edwardsii*.

## 7.2 Methods

### 7.2.1 Handling and Culture

Puerulus, post-*puerulus* and juvenile *J. edwardsii* were collected, by Division of Marine Living Resources (DMLR) personnel, from settlement collectors located along the east coast of Tasmania, with most lobsters collected from Bicheno and Recherche Bay (see Fig. 1.3). These lobsters were held at the DMLR Laboratories at Taroona until there were suitable numbers for tagging.

Prior to tagging, the lobsters were cooled to approximately 9–10° C by placing the holding buckets on a bed of ice. This sedated the lobsters, making them easier to handle. Each lobster was staged according to Hayakawa *et al.* (1990), the carapace length measured to the nearest 0.1 millimetre and the general condition of the body and appendages noted before tag insertion. After tagging, the holding buckets were placed in an air conditioned aquarium room and, when the temperature equilibrated (approximately 14° C), the lobsters were transferred to aquaria according to the experimental design.

Up to 20 lobsters were held in each of the experimental aquaria, measuring 0.6 m wide by 1.1 m long by 0.7 m high and containing 310 L. The water in each aquarium was cleaned and aerated by a recirculating filter and an air-lift undergravel filter. Half the water was replaced approximately every 2 months and the temperature was maintained between 13 to 15° C. The lobsters were fed mussels, pieces of squid, fish and abalone every second or third day, and any uneaten food was removed one day after feeding. Live amphipods and mysids were also supplied on a weekly basis. Each aquarium was examined every one to two days for dead lobsters and moulted exuviae. The exuviae were removed and kept for further examination.

### 7.2.2 Coded Wire Tagging

Individually coded microwire tags of size 1.03 by 0.25 mm diameter were used. These tags were supplied by Northwest Marine Technology on a continuous spool, and were cut from the spool using an automatic tag injecting machine (Northwest Marine Technology). This machine was previously used by the CSIRO to inject batch-coded microwire tags into *P. cygnus* in Western Australia (see Phillips *et al.* 1992). Preliminary trials (this study) found the automatic injector was also effective at injecting batch tags into *J. edwardsii*. However, the use of individually coded tags precludes the use of the machine for direct tag injection because the code on the tag must be checked before injection. The binary code of each tag was determined using a dissecting microscope and then placed into a labelled glass tube ready for injection. The tags were injected, using a hand-held 24 gauge syringe injector, into the right lateral abdominal musculature, between the rear of the thorax and the

first abdominal segment.

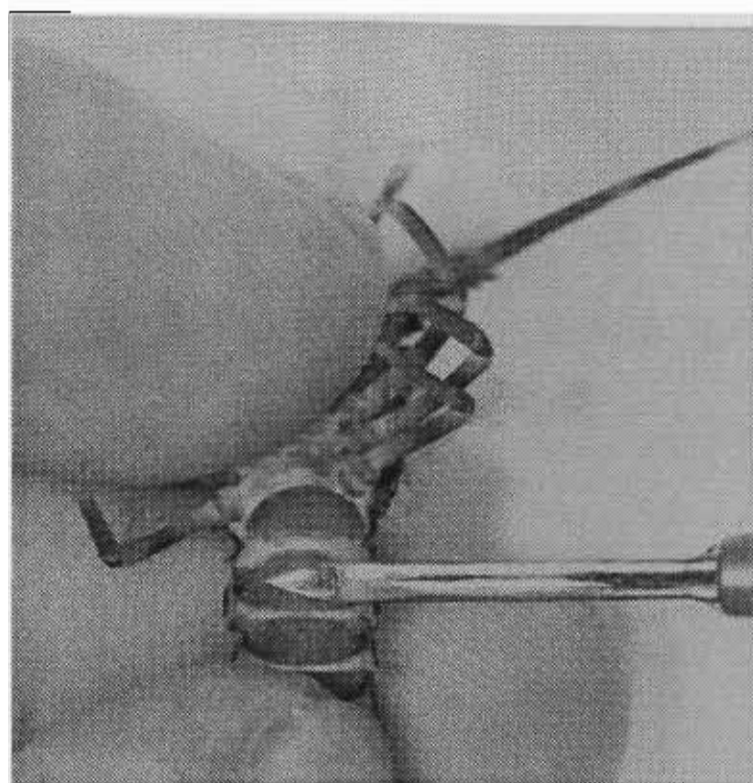
Initially, the tag was magnetised after injection by passing the lobster between the poles of a horseshoe magnet. This followed the methods used for *H. americanus* (Krouse & Nutting 1990b) and *P. cygnus* (David Wright, pers. comm.). However, subsequent post mortems found that the magnet can move the tag inside the lobster (described in the results, Section 7.3.1). After this discovery, tags were magnetised prior to injection. This had the added benefit of reducing the handling time of the lobster. Detection of the tag in the lobster was checked by passing the lobster over a magnetic sensing unit, which emits an audible signal if a tag is detected.

### 7.2.3 Visible Implant Tagging

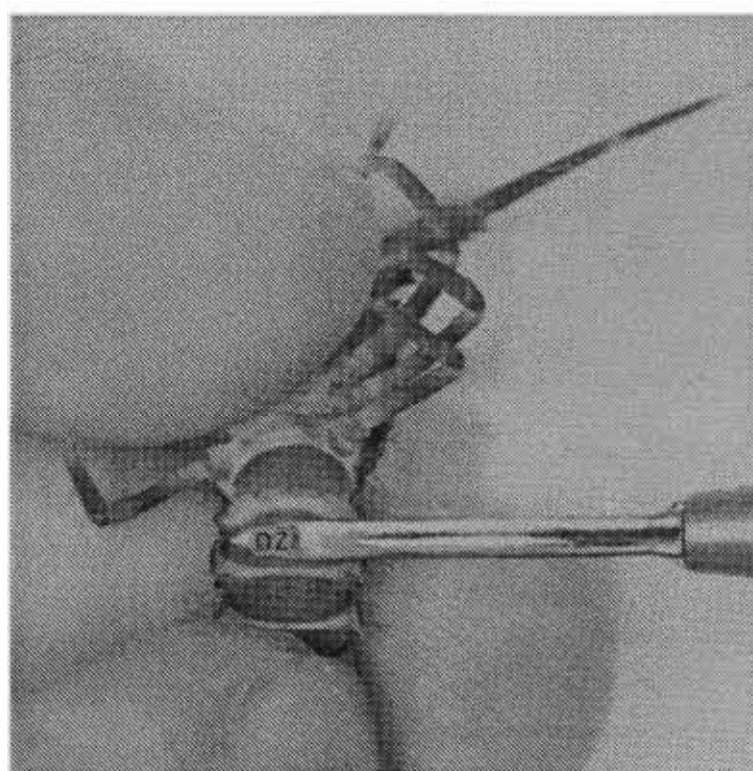
Standard Northwest Marine Technology visible implant tags were used. These tags measure 2.5 x 1.0 x 0.1 mm, and have a three digit alphanumeric code. A handheld injector was used to insert the tag under the clear intersternal membrane between the first and second abdominal segments. The needle of the injector is flat, with external dimensions of 1.75 mm wide by 0.70 mm thick. The tag was placed medially, above the dorsal musculature and ventral nerve cord, and so the end of the tag was clear of the insertion wound. The tagging sequence is shown in Figure 7.1.

### 7.2.4 Tag Assessment Experiments

Seven experiments were used to refine the coded wire and visible implant tagging techniques, to assess any effects on survival and growth and to determine the tag retention rate. Abdominal spine clips and an underwater setting epoxy (Vepox CC48, Vessey Chemicals, Victoria) were also assessed as temporary marking methods. Unmarked controls were initially used to assess the effects of microtagging. However, because batches of each treatment were present in each aquarium, it was difficult to differentiate between lobsters which had shed tags and the control lobsters. Abdominal spine clips were used in later experiments to mark control animals. Details of the experiments are given in Table 7.1. Experiment F included three visible implant tagged lobsters from Experiment E to examine long-term tag retention, but these lobsters were not used to calculate survival rates for Experiment F. Further details of technique development are given with the results. Additional information on the effects of these tags was obtained from the field release program, and is presented with the results of this section.



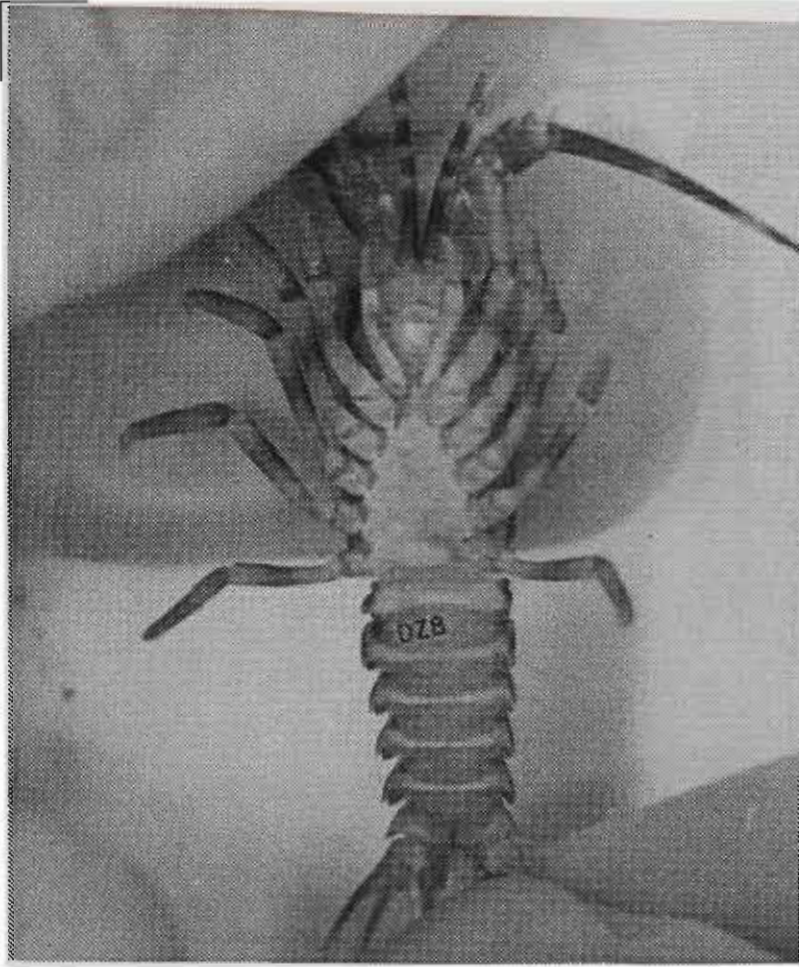
a.



b.

Fig. 7.1. Visible implant tagging of a post-juvenile *Jasus edwardsii*: (a) insertion of needle; (b) injection of the tag. (continued next page)





c.



d.

Fig. 7.1 (continued). Visible implant tagging of a post-juvenile *Jasus edwardsii*: (c) the position of the tag after insertion; and (d) the tag and entry wound two weeks after tagging.

Table 7.1. Details of laboratory experiments to test various tagging methods in *Jasus edwardsii*. Abbreviations: ASC = abdominal spine clips; CWT = coded wire tag; Juv = juvenile; PP = first moult post puerulus; PU = first moult post puerulus; PU = visible implant tag.

Experiment	Date started	Duration (days)	Treatments	No. per treatment	Stages at tagging	Size range (mm CL)	Aims and notes
<b>Coded Wire Tagging</b>							
A	11 Jun 1992	38	Vepox only Coded wire tag Spine clips CWT + ASC	15 15 15 15	PU, PP, Juv	11.2 - 15.6	<ul style="list-style-type: none"> <li>• Trial of coded wire tags</li> <li>• Trial of Vepox and abdominal clips</li> <li>• All lobsters marked with Vepox</li> </ul>
B	30 Jun 1992	26	Unmarked control Coded wire tag Spine clips Vepox CWT + ASC CWT + Vepox	9 9 9 9 9 9	PP, Juv	9.9 - 13.6	<ul style="list-style-type: none"> <li>• Retrieval of Experiment A</li> </ul>
C	31 Aug 1992	88	Control Coded wire tag Spine clips CWT + ASC	12 12 12 12	PU, PP	9.9 - 12.7	<ul style="list-style-type: none"> <li>• Test for effects on survival, growth</li> <li>• Determine mark retention rate</li> </ul>
<b>Visible Implant Tagging</b>							
D	17 Jul 1992	18	Visible implant	20	PU, PP	10.3 - 12.7	<ul style="list-style-type: none"> <li>• Trial of visible implant tags</li> </ul>
E	31 Aug 1992	88	Spine clips Visible implant	10 10	PP	10.3 - 12.6	<ul style="list-style-type: none"> <li>• Retrieval of Experiment D</li> <li>• Test for effects on survival, growth</li> </ul>
<b>Both methods</b>							
F	18 Feb 1993	60	Spine clips Coded wire tags Visible implant	19 19 16+3	PP, Juv	10.4 - 25.6	<ul style="list-style-type: none"> <li>• Repetition of implant tests</li> <li>• Test with larger lobsters</li> <li>• Long term VIT retention</li> </ul>
G	15 Sep 1993	149	Spine clips Coded wire tags Visible implant	15 15 15	PP, Juv	11.3 - 15.5	<ul style="list-style-type: none"> <li>• Test for long term tag retention</li> </ul>



## 7.3 Results

### 7.3.1 Coded Wire Tagging

Few problems were encountered using coded wire tags. The tag was easy to implant and bleeding was minimal. Only a small scar resulted from the puncture wound, which disappeared after the first moult. When returned to the holding bucket after tagging, the lobsters remained motionless for a few minutes, but their behaviour rapidly returned to normal.

The first two trials with the individually coded wire tag (Experiments A & B) were unsuccessful. Only 40% of the lobsters survived to 25 days, with most deaths associated with moulting. The mortality rate was the same for all treatments, including unmarked controls (Experiment B), indicating the mortality was not a tagging effect. Possible causes include chemical effects from the Vepox putty (individuals from all treatments were in each aquarium) and an unsuitable substratum for moulting. Vepox was abandoned as a temporary marking method, regardless of any toxic effects, as it was too time consuming to apply; the air exposure time could be up to 5 minutes. In case there was a lack of suitable substrata for moulting, rough textured rocks were added to each aquarium (in addition to the brick shelters already present), and a layer of coarsely crushed stone was placed over the base. The survival rate was high for all subsequent tests using coded wire tags (Experiments C, F and G).

Information on effects of coded wire tags was also obtained from the field tagging program when removing tags from lobsters which died before release or those which were recaptured. A high incidence of tag displacement occurred, with tags being found on the other side of the body from the insertion point, or in segments anterior or posterior to the tagging position (Table 7.2). Most of the tag displacement observations were from lobsters tagged using the procedure of magnetising tags after insertion. Sample sizes after changing the tagging procedure were not high enough to assess whether the frequency of tag displacement was reduced. Tag displacement was not consistently higher in lobsters which died before release compared with those that survived to recapture (Table 7.2). This suggests that the tag displacement was generally non lethal, although the ventral nerve cord and digestive tract were severed on 2 occasions and tags were found against the ventral nerve cord in 11 other lobsters which died before release. A tag was found in the head region of both a non-released and recaptured lobster.

### 7.3.2 Visible Implant Tagging

A high mortality rate was associated with the first trial using visible implant tags (Experiment D). Of twenty lobsters, only half survived the first 5 days and only two survived 18 days. All dead lobsters had an infection of the haemocoel by facultative protozoan parasites. Other problems noted were tags protruding into the wound, preventing it from healing properly, and reopening of the wound during moulting from puerulus to post-*puerulus*. Half of the lobsters in this trial had the tag injected under the membrane between the thorax and abdomen (as opposed to between the first and second abdominal segments). Tags inserted in this location were more mobile, moving up into the thorax in one case, and appeared to interfere with flexing of the abdomen. Other potential problems were the injection of air with the tag, and bleeding while the needle was inserted, although bleeding stopped within a few seconds of needle withdrawal.

Improvements to the techniques from the first trial included: not tagging pueruli (the puerulus stage is relatively short, giving less chance for the wound to heal before moulting); more attention to hygiene, particularly with disinfection of tagging equipment and holding buckets, and ensuring all uneaten food was collected from the aquaria the next day; and delaying feeding to a week after tagging to allow the wound to seal before introducing potential parasites with the food.

Survival rates were higher in subsequent trials (Experiments E, F and G). Lobsters moulted successfully with no obvious interference from the tag. No entry wound scarring was present on the new integument, but some slight tissue damage was observed on many occasions at the corners of the tag. Examinations of dead lobsters found no obvious damage to the underlying abdominal muscles or the ventral nerve cord.

Table 7.2. Frequency of coded wire tag displacement after insertion in *Jasus edwardsii* tagged for the field program (percentages given in brackets).

Type of displacement	Dead Before Release			Recaptured n = 14
	Puerulus n = 27	Post- <i>puerulus</i> n = 66	Total n = 19	
Anterior - posterior (different segment)	4 (15)	15 (23)	19 (20)	14 (48)
Lateral (toward left side)	16 (59)	27 (41)	43 (46)	9 (31)
Tag near integument (either side)	3 (11)	2 (3)	5 (5)	0
Tag rotated (> 45°)	13 (48)	27 (41)	40 (43)	13 (45)

### 7.3.3 Survival

The survival rate of lobsters tagged with either coded wire or visible implant tags was above 80% for all experiments (excluding the initial trials). The survival rate of lobsters marked with abdominal spine clips was also generally above 80%, and usually higher than lobsters tagged with implant tags (Table 7.3). Lobsters tagged with both coded wire tags and with abdominal spine clips (Experiment C) had the lowest survival rate. The survival rate from pooled experiments was above 90% for all three marking methods (Fig. 7.2). In all cases, the majority of the deaths occurred within 20 days of tagging, and usually occurred at moulting.

### 7.3.4 Growth

The growth of coded wire tagged lobsters was examined in Experiment C. From monitoring the frequency of moulting, three discrete moulting periods were observed between days 2 to 15, 43 to 51 and 71 to 86 after tagging. Lobsters subject to all tagging treatments moulted throughout each of these periods, which suggests that coded wire tags do not influence moulting periodicity. No difference was found in the mean carapace length of coded wire tagged lobsters and other treatments at the start of the experiment and after 75 days ( $t = 0.431$ ,  $df = 47$ ,  $p = 0.669$  and  $t = 1.719$ ,  $df = 35$ ,  $p = 0.094$  respectively). Mean sizes are given in Table 7.4.

From the examination of growth of visible implant tagged lobsters in Experiment E, moulting occurred at similar times to lobsters in Experiment C, occurring between days 43 to 54 and 79 to 85. No puerulus were used in this experiment, accounting for the lack of any earlier moulting. The moulting periods for visible implant tagged lobsters and abdominal spine clipped lobsters were synchronous to within three days. No significant difference was found between the mean sizes at tagging, after 63 days and after 83 days (day 0:  $t = 0.436$ ,  $df = 18$ ,  $p = 0.668$ ; day 63:  $t = 0.319$ ,  $df = 15$ ,  $p = 0.754$ ; day 88:  $t = 0.409$ ,  $df = 15$ ,  $p = 0.689$ ; Table 7.4).

### 7.4.5 Tag Retention

In Experiment C, starting with 25 coded wire tagged lobsters, 2 tags were either shed or undetected from 18 surviving lobsters after 75 days. These lobsters survived until release at 128 days after tagging, and no further tag loss occurred. No tag loss was observed during the 60 days of Experiment F, and no tag loss was observed during the 149 days of Experiment G.

In Experiment E, all surviving lobsters with visible implant tags retained the tag through the first moult. Of 8 surviving lobsters at the second moult, 3 shed their tags with the exuvia

(63% retention to 88 days). In Experiment F, of 19 visible implant tagged lobsters, three lobsters below 14 mm CL shed their tags after 5, 29 and 41 days. This experiment included three of the largest tagged lobsters retained from Experiment E. These three lobsters were tagged as post-*puerulus* and had not shed their tags at release after 231 days in captivity. No tag loss occurred in Experiment G (149 days), but scarring was observed at the position of tag corners of many moults.

Abdominal spine clips were barely discernable after two moults from the post-*puerulus* stage (approximately 80 days).

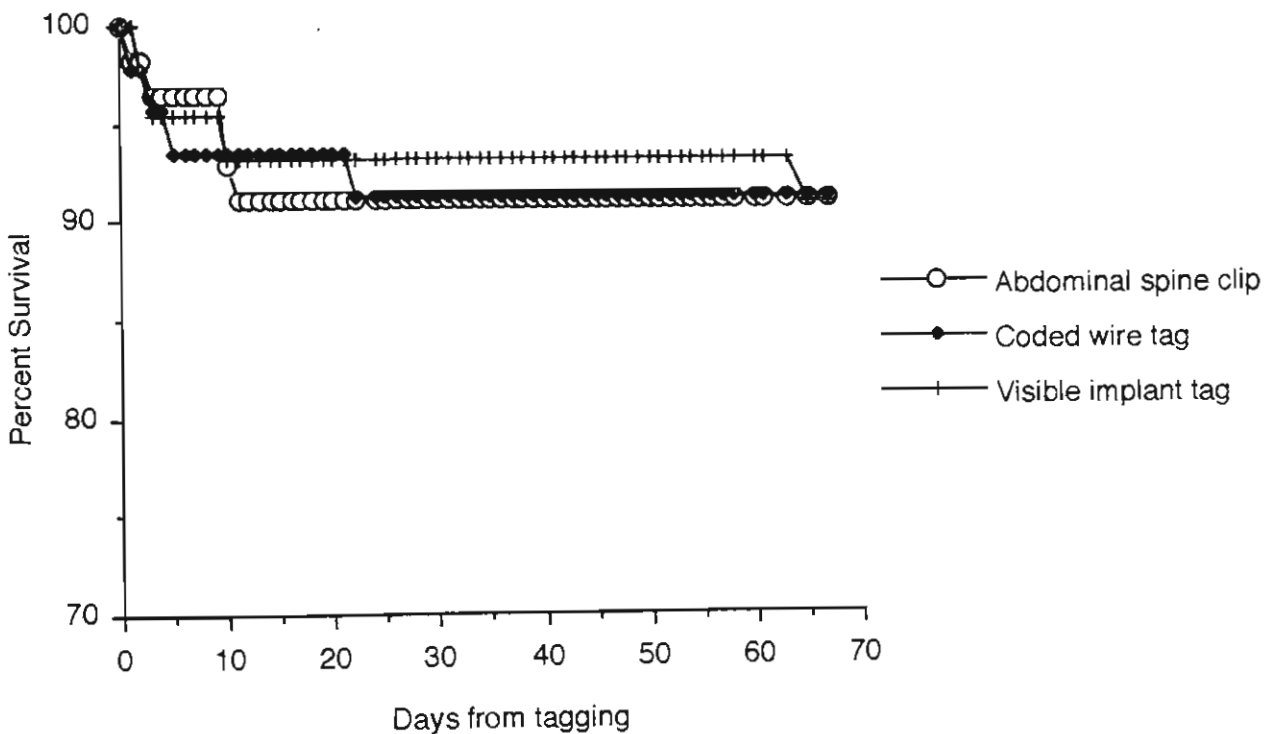


Fig. 7.2. Survival rates of three marking methods on small juvenile *Jasus edwardsii* (pooled results). Pooled sample sizes were 56, 46 and 44 for abdominal spine clipped, coded wire tagged and visible implant tagged lobster respectively.

Table 7.3. Number and percent survival for lobsters of different tagging treatments after 5 and 20 days, and at the end of the experiment (percentages given in brackets).

Treatment	Day 0	Day 5	Day 20	Last day
Experiment C (88 days)				
Unmarked control	12	11 (92)	10 (83)	11 (83)
Abdominal spine clip	12	12 (100)	11 (92)	11 (92)
Coded wire tag	12	12 (100)	10 (83)	10 (83)
Coded wire and spine clip	13	13 (100)	8 (62)	8 (62)
Experiment E (88 days)				
Abdominal spine clip	10	10 (100)	9 (90)	9 (90)
Visible implant tag	10	10 (100)	9 (90)	8 (80)
Experiment F (60 days)				
Abdominal spine clip	19	17 (89)	15 (79)	15 (79)
Coded wire tag	19	17 (89)	17 (89)	16 (84)
Visible implant tag	16	15 (94)	15 (94)	15 (94)
Experiment G (149 days)				
Abdominal spine clip	20	20 (100)	20 (100)	20 (100)
Coded wire tag	15	15 (100)	15 (100)	14 (93)
Visible implant tag	15	14 (93)	14 (93)	14 (93)

Table 7.4. Mean carapace length ( $\pm$  SE) of *Jasus edwardsii* during laboratory tagging experiments.

Treatment	Day 0	Day 63	Day 75	Day 88
Experiment C				
Coded wire tag	11.15 (0.16)		14.33 (0.39)	
Other treatments	11.24 (0.12)		15.32 (0.38)	
Experiment E				
Visible implant tag	11.60 (0.21)	14.38 (0.18)		16.34 (0.36)
Abdominal spine clip	11.71 (0.14)	14.48 (0.25)		16.59 (0.47)

## 7.4 Discussion

Both coded wire tags and visible implant tags can be implanted in small *J. edwardsii* with no detectable long-term biological effects. However, the visible implant tag was not considered suitable for tagging the puerulus stage as this stage is too short for effective healing of the insertion wound before moulting.

Although coded wire tags are restricted to single capture-mark-recapture experiments, these tags were less likely to be shed than visible implant tags, and therefore more suitable for long-term experiments. The incidence of visible implant tag shedding at the second moult in Experiment E indicates that if the tag is not properly implanted it can be incorporated in the new integument and shed at ecdysis. This was also found for coded wire tags implanted in the basal periopod segments of the crab *Callinectes sapidus*, but if the tag was retained through the first few moults then it was retained permanently (van Montfrans *et al.* 1986). This may not be the case for visible implant tags in *J. edwardsii* as the tags are directly under the integument and therefore more easily shed with ecdysis. The tissue damage at the corners of the tags in some lobsters may be because of abrasion with flexing of the abdomen. Tag edges are known to erode overlaying support tissue in 30 g salmonid fish (Kincaid & Calkins 1992). This problem may be improved by increasing the radius of the corners so they are less abrasive and, for lobsters, inducing a prebend in the tag to follow the convexity of the abdomen. However, such improvements may be impracticable.

The loss rate of visible implant tags was not great enough to preclude the use of visible implant tags in field experiments. Where the numbers of lobsters are restricted, or multiple individual capture information is required, visible implant tags provide a valuable alternative to coded wire tags.

# Growth, Survival and Movement

## 8.1 Introduction

The population dynamics of small juvenile palinurid lobsters (< 40 mm CL) are poorly understood, especially compared with that of older stages already recruited to the fishery. This is mostly because of difficulties in sampling, as small lobsters do not readily enter traps and are usually cryptic and sparsely distributed (Herrnkind *et al.* 1994). Considerable advances have been made with the 'discovery' of nursery habitats, particularly for *Panulirus argus* (Marx & Herrnkind 1985a), *P. cygnus* (Jernakoff 1990) and *P. japonicus* (Yoshimura & Yamakawa 1988). High densities of small juvenile lobsters provide adequate data for growth to be determined from the modal progression of size frequency distributions (*e.g.* Norman *et al.* 1994; Jernakoff *et al.* 1994). However, high densities of post-*puerulus* *Jasus edwardsii* are not generally observed (McKoy & Esterman 1981; Annala & Bycroft 1985; Breen & Booth 1989), but two exceptions are Castlepoint in New Zealand (Booth 1979) and Blackfellows Caves in South Australia (Lewis 1977); growth from modal progressions was determined for the Blackfellows Caves population.

Investigations of various parameters of lobster population dynamics, particularly the moult frequency and size increment components of growth, survival, density and movement have also been limited by the lack of an effective means of marking individual animals (reviewed in Chapter 7). The recent availability of internal microtags, and access to pueruli and post-*pueruli* from settlement collectors, means these ecological aspects can now be investigated in more detail (Herrnkind *et al.* 1994).

Coded wire tags have been used in two studies, to determine the growth of post-*puerulus* *P. cygnus* (Phillips *et al.* 1992) and the survival of post-*puerulus* *P. argus* (Herrnkind, Butler & Hunt, unpublished data cited in Herrnkind *et al.* 1994). Laboratory trials (Chapter 7) found both coded wire and visible implant tags to be suitable for use in *Jasus edwardsii*, with minimal biological effect and tag loss. These methods were used to

examine the growth, survival and movement of young *J. edwardsii* in the wild.

## 8.2 Methods

A total of 832 coded wire tagged and 390 visible implant tagged lobsters were released at Crayfish Point (Fig. 1.3), between 10 December 1991 and 30 October 1993. The lobsters were supplied from puerulus collectors by the Tasmanian Division of Marine Living Resources, and the tagging techniques were the same as those used for the laboratory study (Section 7.2). The tagging program was centred around the winter and summer larval settlement periods, particularly the 1991/92 summer and 1992 winter. Because there was a significant decline in larval settlement over the duration of this study (see Chapter 2), only small numbers of puerulus, post-*puerulus* and juvenile lobsters were available for tagging after January 1993.

The tagged lobsters were usually held in the laboratory for 3 to 4 days before release and some deaths occurred during this holding period. The numbers and dates of release for coded wire tagged lobsters are given in Table 8.1, and in Table 8.2 for visible implant tagged lobsters. The size range of released lobsters was between 9.5 mm CL (*puerulus*) and 31.4 mm CL (*juvenile*), but most (94%) were below 15 mm CL.

The first batches of lobsters (December 1991) were released directly onto the reef at Crayfish Point, placing them by hand into holes and crevices. For approximately 5 min after release, the lobsters remained relatively still and appeared to be disorientated. After this initial period, many lobsters left the holes they were placed in, and were immediately eaten by predators. Predation was by wrasse (*Pseudolabrus fucicola*, *P. tetricus* and *Pictilabrus laticlavius*), scorpaenids (*Scorpaena ergastulorum*), dragonets (*Bovichthys variegatus*) and clinids (*Heteroclinus* spp). Some lobsters were also eaten by dragonets while in the holes, indicating that some holes selected for release were not suitable shelters.

Because of the problems of finding suitable holes to release large numbers of tagged lobsters, artificial shelters were constructed. These shelters consisted of two house bricks cemented together. Each brick (approximately 75 x 230 x 135 mm) had five oval holes, and the brick-pairs were aligned such that the backs of the holes were closed off, giving 10 shelters per double-brick. The 'release bricks' were arranged on the reef at Crayfish Point in a 4 x 4 array, 1 m apart. A total of 160 holes were available for the release of lobsters. Surrounding the 'release grid' was a further 16 single bricks (with the backs cemented over) arranged in a 5 m radius circle, and 32 bricks in a 7.5 m radius circle (Fig. 8.1). Lobsters were released onto the release grid from January 1993.



The lobsters were transported to the release site in individual tubes, which were placed in a mesh bag in a 25 L bucket. The tubes were 85 mm long by 35 mm in diameter, with 5 mm holes at each end. The lobsters were kept in water at all times during packing and transport. To minimise the jolting and disorientation of the lobsters, the bag of tubes was not removed from the bucket until the divers were at the release grid. Each lobster was then removed from its tube and placed in the bricks. Once in the holes, the lobsters tended to stay there, and quickly assume normal behaviour. However, if a lobster was accidentally placed in the same hole as another, it would quickly depart and either tail-flip away from the brick, or move into an adjacent hole. The release area was searched for lobsters prior to the release of newly tagged lobsters.

Searches were made for tagged lobsters on 61 occasions between 11 December 1991 and 30 August 1994. The release bricks, surrounding bricks and known holes and crevices near the release area were censused on 46 occasions between 20 January 1992 and 27 January 1993. Searches of other parts of the reef at Crayfish Point were made during this intensive period, and on seven occasions between 17 September 1993 and 30 August 1994. At the start of the tagging programme, only coded wire tagged lobsters were released and, to improve the chances of obtaining long-term data, only approximately 10% of the lobsters encountered after release were recaptured (before April 1992). Recaptured visible implant tagged lobsters were measured at the point of capture, and replaced in the holes in which they were found; the handling time being approximately 3 to 5 min, including capture.

To recover larger tagged lobsters, four modified 'beehive' traps (with closed escape gaps) and six CSIRO western rock lobster research traps (a 'parlour and bedroom' type trap similar to that of De Bruin 1960) were used during intensive trapping sessions on 15 to 19 June 1993 and 15 to 19 March 1994.

## 8.3 Results

### 8.3.1 Census Results

No lobsters released directly onto the reef at Crayfish Point, *i.e.* not onto the bricks, were recaptured. The highest release and recapture rates were between 20 January 1992 and 27 January 1993, with coded wire tagged lobsters released predominantly in the first half of this period, and visual implant tags in the latter half (Table 8.3). Despite high initial abundances of lobsters, the abundance within the release brick area consistently fell below 18 within 2 to 7 days after each batch release.

Table 8.1 Numbers of *Jasus edwardsii* tagged and released using coded wire tags; PU = puerulus, PP = first moult post-puerulus and Juv = juvenile.

Tag Date	No Tagged	Release Date	PU	PP	Juv	No Released
10-12-91	24	11-12-91	3	16	4	23
11-12-91	49	12-12-91	5	38	5	48
12-12-91	50	13-12-91	5	29	6	40
13-12-91	56	17-12-91	8	30	7	45
18-12-91	100	20-12-91	75	22	1	98
19-12-91	100	26-12-91	53	14	4	71
14-1-92	89	20-1-92	1	54	4	59
28/29-1-91	112	30-1-92		77	29	106
13-2-92	70	20-2-92		49		49
		25-2-92		21		21
19-6-92	38	26-6-92	27	11		38
6-7-92	80	7-7-92	47	29	4	80
10-7-92	11	13-7-92	4	6	1	11
3-8-92	63	6-8-92	19	44		63
27-8-92	43	28-8-92		42	1	43
30-9-92	7	6-10-92	2	5		7
27-9-93	30	28-9-93	30			30
Total	965					832

Table 8.2 Numbers of *Jasus edwardsii* tagged and released using visible implant tags; PP = first moult post-puerulus and Juv = juvenile.

Tag Date	No Tagged	Release Date	PP	Juv	No Released
16-9-92	64	22-9-92	49	15	64
30-9-92	23	6-10-92	18	5	23
10-10-92	50	18-10-92	46	4	50
19-10-92	53	23-10-92	36	11	47
24-10-92	1	30-10-92		1	1
2-11-92	50	10-11-92	35	15	50
11-11-92	55	16-11-92	28	15	43
13-1-93	19	14-1-93		19	19
*13-1-93	13	14-1-93		13	13
27-9-93	30	28-9-93		30	30
6-10-93	50	9-10-93	17	33	50
Total	408				390

\* Lobsters with an additional coded wire tag

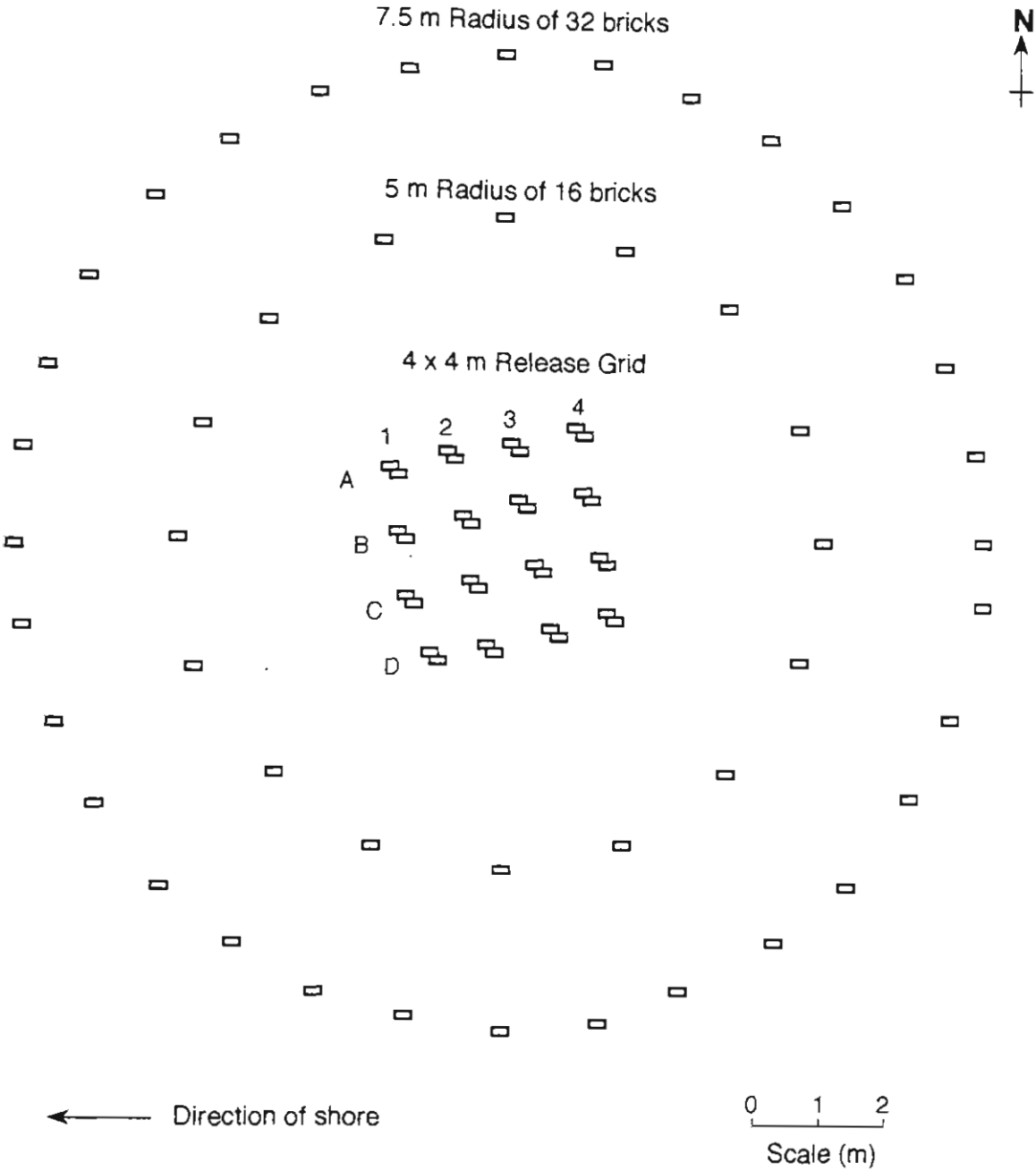


Fig. 8.1. Arrangement of brick artificial shelters at Crayfish Point, Hobart.

Twenty five coded wire tagged lobsters were recaptured, with the period of liberty ranging from 11 to 77 days, and the largest recaptured lobster was 21.8 mm CL (Table 8.4).

Twenty six visible implant tagged lobsters were recaptured, with the longest time of liberty being 76 days. The longest time at liberty for a non-moulting lobster was 38 days (Table 8.5). Of the 26 visible implant tagged recaptures, the number of lobsters recaptured once, twice, three times and four times was 15 (58%), 7 (27%), 2 (8%) and 2 (8%) respectively. The visible implant tags were easy to read underwater, particularly as the optics of diving masks magnify objects by approximately a third.

No microtagged lobsters were captured from searches other than those near the release area, or from the trapping sessions.

### 8.3.2 Growth

Individual growth was examined and compared using a standardised index, where the size increment for the period at liberty was linearly adjusted for a period of 30 days. This index is biased by variations in the time between the recapture date and the last moult.

The growth rates for coded wire tagged lobsters were variable, ranging from 0.3 to 3.8 mm CL per 30 days (Table 8.4). This variability mainly because of seasonal differences. Excluding lobsters which had not grown during the time at liberty, growth rates were significantly higher in the warmer months (mean 2.5 mm CL 30 d<sup>-1</sup>) than in the cooler months of June, July and August (mean = 1.1 mm CL 30 d<sup>-1</sup>; Mann-Whitney U test,  $Z = 2.46$ ,  $p = 0.014$ ; Fig. 8.3). This corresponded with changes in water temperature, from 17° C in February 1992 to 10° C in June 1992.

Only 11 of the visible implant tagged recaptures had changed size, with two slightly decreasing in size at the first moult (Table 8.5). The growth of visible implant tagged lobsters, which were predominantly at liberty from October 1992 to January 1993, was generally within the range of the growth rates of coded wire tagged lobsters for the warmer months (mean = 2.2; Table 8.5; Fig. 8.3).

Individual growth rates obtained from laboratory reared lobsters were mostly between 1 to 2 mm CL per month (mean for 63 days = 1.3). This range was intermediate between the winter and summer growth rates of coded wire tagged lobsters released in the wild (Table 8.6; Fig. 8.4). The culture temperature of 13–15° C, was intermediate to the range of temperatures at Crayfish Point.

Table 8.3. Numbers of juvenile *Jasus edwardsii* released, censused and recaptured in the artificial 'release grid', at Crayfish Point.

Date	Day	Census Total	Coded Wire Tagged Released	Recaptured	Visible Implant Tagged Released	Recaptured
20-1-92	0	0	59			
21-1-92	1	17				
29-1-92	9	10				
30-1-92	10	7	106			
11-2-92	22	17				
12-2-92	23	14				
20-2-92	31	11	49			
26-2-92	37	17	21	2		
5-3-92	45	11		2		
6-3-92	46	11				
9-3-92	49	9		1		
5-4-92	76	6		6		
3-5-92	104	1				
29-5-92	130	0				
26-6-92	158	0	38			
7-7-92	169	3	80	3		
9-7-92	171	12				
13-7-92	175	12	11			
15-7-92	177	8				
4-8-92	197	0				
6-8-92	199	0	63			
25-8-92	218	3		3		
28-8-92	221	1	43	1		
4-9-92	228	4				
10-9-92	234	6				
11-9-92	235	0				
22-9-92	246	4		2	64	2
24-9-92	248	4				
29-9-92	253	4				
2-10-92	256	6		3		3
6-10-92	260	5	7		23	3
18-10-92	272	4			50	4
23-10-92	277	12		1	47	6
30-10-92	284	11		1	1	10
6-11-92	291	11				6
10-11-92	295	3			50	1
16-11-92	301	2			43	1
6-12-92	321	3				3
30-12-92	345	6				2
7-1-93	353	4				3
13-1-93	359	0				
14-1-93	360	0			32	
27-1-93	373	2				1
17-9-93	606	0				
28-9-93	617	0	30		30	
10-9-93	599	0				
9-10-93	628	0			50	

Table 8.4. Individual growth increments of coded wire tagged *Jasus edwardsii* (all recaptured lobsters). Abbreviations: Days = days at liberty;  $CL_i$  = carapace length (mm) at tagging;  $CL_{ii}$  = carapace length (mm) at recapture;  $\Delta CL$  = size increment; PU = puerulus; PP = first moult post-*puerulus*; and J = juvenile.

Tag	Release	Capture	Days	$CL_i$	$CL_{ii}$	$\Delta CL$	$\Delta CL \cdot 30 d^{-1}$	Stage
818	30-1-92	25-2-92	26	12.0	14.1	2.1	2.4	PP-J
835	30-1-92	25-2-92	26	11.7	12.2	0.5	0.6	PP-J
1025	20-2-92	4-3-92	13	13.8	13.8	0	0	PP
1071	20-2-92	4-3-92	13	13.2	14.3	1.1	2.5	PP-J
954	30-1-92	9-3-92	39	12.3	16.9	4.6	3.5	PP-J
746	20-1-92	5-4-92	76	12.1	19.9	7.8	3.1	PP-J
785	20-1-92	5-4-92	76	12.1	21.8	9.7	3.8	PP-J
807	20-1-92	5-4-92	76	12.0	19.4	7.4	2.9	PP-J
825	30-1-92	5-4-92	66	13.3	20.1	6.8	3.1	PP-J
942	30-1-92	5-4-92	66	12.2	17.2	5.0	2.3	PP-J
1113	22-2-92	5-4-92	45	12.2	17.8	5.6	3.7	PP-J
1265	26-6-92	7-7-92	11	11.55	11.55	0	0	PU
1279	26-6-92	7-7-92	11	10.75	10.75	0	0	PU
1290	26-6-92	7-7-92	11	11.35	11.35	0	0	PU
1472	6-8-92	25-8-92	19	12.75	13.95	1.2	0.3	PP-J
1511	6-8-92	25-8-92	19	11.50	11.50	0	0	PP
1543	6-8-92	25-8-92	19	12.15	13.05	0.9	1.9	PP-J
1504	6-8-92	28-8-92	22	12.45	12.45	0	0	PP
1358	7-7-92	22-9-92	77	11.80	13.80	2.0	1.4	PP-J
1474	6-8-92	22-9-92	57	11.75	13.25	1.5	0.8	PP-J
1503	6-8-92	2-10-92	57	11.95	14.15	2.2	0.8	PP-J
1578	28-8-92	2-10-92	35	11.85	13.05	1.2	1.2	PP-J
1586	28-8-92	2-10-92	35	12.35	14.05	1.7	1.0	PP-J
1605	28-8-92	23-10-92	56	12.65	14.75	2.1	1.5	PP-J
1706	6-10-92	30-10-92	24	11.05	11.85	0.8	1.0	PU-PP

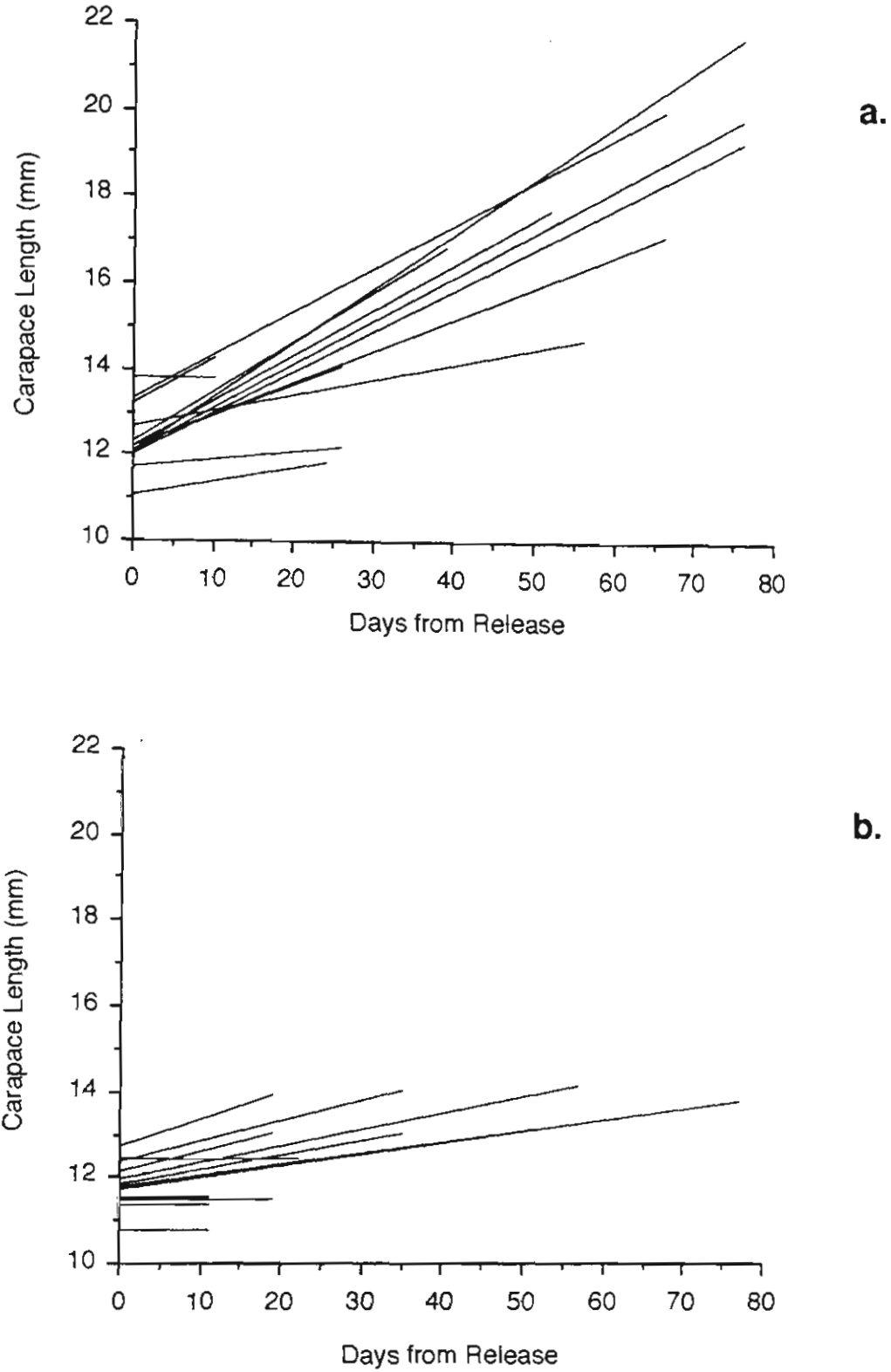


Fig. 8.2. Growth of coded wire tagged *Jasus edwardsii*: (a) at liberty during spring summer and autumn; and (b) at liberty during winter (June, July and August).

Table 8.5. Individual growth increments of visible implant tagged *Jasus edwardsii*. Abbreviations: Days = days at liberty;  $CL_i$  = carapace length (mm) at tagging;  $CL_{ii}$  = carapace length (mm) at recapture;  $\Delta CL$  = size increment from release; PP = first moult post-plerulus; and J = juvenile.

Tag	Release	Capture	Days	$CL_i$	$CL_{ii}$	$\Delta CL$	$\Delta CL \cdot 30 d^{-1}$	Stage
MP7	22-9-92	2-10-92	10	11.90	12.80	0.9	2.7	PP-J
MM6	6-10-92	18-10-92	12	12.80	14.00	1.2	3.0	PP-J
DB0	18-10-92	23-10-92	5	11.30	11.50	0.2	1.2	PP-J
MM7	6-10-92	18-10-92	12	12.30				PP
		30-10-92	24	12.30	14.00	1.7	2.1	PP-J
		6-11-92	31	14.00		1.7	1.6	J
		16-11-92	41	14.00		1.7	1.2	J
DA3	18-10-92	23-10-92	5	12.30				PP
		30-10-92	12	12.30	13.55	1.3	3.1	PP-J
MN8	6-10-92	30-10-92	24	13.45	13.15	-0.3	-0.4	PP-J
MP0	6-10-92	23-10-92	17	12.90				PP
		6-11-92	31	12.90	14.50	1.5	1.5	PP-J
DK4	23-10-92	16-11-92	24	12.65				PP
		6-12-92	44	12.65	16.10	3.5	2.4	PP-J
		7-1-93	76	16.10	19.7	7.1	2.8	J
DX5	16-11-92	6-12-92	20	12.35	12.25	-0.1	-0.2	PP-J
		7-1-93	52	12.25	15.1	2.75	1.6	J
DM0	23-10-92	6-11-92	14	11.65	13.75	2.1	4.5	J
		30-12-92	67	13.75	13.75	2.1	0.9	J
DY0	16-11-92	30-12-92	54	11.85	14.00	2.2	1.2	PP-J
		7-1-93	62	14.00	17.2	5.4	2.6	J



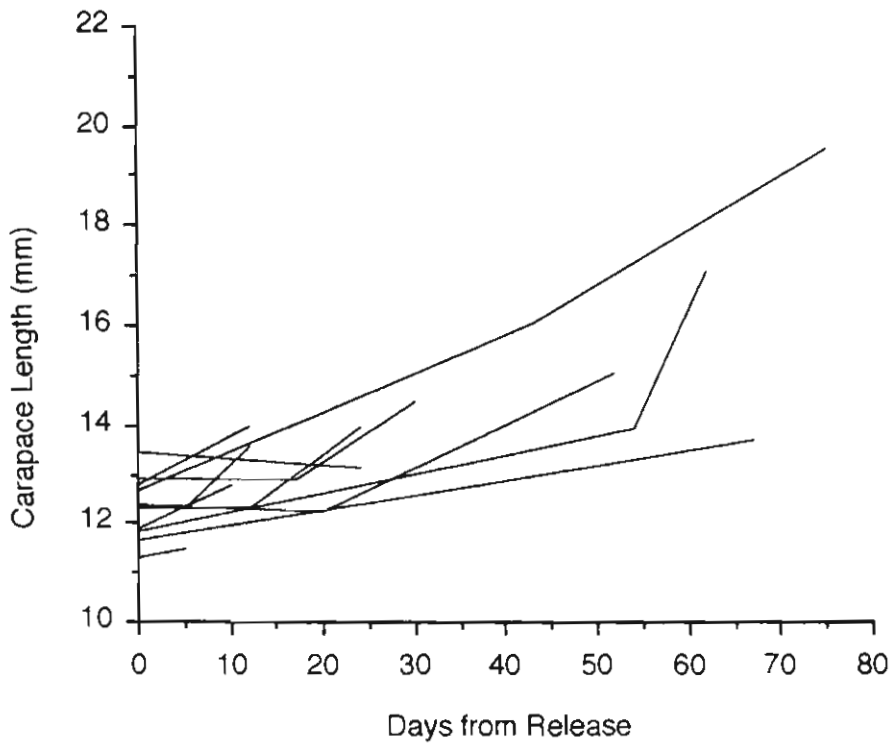


Fig. 8.3. Growth of visible implant tagged *Jasus edwardsii*. Lines indicate size increments of individuals between recaptures and not the growth pattern.

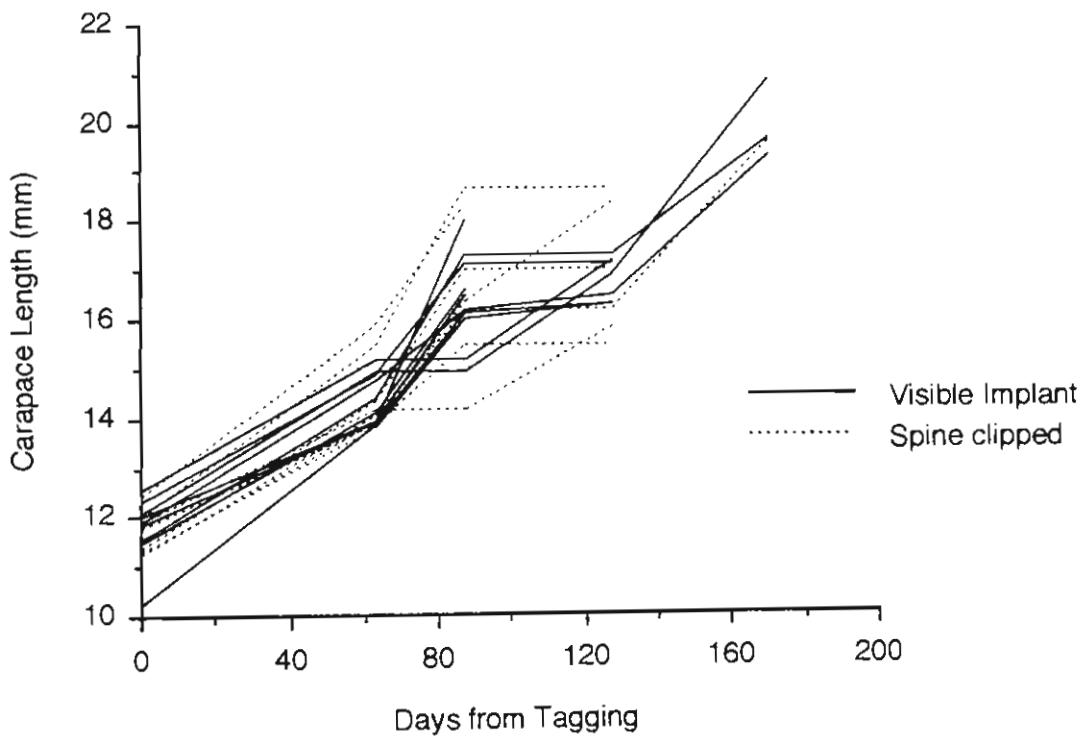


Fig. 8.4. Individual growth of laboratory reared *Jasus edwardsii* (Experiment E). Lines indicate size increments of individuals between measurement days and not the growth pattern.

Table 8.6 Individual growth rates (mm CL per 30 days) for laboratory reared lobsters (from Experiment E, described in Chapter 7).

Tag Code	Day 63	Day 88	Day 128	Day 171
Visible Implant Tag				
MX7	1.36	0.97	1.13	
MX6	1.24	0.89	1.09	
MX4	1.00	2.10		
MX3	1.71	1.99	1.42	
MX2	1.36	1.45	1.07	1.30
MX1	1.36	1.96	1.35	1.43
MX0	0.90	1.53		
MW9	1.24	1.74		
Abdominal Spine Clip				
R1	1.07	0.77	0.91	
R2	1.64	2.28	1.57	
R3	1.19	1.60	1.17	
R4	1.64	1.99		
L1	1.43	1.93	1.32	
L2	1.26	1.74	1.68	
L3	0.98	1.24	0.86	
L4	1.24	1.65	1.14	
L5	1.33	1.69	1.16	1.46

### 8.3.3 Loss Rates (Survival and Dispersion)

There was a rapid loss rate (disappearance) of tagged lobsters from the bricks soon after release. This was indicated by low numbers of lobsters in the first recapture session. The proportion of lobsters first caught after release ranged from 2% to 14% over periods of 5 to 26 days (Table 8.7). These initial recapture proportions were similar for most release batches, when standardised for a period of 30 days, ranging from 1% to 8%. No lobsters were recaptured from two batches of coded wire and one batch of visible implant tagged lobsters released onto the bricks (total of 82 lobsters).

The loss rate was estimated using two methods. The first method examined the differences in recapture proportions for a single batch of lobsters through time. The reduction in proportion of recaptured lobsters ( $p$ ) after time  $t$  can be given by the exponential relationship:

$$p = \alpha e^{-Xt} \quad (8.1)$$

where  $X$  is the instantaneous loss rate, including loss because of mortality and emigration. The coefficient  $\alpha$  is proportional to tag loss and searching efficiency (Treble *et al.* 1993) and, in this case, is assumed to be constant. On this basis, the log transformed relationship

of (8.1) was used to estimate the loss rate from the linear regression between  $\ln p$  against time, where:

$$\ln p = \ln \alpha - X t \quad (8.2)$$

Only four batches, one coded wire tagged and three visible implant tagged (Table 8.8), yielded data suitable for this method of loss rate estimation. These batches had reasonable recapture rates from sequential census times. The instantaneous loss rate from these batches were reasonably similar, ranging from 0.024 to 0.086 (per day), with the coded wire batch having the highest loss rate (Table 8.8, Fig. 8.5). These loss rates are equivalent to monthly retention rate probabilities ( $\phi$ ) of 0.07 to 0.51 (Table 8.8).

Retention rates (the converse of loss rates) were also examined using the multiple capture-mark-release data from the visible implant tagged lobsters, and the Jolly–Seber estimation method for open populations (Jolly 1965). For an 85 day period, the retention rate probability generally ranged between 0.07 and 0.93 for periods of 4 to 20 days. Standardised survival probabilities were usually between 0.001 and 0.05, with the retention rate for one period being 0.834 (mean = 0.0119; Table 8.9).

#### 8.3.4 Movement

Small scale movement patterns of visible implant tagged lobsters were determined from the release and recapture positions within the grid of release bricks (Fig. 8.6). Although the array of release bricks only covered a small area (4 x 4 m), most lobsters were recaptured either at the release point, or in an adjacent brick (1 m away). In 8 cases, lobsters left the release area (or were not found) for a period of time and returned to the same brick (*e.g.* DM0 at brick A4; Fig. 8.6). This site fidelity was not as evident for DA3 (moving from B1 to A3), MV7 (D3 to A2) and MN8 (A2 to A4). No tagged lobsters were found outside the 7.5 m ring of bricks, including the release areas used prior to introducing the bricks. This may be due, in part, to the reduced search effort outside the release area. Consequently, no information was obtained to estimate the emigration rate from the release area.

Table 8.7. Initial recapture rates for each batch of tagged *Jasus edwardsii* after release.

Batch Release Date	Release No.	1st Recapture No.	Period (d)	Proportion recaptured	Recapture Rate (d <sup>-1</sup> )
Coded wire tagged					
20-1-92	59	7	10	0.120	1.19
30-1-92	106	2	26	0.019	0.49
20-2-92	49	2	14	0.041	0.57
25-2-92	21	0	-	0	0
26-6-92	38	3	11	0.079	0.87
7-7-92	80	1	77	0.013	0.96
13-7-92	11	0	-	0	0
6-8-92	63	3	19	0.048	0.91
28-8-92	43	2	25	0.047	1.16
6-10-92	7	1	17	0.143	2.43
Visible implant tagged					
22-9-92	64	3	10	0.046	0.47
6-10-92	23	4	12	0.174	2.09
18-10-92	50	3	5	0.060	0.30
23-10-92	47	3	7	0.064	0.45
10-11-92	50	0	0	0	0
16-11-92	43	2	20	0.047	0.93

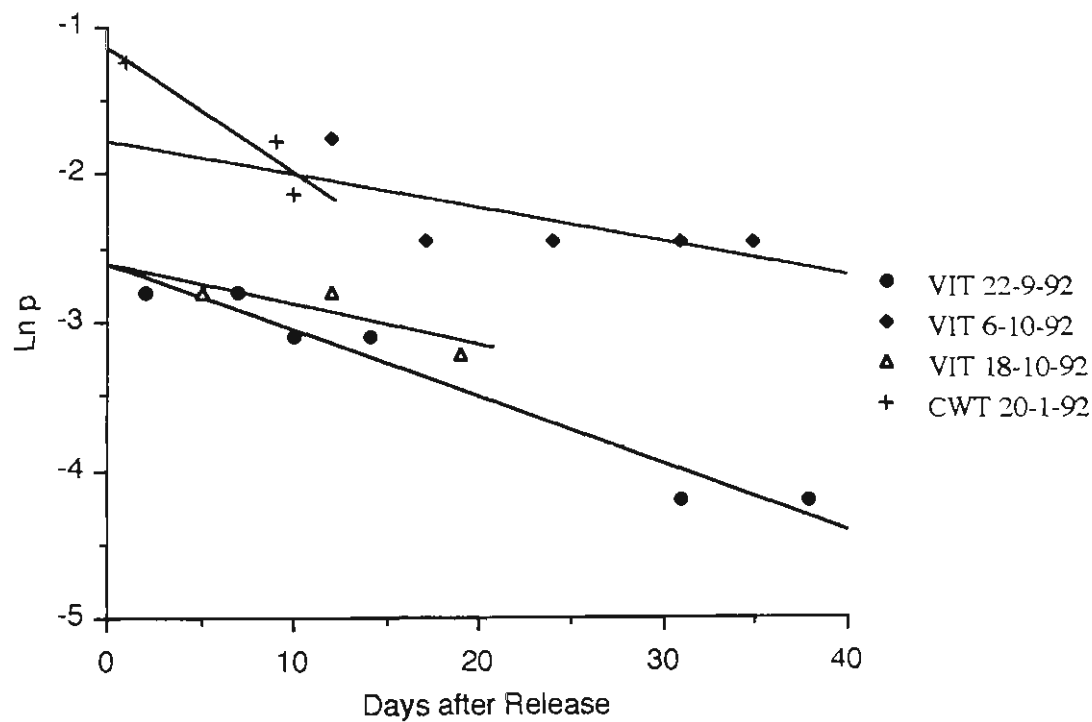


Fig. 8.5. Decrease in proportion (natural log) of recaptured *Jasus edwardsii* with time after release. The slope equals  $-X$  where  $X$  is the instantaneous loss rate. Abbreviations: VIT = visible implant tagged; CWT = coded wire tagged; dates are the date of release for that batch.

Table 8.8. Retention rates (accounting for survival and dispersion) of four batches of tagged *Jasus edwardsii* calculated from the rate of decline in recapture numbers, in terms of (X) the instantaneous loss rate and ( $\phi$ ) the probability of being retained in the study area for a period of time.

Batch Release Date	Intercept $\alpha$	X ( $d^{-1}$ )	$\phi$ ( $d^{-1}$ )	$\phi$ (30 $d^{-1}$ )
Coded wire tagged				
20-1-92	-1.14	0.086	0.92	0.07
Visible implant tagged				
22-9-92	-2.60	0.045	0.96	0.26
6-10-92	-1.77	0.024	0.98	0.51
18-10-92	-2.60	0.029	0.97	0.42

Table 8.9. Retention rate estimates ( $\phi$ ) of visible implant tagged lobsters using the Jolly-Seber method. Starting date was 22 September 1992. Also given are estimates of: ( $\alpha$ ) the proportion of recaptures; (M) number of marked animals; (N) total population size; (B) and number of new animals.

Day	$\alpha$	M	N	B	$\phi$	SE $\phi$	$\phi$ (30 $d^{-1}$ )
0	-	0	-	-	0.07		<0.001
10	1.000	4.5	5	23	0.67	0.19	0.050
14	0.115	3.0	26	303	0.93	0.45	0.834
26	0.074	24.3	327	157	0.48	0.27	0.012
31	0.047	24.3	327	-67	0.30	0.28	0.006
38	0.909	24.7	27	-1	0.35	0.53	0.011
48	1.000	9.0	9	0	0	0	0
59	0.020	0	0	528	0.24	0.43	0.001
65	0.023	12.0	528	-52	0.11	0.55	0.036
85	-	-	-	-	-	-	-
						mean	0.119

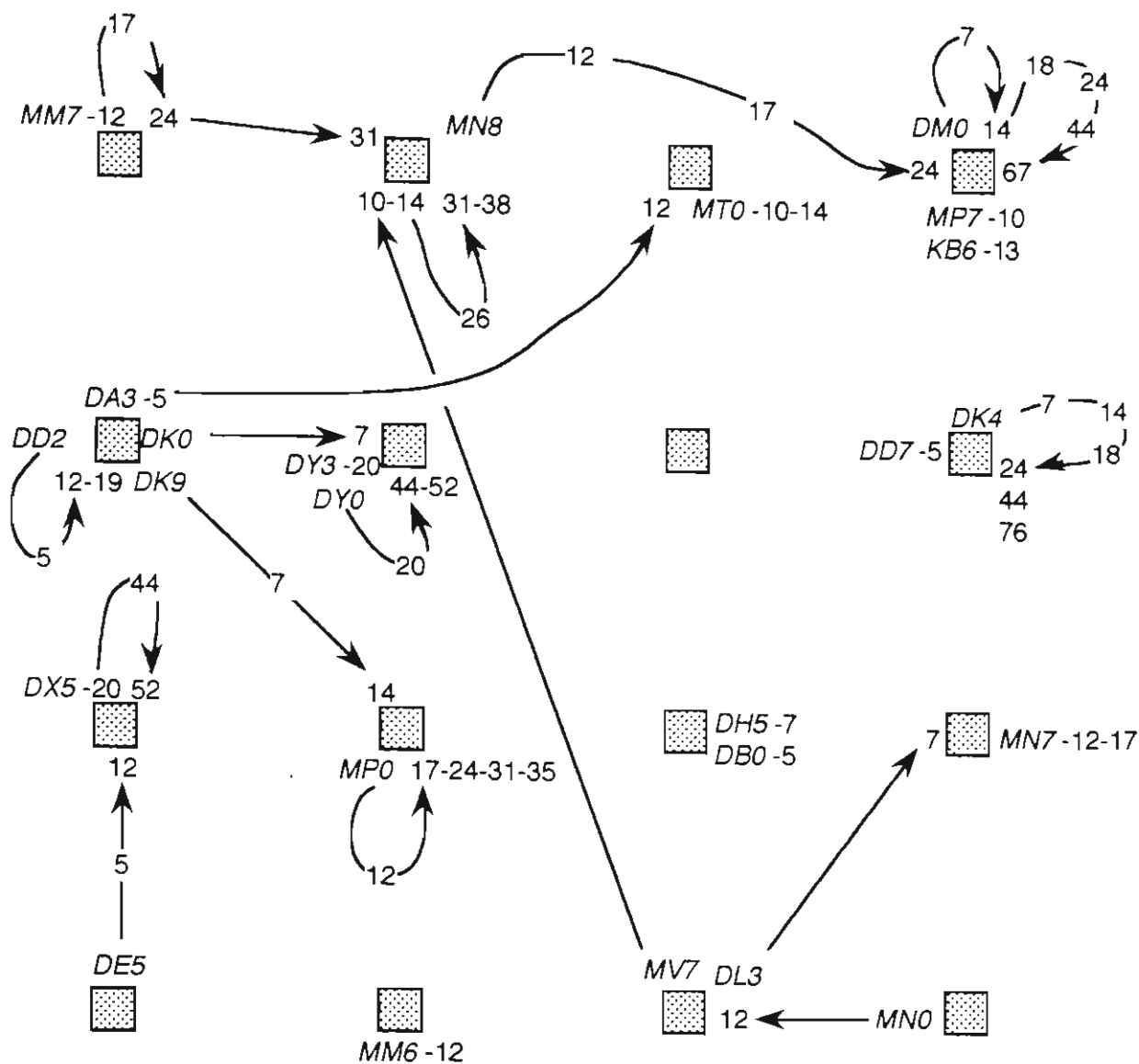


Fig. 8.6. Movement of visible implant tagged *Jasus edwardsii* between artificial shelters at Crayfish Point. The position of the tag code indicates position of release and numbers indicate the position and day of subsequent capture. Numbers on the lines indicate that the lobster was not found on that day. Shelters were spaced 1 m apart.

## 8.4 Discussion

The use of bricks as artificial shelters at the release and recapture locations solved two major problems: releasing tagged lobsters without subjecting them to predation and inefficient recapture rates from searches of the natural reef (involving long search times for few recaptures). The observed predation of the first batches released suggests that recapture rates and natural mortality estimates would have been severely compromised if this method continued. The need for placing individual lobsters in artificial shelters in this study contrasts with the release of hatchery reared, microtagged stocks of *Homarus gammarus* in the United Kingdom. Over 49 000 three month old *H. gammarus* were released *en masse* from the surface, a surface to substratum funnel or by divers at the seabed, and the recapture rate was above 50% after 4 to 8 years (Bannister *et al.* 1994).

The apparent fidelity of many recaptured lobsters to particular bricks indicates that the bricks provide suitable shelter, and probably approximate the features of natural shelters. On this basis, bricks or other similarly structured artificial habitats may prove to be an effective tool for integrating cultured lobsters into the natural environment for stock enhancement programs, increasing the carrying capacity of reefs where the natural availability of shelters is low and for further ecological research.

The artificial shelters used in this study may have influenced the population parameters being measured. Effects on growth, survival and movement may have occurred because of unnaturally high densities near the artificial habitats. Survival and movement may also have been affected if the bricks are of a different quality to natural shelters. For example, if the bricks provided better protection from predators and physical forces than natural shelters, then survival may be increased and emigration (to less suitable areas) reduced. However, more common techniques of trapping and diver-searches are also associated with sampling bias. Although trapping small juvenile lobsters in this study was unsuccessful, other problems of trapping studies include an unknown census area (at small scales), as well as temporal changes in catchability of traps and probability of recapturing tagged lobsters (Morgan 1974a, 1974b; Jernakoff & Phillips 1988; Phillips 1990). Diver-search methods to capture and recapture lobsters may be biased by difficulties in standardising the sampling effort between times and low statistical power where the capture efficiency is low.

This study was also different from standard capture-mark-recapture studies in that lobsters were initially captured from puerulus collectors outside the study area. The release of lobsters therefore artificially increased the stocks on the reef. However, the release rates were not considered greater than potential natural settlement rates, with hundreds of pueruli

settling into collectors over a similar area at Bicheno (see discussion in Chapter 2). Despite the possible biases of using artificial shelters and transferring lobsters into the study area, there were no feasible alternatives. More comprehensive studies are required to test the validity of this methodology. However, until such time it is assumed that the sampling biases were minimal.

The growth of coded wire tagged lobsters was clearly seasonal, with mean growth ranging from 2.5 mm CL to 1.1 mm CL between the summer and winter months. This difference corresponded with changes in water temperature. The summer growth rate was similar to estimates of 2.18 to 2.19 mm CL per month for post-*puerulus J. edwardsii* in South Australia (Lewis 1977). The combined winter and summer growth rates are also consistent with *J. edwardsii* at Stewart Island, New Zealand, attaining a size of 31-34 mm CL in the first year after settlement (Annala & Bycroft 1985). Although Stewart Island is approximately 5° latitude further south than Crayfish Point, the summer and winter temperatures are similar (between 17° C and 12° C; Annala & Bycroft 1985). Tagging studies of the tropical *Panulirus argus* found similar growth rates of 1.3 mm CL per month at 20-25 mm CL, but this increased to approximately 5.0 mm CL per month for 40-45 mm CL juveniles (Forcucci *et al.* 1994). Growth was also seasonal in *P. argus*, with longer intermoult periods in winter (Forcucci *et al.* 1994).

For *Jasus edwardsii* in New Zealand, there is considerable variation in growth between areas and years and, from marked lobsters above 40 mm CL, individual variation can also be high. In this study, the short times at liberty make it difficult to assess individual variations in growth, with lobsters probably only moulting one or two times (based on moulting frequencies in the laboratory). However, a high amount of individual variability was apparent, with up to 1 mm CL per month difference in the summer and less variability in the winter.

The low recapture rates and 'survival' estimates indicated a high loss rate from the study site. Factors contributing to this loss may include high initial mortality from tagging and handling effects, natural mortality, movement from the brick shelters to unsearched 'natural' shelters in the study area and a rapid dispersal rate. The laboratory experiments showed that tagging effects are unlikely to be a major factor contributing to mortality. However, Jernakoff (1990) found that up to 50% of transferred and handled *P. cygnus* post-*pueruli* leave their shelters within 24 hours. In this study, lobsters remained in the bricks for at least 1 h after release, but if lobsters left their holes during daylight they were likely to be at a high risk of predation. Although the handling of lobsters may have caused them to move out of the artificial shelters, handling effects are not thought to cause



emigration from the study area. Only four of the eleven visible implant tagged lobsters recaptured more than once were not found on the census day subsequent to capture; and three of these four had returned to the same brick by the following census.

A high dispersal rate would be expected if there were agonistic interactions between the lobsters, even though the availability of shelters always exceeded the lobster numbers. This is supported by the observations: that a lobster would immediately leave if placed in a hole already occupied by a lobster; that remaining lobsters had a reasonable fidelity to certain bricks, suggesting that dispersal is not an inherent behavioural trait; and that recaptured lobsters were usually evenly distributed between the bricks, with only one to two lobsters per brick. Apart from influencing survival estimates, natural processes causing the dispersal of newly settled lobsters, such as intraspecific interactions, may have implications for limiting the carrying capacity of the reef.

The analysis of loss rates, from both the decline in abundance of batches and the Jolly-Seber mark-recapture method, gave variable results. Estimates of the probability a lobster will survive or not emigrate from an area generally ranged from 0.07 to 0.51 (per month). Lower estimates, but with high standard errors, were obtained from some periods of the Jolly-Seber analysis. Both the accuracy and precision of these estimates would have been affected by the low numbers of recaptures. Estimates from the decline in batch abundance were higher than those from the Jolly-Seber model and this is probably because of only analysing the four batches with a suitable number of recaptures, and hence having lower loss rates. The high loss rate estimates may also be biased by movements of lobsters from the brick shelters to natural shelters within the study area. Although not many suitable natural shelters were observed within the 5 m ring of bricks, the reappearances of lobsters in the release bricks after long absences suggests there are suitable natural shelters nearby. The variability in loss rates, between batches or times, may have been because of natural influences such as storms. Several storms occurred during the study and were severe enough to move the bricks. Changes in prey availability, predation and emigration rates may have also influenced the loss rates.

The upper retention, or survival estimates for early benthic *J. edwardsii* were similar to those for first benthic stage, algal dwelling *P. argus*, of approximately 0.65 to 0.77 per month (transformed from reported values of 0.6% to 4% survival in the first year: Herrnkind & Butler 1994; Herrnkind *et al.* 1994). Survival of post-algal *P. argus*, from approximately 20 mm CL, is higher at approximately 0.80 per month (Forcucci *et al.* 1994). The survival rate of early benthic *J. edwardsii* is also expected to rapidly improve with increased size, as the natural survival rate of adult *J. edwardsii* is comparatively high

at over 0.99 per month (transformed from an annual instantaneous mortality rate of 0.11; Annala 1977).

In summary, this study was the first to examine the population dynamics of post-*puerulus* *Jasus edwardsii*, using novel microtagging techniques, and represents a considerable step towards the quantitative evaluation of various ecological parameters. Estimates of growth and survival were variable, with variation in growth because of both seasonal changes and individual differences. Survival within the study area (as a function of mortality and emigration) was quite low, suggesting that recruitment to maturity and the fishery may be substantially limited by immediate post-settlement processes.

# General Discussion

## 9.1 Introduction

This chapter presents an overview of the ecology of juvenile *Jasus edwardsii*, and is a synthesis of the results for each of the ecological aspects examined.

## 9.2 Natural History and Ontogenetic Niche Shifts

Substantial changes were found in the habitat use and diet of juvenile *Jasus edwardsii*. The ecology of newly settled lobsters was distinct from older juveniles and, using the terminology of other lobster researchers (Cobb & Wahle 1994), is referred to as the early benthic phase.

The early benthic phase begins with the settlement of puerulus onto the reef, with pulses of settlement observed in the winter and summer months in eastern Tasmania. Soon after settlement, puerulus and post puerulus were found in shelters on the reef substratum. Early benthic lobsters that remained within an area had a high fidelity to certain shelters, and only specific shelter types were used: having a similar size to the lobster and only one opening. The distribution over the reef was randomly to evenly dispersed, and positively correlated with the distribution of larger juveniles and adults. Foraging was for highly cryptic animals, particularly ophiuroids, isopods and bivalves, which were mostly present in clumps of small algae, in kelp holdfasts and within small crevices in the substratum.

The transition from the early benthic phase is at approximately 35 mm CL, or one year after settlement (based on estimates of Lewis 1977 and Annala & Bycroft 1985). Lobsters larger than 35 mm CL occupied a wider variety of shelter types, and there was a strong tendency to cohabit with peers of a similar size, in comparatively larger shelters. The distribution of occupied shelters also tended to be aggregated. Accompanied by the changes in shelter use and distribution patterns were changes in diet, to predominantly hiatellid bivalves, crabs and sea urchins. More gradual changes occurred with increased sizes, to increased volumes of sea urchins, crabs and chitons. The tendency for aggregation (especially between shelters) was reduced at larger sizes (> 60 mm CL).

Predation is a highly influential factor in the solitary and cryptic sheltering behaviour of other early benthic lobsters, particularly for *Homarus americanus* and *Panulirus argus* (Howard 1988; Smith & Herrnkind 1992; Wahle & Steneck 1992), and is also probably an important influence on the habitat use of *J. edwardsii*. Many of the larger fishes on Tasmanian reefs are capable of consuming small lobsters, based on their gape size and predominance of macrocrustaceans in the diet (Edgar *et al.* 1982), as well as from direct observations in this study. Potential predatory fish occur in guilds of open roamers (labrids and monacanthids), algal dwellers (clinids and labrids) and crevice dwellers (bovichthyids and scorpaenids), and the small enclosed shelters of early benthic *J. edwardsii* are likely to afford the best protection from such predators. In other lobsters, the shift from solitary, cryptic phases to more widely ranging phases is often accompanied by a decreased susceptibility to predation at larger sizes (prey escape) and increased energetic demands (Marx & Herrnkind 1985a, 1985b; Smith & Herrnkind 1992; Wahle 1992a). These processes may also influence the ecology *J. edwardsii*, and experimentation is required to examine these aspects. Possible changes in susceptibility to predation and physical forces, as well as feeding efficiency, may also be mediated by changes in morphology.

According to theories outlined by Caddy (1986), early benthic lobsters experience a decline in shelter availability with increased size, and this decline in availability may induce a shift in the types of shelters use. The underlying fractal principles to Caddy's hypotheses (Caddy 1986; Caddy & Stamatopoulos 1990) were applicable to the reefs examined in this study, but the rate of decline in shelter availability was quite different between substratum types, suggesting this is not a general factor influencing shifts in habitat use.

### 9.3 Implications for Ecological Interactions

The early benthic phase occupies the same reefs as older juveniles and adults, as opposed to the spatially separated populations of *P. cygnus*, *P. interruptus* and *P. argus* (Chittleborough 1970; Engle 1979; Forcucci *et al.* 1994). This provides the opportunity for juvenile-adult interactions. Negative interactions may include antagonism, competition and cannibalism. Interactions may also be positive, in that settling puerulus may be attracted to adult populations, as found for the post larvae of *H. americanus* (Boudreau *et al.* 1993).

The differences in shelter use and diet suggest the niche overlap between early benthic and larger *J. edwardsii* is small, and strong competitive effects are unlikely to occur. The positive correlation of early benthic and larger lobster distributions may be because of behavioural responses or attraction cues. An effect of coincidental distributions of available shelters could not be discounted in this study, especially given that the correlations were

more apparent at higher densities. Cannibalism in *J. edwardsii* was reported by both Hickman (1945) and Fielder (1965) but it is unclear whether these observations were of actual lobsters or moulted exuviae. This study also found exoskeleton pieces in the stomach contents.

The ontogenetic niche shifts indicate that interspecific interactions may also change with lobster size. As discussed (Chapter 5), differences in feeding may result in different community structuring processes at different sizes, and complicate the flow of matter and energy through reef ecosystems. Other important interspecific interactions may be the competition for shelter with other crevice dwellers such as molluscs, sea urchins or crabs. The intensity of any such competition would be greatest for early benthic phase lobsters as this stage has the most specific shelter requirements.

## 9.4 Implications for Recruitment

The tagging study indicated that the retention rates of early benthic phase *J. edwardsii* within a certain area are low, due to either mortality or dispersion. Low survival rates may be because of effects of predation, or physical processes such as storms. On this basis, survival and dispersion during the early benthic phase may be critical in determining recruitment between the settlement of puerulus and maturity. The importance of the ecological processes during the early benthic phase in determining recruitment is supported by evidence of density dependent survival between puerulus and first year cohorts at Stewart Island, New Zealand (Breen & Booth 1989).

The relationship between settlement rates and later recruitment may be decoupled by either density dependent effects or stochastic events. Although the tagging results were limited to a low degree of precision (because of low numbers of recaptures), there was considerable variability in the recapture rates between batches, suggesting that variable mortality processes, possibly stochastic, were occurring. Stochastic mortality processes may include storms and severe floods (Street & Booth 1985).

Predation rates may also have a stochastic element, depending on the behaviour and population fluctuations of predators. However, predation rates may also induce density dependent survival, particularly if predators develop a search image at higher lobster densities, or if lobsters are more easily detected at higher densities (particularly if aggregations occur). In this context, the observed random to regular distribution of early benthic phase lobsters would be advantageous in limiting predation.

Prey availability for early benthic lobsters is unlikely to be limiting on a population wide

scale, given the high densities of prey found at Watsons Bay. However, prey availability may be limiting at the scale of individuals, especially if there is a high fidelity to one shelter and the foraging range is small.

The timing of settlement may also affect recruitment, especially given the likelihood of a low probability of survival during the early benthic phase. The recruitment rate from winter settling cohorts is expected to be much lower than lobsters settling in the summer because of reduced growth rates, and a corresponding extension of the time exposed to significant mortality events.

The availability of shelter is another important factor possibly affecting recruitment. As discussed in Chapter 4, shelter availability is highly dependent on the substratum composition and structure, affecting both the total availability, and the changes in availability with lobster size. Limitations in shelter availability are likely to be more prevalent during the early benthic phase, with the potential for bottlenecks in recruitment occurring at either the settlement stage or toward the end of the early benthic phase. The estimates of shelter availability at Watsons Bay were much higher than the observed densities of lobsters, and shelter limitations were not apparent during this study. However, these observations were made during an exceptionally low settlement period (Chapter 2) and it is quite feasible that shelter is a limiting resource at higher settlement rates.

Density dependent processes may also occur after the early benthic phase. Juveniles between 35 and 60 mm CL were highly aggregated, both within and between shelters. Because the levels of aggregation were higher at increased densities, this may lead to localised density dependent effects, possibly in the form of reduced food abundance near the aggregation. This is especially given the small foraging range of *J. edwardsii* (MacDiarmid *et al.* 1991). Breen and Booth (1989) found evidence of density dependent growth for this size range at Stewart Island.

## 9.5 Conclusions

The life history of benthic *J. edwardsii* is complex, with considerable ontogenetic shifts in ecology. The distinct ecological differences between early benthic phase lobsters and larger lobsters suggests there is little niche overlap, and that these groups are essentially separate components of the reef ecosystem. For early benthic phase lobsters, the specific habitat requirements, possibly increased susceptibility to predation and the dynamics of growth, survival and movement suggests that this phase is a critical one in determining recruitment to maturity and the fishery.

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