FINAL REPORT TO THE FISHING INDUSTRY
RESEARCH AND DEVELOPMENT COUNCIL

FIRDTF PROJECT 86/83

AN INVESTIGATION OF THE HABITAT REQUIREMENTS OF THE POST-PUERULUS STOCKS OF THE WESTERN ROCK LOBSTER.

CSIRO
Marine Laboratories

FINAL REPORT TO THE FISHING INDUSTRY RESEARCH AND DEVELOPMENT COUNCIL

FIRDTF PROJECT 86/83

AN INVESTIGATION OF THE HABITAT REQUIREMENTS OF THE POST-PUERULUS STOCKS OF THE WESTERN ROCK LOBSTER.

J. Fitzpatrick

P. Jernakoff

B.F. Phillips

CSIRO Division of Fisheries

CONTENTS

EXECUTIVE SUMMARY

Post-puerulus western rock lobsters are smaller than 25 mm carapace length and are within their first year after settlement from the planktonic puerulus stage. Prior to this study the habitat of the post-puerulus western rock lobster was unknown and consequently there was little other information on the lobsters during this stage.

The objectives of this 3 year investigation, aimed at redressing this lack of knowledge, were;

1. To determine the natural habitat and habitat requirements of the post-puerulus stage of the western rock lobster.
2. To measure the densities at which post-pueruli naturally occur.
3. To compare the densities of post-pueruli in natural habitats with the densities of post-pueruli found on artificial collectors, and hence to measure and improve the accuracy with which predictions of commercial catch are made.
4. To investigate the suitability of artificial habitats as a possible means of enhancing post-puerulus survival.

Assessment of Objective 1

This objective was successfully completed.

Natural habitat

- At the two major study sites, Seven Mile Beach and Cliff Head in Western Australia, the natural habitat was shallow coastal limestone reefs (less than 5 m deep). On the limestone reefs post-pueruli inhabit small holes in the reef surface, mainly on the reef face/top but also in ledges and caves. Post-pueruli inhabit small holes in the reefs until about 16 - 20 mm carapace length, when they move into the reef den habitat of the juvenile stage. Post-pueruli were also found on deeper reefs, to at least 30 m, near Seven Mile Beach and Cliff Head and in coral habitat at the Abrolhos Islands.

Habitat requirements

- Post-pueruli prefer shelters covered by seagrass and/or algae, and of a size positively related to their carapace length.

Assessment of Objective 2

This objective was successfully completed.

- Densities of post-pueruli varied significantly on spatial and temporal scales -ie. differences between locations, reefs, habitats, months and years. In general, densities at Seven Mile Beach (0.11 - 0.93 post-pueruli m^{-2}) were higher than at Cliff Head (0.04 -0.90 post-pueruli m^{-2}).

Assessment of Objective 3

The first part of this objective was successfully completed.

- The densities of pueruli and post-pueruli (<10 mm C.L.) on the reefs at Seven Mile Beach correlate strongly with the densities of similar sized lobsters on artificial collectors at the same site. This indicates that, the index of settlement derived from the collectors is an accurate representation of natural settlement, as determined by diver surveys, over a large and spatially variable area at Seven Mile Beach.

The second part of this objective was found to be impractical.

- High variability in searching efficiency, attributable mainly to weather conditions and the topographical complexity of the habitat, reduced the accuracy of estimates of post-puerulus density, made by divers, and hence decreased the usefulness of these density estimates in improving the existing predictive model.

Assessment of Objective 4

This objective was successfully completed.

- Two types of artificial habitat, limestone blocks with holes drilled in them and covered by seagrass, and habitats constructed from "Tanikalon" fibres, were used as shelter by early post-pueruli. Three other types of artificial habitat were not used by post-pueruli.

- Experiments on disturbance and transfer of post-pueruli between and within natural and artificial shelters indicate that the majority of animals do not remain in selected shelters after relocation.

Additional research

Additional research on the nocturnal activity and movement, the natural diet, growth and behaviour of post-pueruli was conducted during this study.

Major implications of the study

Fisheries models

- Models may be refined using information on the natural densities and growth rates of post-pueruli.

- The discovery of recruitment of post-pueruli to depths of at least 30 m, greatly increases the area of habitat known to be potentially suitable for puerulus settlement, and hence needs to be taken into account in stock assessment models.

Artificial habitats for stock enhancement

- The success of artificial habitats as post-puerulus shelters indicates that, providing areas can be identified where habitat is limiting, it may be possible to enhance post-puerulus survival by provision of artificial habitats.

- The behaviour of post-pueruli after transfer to shelters probably increases the already high risk of predation. Therefore, stock enhancement (as suggested in the literature) by transfer of post-pueruli between areas of high and low density, or release of aquarium reared post-pueruli into natural habitats, is unlikely to be successful.

Environmental conservation

- Knowledge of the natural habitat of post-pueruli will allow us to identify important conservation areas and hence protect the stock from anthropogenic disturbance during this stage of their life.

Transfer of information to Industry and other bodies

To date, seminars on this research have been presented to:

- The Rock Lobster Industry Advisory Committee and to rock lobster fishermen at Geraldton, Jurien Bay, Ledge Point and Fremantle in 1987, 1988 and 1989.
- The 1987 and 1989 meetings of the Western Fisheries Research Committee.
- The 1987 Australian Marine Sciences Association conference.
- The 1988 CSIRO Fisheries Divisional seminars.
- The Bureau of Rural Resources, during 1989.

An article on the research, written for the Industry, has been published in FINS and a written report was submitted to the Western Fisheries Research Committee in 1988. Further reports on the study will be submitted to the Australian Fisheries Magazine and to scientific journals.

ACKNOWLEDGEMENTS

Grateful thanks for the able and cheery assistance from the people that made the, sometimes not so pleasant, field sampling possible; Kevin Smith, Mike Forde, Boze Hancock, Sean Finn and the people of Dongara. Thanks also to Dave Wright for his assistance in accessing references in the computer based bibliography he is working on. Bert de Boer and Richard Litchfield, of the CSIRO LRR Biometrics Unit, were most helpful with statistical assistance.

INTRODUCTION

The biology of the Western Rock Lobster, Panulirus cygnus George (1962), has been intensively studied and consequently there exists a considerable amount of published information on various stages of its life history (e.g. George 1958, Sheard 1962, Chittleborough 1970, Chittleborough and Phillips 1975, 1979, Joll 1982, Phillips et al. 1977, 1984, Phillips 1986 and Jernakoff et al 1987). However, one stage of the life history of this species has remained relatively unknown, the post-puerulus stage. This stage begins with moulting from the puerulus stage and persists until the lobsters reach juvenile size. For the purposes of this study, minimum juvenile size has been defined as 25 mm C.L. which is the size at which Phillips et al (1977) suggested the lobsters become gregarious and first move into the reef den habitat of the juveniles.

The paucity of information concerning post-puerulus western rock lobsters is largely due to the lack of success, despite considerable effort, in finding post-pueruli in their natural habitat (Phillips et al 1977). It is only when the lobsters reach juvenile size at about 2+ years old that they are found in the juvenile den habitat (Cobb 1981) on shallow coastal reefs and will readily enter baited pots (Chittleborough 1970).

Although puerulus and post-puerulus P. cygnus have rarely been found in their natural habitat, they have been found clinging to ropes attached to commercial rock lobster pots (George 1958) and large numbers of post-pueruli have been collected on frames made from artificial seaweed (Phillips 1972). Phillips et al (1977) suggested that the natural settlement of the pueruli occurred in shallow benthic habitats distinct from the juvenile habitat, probably the coastal seagrass beds. On the basis of aquarium experiments, Phillips et al (1977) further suggested that following settlement the post-pueruli remain solitary in the seagrass beds, until about 1.5 years old. At this age they were proposed to develop gregarious behaviour and gradually move into the juvenile habitat.

The lack of success in finding post-puerulus *P. cygnus* in their natural habitat has, up to now, made direct studies of their population dynamics and ecology e.g. densities, diets, growth rates impossible. In the present study our aim was to determine the habitat of post-puerulus *P. cygnus* and thus to open the way to these much needed investigations of habitat use, population dynamics and ecology of the western rock lobster during this stage of its life cycle.

The objectives of this study were;

1) to investigate the habitat requirements of the post-puerulus stocks of the Western Rock Lobster;
2) to compare the densities of puerulus settlement on artificial collectors and in natural habitats;
3) to measure and improve the accuracy with which commercial catches are predicted from the post-puerulus densities on artificial collectors;
4) to enhance the abundance and survival of post-pueruli, and hence of adult, western rock lobsters through a knowledge of the habitat requirements of the post-puerulus.

MATERIALS AND METHODS

STUDY SITES

The study was mainly carried out at two shallow locations on the Western Australian coast, Seven Mile Beach and Cliff Head (Figure 1). Some additional, preliminary work was carried out on a set of reefs in deeper water (up to 30 m deep), near Seven Mile Beach and Dongara, and at Rat Island of the Houtman Abrolhos (Figure 1).

Shallow coastal locations

Seven Mile Beach is in the centre of the geographic range of the western rock lobster and is a location where artificial seaweed collectors are deployed to monitor the settlement of puerulus stage western rock lobsters (Phillips 1972, 1986). Seven Mile Beach receives a high level of puerulus settlement and supports high densities of juvenile lobsters (Chittleborough and Phillips 1975). Therefore it is likely that this location also supports high densities of the intermediate post-puerulus stage.

Seven Mile Beach is characterised by limestone patch reefs, covered and surrounded by dense seagrass beds (*Amphibolis antarctica*, *A. griffithii*) interspersed with sparse seagrass beds (*Heterzostera tasmanica* and *Halophila ovalis*) and areas of sand and rock rubble (Figure 2). This location is in 2 - 5 metres of water which is relatively calm due to a protective outer reef. The tops of many of the limestone reefs are covered in a dense canopy of *A. antarctica* and *A. griffithii* growing on a layer of sand, with coralline algae growing on bare patches of the rock substratum. Ledges, caves and reef faces are covered by algae and encrusting invertebrates e.g. ascidians and sponges, whose densities vary from almost zero (bare rock) to extremely dense cover. At times of high tide the swell crosses the outer reef and creates very strong surge and low under water visibility. These conditions are prevalent during winter and disrupt sampling programs involving divers.

The study area at Cliff Head is characterised by seagrass growing on small lumps of limestone (0.5-2 m long x 0.5-1 m high) and limestone reef on a sandy bottom in 1 - 3 m of water. The reef at Cliff Head is much less topographically complex than the reef at Seven Mile Beach. There are usually large amounts of coarse and fine seagrass detritus around the reef. Fine detritus is readily resuspended during a swell, causing a severe increase in turbidity and creating poor conditions for visual sampling by divers.

Deeper coastal locations

To examine the distribution of post-pueruli over a range of water depths, preliminary work was carried out at 5 deeper, coastal locations during November 1988, January 1989 and March 1989. The locations were; Leander Reef, Irwin Reef, Pearse Break, North Bank and Field Lump (Figure 1). Sites on these reefs were selected to cover the maximum range of depths available on each reef.

Two sites were selected on Leander Reef, which at about 13 km from shore, was the furthest offshore of the study sites. The main site (LR1) was an area of reef in 27 - 30 m of water with a sparse cover of seagrass Thallassadendron pachyrhizum and brown macroalgae Sytothalia dorycarpa and dense encrustation of invertebrates, especially sponges. The second site (LR2) was a large hole on top of the reef in 4 - 6 m of water and had similarly dense invertebrate cover.

Three sites were selected along an approximately east-west line across Irwin Reef which lies about 6 km from shore. One site was in 20 m of water on the west of the reef (IR3) and a second site was on top of the reef (IR2) in 6 m of water. The sea bed between Irwin Reef and the shore reaches a maximum depth of 16 -17 m however the third site (IR1), the deepest reef found in this area, was only 10 m deep. The Irwin Reef sites were characterised by seagrasses, T. pachyrhizum, A. antarctica, and macroalgae, S. dorycarpa, E. radiata, growing on limestone reef. The western site (IR3) was characterised by several metre high ledges with dense sponge and ascidian encrustation, whereas the eastern site (IR1) had denser plant cover and low ledges (< 1 m).

Three slightly shallower sites were selected on Pearse Break, a reef about 3.5 km from shore. The first site (PB3), on the west side of the reef lies in 16 m of water, and has very tall (> 5 m) vertical reef faces densely covered in sponges and other invertebrates. E. radiata grows on the top of the reef and there are beds of A. antarctica in some places on the sand around the reef. The second site (PB2), in 4 - 6 m of water, was subject to much higher wave energy and had more bare and coralline algal encrusted reef with a sparse cover of macroalgae. The third site (PB1), on the east of the reef, lies in 10 m and is characterised by numerous deep ledges and caves on sand and a cover of A. antarctica on the reef tops.

The fourth offshore location was a transect running west from the Seven Mile Beach study site across North Bank, about 5 km from shore. Four sites were selected along this transect. One site on the west of North Bank (SMB4) in 20 metres of water, was characterised by low ledges sparsely covered in seagrass (*Thalassodendron* and *Amphibolis*), and was surrounded by a large expanse of sand. Another site was on top of North Bank (SMB 3) in 10 metres of water with a denser seagrass cover. The other two sites were between North Bank and the onshore study site, SMB 2 in 18 metres of water, and SMB1 in 10 metres of water.

Rat Island sites

Preliminary surveys were conducted at four sites around Rat Island in May 1988 (Figure 1).

1) "Cacker Flats", where puerulus collectors are deployed, is an area of reefs composed of consolidated coral, covered in short brown algae (probably *Giffordia* sp.) in about 5 m of water.

2) "The Nursery", an area of living coral and dead, algal covered plate and staghorn *Acropora* sp. coral in about 5 m of water.

3) The "Southern coral country", characterised by large colonies of living and dead, plate and staghorn *Acropora* sp. and kelp beds *E. radiata* in 2 - 9 m of water.

4) The "Northern coral country", of similar depth and coral species composition to 3) but without kelp.

SEARCHING AND SAMPLING METHODS

Seagrass beds were surveyed in October 1986 using 1 m^2 steel quadrats with a 40 cm high fence of flexible plastic mesh (1.5 mm X 3 mm) supported by floats and with a 15 cm wide, plastic mesh, skirt weighted down by chain to prevent the escape of post-pueruli under the frame during searching. Blocks of four quadrats, covering 4 m^2 of seagrass, were randomly placed in the seagrass beds. Each quadrat was searched twice (in a north-south then an east-west direction) by a pair of divers working side by side. During October 1986, divers searched 75 quadrats (75 m^2) and 73 m^2 of unfenced transect in the *Amphibolis* beds and 32 m^2 in the *Heterozostera* and *Halophila* beds.

To determine whether animals had been missed during quadrat searches of *Amphibolis* beds, the entire contents of an additional 60 quadrats, 20 on the reef top and 40 in surrounding beds, were searched and then removed. The seagrass stems were cut and the canopy was sucked into a plastic mesh bag using a suction pump. Sand to a depth of about 2 cm was also removed in case post-pueruli were buried in the substratum as Engle (1979) reported for *Panulirus interruptus*. The samples of seagrass and sand were subsequently sorted on the beach. Another 28 m^2 of seagrass were similarly sampled in April 1987.

There were some areas of limestone on the top of some reefs which were devoid of seagrass, macroalgae and invertebrate growth. In November 1986, divers searched 40 m^2 of this 'bare limestone' habitat and 55.5 m^2 of rock rubble, without quadrats.

Subsequent to the extensive surveys of the seagrass beds and other habitats in October and November 1986, searching effort was concentrated on the limestone reefs at Seven Mile Beach. During November 1986, systematic surveys were conducted on 12 limestone reefs at Seven Mile Beach. Reef habitats were intensively examined by divers using powerful torches to illuminate every hole or fissure in the rock surface and similar interstices in the algal and invertebrate cover.

From February 1987 until the end of the field work in March 1989, the focus of searching effort was maintained on the reef habitats. Divers searched the shallow reefs at Seven Mile Beach and Cliff Head in February 1987, March/April 1987, September 1987, November 1987, January 1988, March 1988, September 1988, November 1988, January 1989 and March 1989.

The sampling method used on the inshore reefs at Seven Mile Beach and Cliff Head was also employed on the deeper reefs offshore from Dongara in November 1988, January 1989 and March 1989. The survey of post-puerulus distribution at Rat Island in May 1988, involved searches of live and dead coral (plate and staghorn Acropora spp.) and areas of consolidated coral and coral rubble, using the non-destructive techniques employed at the coastal sites.

POST-PUERULUS HABITAT AND HABITAT PREFERENCE

Shelters and surrounding cover

Preliminary observations in November 1986 identified 2 factors which appeared to have a major influence on the selection of shelter sites, hereafter refered to as shelters, by post-pueruli. These factors, the presence of cover around the shelters and the size of the shelter were examined, both through survey of a large number of natural shelters and by field experiments.

During November 1986, the type of cover/growth e.g. algae, seagrass, invertebrates, around post-puerulus shelters was recorded for all post-pueruli that were found. In February and March/April 1987, data on the size of post-pueruli and the approximate area of the opening of their shelters, were collected. It was not possible to measure the depth of the shelters, without disturbing the post-pueruli. Disturbance was observed to cause post-pueruli to leave their shelters, and thus may increase the probability of repeated sampling of individuals.

An experiment was conducted at Seven Mile Beach in 1986/7 to examine the influence of cover around the shelter, and the size of the shelter, on post-puerulus habitat preference. Six limestone blocks (60 cm long x 30 cm wide x 25 cm high) with 32 drilled holes, four of each combination of four diameters (8 mm, 10 mm, 12 mm, 14 mm) and two depths (25 mm or 50 mm), were randomly placed in dense *Amphibolis* beds at 2 sites 750 m apart. The position on the blocks of the different sized holes was randomly assigned within a regular grid on 1 face, such that the holes were 100 mm apart. The effect of cover around the shelter was examined by removing the seagrass from around half (3) of the blocks at each site. The blocks were checked for the presence of post-pueruli 7 times between December 1986 and November 1987 and the size and number of post-pueruli present was recorded.

Post-pueruli were observed to occupy shelters in all parts of the reefs, ie caves, ledges and reef face/top. In order to examine patterns of habitat use exhibited by post-pueruli, their shelters were recorded as either cave, ledge or reef face/top during the surveys following November 1986.

To determine the size range during which the change from the post-puerulus habitat to the juvenile habitat occurs, in November 1988, January and March 1989, we recorded post-puerulus size and whether the post-pueruli were in small holes or in larger spaces.

The number of post-pueruli sheltering together

The number of post-pueruli found in the same shelter was recorded in February/March 1987. Additionally, in order to examine the natural development of gregarious behaviour over time, the presence of post-pueruli in groups or singularly was recorded in November 1988, January 1989 and March 1989.

DENSITIES OF POST-PUERULI IN NATURAL HABITATS

-Accuracy, Precision, Natural Densities

Accuracy tests

As the density estimates are based on estimates of the number of animals and the area of habitat searched, it is important to have a measure of the accuracy and precision of these estimates and hence of the density estimates. Attempts were made to obtain such measures of error.

There was no simple way to assess the accuracy of area estimates, due to the complexity of the reef surface, and hence the area of habitat searched was approximated only to the nearest 0.25 m^2.

To assess the accuracy of diver estimates of post-puerulus numbers mark/recapture and depletion experiments, aimed at deriving alternative measures of post-puerulus abundance, were attempted. In mark/recapture experiments it is necessary to be able to mark post-pueruli and hence to be able to recognize them on recapture. Two methods of marking that were attempted, marking with epoxy paint or oil-based crayons, were unsuitable as the animals had to be captured and handled and this often resulted in injury to the post-pueruli or refusal to re-enter their shelters when released. The most successful method of marking post-pueruli was antennal clipping while the post-pueruli were still in their holes. This avoided the problem of having to capture the post-pueruli and reintroduce them to their holes. During antennal clipping, some post-pueruli showed no or little reaction while others retreated into their holes but appeared to resume normal behaviour after about 5 minutes. However, not all post-pueruli could be marked as many would retreat into their holes out of reach. Another limitation of this method was that clipped lobsters could only be identified as part of the marked subset of the population, not as individuals.

Mark/recapture experiments were attempted on 2 reefs at Seven Mile Beach, in March/April 1987. On the first reef, 51 of the 94 post-pueruli found could be marked by antennal clipping. On the second reef 28 of the 50 post-pueruli found could be marked. After 9 days the reefs were searched again and the proportion of marked to unmarked post-pueruli recorded.

Two depletion experiments, aimed at deriving additional, alternative estimates of the total number of post-pueruli on 2 reefs, were attempted in November 1987 and in March 1988. In these experiments the cumulative numbers of post-pueruli found on successive searches of the reefs were plotted and the total theoretical abundance calculated (using Ricker's (1975) method where applicable).

Precision tests

To determine whether divers searching the same area of reef found the same number of post-pueruli, repeated searches were conducted at Seven Mile Beach in November 1986. Five divers marked an area of reef which they searched and recorded the number and location of all post-pueruli they found. Divers then swapped areas and searched for post-pueruli in the area that had been searched by the first diver, again recording the numbers and locations of post-pueruli.

The study was expanded in February 1987 to examine precision in counts made by;

i) the same diver during 2 searches on the same day,

ii) by the same diver during 2 searches on different days,

iii) by different divers on the same day, and

iv) by different divers on different days.

The between diver precision in estimating the area of habitat searched and the number of post-pueruli found, by 2 divers who separately searched the same area of a reef, on the same day, was re-assessed in September 1988 and in November 1988.

Natural densities

Natural densities, in each habitat (cave, ledge, face/top), were calculated for parts of reefs at Seven Mile Beach in February and March/April 1987. Densities were also calculated for a standard set of 13 reefs at Seven Mile Beach and 4 transects at Cliff Head, which were searched completely, during field surveys in September 1987, November 1987, January 1988, March 1988, September 1988, November 1988, January 1989 and March 1989. Analysis of variance was used to examine differences in post-puerulus densities within and between habitats, reefs, years and months.

NATURAL DENSITIES vs COLLECTOR DENSITIES

The size of the puerulus and post-puerulus lobsters that are regularly removed from the artificial collectors ranges from about 7 to 9 mm C.L. (Phillips 1972). The comparison between collector densities and natural densities is therefore restricted to the subset of the natural population of post-pueruli that are < 10 mm C.L.. The natural density of post-pueruli < 10 mm C.L. was calculated for a set of reefs at Seven Mile Beach which were sampled on each occasion in September and November 1987, January, March, September and November 1988 and January, March 1989.

ARTIFICIAL HABITATS

In addition to the limestone blocks (described under POST-PUERULUS HABITAT AND HABITAT PREFERENCE above), four other types of artificial habitat (Figure 3) were constructed and deployed at Seven Mile Beach to examine the suitability of such structures for puerulus settlement and post-puerulus habitation.

The first type of artificial habitat was a hollow concrete cylinder with 12 holes (20 mm diameter x 70 mm depth). The ends of the cylinder were sealed with plastic mesh to allow water movement but exclude predatory octopi and fish. The second type of artificial habitat was a block of 12 PVC mesh cylinders, 20 mm diameter x 80 mm length, clamped at one end and strapped together on a flat steel anchor. The third type consisted of a mat of "Tanikalon" (Taniyama Chemical Industries Ltd, Okayama, Japan) synthetic rope fibres (350 mm x 300 mm x 250mm) attached to a plastic sheet, as is used in the puerulus collectors (Phillips 1972), mounted on a steel frame such that the fibres were hanging down. The fourth type consisted of a concertina (approx. 300 mm diameter x 700 mm long) of a fibre mesh, suspended on a rope between a float and a flat steel anchor.

Five of each of these types of artificial habitat were set out at 2 sites 750 m apart within the *Amphibolis* beds at Seven Mile Beach during October 1986. The habitats were left for about 2 months and then checked for pueruli and post-pueruli in November 1986, February 1987 and March 1987. The number of pueruli and post-pueruli found in the artificial habitats and in nearby control plots of *Amphibolis*, was recorded and the animals were removed.

Transfer of post-pueruli between shelters

Three experiments were conducted at Seven Mile Beach to examine the likelihood that post-pueruli, transferred between shelter sites would remain in the new shelter site.

In the first experiment, 32 post-pueruli were collected from artificial collectors (Phillips 1972), 20 of which were transferred to holes in limestone reef and 12 were transferred to holes (14 mm diameter x 50 mm depth) in 6 limestone blocks (2 per block). The second experiment involved taking 17 post-pueruli from their natural shelter sites and returning them to the same sites. The third experiment compared the residence time of 8 post-pueruli removed from limestone blocks and returned to the same hole, with the residence time of 8 post-pueruli left undisturbed in limestone blocks.

In the second and third experiments, some post-pueruli were given the choice of entering a hole or ecaping into the surrounding seagrass. The number of post-pueruli that chose to enter the hole and the number that chose to flee was recorded.

SIZE/FREQUENCIES AND GROWTH

It was not possible to monitor the size of individual lobsters in the field, as they could not be individually marked, and hence the growth of post-pueruli could only be measured indirectly, in terms of increase in the mean size of cohorts. The mean cohort sizes were calculated by analysis of size/frequency data collected during bimonthly surveys throughout the summers of 1986/87, 1987/88 and 1988/89.

During the initial surveys in November 1986, the sizes of post-pueruli were estimated visually as <10 mm C.L., 10 - 15 mm C.L., 16 - 20 mm C.L. or 21 - 25 mm C.L.. These data were not used in cohort analysis. In February 1987, as divers were more experienced at finding the post-pueruli and estimating their sizes, the size classes were reduced to 1 mm C.L. and the range of classes was extended to 55 mm C.L.. This size range was chosen to cover the 1+, 2+ and 3+ age groups, based on the upper size limits estimated by Chittleborough (1976), such that the growth of cohorts could be followed through several years.

A size reference collection of lobsters was used to familiarize divers with the different lobster sizes before visual estimation was conducted. A measure of the error associated with visual size estimation was obtained by measurement of post-pueruli that were captured after their sizes had been estimated visually. Measurement of post-pueruli was conducted during routine searches for post-pueruli in March 1988, September 1988, November 1988, January 1989 and March 1989.

Whereas in February and March/April 1987, the team of divers searched a number of reefs simultaneously, from September 1987 the strategy was changed such that the team searched a single reef per dive and covered the whole reef. This strategy allows assessment of the total number of post-pueruli on a reef. The size/frequency data subsequently collected in this manner provide comparable indications of the population structure at Seven Mile Beach and Cliff Head at each sampling time. The survey at Cliff Head in September 1988 had to be abandoned due to the extreme turbidity at this site and hence only Seven Mile Beach data were collected during that month.

Maximum likelihood estimates, of the mean size of each of the cohorts that were expected to be present at each sampling time, were calculated using MIX analysis (MIX release 2.3, Macdonald and Green 1988). Mixture distributions were fitted to the data, which were assumed to be normally distributed unless this assumption was obviously violated by a severe truncation due to the minimum size at settlement effect. In these cases, a truncated normal distribution was fitted to the data using the fortran program CENSOR (N. Campbell, CSIRO Div. of Math. & Stats).

NATURAL MOVEMENTS OF POST-PUERULI

To provide an indication of the natural movements of post-pueruli, observations were made of the distance that the marked post-pueruli moved between shelters during a night. Twenty one post-pueruli within an area of 8 m^2, on a reef at Seven Mile Beach, had their right antenna clipped and the straight line distance they travelled overnight, relative to the closest boundary of the marked area, was recorded. In some cases individuals could be distinctly recognised and the distance these lobsters had travelled from their original shelters was recorded.

Shelter occupancy

To examine the number of consecutive days over which shelters were occupied by post-pueruli, the presence of post-pueruli in 52 marked shelters on 5 reefs was examined daily for 10 days in November 1986. The original occupants of the shelters were not marked because disturbance may have influenced their behaviour. Consequently, there is no evidence that a post-puerulus observed in a shelter on different days was the same individual.

NOCTURNAL ACTIVITY

The nocturnal activity of post-pueruli was observed in the field. Post-puerulus shelters were marked during the day and the presence or absence of post-pueruli, and the size of post-pueruli, in each shelter was recorded at regular intervals during the following night. The initial set of observations in February 1987 were made over the 2 hours around sunset, in order to determine the time at which 26 post-pueruli left their daytime shelters. The second set of observations were conducted every 2 hours from sunset to sunrise on one night in January 1988, in order to determine the time at which 42 shelters were occupied, indicating the end of an activity period.

DIET

An indication of diet was derived by examining the gut contents of 91 post-pueruli collected between 1 and 2 hours after sunset in November 1986, February 1987 and April 1987. The foreguts were preserved and examined using the methods of Joll and Phillips (1984). The moult stage of each post-puerulus was also defined according to the system used by Joll and Phillips (1984), such that the interaction between diet and moult stage could be examined.

POST-PUERULUS COLOURATION

The colouration of post-pueruli was recorded during the surveys at Seven Mile Beach, Cliff Head and the deeper offshore reefs in 1988/89. Divers recorded the colouration of all post-pueruli that could be clearly seen and, when matched with the size data, these data can be used to determine the stage at which the colouration changes occur. Post-pueruli in a transitional phase were recorded as belonging to the colour group they were changing to e.g a clear animal with a stripe = striped.

RESULTS

POST-PUERULUS HABITAT AND HABITAT PREFERENCE

Seven Mile Beach, Cliff Head and Deeper sites

In November 1986 12 post-pueruli were found and in February 1987 188 post-pueruli were found. All of these animals were sheltering on the limestone reefs at Seven Mile Beach. No post-pueruli were found in the rock rubble, sand or bare reef tops and only 2 were found in seagrass beds, both under a small rock amongst the seagrass.

Newly settled pueruli and post-pueruli were found sheltering in small holes and cracks in the reef face/tops, caves and ledges of the limestone reefs. Their shelters were usually surrounded by algae (e.g *Caulerpa* sp., *Codium* sp.), seagrass, invertebrate growth, seagrass detritus or a combination of these. In the majority of cases, the shelters were surrounded by *Amphibolis*, algae or a combination of both (Figure 4). Post-pueruli in 'bare' shelters (Figure 4), were generally found in caves and >10 mm C.L..

The small post-pueruli appeared to occupy holes that were only slightly larger than their body size. The areas of the entrances to 589 post-puerulus shelters were calculated (as ellipses) and then regressed against the estimated carapace lengths of the post-pueruli in the holes. There was a significant, positive relationship between the logarithm of the area of the holes and the carapace lengths of the post-pueruli inhabiting them ($R^2 = 0.59$; $p < 0.05$).

The selection of shelters surrounded by seagrass, and of specific hole size, which was apparent from observations of natural shelters, was also demonstrated experimentally. Post-pueruli exhibited a highly significant preference for holes in limestone blocks that were surrounded by Amphibolis ($Chi^2 = 33.03$; d.f. = 1; $p < 0.001$). There was also a highly significant, positive relationship between post-puerulus size and the diameter of the hole in the limestone block that they inhabited ($Y = 4.68 + 0.71X$; $R^2 = 0.92$; $n = 35$; $p < 0.001$). Additionally, post-pueruli exhibited a highly significant preference for deeper holes given the choice of 25 mm or 50 mm deep holes ($Chi^2 = 29.26$; d.f. = 1; $p < 0.001$).

Towards the end of summer, the larger post-pueruli (> 20 mm C.L.) were frequently observed sheltering in more open spaces under ledges and in caves, rather than inhabiting small holes in the rock substratum. Analysis (log-linear model fitted to a contingency table - GENSTAT) of data collected in the 1988/89 summer, indicates that the proportion of post-pueruli occupying small holes decreases as post-puerulus size increases ($Chi^2 = 154.4$, df = 3, $p < 0.001$). There is a comparatively large decrease in the percentage of post-pueruli in holes between the 11 - 15 mm C.L. and 16 - 20 mm C.L. size classes (Figure 5).

Post-pueruli occupied similar shelters at each of the limestone reef locations at Seven Mile Beach and Cliff Head, and on the deeper reefs offshore from Seven Mile Beach and Dongara.

Rat Island sites

Post-pueruli inhabited holes and ledges in consolidated-coral reef or the spaces between plates of Acropora sp. coral at 3 of the sites examined in May 1988. The number, and the size range, of post-pueruli at each site are given in Table 2. No post-pueruli were found in areas of coral rubble.

Most of the post-pueruli at Rat Island were in the company of juvenile lobsters, in what appeared to be the equivalent of a den on the coastal limestone reefs. However, the structure forming the dens was different between the coastal and offshore locations. The post-puerulus found at "The Nursery" was in the space between the algal covered plates of a dead coral colony and the four at the "southern coral country" were found in the space between plates of live Acropora coral.

NUMBER OF POST-PUERULI SHELTERING TOGETHER

The number of post-pueruli sheltering either alone or in groups was examined in February 1987 and indicated that, although shelters containing a single post-puerulus were most frequent, the largest proportion of the total number of post-pueruli were in groups (Figure 6). Eight groups of more than 10 animals, represented a large proportion of the total number of post-pueruli that were sheltering in groups. One group, in a small cave in the reef face, contained a large number of post-pueruli and some juveniles, of which most were caught and measured. The sizes of these 93 lobsters ranged from 7 to 30 mm C.L. (Figure 7).

Whereas most of the small post-pueruli occurred alone, more than 80% of the post-pueruli > 20 mm C.L. were found in groups (Figure 8). The interaction, between post-puerulus size (pooled within 5 mm classes to boost sample sizes) and the number of post-pueruli occurring alone, was shown by log-linear analysis of the contingency table to be highly significant ($p < 0.001$, $Chi^2 = 114.1$, $df = 7$). This interaction indicates that the proportion of animals occurring alone decreases as post-puerulus size increases. The change from solitary habits to living in a group appears to follow a fairly linear development through the post-puerulus size range (Figure 8).

NATURAL DENSITIES OF POST-PUERULI

-Accuracy, Precision, Natural densities

Accuracy of diver surveys

-mark-recapture experiments

Divers could only mark (by antennal clipping) 51 of the 94 post-pueruli seen on the first reef and 28 of the 50 post-pueruli seen on the second reef. When the same reefs were surveyed 9 days later, 57 post-pueruli (21 marked) were found on the first reef, and 77 post-pueruli (11 marked) were found on the second. The ratio of marked to unmarked animals at the first sampling was assumed to be the same as at the second sampling and an adjusted estimate (including animals seen but not marked initially) of the "marked" animals was derived. Using Bailey's (1951) equation, the size and variance of the population on these reefs has been calculated. This calculation assumes no movement to or from the reefs. The estimate of the total number of post-pueruli on the first reef is 138 (variance = 140.62) and for the second reef is 148 (var. = 540.83). The numbers of post-pueruli found during the first searches on these 2 reefs were therefore approximately 70 % and 30 % respectively of the total number estimates generated by Bailey's (1951) equation.

-depletion experiments

The first depletion experiment in November 1987 involved removal of all post-pueruli found on a reef, during six searches over 3 days. Ricker's (1975) method for estimating the total theoretical catch, relies on the assumption that the number of animals caught on each successive sampling drops substantially. This was not the case and consequently there was a very poor correlation between the cumulative catch and the log-transformed catch per search ($r^2 = -0.32$, df = 4, $p = 0.54$). The second depletion experiment was also unsuccessful.

Precision of diver surveys

Pilot sampling conducted in November 1986 indicated that divers searching the same area of reef found approximately the same number of post-pueruli (± 1), however about 25 - 50 % of those found on the second search were different individuals. The precision tests in February 1987 also indicated that there is within and between diver variation in the number of post-pueruli found on the same and consecutive day.

Precision between divers, in finding post-pueruli and estimating areas was re-evaluated, during 2 repeated searches in September and November 1988. Data were examined using paired comparison t-Tests. The frequency data were assumed to follow a Poisson distribution and were converted to a normal distribution by square root transformation. The analysis on the transformed data, indicated that there was no significant difference between the number of post-pueruli found by the first diver and the number found by the second diver ($p > 0.1$; $n = 5$ comparisons), for either month. The area-of-habitat data were assumed to be normal and the t-Tests indicated that there is no significant difference between estimates, of the area of habitat searched, made by the first and second diver ($p > 0.1$; $n = 5$), for either month.

The precision tests indicate that the variation between divers in finding post-pueruli and estimating areas is not significant. Therefore the estimates of post-puerulus density based on these data can also be expected to be consistent between divers.

Natural densities

Preliminary analyses of the variation in post-puerulus densities were conducted using the data collected in February and March/April 1987.

The variation in post-puerulus densities within and between reefs was examined on a subset of the data (to acheive a balanced design) from February and March 1987. In February, the number of post-pueruli in three replicate sub-areas within three areas within seven reefs were analysed by a nested analysis of variance. A similar analysis was carried out on the March data, except that there were two areas nested within 11 reefs.

There was no significant difference in the density of post-pueruli within areas of a reef during both sampling times (February: $p = 0.41$, March: $p = 0.83$). In February, there was a significant difference detected between the seven reefs ($p < 0.005$), however a Student-Newman-Keuls multiple range test

(SNK) was unable to detect clear differences between the means for each reef (combined mean = 0.74 ± 0.10 S.E., n = 63, range 0.08 to 1.69). In March there was no significant difference between densities of post-pueruli on each of the 11 reefs (p = 0.96; mean = 0.87 ± 0.11 S.E., n = 66).

A separate analysis was conducted to examine the variation in post-puerulus densities between habitats and reefs. Many of the areas of reefs sampled in February did not contain all of the three habitats (cave, ledge and face). It was not possible to use a balanced, factorial (factors: habitat, reef) analysis of variance to analyse the small balanced subset of data for this sampling period. However this was possible with a balanced subset of the March data. Orthogonal analysis of these data demonstrated no significant interaction in the densities of post-pueruli between the reefs and the habitats (p = 0.89, df = 20, 66). Independence of reef and habitat data were assumed for the February data also. The analysis of the separate factors of habitat and reef were made more powerful by being able to use additional data unsuitable in the two factor design (e.g. all habitats in all areas of a reef were available for analysis of the differences between reefs). The assumption of homogeneity of variances was satisfied by $\log_{10}[x + 1]$ transformation. (All means and ranges given below are untransformed and describe the number of post-pueruli m^{-2}).

The analysis demonstrated that there was no significant difference in the densities of post-pueruli found in caves (mean = 0.64, n = 44) ledges (mean = 0.57, n = 65) or reef faces (mean = 0.57, n = 56) during February 1987 (p = 0.978, df = 2,162). However in March 1987 there was significant variation between habitats (p = 0.005, df = 2,107). The density in ledges (mean = 1.36, n = 52) was shown to be significantly higher than in caves (mean = 0.91, n = 20) and cave densities were higher than face densities (mean = 0.51, n = 38). While the densities of post-pueruli in the face habitat were similar during February and March, the densities of post-pueruli in ledges and caves were higher in March.

There was significant variation in the densities of post-pueruli between reefs during the February sampling (p = 0.000, df = 10,130). A SNK test showed that the reefs could be split into three groups on the basis of their mean densities (p = 0.05). Reefs 45, 3, 29, 35 (range 0.09 - 0.20) had significantly lower densities than reefs 5, 22, 21, 17 (range 0.42 - 0.47) which were lower than densities on reefs 1s, 4, 1n (range 1.21 - 1.49).

There was no significant difference in the densities of post-pueruli between reefs during the March (p = 0.098, df = 10,88). Mean reef densities (for reefs sampled during both periods) were generally higher in March (range 0.57 - 1.69) than in February (range 0.09 - 1.49).

In the analysis of the data from subsequent sampling periods a different design of ANOVA was used as there were insufficient data to acheive a balanced design, using subsets of the data, and to include temporal factors (month and year) in the analysis. Therefore, analysis of the temporal and spatial variation in post-puerulus density was conducted by non-orthogonal analysis of variance, via regression (E. de Boer, CSIRO LRR Biometrics Unit). The data from the sampling periods September and November 1987, January, March, September and November 1988, January and March 1989 were analysed separately for the Seven Mile Beach and Cliff Head sites. Within each site reefs were split into habitats, habitats were split into years and years were split into months.

As the same set of reefs was examined during each sampling period, the density data from each month within a year describe the same cohort of post-pueruli. Therefore the density data collected each month are non-independent within years. Consequently, the significance of terms in the ANOVA which include 'month' was tested using the conservative test of Greenhouse and Geisser (1959). This test excludes the degrees of freedom contributed by the repeated measure. Henceforth, where the significance of terms including 'month' is reported the Greenhouse and Geisser test has been used.

In order to reduce the number of 0 values (no post-pueruli found) in the dataset, the data collected by the 5 divers were pooled within reefs, such that for each reef there was a single estimate of post-puerulus density for each habitat. The absence of a statistical difference between the divers in February and March/April 1987 (see above) and in September and November 1988 (see Precision Tests) further justifies this pooling.

Seven Mile Beach

Examination of the raw data from Seven Mile Beach revealed high frequencies of 0 density values leading to an unacceptable skew in the distribution. Apart from causing the departure from normality, the 0 values also have a different measure of error and hence violate the homogeneity of variances assumption of ANOVA. For these reasons the 0s were excluded from the analysis. It is important to note that most (78%) of the 0 values occurred in the cave habitat. Examination of histograms of the raw data, with the zeroes removed, indicated that the distribution was still skewed. This, and the non random association of residuals vs fitted values, indicated that some form of transformation was required. A non-orthogonal ANOVA was carried out (via regression) on the log. transformed data using the statistical package Genstat V.

The initial ANOVA on the whole data set (0s removed) identified several significant main effects and interactions (Table 3). Reef ($p < 0.05$), habitat ($p < 0.001$), year ($p < 0.01$) and the interactions between them, reefXhabitat ($p < 0.001$), yearXhabitat ($p < 0.01$) and yearXreef ($p < 0.001$) had significant effects on post-puerulus density. Interactions between monthXreef ($p < 0.05$) and monthXyear ($p <0.01$) were also significant.

It was not appropriate to use multiple comparisons tests, as there was a small number of samples and the data were highly non-orthogonal. Therefore, multiple comparisons tests could only provide approximations of the significance of the differences between individual means (E. de Boer, CSIRO LRR Biometrics Unit). Tables of means were examined to identify subsets of the data which were making major contributions to the variance associated with the significant terms in the initial ANOVA. The subset was then removed and the ANOVA re-run. Changes in significance levels (and MS) reflect the contribution towards the term's original variance of the missing subset. The breakdown of the significant terms is outlined below:

-A large proportion of the variation between reefs was shown to be due to a single reef '1s' as when this reef is excluded, the reef term is no longer significant and there is a large reduction in the mean sums of squares (Table 3 - MS).

-The variation between habitats was not so easily partitioned. Although the table of means (Table 4) indicates that post-puerulus densities in the cave habitat are highest, the mean cave densities have been overestimated by the removal of the 0s (as most of the 0s are from caves). When the cave data were excluded from the analysis, there was still significant ($p < 0.01$) variation between habitats (Table 3). This variation indicates that post-puerulus densities are higher in ledge habitats than face habitats (Table 4).

-The variation due to the reefXhabitat interaction also decreased greatly in response to exclusion of the cave data (Table 3).

-Post-puerulus densities were significantly higher ($p < 0.01$) in 1988/89 than in 1987/88 for all habitats and months (Table 4).

-The significance of the reefXyear interaction was largely due to 2 reefs, '46' and '5', being higher in 1987/88 whereas all of the other reefs were higher in 1988/89 (Table 5). Exclusion of the data from these reefs lead to a large decrease in the significance level of the interaction (Table 3).

-Removal of data for Reefs '46' and '5' also lead to the variation due to the month term becoming significant.

-The major contributor to the significant yearXhabitat interaction may be the high density in the cave habitat in 1988/89 (Table 4). However, removal of data from the cave habitat has little effect on the significance of this term (Table 3).

-The yearXmonth interaction is largely due to the very low density recorded for January 1988 compared to the high density recorded for January in 1989 (Table 4). When the data from the January 1988 period are removed the interaction is no longer significant (Table 3).

-The extremely high density of post-pueruli on reef '46' in September (Table 5) was the major contributor to the variance in the monthXreef interaction (Table 3). A very high density of post-pueruli in September 1987 was an overestimate due to a group of lobsters from 25 to 70 mm C.L., whose sizes could not be individually estimated, and for the purposes of this study had to be used as 200 at at least 25 mm (200 x 25 mm C.L.). No survey was conducted in September 1988, and hence the mean value is solely from 1987.

Cliff Head

About half (49%) of the zero values in the Cliff Head data set are estimates of post-puerulus density in the cave habitat. Of the remaining 0s, 44% are for the most southern transect. In order to reduce the skewness of the distribution, the data for the cave habitat, the southern transect, and all remaining 0s, have been excluded from the analysis. The structure of the analysis was consistent with the structure of the Seven Mile Beach analysis.

The initial ANOVA was run (via regression) including all terms -ie. HabitatXTransectXMonthXYear. There were insufficient data to permit inclusion of the fourth order interaction in the model. Therefore the third order interactions were used to test the significance of the lower order interactions and main effects (E. de Boer, personal communication). The results of this ANOVA indicate that there was no significant effect of any of the third order interactions on post-puerulus density ($p > 0.05$).

A second ANOVA was run excluding these higher order interactions. The effect of habitat on post-puerulus density was shown to be significant ($p < 0.05$). Post-puerulus densities in the ledge habitat were always higher than in the face habitat (Table 6).

NATURAL DENSITIES vs COLLECTOR DENSITIES

The numbers of post-pueruli which had settled on the 6 artificial collectors at Seven Mile Beach, during each month in 1987/88 and 1988/89, were supplied by B. Phillips (unpublished data). The monthly puerulus counts were converted to densities by division by the surface area of the collectors (0.549 m^2, B. Phillips personal communication). The natural densities of post-pueruli < 10 mm C.L. on the shallow reefs at Seven Mile Beach were calculated from the data (pooled for diver, habitat and reef) for each of the 8 sampling periods from September 1987 to March 1989.
There was a strong correlation between the density of pueruli and post-pueruli on the collectors and the densities of pueruli and post-pueruli < 10 mm C.L. on the reefs (pooled within site) at Seven Mile Beach ($r = 0.85$, $p < 0.01$). A plot of these data revealed a possibly logarithmic relationship (Figure 9). However, the correlation was weakened slightly ($r = 0.83$, $p < 0.05$) when log(reef density + 0.01) was used. Examination of the density data, pooled over reefs, revealed that most of the newly settled post-pueruli

(< 10 mm C.L.) inhabited the reef face habitat (Table 7). However, the correlation between collector densities and reef densities was little changed by dropping the ledge and cave habitat data ($r = 0.84$, $p < 0.05$).

ARTIFICIAL HABITATS

Thirty five post-pueruli were found in holes in the limestone blocks covered by seagrass in the seagrass beds at Seven Mile Beach. This indicates that limestone blocks, especially with 50 mm deep holes, a range of hole diameters and seagrass cover, provide suitable habitat for post-pueruli.

On each occasion when the other 4 types of artificial habitat and the control plots of Amphibolis were examined, it was only the "Tanikalon" habitats that were occupied by post-pueruli. A total of 25 post-pueruli were found in the "Tanikalon" habitats, 5 at the first site and 20 at the second site. The small mean size of the post-pueruli, 9.27 ± 0.44(SE) mm C.L., suggests that these lobsters had settled into the "Tanikalon" habitat as pueruli.

Transfer of post-pueruli between shelters

Experiments on the response of post-pueruli to capture and transfer between shelters indicated that the disturbance is likely to cause the post-pueruli to abandon their shelters soon after transfer (Table 8).

All of the 20 post-pueruli transferred from artificial collectors to natural shelters in reefs initially refused to enter the shelters. After continued prodding 10 entered the shelters tail first. Four of these animals deserted their shelters and walked off into the surrounding seagrass immediately after the plastic vials used for release were removed. One left its shelter 15 minutes later and the remaining 5 animals had left by the following day. The 12 post-pueruli introduced into shelters in limestone blocks behaved in a similar manner and all shelters had been abandoned by the next day.

Nine of the 18 post-pueruli that were taken from natural shelters were given the choice of re-entering the same shelter or moving off into the seagrass. Of these animals, 7 refused to enter their old shelters and by the following day only 1 shelter was occupied. The other 9 post-pueruli were not given the choice of escape during release into their original shelters and the proportion of shelters occupied the next day was much higher. Five animals stayed in their shelters after the plastic vials used for release were removed and 4 moved off into the seagrass. By the following day, there were 6 animals in the original shelters. Fifteen post-pueruli in natural shelters nearby were observed but left undisturbed, 10 shelters were still occupied the following day.

Eight post-pueruli, taken from shelters in limestone blocks, were given the choice of re-entering their shelters or escaping into the seagrass. Only 2 of these post-pueruli chose to enter the shelters and 3 shelters were occupied the following day. When 8 post-pueruli in shelters in blocks were left undisturbed, all shelters were still occupied the following day.

SIZE/FREQUENCY DATA AND GROWTH

Seven Mile Beach and Cliff Head

Preliminary estimates of post-puerulus size during 1986/87 were generally within 2 mm of the actual size. The precision of size estimates was reassessed in more detail during 1988/89.

During the collection of size/frequency data in 1988/89, 97 post-pueruli and 223 juveniles were measured after their sizes had been estimated visually. The mean of the errors (absolute) associated with visual estimates of lobster size, was calculated for each survey period. Comparison of the standard deviations, shows that the precision of size estimates was always lower for juvenile lobsters than for post-pueruli (Table 9). The pooled mean error was less than 1 mm for post-pueruli and less than 2.5 mm for juveniles. On the basis of these error estimates the size/frequency data were grouped, into 2 mm size classes for lobsters < 25 mm C.L., and 5 mm size classes for lobsters ≥ 25 mm C.L., before analysis. This grouping resulted in considerable smoothing of the size/frequency distributions.

Normal curves were fitted to the smoothed distributions using the MIX or CENSOR programs. Most of the distributions examined had 2 obvious components, the first corresponding to the post-pueruli and the second probably representing the 2+ and 3+ year old juveniles. In the cases where there was little overlap between the 2 components (e.g. Figure 10a) the 2 distributions were fitted separately. Otherwise (e.g. Figure 10b) the components were fitted simultaneously. In some cases, due to truncation in the size distribution corresponding to the minimum size at settlement, a truncated normal distribution had to be fitted to the data.

A growth curve for post-pueruli was derived by plotting the means of the distributions fitted to the first component for each sampling period and site (Figure 11). The means of the distributions fitted by the different methods are identified in the figure. In the case of the data for March 1988 (Chi^2 = 38.31, df = 9, p = 0.0000) and March 1987 (Chi^2 = 22.08, df = 8, p = 0.0048) from Seven Mile Beach, it was not possible to fit a distribution that was not significantly different to the observed distributions (Figure 10b). In the case of March 1988 the post-puerulus and juvenile components of the data were highly overlapped. In March 1987 there was a severe truncation at 25 mm C.L. as only post-pueruli were included in this survey.

The large degree of overlap of cohorts within the juvenile component, in conjunction with the low levels of precision in estimating juvenile sizes, usually made it impossible to fit separate distributions to these cohorts. In the cases where normal distributions could be fitted to the observed juvenile data, the mean sizes of the fitted distributions were plotted (Figure 12). The curves in this figure represent the growth of lobsters for about 2 years from the time of settlement, or until about 3 years of age.

Deeper reefs

Size/frequency data were collected for post-puerulus lobsters at the deeper sites, however the number of post-pueruli found was too small for statistical analysis.

There appeared to be a relatively low abundance of large post-pueruli on some of the deepest reefs towards the end of summer, the time of year when these animals were observed to become more abundant on the coastal reefs. In order to determine whether this is a statistically significant pattern, we calculated the proportion of the total number of post-pueruli that were > 20 mm C.L. at each offshore site, in March 1989. Preliminary analysis indicated that the proportion of post-pueruli > 20 mm C.L. correlates poorly with water depth ($p > 0.05$). The poor correlation is due to the datum for the site on top of Leander Reef, LR1 (Figure 1). This site may be considered atypical in that it lies in an area of extremely high wave energy (sampling at LR1 was conducted during a rare period of very low swell). When this datum is dropped from the analysis, the correlation between water depth and the proportion of post-pueruli > 20 mm C.L. is highly significant ($r = -0.75$, $P < 0.005$).

MOVEMENT BETWEEN SHELTERS

In an experiment examining the distance post-pueruli move overnight, 21 post-pueruli within a 8 m^2 area were marked (by antennal clipping) in their shelters. By the following day 5 were found outside the original area, 11 were found within the original area, and 5 could not be found. The minimum distance moved from the edge of the marked area to the new shelter of 3 post-pueruli (sizes 11, 10, 10 mm C.L.) was 2.6, 3.1, and 3.6 m respectively. Two individuals (sizes 25, 7 mm C.L.) which could be positively identified had moved 5.1 and 4.1 m respectively. The mean minimum distance that the post-pueruli had moved was 3.7 m (S.D. = 0.96, n = 5).

Shelter occupancy

Of the 52 shelters that were observed over 10 consecutive days, 49 % were occupied for at least 2 days and 19 % were occupied on at least 10 days. No shelters were occupied by post-pueruli larger than 15 mm C.L. for longer than 3 days, whereas 22 % of shelters occupied by post-pueruli smaller than 15 mm C.L. were occupied for at least 10 days (Figure 13). This may be an indication that the larger post-pueruli are more likely to leave their shelters, however the sample size of post-pueruli > 15 mm C.L. was too small to test this statistically. Furthermore, we did not know whether the post-pueruli occupying a shelter on consecutive days were the same animal.

NOCTURNAL BEHAVIOUR

Combining the 2 sets of observations of the post-puerulus shelters, conducted at regular intervals over two nights, revealed a pattern in which the lobsters vacated their shelters soon after sunset and occupied shelters just before sunrise. By the time observations were halted, soon after daybreak, nearly 80 % of the shelters were occupied. Although individual post-pueruli could not be identified, the lobsters occupying shelters at dawn were the same size as those that had vacated them at dusk.

FORAGING HABITAT AND DIET

All post-pueruli observed during night dives were in the limestone reef habitat. The post-pueruli appeared to be foraging amongst the algal and seagrass cover on the reef face/tops, ledges and caves and in seagrass detritus. No post-pueruli were observed foraging in the seagrass beds surrounding the reefs. These observations suggest that, although limited to the limestone reefs, the post-pueruli forage over all parts of the reefs.

The foreguts of 91 post-pueruli were examined for dietary components. Forty six of these post-pueruli, had foreguts > 10 % full and it was assumed that these lobsters had been feeding immediately prior to capture. Most (72%) were in inter-moult condition whereas about 50% of the post-pueruli with foreguts < 10 % full were in pre-moult condition (Table 10). The analysis of the foregut contents of the post-pueruli, with foreguts > 10 % full, indicated that a few of the food types make up major proportions of the post-puerulus diet at these sites. Coralline algae (39.95% ± 5.03 S.E.), molluscs (30.59% ± 3.95 S.E.) and unidentifiable digested material (22.78% ± 3.01 S.E.) were the most voluminous constituents of the foregut contents.

The percentage of the 3 most voluminous, identifiable, food categories, coralline algae, molluscs and crustaceans, were compared between post-pueruli of various moult stages (Figure 14). There was a significantly greater percentage of coralline algae in the foreguts of pre- and post-moult animals compared with inter-moult animals (ANOVA $p < 0.05$). There was no significant difference between the moult stages in the percentage of molluscs or crustaceans in the foreguts (ANOVA $p > 0.05$).

POST-PUERULUS COLOURATION

The data collected in September and November 1988 and January and March 1989, indicate without need for statistical confirmation that there is a strong relationship between post-puerulus size and colouration (Figure 15). After settling as clear pueruli, the lobsters moult into post-pueruli and develop the striped colouration which persists until the 11 - 15 mm C.L. size range. By the time the post-pueruli have reached the 16 - 20 mm C.L. size range, they have taken on the non-striped juvenile colouration (Figure 15).

DISCUSSION

The investigation at Seven Mile Beach and Cliff Head was successful in identifying the habitats used by western rock lobsters from the time of puerulus settlement through the post-puerulus stage. The pueruli and the early post-pueruli inhabit small holes in the reef, usually on the reef face and where there is some algae or seagrass growing on the reef. The reef face is covered in dense growth of algae and seems to provide very similar habitat to the artificial seaweed collectors. This supports Phillips (1972) suggestion that puerulus settlement on the collectors simulates natural settlement. For some time after settlement the post-pueruli continue to inhabit small holes in the reef, however the relationship between carapace length and hole size suggests that they move to larger holes as they grow.

The combination of algae/seagrass and rocky substratum used by P. cygnus post-pueruli is similar to the habitats used by other species. Newly settled post-puerulus Panulirus argus inhabit clumps of algae and algal covered rock rubble off the coast of Florida (Andree 1981, Marx 1983, Herrnkind and Butler 1986). Post-puerulus Panulirus interruptus inhabit seagrass beds, in predominantly rocky habitat with dense plant cover, off the Californian coast (Parker 1972, Serfling 1972, Engle 1979). In Japan, post-puerulus Panulirus japonicus inhabit small holes near algae on the side or underside of rocks and boulders in shallow coastal waters (Yoshimura and Yamakawa 1988).

At some time before reaching juvenile size, usually by the 16 - 20 mm C.L. size range, the post-puerulus western rock lobsters move into larger spaces and the company of other lobsters and thus begin to share the den habitat of the juveniles. It is unknown whether the post-pueruli move because they can no longer find holes of the right dimensions or whether they actively seek to enter the juvenile habitat and the company of larger lobsters. In an aquarium study, Phillips et al (1977) observed that post-pueruli "were not particularly gregarious" until reaching about 20 - 25 mm C.L.. At about this size the post-pueruli gradually abandoned their solitary habits and formed groups under a larger shelter.

Post-pueruli commonly occur in the juvenile den habitat from around 15 mm C.L. and it is perhaps only a matter of chance that they had never been found at this size in any numbers before. The definition of the post-puerulus stage can be refined now that aspects of the physical and behavioural transition to the juvenile stage have been documented. Post-pueruli develop juvenile colouration, habitat use and gregarious behaviour during the 15 - 20 mm C.L. size range. By the time they reach the 20 - 25 mm C.L. range most lobsters exhibit juvenile characteristics. On the basis of this, the most appropriate size of dilineation between post-pueruli and juveniles is probably 20 mm C.L., although the transition is a gradual process through the 15 - 25 mm C.L. range. This is also consistent with the development of adult spination of the antennal plates and carapace in post-pueruli of this species at 21 mm C.L. (George 1958).

Once the habitat of the post-pueruli had been determined, the natural densities at which the post-pueruli occurred were assessed. Diver estimates of post-puerulus abundance and density were found to be acceptably (5 % level) consistent between divers. Fortunately large differences between divers in levels of experience were avoided by maintaining the same group of divers through out the study. Engle (1979) attributed different encounter and capture rates during visual surveys of post-puerulus P. interruptus to different levels of diver experience.

The precision of the diver estimates of post-puerulus density indicates that they provide a useful index of natural densities and hence meaningful assessment can be made of variation in densities. Inaccuracy in density estimates, assuming that the error is randomly distributed, may tend to obscure patterns of post-puerulus density. However, analyses of the density data identified considerable spatial and temporal variation.

Spatial variation in post-puerulus densities was demonstrated for between site, reef and habitat comparisons. The mean densities at Seven Mile Beach, ranging from 0.11 to 1.93 post-pueruli m^{-2}, were consistently higher than at Cliff Head (0.04 to 0.90 post-pueruli m^{-2}). This is consistent with the impression Joll and Phillips (1984) gained of the densities of juveniles at the same sites in 1977/78.

There was significant variation between reefs at Seven Mile Beach, however there were no obvious spatial patterns in the variation except the consistently high densities on a single reef '1s'. There are several plausible explanations as to the source of the variation between reefs e.g.

the vagaries of the currents carrying the pueruli into the study area, different amounts of suitable settlement habitat on different reefs, different levels of topographic complexity leading to different levels of searching efficiency. Another factor which must be taken into account is the release, as part of a tagging study (Phillips unpublished data), of numerous post-pueruli on Reef '4' which is close to the reef with the highest densities. The densities on Reef 4 were not particularly high and it is possible that there had been some movement of post-pueruli to Reef '1s'. Post-pueruli on these reefs were not checked for the internal tags as the capture and handling would have caused considerable disturbance and possibly injury to the post-pueruli, which may have affected the experiment in progress.

The significance of the variation in reef densities in relation to month and year may indicate changing patterns of puerulus input into the area or reflect the dynamic nature of the reef habitats. There was often considerable movement of sand around reefs between survey periods which could lead to some ledges being filled in and others being excavated. Newly excavated ledges usually had less algal and invertebrate growth and hence the movement of the sand could lead to changes in the amount of suitable habitat.

Densities in the ledge habitat were generally higher than in the face habitat at both Seven Mile Beach and Cliff Head. Although the densities in the cave habitat were shown to be the highest, this is probably an effect of excluding zero values from the analysis. As cave densities were calculated only for caves where post-pueruli were present, and the area of these caves was usually small, the estimate of mean cave density is overestimated and the variance is underestimated. Furthermore, as the distinction between caves and ledges could not always be made on an objective basis and there appeared to be little biological reason to make the distinction, the cave and ledge habitats should be treated as one.

There was a significant pattern of increasing density through time. Post-puerulus densities increased from month to month within years and were higher in 1988/89 than in 1987/88. The increases within years are due partly to the cumulative addition of newly settled post-pueruli to the population. There was probably also some increase in the divers' searching efficiency due to increasing post-puerulus size and diver experience.

The significant level of variation in monthly densities, within habitats, also indicates that there is a seasonal movement of post-puerulus between the habitats. The density of newly settled lobsters (< 10 mm C.L.), mainly in the reef face habitat, has a seasonal peak in September to November as demonstrated by the indices of both natural and collector settlement. However this is not reflected in the densities in the face habitat being significantly higher than in the ledge habitat during the settlement period, probably due to the presence of large post-pueruli in the ledges. These large post-pueruli presumably settled late in the previous season and grew slowly in the colder water during winter. The movement of post-pueruli into the ledge habitat, the increase in abundance due to continual settlement and an apparent increase due to increasing catchability (likelihood of being seen) with increasing size, through time also affect seasonal trends. The change from early post-puerulus habitat to juvenile habitat is also reflected in the data from February and

March 1987. In February the post-pueruli were evenly distributed over the habitats on the reef, whereas by March they had aggregated in the ledge/cave habitat.

It was hoped that by accurately measuring the actual densities of post-pueruli in natural habitats we could determine natural settlement densities in relation to collector densities and natural post-puerulus mortality rates. This would then facilitate refinement of the population models used in predicting the commercial catch of lobsters (Phillips 1986). However the difficulties encountered in finding post-pueruli and subsequently measuring their abundance lead to inaccurate estimates of natural density and hence the inability to assess natural mortality rates.

The cryptic nature of the early post-pueruli, acheived through camoulflage and behaviour, is undoubtedly the major contributor to the low accuracy levels of diver surveys. The depletion experiment assessments of diver accuracy indicated high levels of error which were also partly attributable to areas that were inaccessible to visual survey e.g the roof of caves with entrances which were too low for a diver to fit his head under. Other major causes of inaccuracy in diver surveys were low visibility and strong surge underwater, and factors such as water temperature and carnivorous eels with great gnashing fangs which affect divers' concentration and hence searching efficiency.

Mark/recapture experiments indicated that 30 - 70 % of the post-pueruli were not found on the first search, however there is some doubt about the assumption of equal catchability of marked and unmarked post-pueruli. Many post-pueruli, particularly small ones, can only be seen when they move their antennae and sometimes only one antenna is visible. Hence, in some cases the catchability (likelihood of being seen) of post-pueruli with a clipped antenna would be reduced. This would lead to an overestimate of the population size.

The density estimates from visual surveys and from mark/recapture experiments were of the same order of magnitude. However, the inaccuracy in density estimates, made by divers, indicates that this method is useful only for deriving an index of settlement. The high correlation between this index of natural settlement and the collector index of settlement, suggest that the two indices may be equally useful for the current models predicting recruitment to the catchable stock of lobsters. Therefore, the diver survey method may provide a useful, alternative, means of monitoring settlement in places where collectors cannot be deployed.

Settlement on collectors is monitored over a month (Phillips 1972, 1986), however this is not practical in areas of rough water where there is a high likelihood of damage or loss of collectors. In such areas a team of divers could choose a short period of good weather and assess the last months settlement rapidly.

Howard (1988) found that predation by fish on the nursery reefs was concentrated on the newly settled post-pueruli (8 - 15 mm C.L.). He estimated that fish predators annually remove thousands of lobsters per hectare and suggested that predation is a major factor limiting the survival of P. cygnus on the nursery reefs. As the fishery yield is tightly linked to the production of juveniles on the nursery reefs it is strongly influenced by mortality events on these nursery reefs (Howard 1988). Therefore, if the mortality rate of post-pueruli can be reduced e.g by providing protection from predators, there may be significant benefits in terms of increased juvenile production and hence increased yield to the fishery. Chittleborough (1970) suggested that a practical approach to increasing recruitment of P. cygnus would be the distribution of artificial shelters along the coast.

Knowledge of the natural habitat requirements of post-pueruli was used in the design of artificial habitats with some success. The "Tanikalon" fibres have previously been shown to be suitable habitat for pueruli and post-pueruli (Phillips 1972), this was supported by our findings. In this study the limestone block habitat was also found suitable for post-puerulus habitation. However the success of an artficial shelter program, incorporating the tested designs, would depend on several factors which require further investigation.

The design of artificial shelters would have to take into account the changing habitat requirements of the lobsters from puerulus, through post-puerulus to migratory juvenile size. The sites chosen for the deployment of artificial shelters would need to be in areas of high puerulus settlement, where survival is limited by natural shelter and there is suitable foraging habitat and an adequate food supply for all stages. It is important to stress the need for further research on these factors, and the impact of such a program on the marine ecosystem, before attempting stock enhancement through provision of artificial shelter.

Another approach to enhancing post-puerulus survival is to manipulate stocking densities on the nursery reefs. Chittleborough (1970) and Chittleborough and Phillips (1975) suggest that transfer of early juveniles (post-pueruli), from areas of high puerulus settlement to areas of low puerulus settlement, could increase productivity of the low settlement area without having a significant effect on the high settlement area. Fluctuations in the level of puerulus settlement, detected by trends on the collectors, are apparently smoothed by density dependent processes operating on the early juvenile lobsters (post-pueruli) soon after settlement (Chittleborough and Phillips 1975). During periods of high settlement, the limited carrying capacity of the nursery reefs limits recruitment to the adult stock (Chittleborough 1970). At the same time, other areas may receive low levels of puerulus settlement which prevent the reefs from reaching their potential carrying capacity (Chittleborough 1970).

To gain an indication of the suitability of post-pueruli for stocking areas of low puerulus settlement, it is necessary to know whether post-pueruli can be transferred between shelters ie. will they accept the new shelter? Evidence from this study suggests that post-pueruli would be poor candidates for such transfers. The percentage of post-pueruli that remained in the shelter they had been transferred to was extremely low. After disturbance post-pueruli tend either not to enter the new shelter or to leave by the following day. Observations of post-pueruli out in the open during the day or night indicate that mortality due to predation would be very high on post-pueruli rejecting a shelter. Psammaperca waigiensis is the most consistent predator on post-pueruli at Seven Mile Beach (Howard 1988) and as this fish is a nocturnal or crepuscular hunter (Howard 1988) it may represent a grave threat to post-pueruli changing shelters during the night.

Different growth rates of juvenile *P. cygnus* were observed at Seven Mile Beach and Cliff Head in 1972/73 (Chittleborough 1976). Juvenile growth at Seven Mile Beach was retarded in comparison with rates observed in aquaria, while the growth at Cliff Head was faster than at Seven Mile Beach and equal to the aquarium rates (Chittleborough 1976). Chittleborough concluded that population density plays a role in depressing growth rates at high density sites, but that there are also other factors involved. Joll and Phillips (1984) also reported lower densities and faster growth at Cliff Head in comparison with Seven Mile Beach in 1987/88. However, they observed an "obvious association" between diet and growth rate at these sites.

There is some evidence from the present study that a density:growth relationship existed for post-pueruli at Seven Mile Beach and Cliff Head in 1987/88. In 1987/88, Seven Mile Beach supported higher densities of post-pueruli than Cliff Head and the growth of post-pueruli at this site was lower. At Cliff Head, where the densities were lower, growth in 1987/88 was higher than at Seven Mile Beach and equal to, or in excess of, that in aquaria. In 1988/89 however there was still a discrepency in post-puerulus densities, yet the growth was consistent between sites.

The nocturnal activity pattern of post-pueruli is similar to that of older *P. cygnus* (Cobb 1981, Phillips *et al* 1977, Jernakoff 1987), but the post-pueruli were observed to forage in different habitats. Juveniles forage mainly in the *Amphibolis* and *Heterozostera*/*Halophila* seagrass beds in the Seven Mile Beach area (Jernakoff 1987), whereas post-pueruli were only observed on the limestone reefs. However, more thorough sampling of the seagrass beds needs to be conducted at night. Chittleborough (1976) suggested that the relatively good growth during the first post-larval year (post-pueruli) indicated that post-pueruli and juveniles were not in direct competition with each other. The apparent separation of foraging habitats observed in this study is a possible mechanism for reducing intraspecific competition.

Comparison of the diet of post-pueruli, from this study, with that of juveniles (Joll and Phillips 1984), indicates that both groups consume large amounts of coralline algae and varying quantities of molluscs. The proportion of molluscs in the diet of post-pueruli was related to moult stage, and the proportion in the juvenile diet was related to study site. Most of the post-pueruli and juveniles (Joll and Phillips 1984) that had been feeding (foreguts > 10% full) were in intermoult condition, suggesting that post-pueruli in pre- and post-moult are less likely to feed. This is consistent with the observations of Chittleborough (1974) that *P. cygnus* in aquaria cease to eat for several days immediately before and after moulting.

The settlement of shallow water Palinurids is generally restricted to areas in depths of 1-4 metres, although the pueruli of some species may be able to settle in both shallow and slightly deeper areas (Kanciruk 1980). In the case of *P. cygnus*, Chittleborough (1970) states that juveniles are mainly concentrated in depths less than 10 metres, with some larger juveniles to 18 metres. However, post-puerulus *P. cygnus* have been pulled up on the ropes of lobster pots which were fishing in about 80 metres of water (George 1958) and juveniles (< 50 mm C.L.) have been caught at about 40 metres depth (R.Brown Fisheries Dept. of W.A. personal communication). The discovery of pueruli and post-pueruli at the deeper Leander Reef site indicates that settlement of *P. cygnus* occurs to at least 30 m, and there is no reason to predict that settlement does not occur in water deeper than 30 m. Heydorn (1969c) reported 40 mm C.L. Jasus lalandii at 140 feet (approx. 45 m) at Vema Seamount, which as it is isolated by depth indicates that settlement occurred on the seamount which is 20 m deep at the apex (Kanciruk 1980). The observations of these two species suggests that deeper water settlement of pueruli may be more common in Palinurid species than previously thought.

The presence of a large population of J. lalandii on Vera Seamount before 1966, presumably originating from deeper water settlement (Heydorn 1969c), indicates that such settlement is successful, in terms of survival to adulthood, in this species. However, in the case of P. cygnus there was a decrease in the proportion of large post-pueruli (> 20 mm C.L.) with increasing water depth. There may be several reasons for this e.g. higher mortality of the post-pueruli at the stage when they initially occupy the juvenile den habitat on the deeper reefs, retarded growth rates in deeper water, or failure to find aggregations of the large post-pueruli during the preliminary surveys in deeper water. Further research is needed to clarify this and other questions raised by the study.

LITERATURE CITED

Andree, S.W. (1981). Locomotory activity patterns and food items of benthic postlarval spiny lobsters, Panulirus argus. M.Sc. Thesis. Florida State University. 50 pp.

Bailey, N.T.J. (1951). On measuring the size of mobile populations from capture - recapture data. Biometrika 38: 293-306.

Chittleborough, R.G. (1970). Studies on recruitment in the western Australian rock lobster Panulirus longipes cygnus George: density and natural mortality of juveniles. Aust. J. Mar. Freshw. Res. 21: 131-148.

Chittleborough, R.G. (1974). Review of prospects for rearing rock lobsters. Australian Fisheries 4 (33)

Chittleborough, R.G (1976). Growth of juvenile Panulirus longipes cygnus George on coastal reefs compared with those reared under optimal environmental conditions. Aust. J. Mar. Freshw. Res. 27: 279-95.

Chittleborough, R.G., Phillips, B.F. (1975). Fluctuations of year-class strength and recruitment in the western rock lobster Panulirus longipes (Milne-Edwards). Aust. J. Mar. Freshw. Res. 26: 317-328.

Cobb, J.S. (1981). Behaviour of the Western Australian spiny lobster, Panulirus cygnus George, in the field and laboratory. Aust. J. Mar. Freshw. Res. 32: 399-409.

Engle, J.M. (1979). Ecology and growth of juvenile California spiny lobster, Panulirus interruptus (Randall). Ph.D. Thesis. University of Southern California. 298 pp.

George, R.W. (1958). The biology of the Western Australian commercial crayfish Panulirus longipes. PhD Thesis, University of Western Australia.

Greenhouse, S.W., Geisser, S. (1959). On methods in the analysis of profile data. Psychometrika 24: 95-112.

Herrnkind, W.F., Butler, M.J. (1986). Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters Panulirus argus. Mar. Ecol. Prog. Ser. 34: 23-30.

Heydorn, A.E.F. (1969c). The South Atlantic rock lobster *Jasus tristani* at Vema Seamount, Gough Island and Tristan Da Cunha. Investl. Rep. Div. Sea Fish. S. Afr. 73: 1-20.

Howard, R.K. (1988). Fish predators of western rock lobster (*Panulirus cygnus* George) in a nearshore nursery habitat. Aust. J. Mar. Freshwat. Res. 39: 307-316.

Jernakoff, P. (1987). Foraging patterns of juvenile western rock lobsters *Panulirus cygnus* George. J. Exp. Mar. Biol. Ecol. 113: 125-144.

Jernakoff, P., Phillips, B.F., Maller, R.A. (1987). A quantitative study of nocturnal foraging distances of the western rock lobster *Panulirus cygnus* George. J. exp. mar. Biol. Ecol. 113: 9-21.

Joll, L.M. (1982). Foregut evacuation of four foods by the western rock lobster *Panulirus cygnus* in aquaria. Aust. J. Mar. Freshw. Res. 33: 939-943.

Joll, L.M., Phillips, B.F. (1984). Natural diet and growth of juvenile western rock lobsters *Panulirus cygnus* George. J. Exp. Mar. Biol. Ecol. 75: 145-169.

Kanciruk, P. (1980). Ecology of juvenile and adult Palinuridae (spiny lobsters). Chapter 2 in Cobb, J.S and Phillips, B.F. (1980) The biology and management of lobsters, Volume II: Ecology and management. Academic Press, Inc.

Marx, J. (1983). Aspects of microhabitat use by young juvenile spiny lobsters, *Panulirus argus*. M.Sc. thesis, Florida State University, Tallahassee. 57 pp.

Parker, K.P. (1972). Recruitment and behaviour of puerulus larvae and juveniles of the California spiny lobster *Panulirus interruptus* (Randall). M.Sc. thesis, San Diego State University. 95 pp.

Phillips, B.F. (1972). A semi-quantitative collector of the puerulus larvae of the western rock lobster *Panulirus longipes cygnus* George (Decapoda, Palinuridae). Crustaceana. 22: 147-154.

Phillips, B.F. (1986). Prediction of commercial catches of the western rock lobster *Panulirus cygnus*. Can. J. Fish. Aquat. Sci. 43: 2126-2130.

Phillips, B.F., Campbell, N.A., Rea, W.A. (1977). Laboratory growth of early juveniles of the western rock lobster Panulirus longipes cygnus. Mar. Biol. 39: 31-39.

Phillips, B.F., Joll, L.M., Ramm, D.C. (1984). An electromagnetic tracking system for studying the movements of rock (spiny) lobsters. J. exp. mar. Biol. Ecol. 79: 9-18.

Ricker, W.E. (1975). Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Canada 191: 382 pp.

Serfling, S.A. (1972). Recruitment, habitat preference, abundance and growth of the puerulus and early juvenile stages of the California spiny lobster, Panulirus interruptus (Randall). M.Sc. thesis San Diego State University 124 pp.

Sheard, K. (1962). The Western Australian crayfishery, 1944 - 1961. Peterson Brokensha Pty, Ltd., Perth Australia 107 pp.

Yoshimura, T., Yamakawa, H. (1988). Ecological investigations of settled puerulus and juvenile stages of the Japanese spiny lobster Panulirus japonicus at Kominato, Japan. J. Crustac. Biol. 8: 524-531.

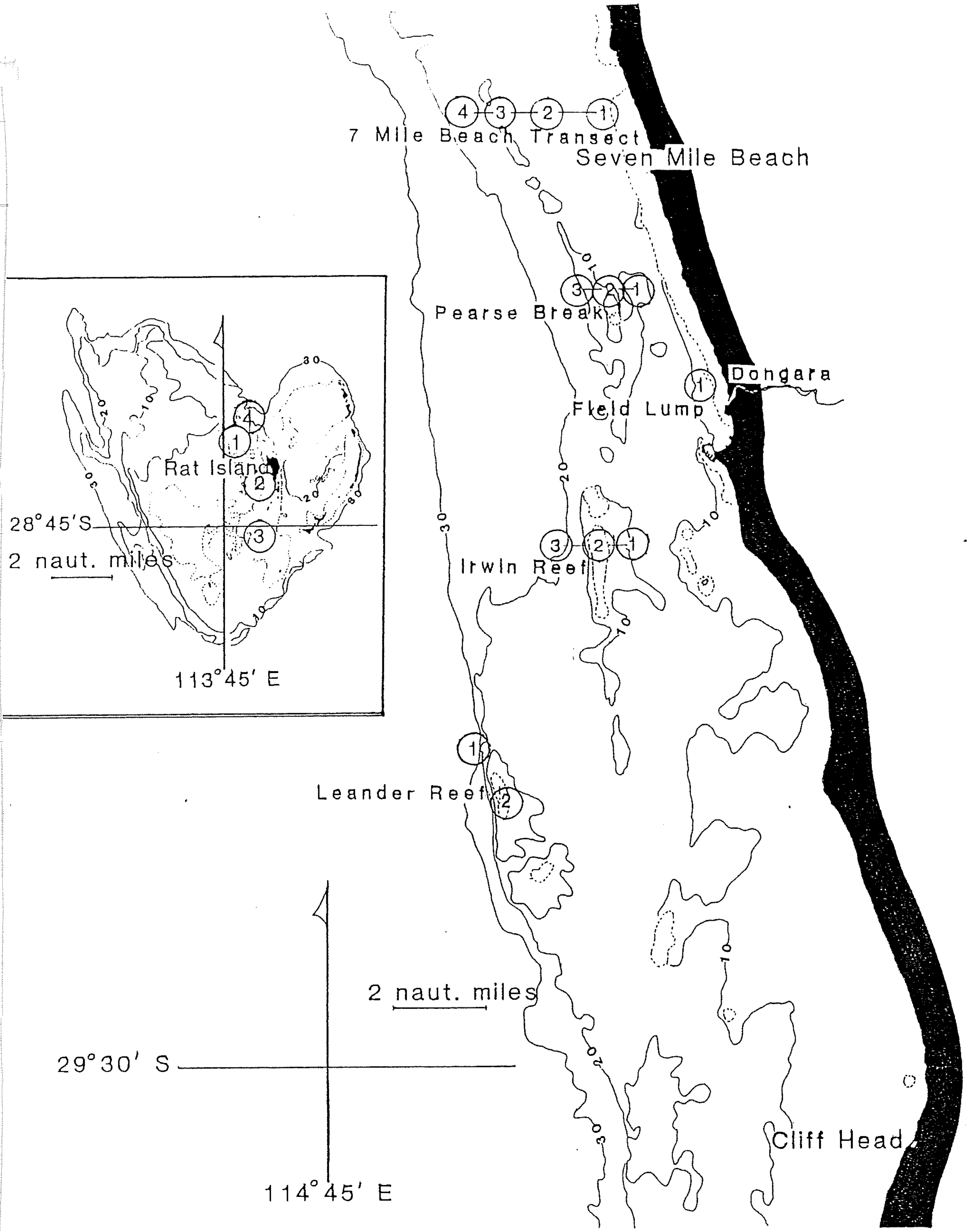

Figure 1: Map of study sites where searches for post-puerulus *P. cygnus* were conducted. The shallow coastal, locations, Seven Mile Beach and Cliff Head and the deeper, offshore reefs; Leander Reef, Irwin Reef, Pearse Break, Field Lump and the Seven Mile Beach transect are marked. Rat Island is also marked (inset). The circled numbers indicate the approximate position of the study sites at each location. Depths in metres.

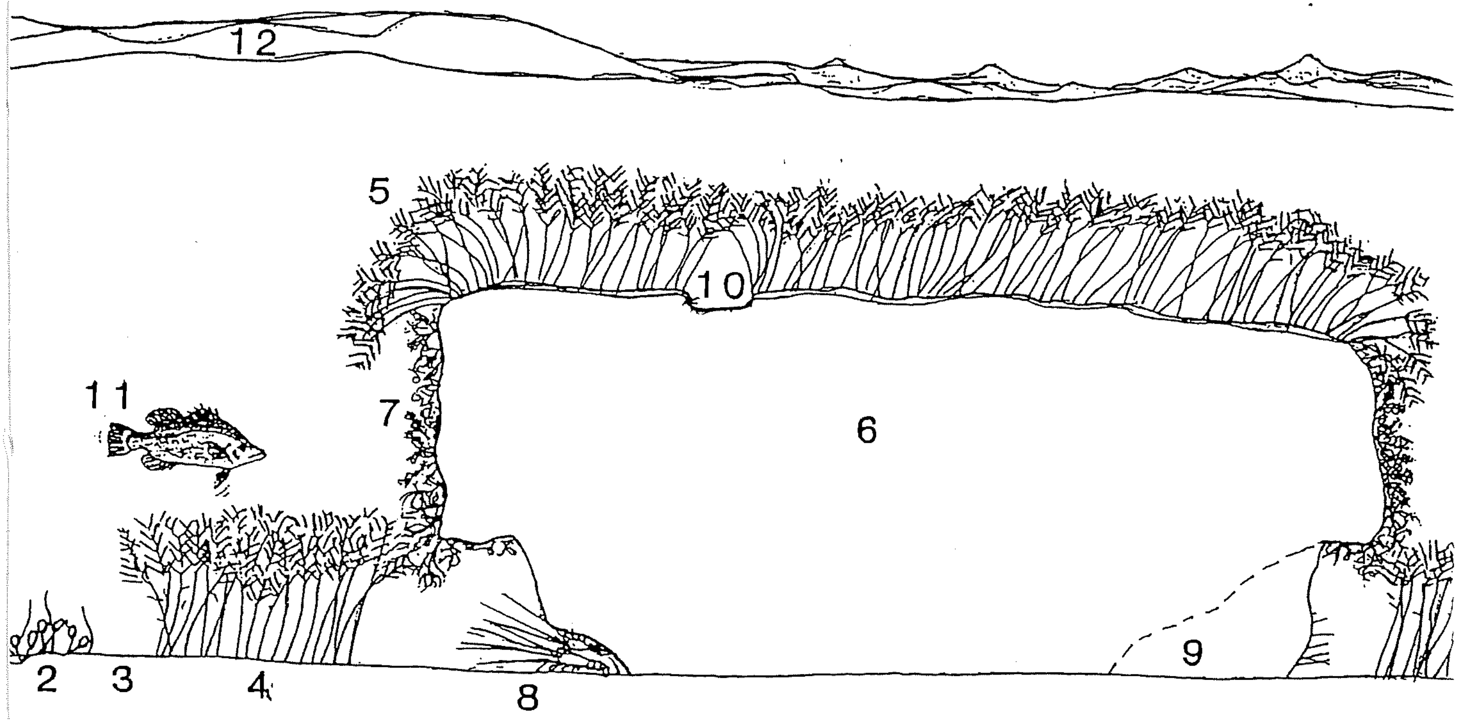

Figure 2: Stylised cross-section of a limestone reef at Seven Mile Beach. 1 = rock rubble, 2 = *Heterozostera*/ *Halophila*, 3 = sand, 4 = *Amphibolis* on seabed, 5 = *Amphibolis* on reef top, 6 = limestone reef, 7 = reef face with algal/invertebrate cover, 8 = ledge in use as juvenile lobster den, 9 = cave, 10 = coralline algal encrusted limestone, 11 = predatory fish *Psammaperca waigiensis*, 12 = water surface.

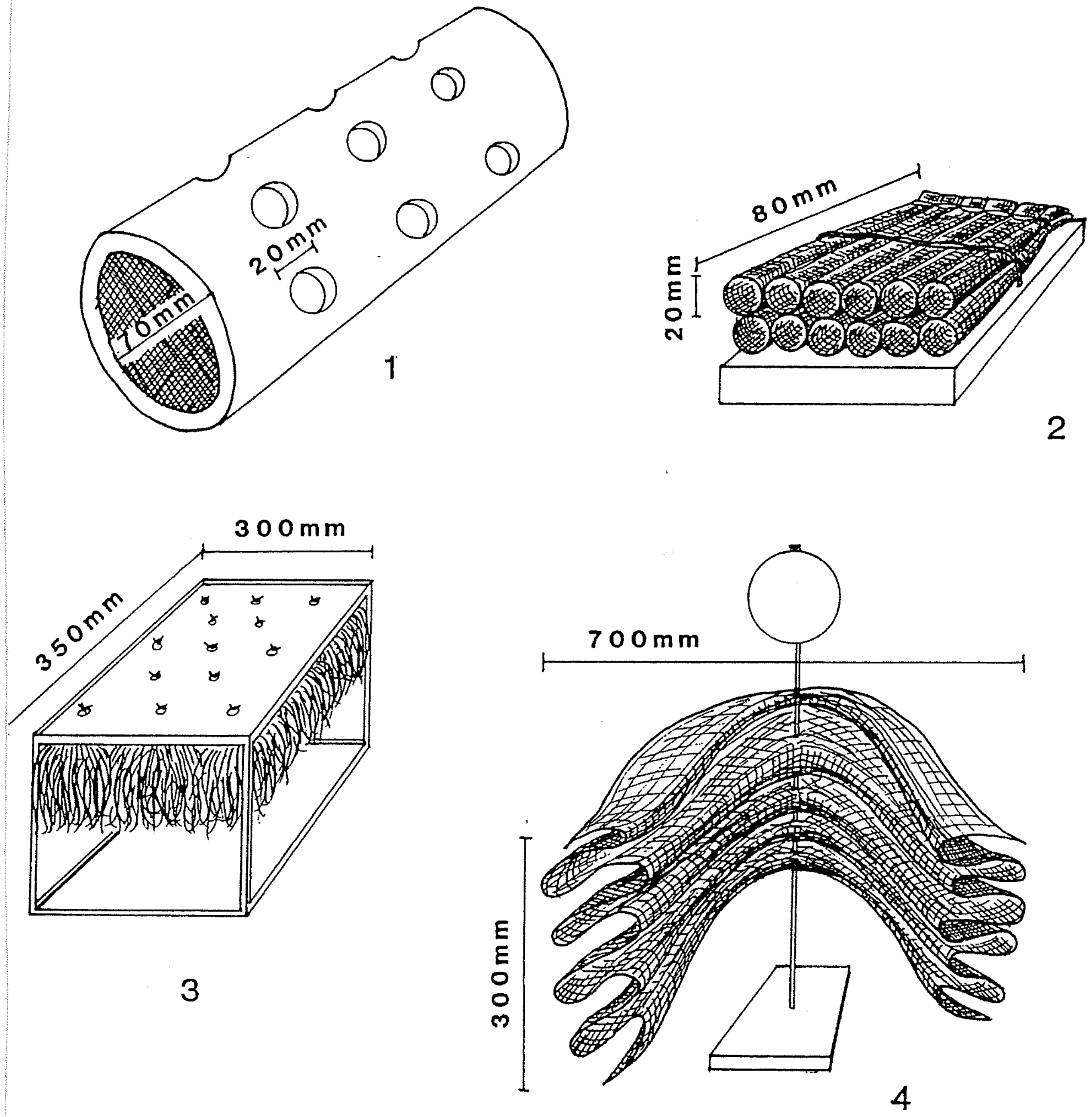

Figure 3: Artificial habitat types. Type 1 is a concrete cylinder with 12 holes drilled in it, both ends are blocked with plastic mesh. Type 2 is a set of black PVC mesh cylinders, clamped at one end and wired to a steel weight. Type 3 is a mat of synthetic rope fibres attached to a plastic sheet, mounted on a steel frame such that the fibres hang down. Type 4 is a concertina of fibre mesh on a rope suspended between a float and a steel weight.

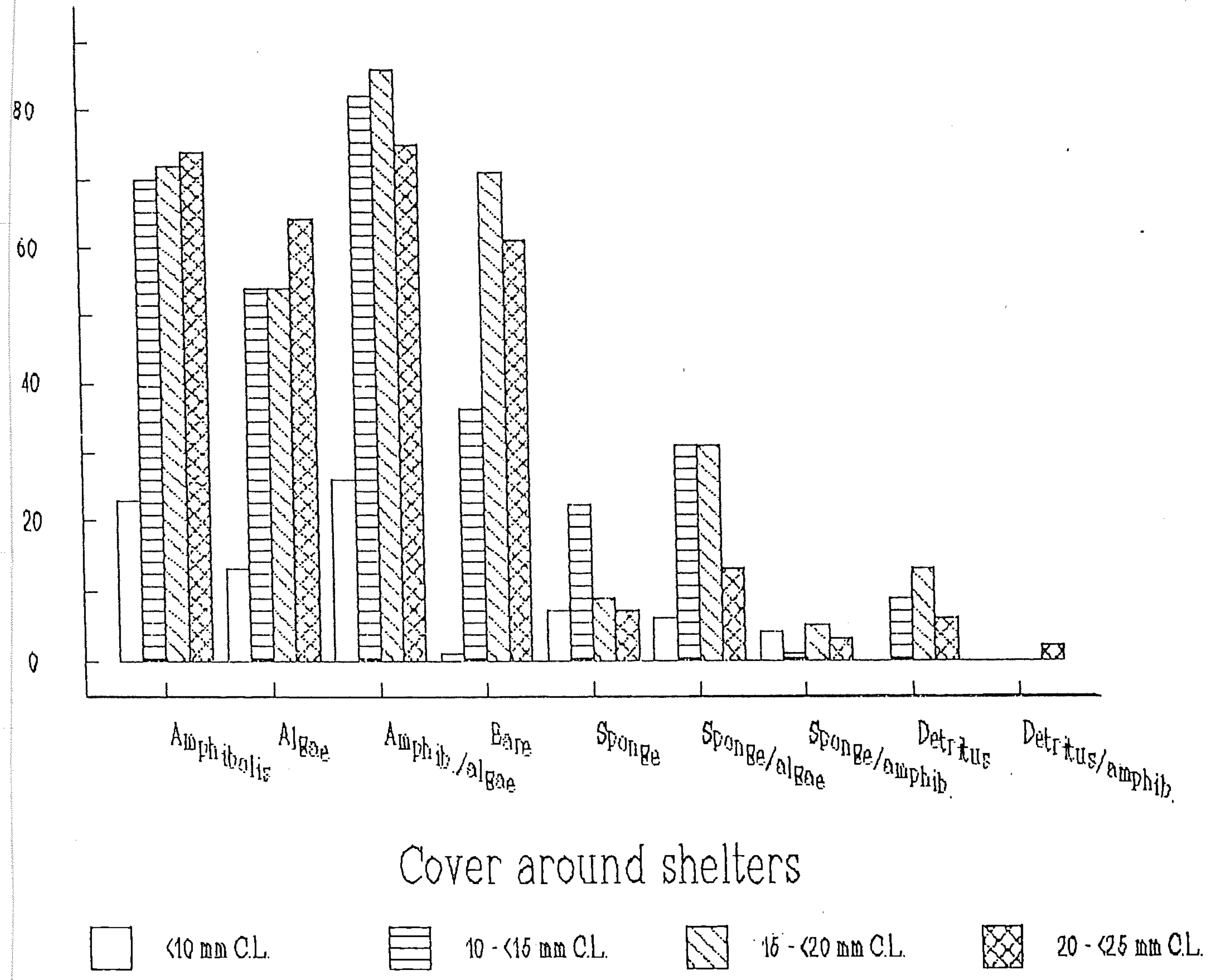

Figure 4: Cover around post-puerulus *P. cygnus* shelters. The frequency of post-puerulus shelters that were surrounded by various types of cover/growth. The 4 bar types represent the 4 size classes (mm carapace length) of post-pueruli in the shelters. Amphib. = *Amphibolis*.

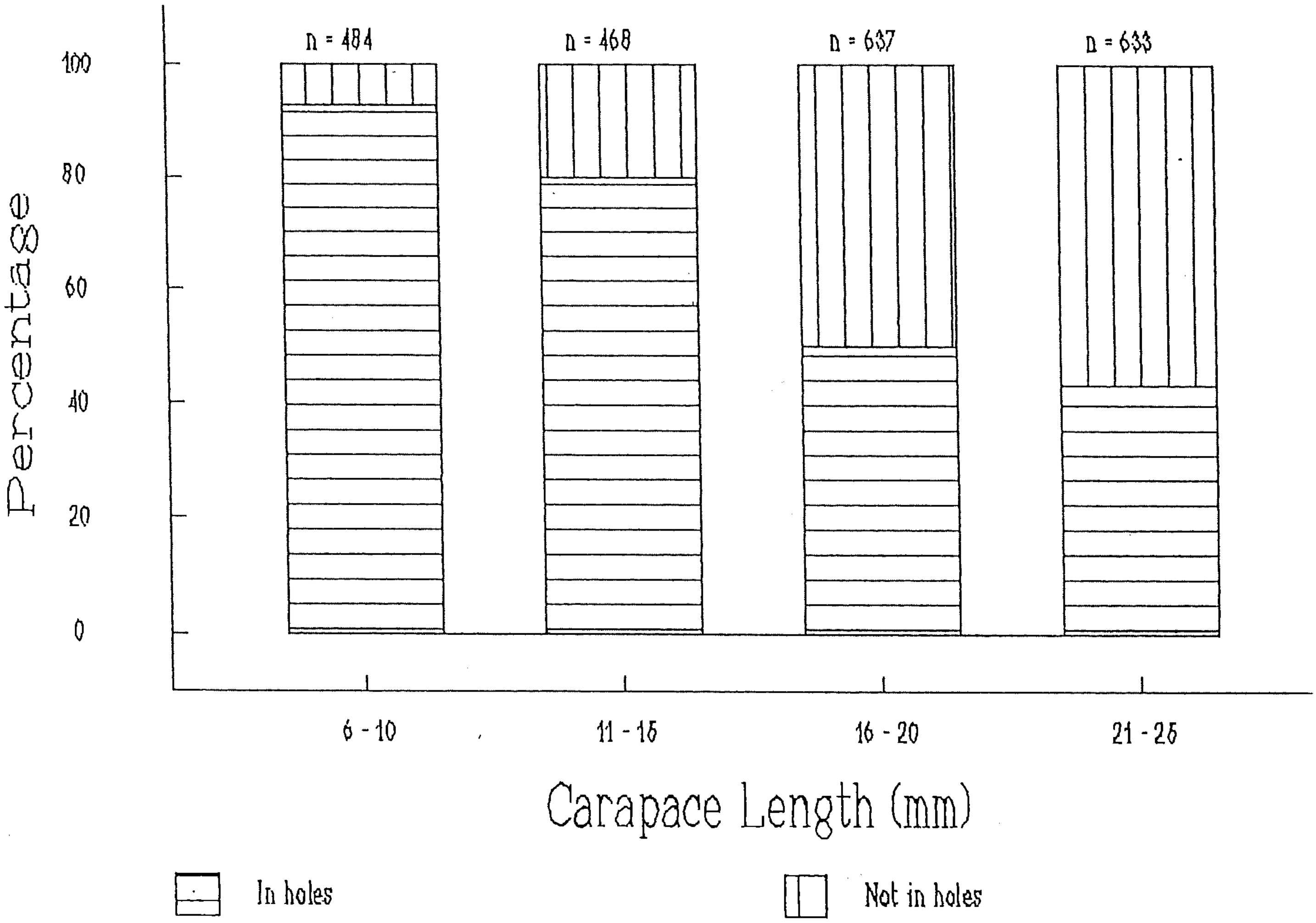

Figure 5: The percentage of post-puerulus P. cygnus that were found in holes of about body size and the percentage found in larger spaces. Data are from sites at Seven Mile Beach, Cliff Head and deeper reefs off Dongara sampled in 1988/89.

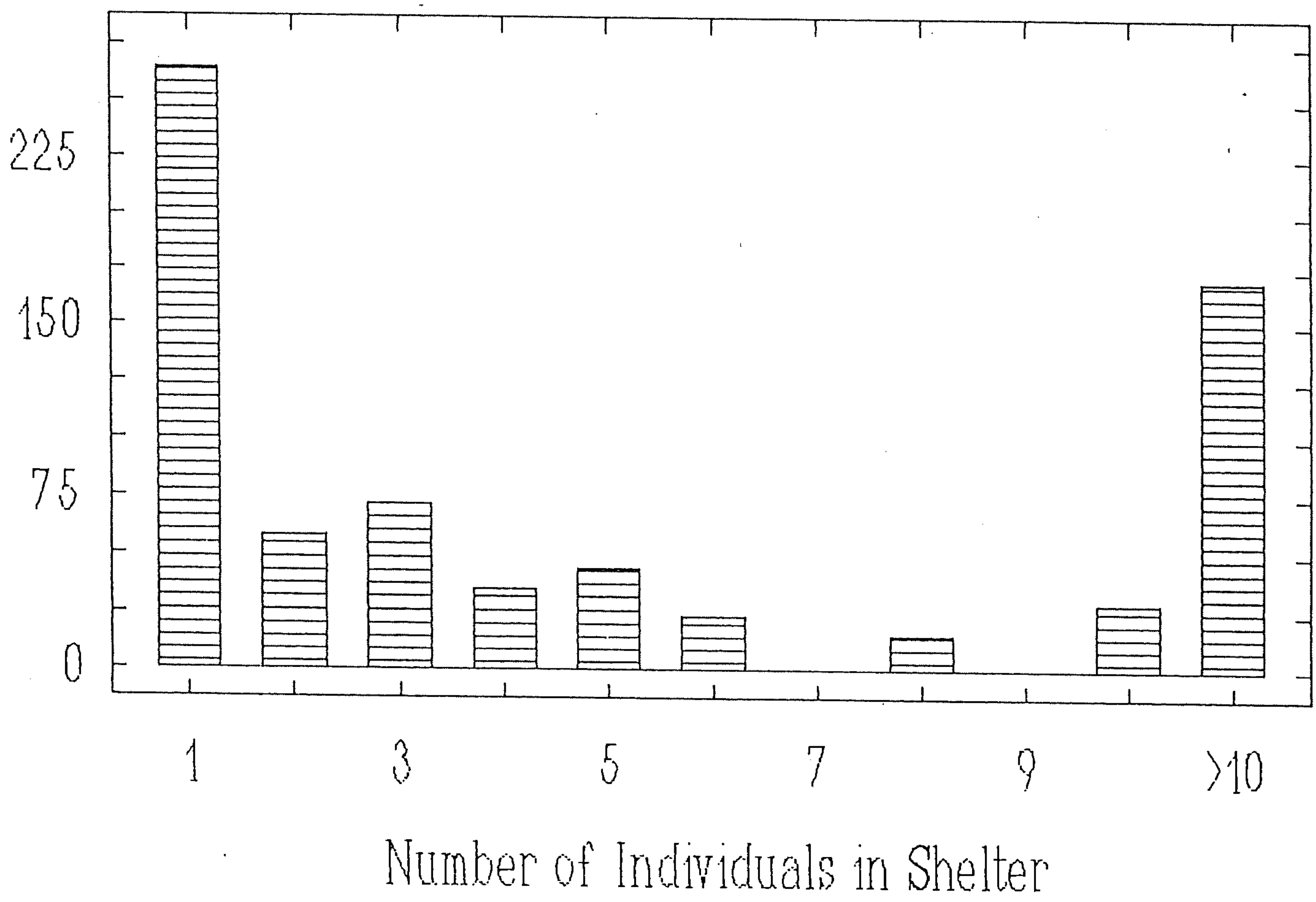

Figure 6: Number of post-puerulus P. cygnus sheltering together. The histogram shows the number of post-pueruli that were found either alone or in groups of various numbers of individuals, in February 1987.

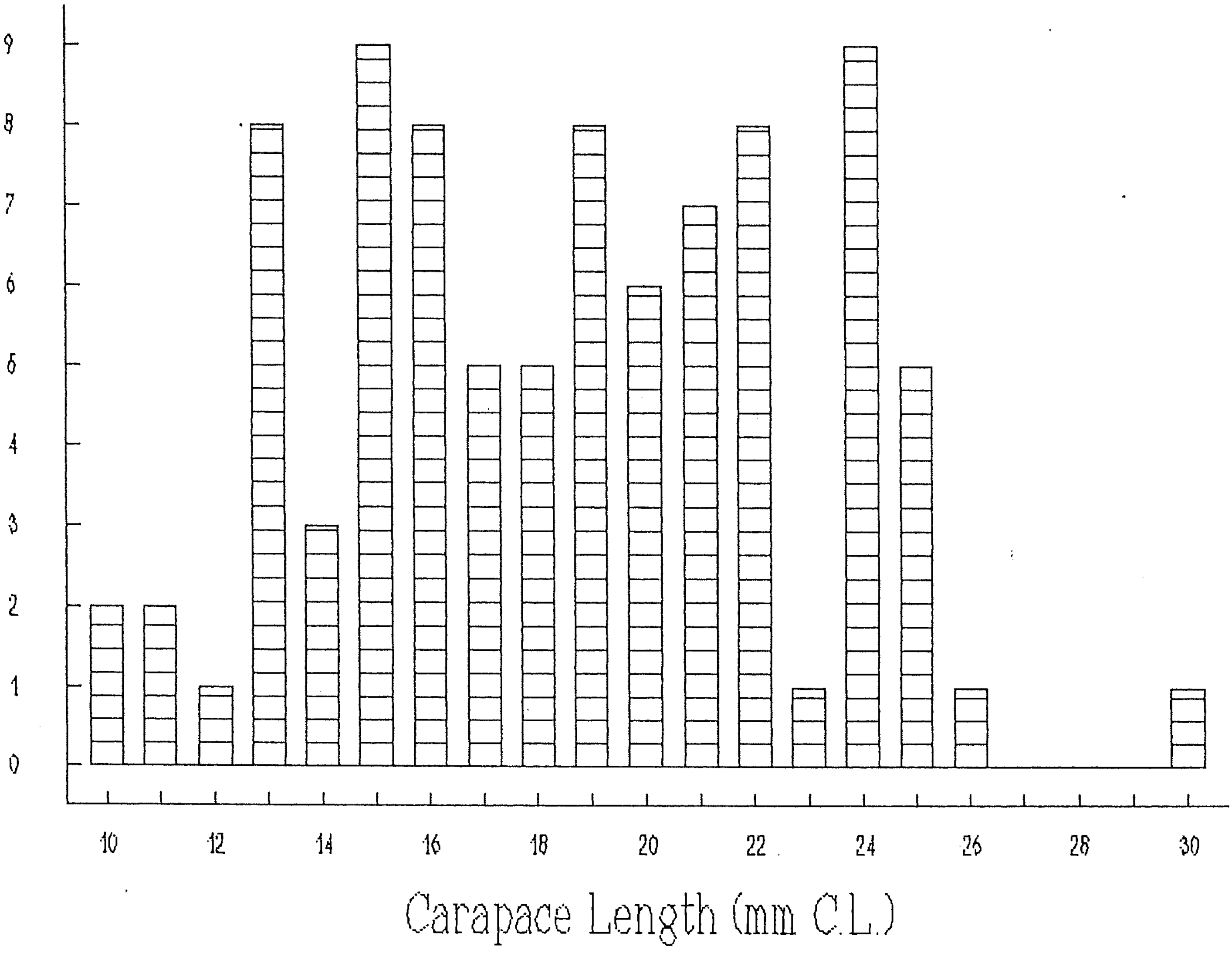

Figure 7: Size distribution of P. cygnus post-pueruli and juveniles in the same cave. The size/frequency plot describes 91 post-pueruli and 2 juveniles that were found sheltering together in a small cave on a reef at Seven Mile Beach.

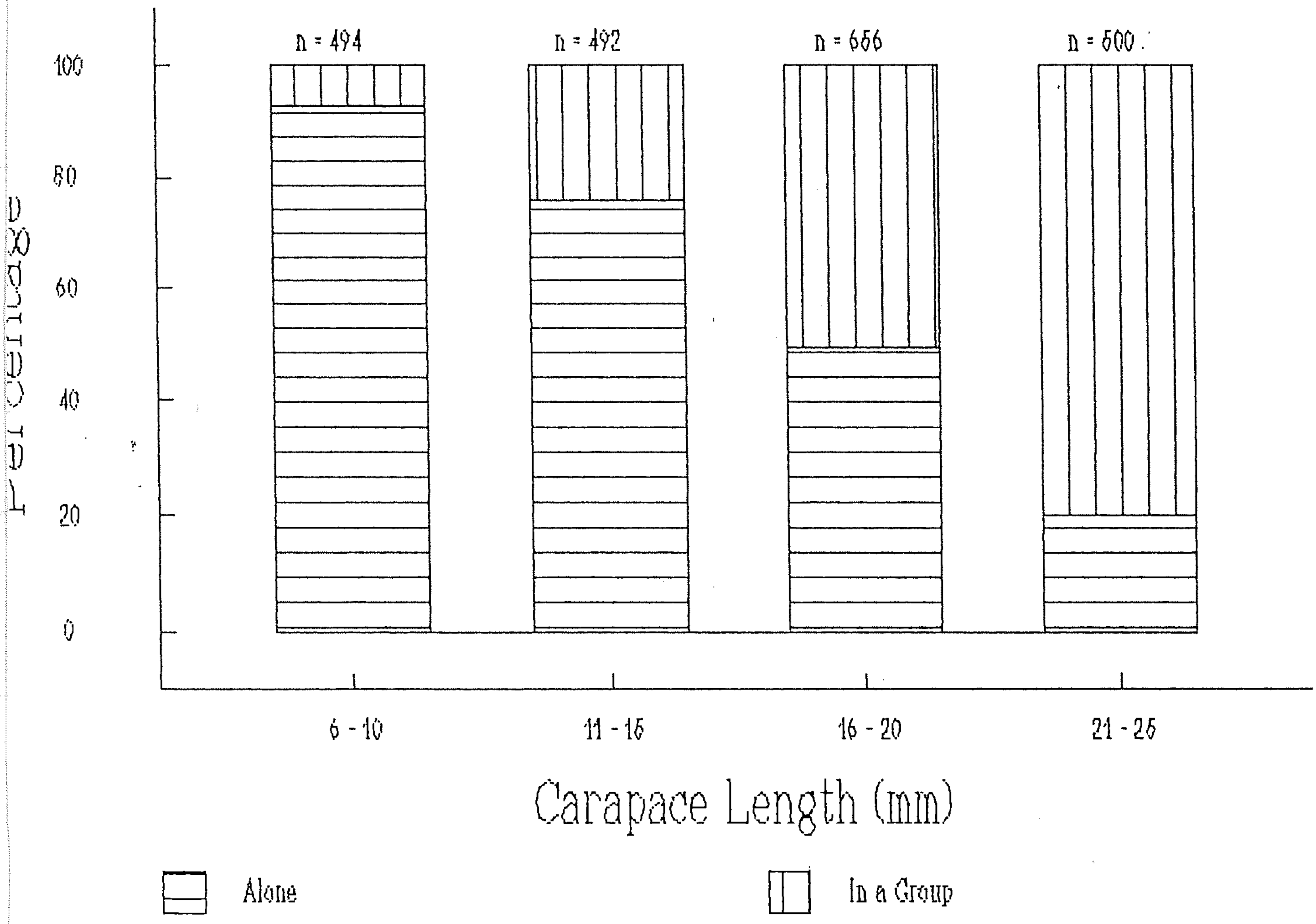

Figure 8: Percentage of post-puerulus P. cygnus in groups or alone vs carapace length. Data for post-pueruli found during September, November 1988 and January, March 1989, were pooled and then split into 4 size classes. The plot shows the percentage of post-pueruli in each size class that were found alone or in the company of other lobsters.

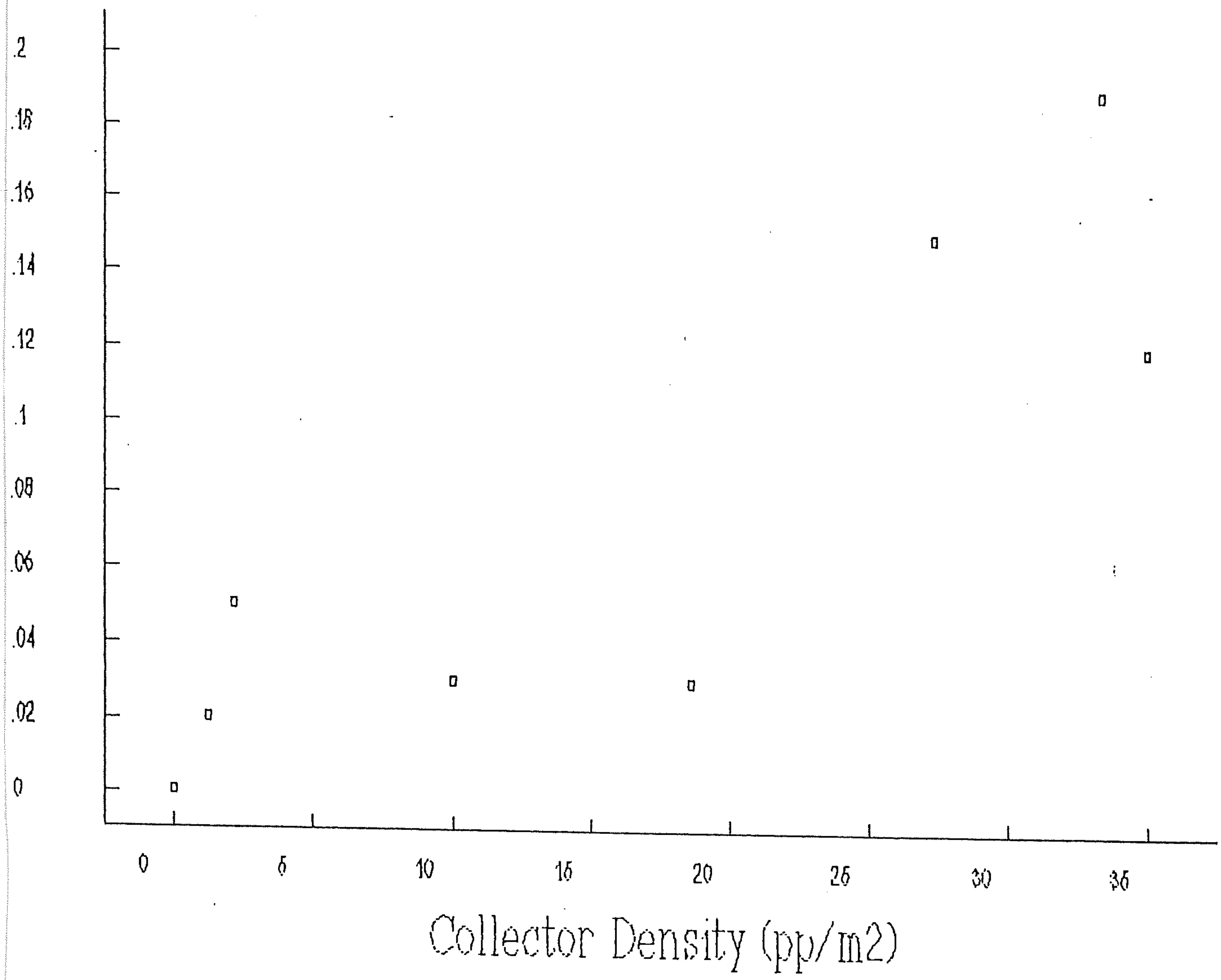

Figure 9: Natural vs Collector settlement densities. Natural settlement densities refer to the densities of P. cygnus post-pueruli < 10 mm C.L. found on 13 reefs at Seven Mile Beach, during 8 field surveys in the summers of 1987/88 and 1988/89. Collector densities refer to the densities of post-pueruli found on artificial collectors during the same months (B. Phillips unpubl. data). The correlation between the 2 measures is highly significant (r = 0.85, p < 0.01). pp = post-pueruli.

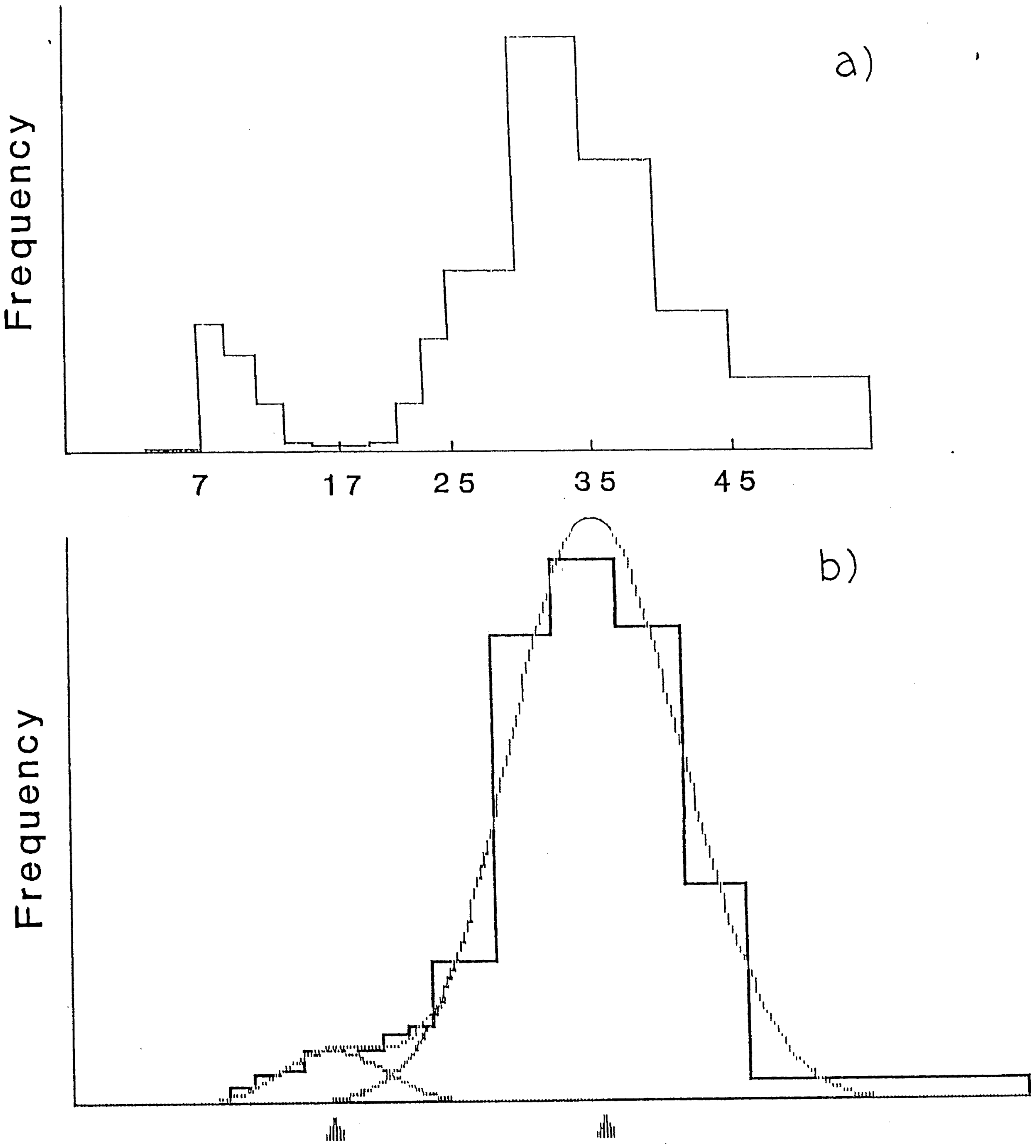

Figure 10: Size/frequency distributions of post-puerulus *P. cygnus* at Seven Mile Beach, fitted by the MIX program. a) November 1987 - little overlap of post-puerulus and juvenile components; b) March 1988 - post-puerulus and juvenile components overlap. The arrows under the x axis indicate the means of the fitted distributions, Xi = 17.15 mm C.L. (SE = 0.55), Xii = 38.24 mm C.L. (SE = 0.13). The y axis is frequency of post-pueruli, but is unscaled.

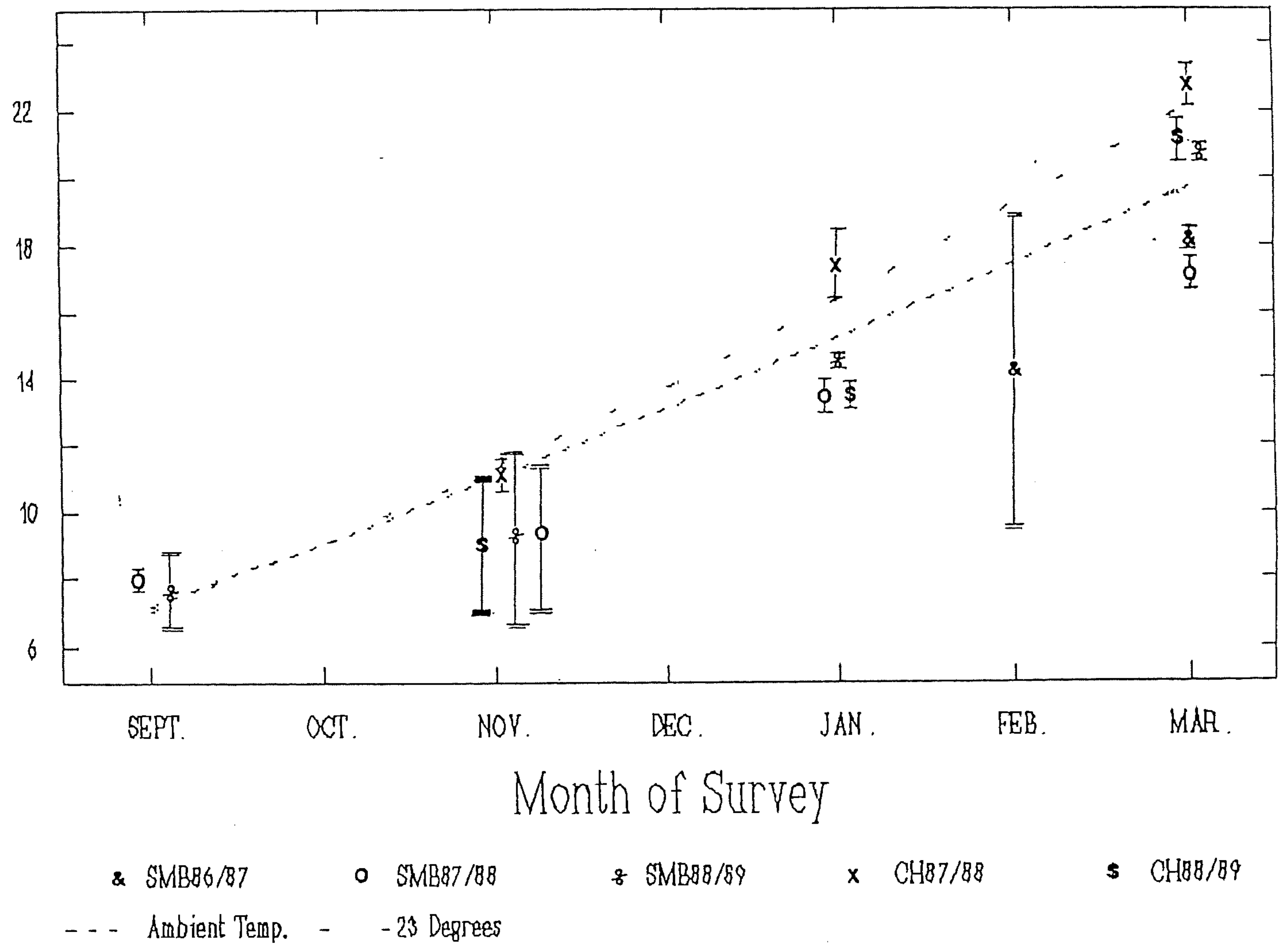

Figure 11: Mean sizes of P. cygnus post-pueruli during each month of sampling. The data are from Seven Mile Beach (SMB) and Cliff Head (CH), sampled over 3 years. The 2 lines are derived from published growth equations for post-pueruli raised in aquaria at ambient temperatures and at constant 23° c. The different types of error bar indicate the method/program used to derive each mean, as follows; CENSOR I MIX I Mode and range I .

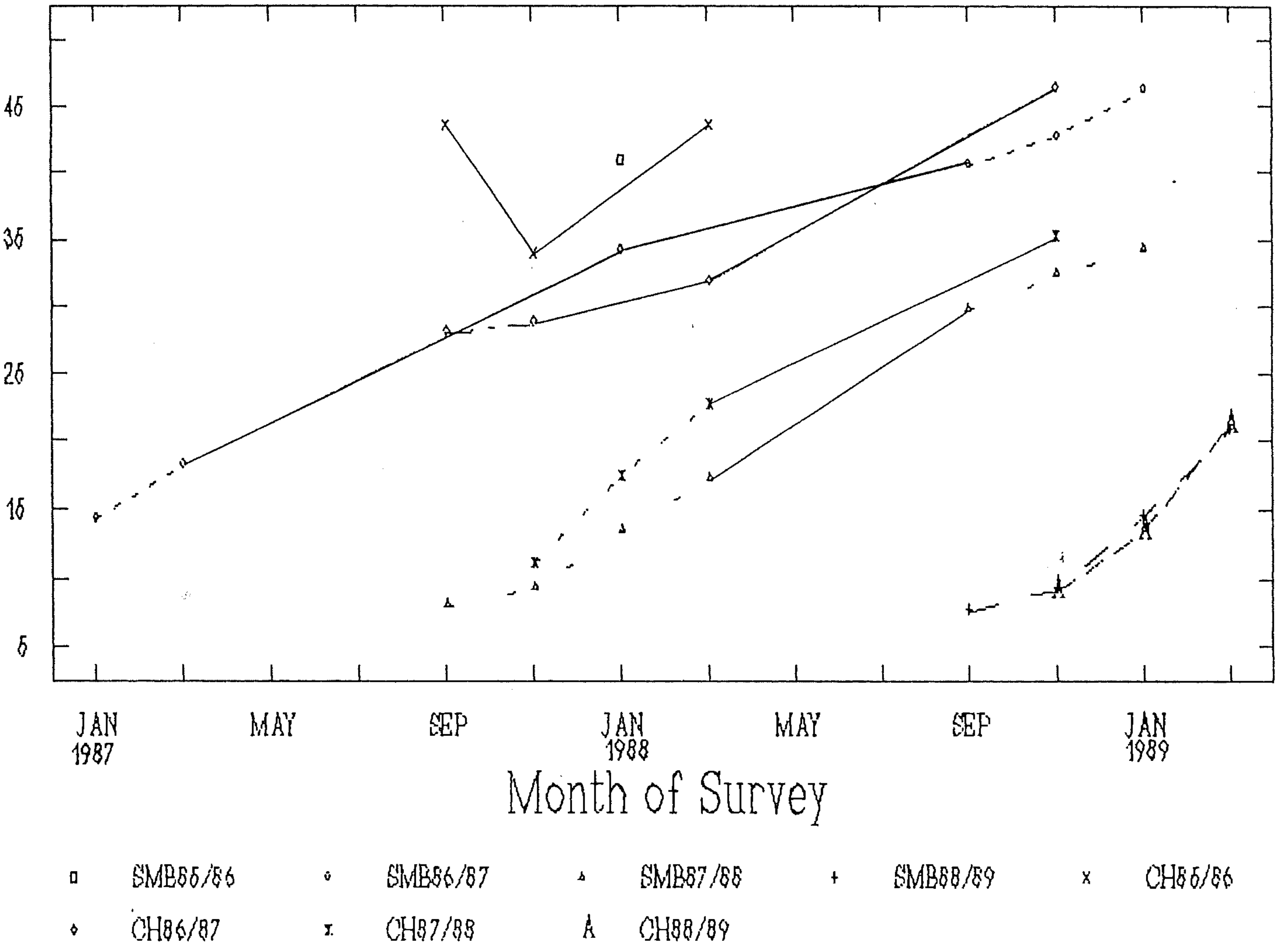

Figure 12: Growth of post-puerulus and juvenile *P. cygnus* at Seven Mile Beach and Cliff Head. The points are the means of all cohorts present at each sampling time, fitted using the MIX program. The lines connecting the points approximate the growth of successive cohorts of lobsters over 2 years. The symbols indicate the site and the most likely year in which the cohort settled, backcalculated from the probable year class of the cohort at the sampling time.

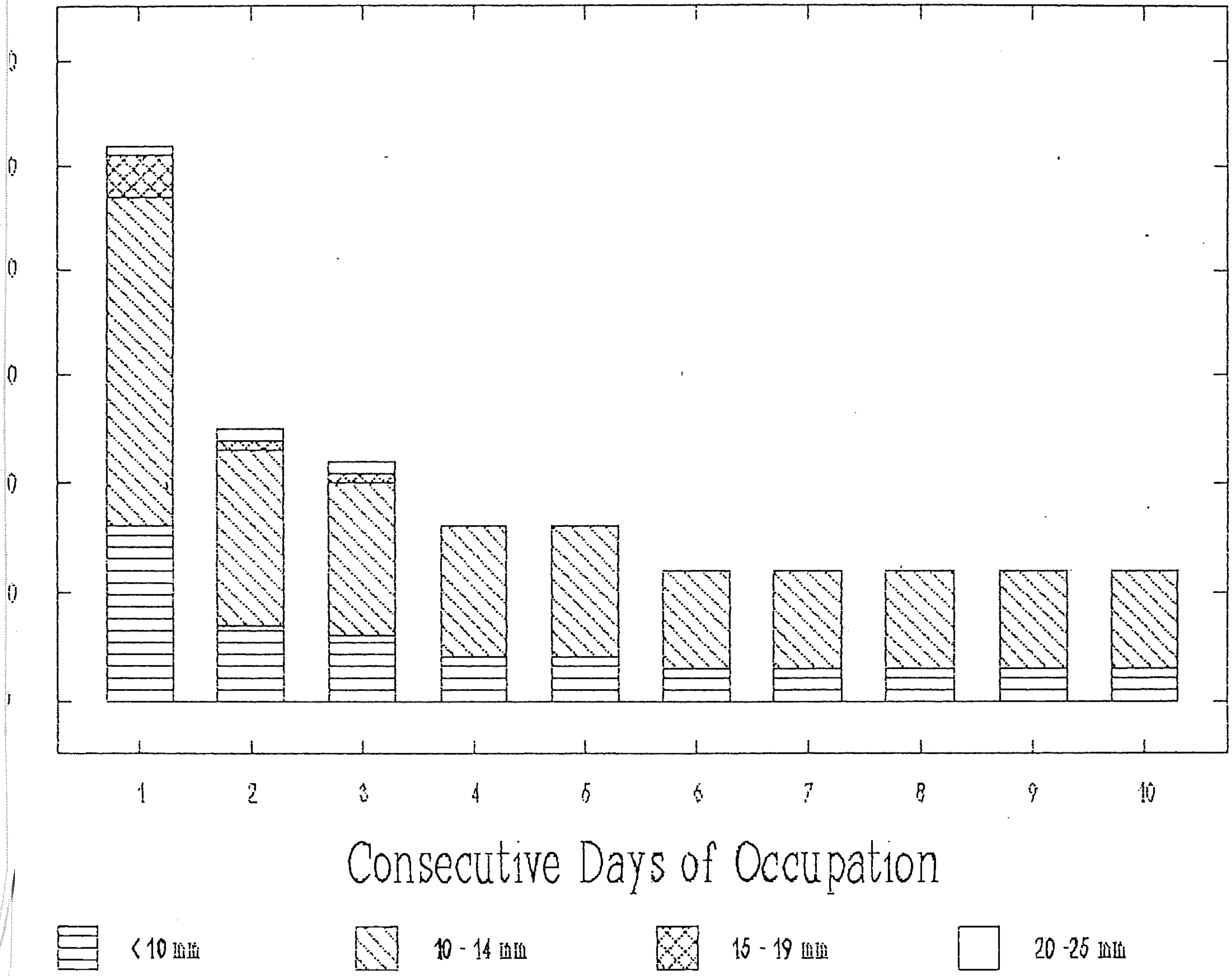

Figure 13: Occupation of post-puerulus P. cygnus shelters over 10 days. 52 post-puerulus shelters at Seven Mile Beach were observed over 10 consecutive days. The bars represent the number of shelters that were still occupied each day. The different bar types indicate the size (carapace length) of the post-pueruli in the shelters.

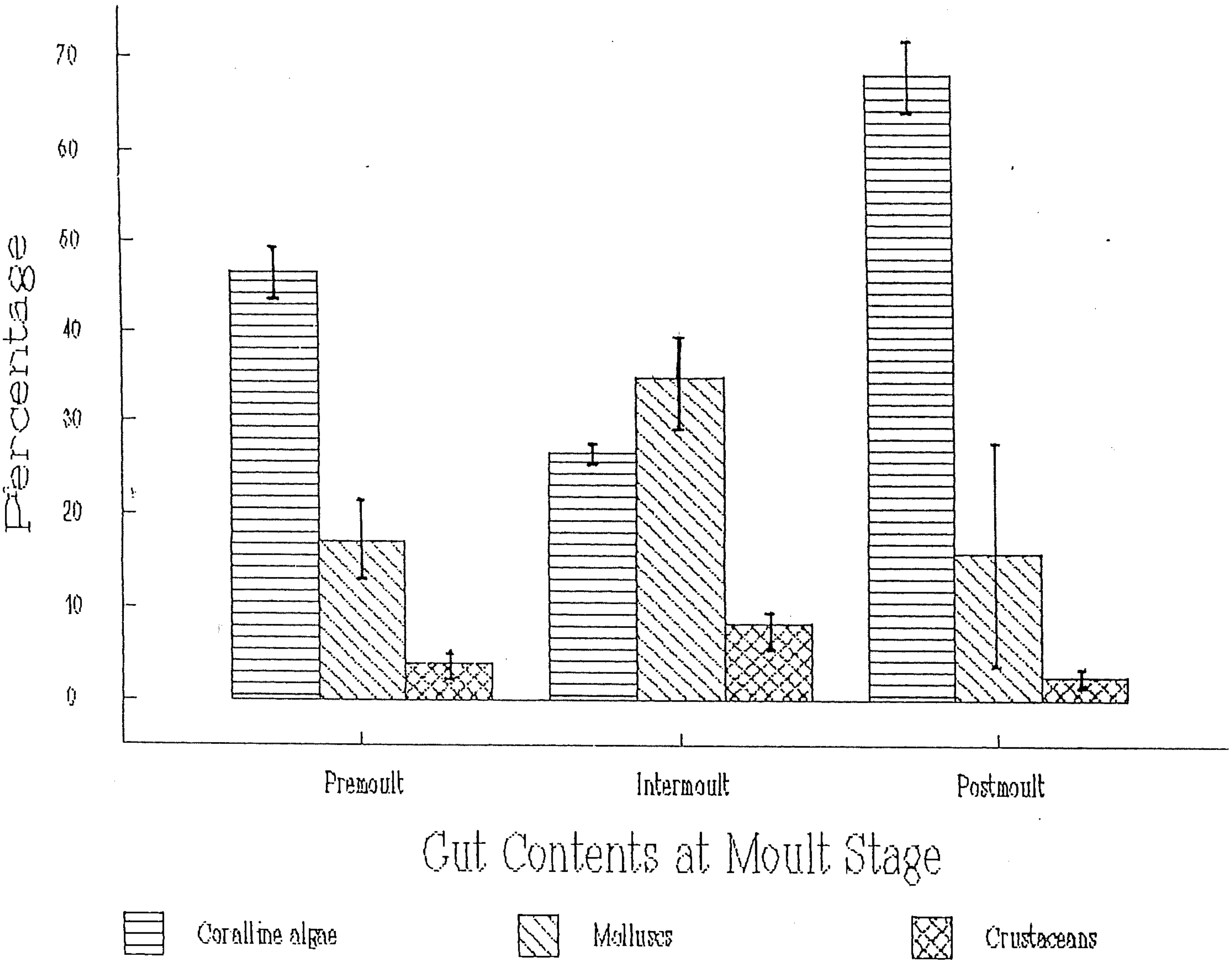

Figure 14: Fore-gut contents analysis. The fore-gut contents of 46 P. cygnus post-pueruli, collected in November 1986, February and April 1987. The proportion of the total fore-gut contents made up by the 3 most voluminous, identifiable food types was compared between moult stages. All fore-guts were > 10 % full. Standard error bars are given.

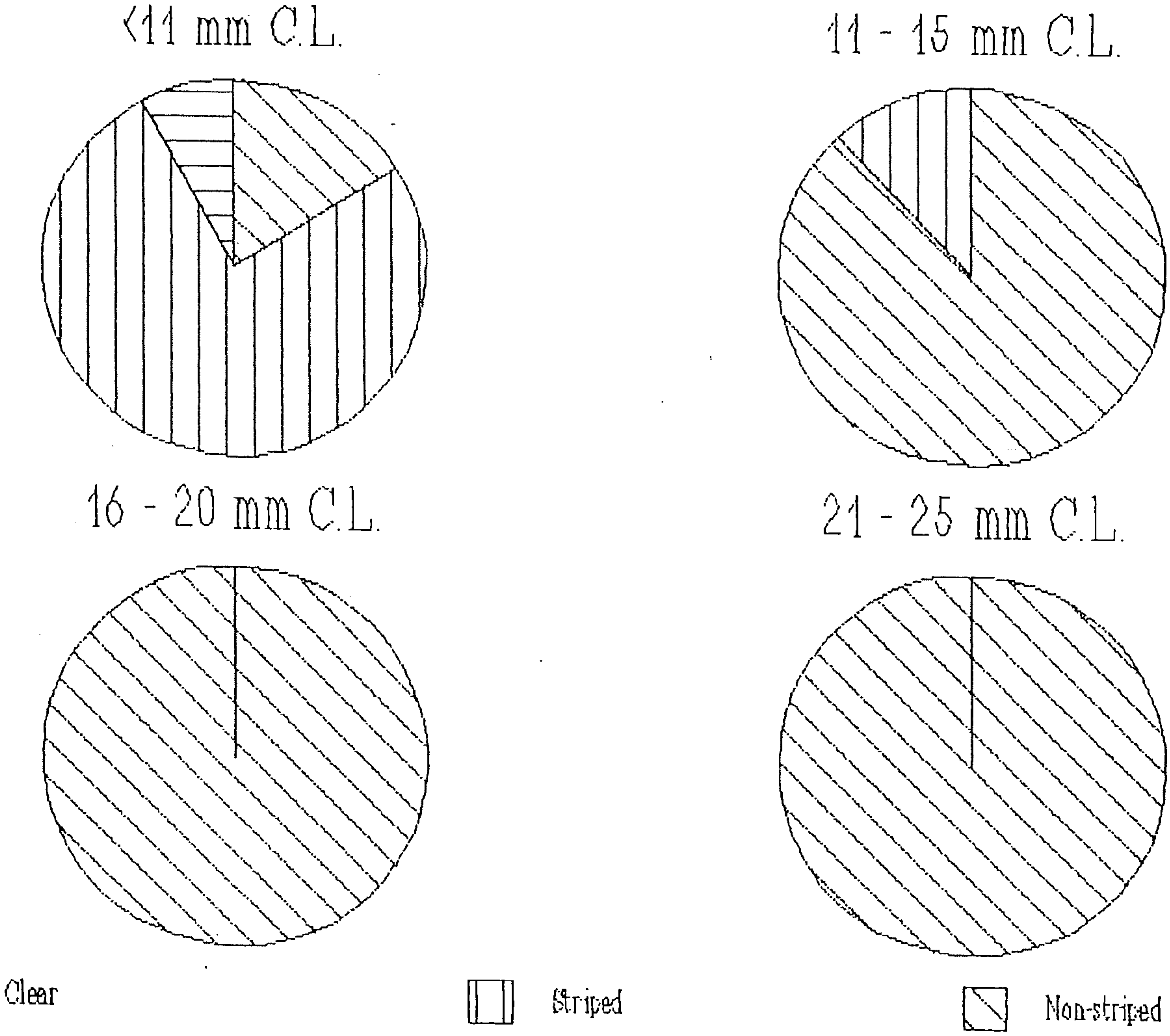

Figure 15: Post-puerulus *P. cygnus* colouration vs size. The proportion of lobsters that are clear pueruli, striped post-pueruli or non-striped post-pueruli within 4 size classes. The data were collected in September and November 1988, January and March 1989.

Table 1: Areas covered during initial searches for post-pueruli at Seven Mile Beach. The area in square metres of each habitat type that was searched for post-pueruli in October 1986 and April 1987, and the number of post-pueruli that were found. Searching on the limestone reefs was conducted in November 1986.

HABITAT	Area	Number of p-p
Amphibolis, seabed		
- quadrat	75	0
- transect	73	2
- canopy removed	56	0
Amphibolis, reef top		
- canopy removed	32	0
Heterozostera/*Halophila*		
- quadrat	32	0
Rock rubble	55.5	0
Bare reef top	50	0
Limestone reef	87	12

Table 2: Post-pueruli found during preliminary survey at Rat Island in May 1988.

Site	Number of Post-pueruli	Size Range
"Cacker Flats"	14	14 - 25 mm C.L.
"Nursery"	1	17 mm C.L.
"Southern coral"	4	13 - 20 mm C.L.
"Northern coral"	0	

Table 3: Analyses of the variance in post-puerulus densities at Seven Mile Beach. Six analyses were conducted on the log. transformed density data after the zeroes were removed. Additional subsets of the data were excluded from 5 of the analyses. The mean sum of squares, degress of freedom and significance level of each term and interaction is given. R = reef, H = habitat, Y = year, M = month. Probability levels: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	Subset excluded from analysis																	
	Zeroes			Reef 1s			Cave			Jan 1988			Reef 46/Sept.			Reefs 5&46		
	df	MS	Sign.	df	MS	Sign.	df	MS	Sign.	df	MS	Sign.	df	MS	Sign.	df	MS	Sign.
Reef (R)	12	4.591	*	11	2.849		12	3.321	*	12	4.185	*	12	4.213	*	10	4.359	*
Habitat (H)	2	22.551	***	2	17.325	***	1	16.105	**	2	22.102	***	2	22.055	***	2	23.625	***
R*H	24	1.588	***	22	1.680	*	12	1.721		23	1.527	***	24	1.447	**	20	1.113	**
Year (Y)	1	28.339	**	1	29.392	**	1	21.519		1	15.905	*	1	29.895		1	36.266	***
R*Y	12	1.764	***	11	1.797	***	12	1.576	**	12	1.788	***	12	1.694	**	10	1.184	*
H*Y	2	1.539	**	2	1.272	*	1	2.299	**	2	0.835		2	1.753	*	2	1.455	
R*H*Y	19	0.208		17	0.225		12	0.227		19	0.267		19	0.206		16	0.207	
Month (M)	3	3.652		3	3.035		3	2.722		3	5.512		3	4.472		3	5.362	**
R*M	36	1.163	*	33	1.245	*	36	1.069	*	36	1.190	*	35	0.963		30	0.648	
H*M	6	1.181		6	1.280		3	2.083	*	6	0.965		6	1.181		6	1.134	
Y*M	3	4.419	**	3	3.370	*	3	3.889	**	2	1.177		3	4.419	**	3	4.743	**
R*H*Y*M	112	0.544		98	0.533		97	0.484		84	0.494		112	0.544				
R*H*M	47	0.565		41	0.521		35	0.419		45	0.487		47	0.565		41	0.545	
R*Y*M	32	0.601		29	0.628		32	0.574		20	0.553		32	0.601		27	0.434	
H*Y*M	5	0.214		4	0.248		3	0.087		3	0.134		5	0.214		5	0.410	
Residual	28	0.504		24	0.486		27	0.504		16	0.509		28	0.504		24	0.455	

Table 4: Mean density values from ANOVA on Seven Mile Beach data: Habitat*Year and Month*Year. Table shows means (exponetiated), log. transformed means, standard error of trans. means and number of observations.

	1987/88				1988/89				Pooled Years			
HABITAT	$\bar{X}$	Log.$\bar{X}$	SE	N	$\bar{X}$	Log.$\bar{X}$	SE	N	$\bar{X}$	Log.$\bar{X}$	SE	N
Cave	0.71	-0.338	0.157	22	2.11	0.746	0.179	17	1.14	0.135	0.118	39
Ledge	0.35	-1.045	0.105	49	0.80	-0.232	0.107	48	0.53	-0.643	0.075	97
Face	0.23	-1.471	0.108	4	0.36	-1.016	0.104	50	0.29	-1.237	0.075	97
Pooled	0.34	-1.083	0.068	118	0.65	-0.428	0.069	115	0.47	-0.760	0.048	233

	1987/88				1988/89				Pooled Years			
MONTH	$\bar{X}$	Log.$\bar{X}$	SE	N	$\bar{X}$	Log.$\bar{X}$	SE	N	$\bar{X}$	Log.$\bar{X}$	SE	N
Sept.	0.31	-1.167	0.139	28	0.33	-1.120	0.139	28	0.32	-1.143	0.099	56
Nov.	0.45	-0.789	0.139	28	0.58	-0.549	0.139	28	0.51	-0.669	0.099	56
Jan.	0.23	-1.452	0.135	30	1.07	0.064	0.135	30	0.50	-0.694	0.095	60
Mar.	0.40	-0.920	0.130	32	0.86	-0.154	0.137	29	0.57	-0.556	0.095	61
Pooled	0.34	-1.083	0.068	118	0.65	-0.428	0.069	115	0.47	-0.760	0.048	233

Table 5: Mean density values from ANOVA on Seven Mile Beach data: A)Reef*Year and B)Reef*Month. The table shows means (exponentiated), log. transformed means, standard errors of trans. means and the numbers of observations.

A)

	1987/88				1988/89				Pooled Years			
REEF	$\bar{X}$	Log.$\bar{X}$	SE	N	$\bar{X}$	Log.$\bar{X}$	SE	N	$\bar{X}$	Log.$\bar{X}$	SE	N
22	0.43	−0.854	0.246	9	1.01	0.013	0.261	8	0.64	−0.446	0.179	17
21	0.31	−1.158	0.233	10	0.49	−0.711	0.246	9	0.39	−0.947	0.169	19
20	0.12	−2.098	0.261	8	0.41	−0.881	0.233	10	0.24	−1.422	0.174	18
5	0.38	−0.956	0.233	10	0.24	−1.435	0.246	9	0.31	−1.183	0.169	19
6	0.26	−1.363	0.246	9	0.29	−1.224	0.261	8	0.27	−1.298	0.179	17
29	0.25	−1.378	0.223	11	0.45	−0.793	0.246	9	0.33	−1.115	0.165	20
46	1.11	0.103	0.279	7	0.94	−0.057	0.301	6	1.03	0.029	0.205	13
59	0.12	−2.080	0.261	8	1.13	0.118	0.233	10	0.42	−0.859	0.174	18
1s	1.04	0.036	0.223	11	1.43	0.360	0.213	12	1.23	0.205	0.154	23
1n	0.31	−1.163	0.233	10	0.93	−0.077	0.233	10	0.54	−0.620	0.165	20
4	0.36	−1.010	0.279	7	0.65	−0.437	0.261	8	0.49	−0.704	0.191	15
60	0.19	−1.643	0.261	8	0.55	−0.591	0.261	8	0.33	−1.117	0.185	16
2	0.48	−0.736	0.233	10	0.94	−0.061	0.261	8	0.65	−0.436	0.174	18
Pooled	0.34	−1.083	0.068	118	0.65	−0.428	0.069	115	0.47	−0.760	0.048	233

B)

	September				November				January				March			
REEF	$\bar{X}$	Log.$\bar{X}$	SE	N	$\bar{X}$	Log.$\bar{X}$	SE	N	$\bar{X}$	Log.$\bar{X}$	SE	N	$\bar{X}$	Log.$\bar{X}$	SE	N
22	0.71	−0.336	0.522	2	0.72	−0.334	0.330	5	0.67	−0.404	0.330	5	0.52	−0.646	0.330	5
21	0.49	−0.717	0.301	6	0.31	−1.165	0.330	5	0.33	−1.102	0.369	4	0.42	−0.862	0.369	4
20	0.15	−1.989	0.330	5	0.19	−1.648	0.369	4	0.37	−1.008	0.330	5	0.37	−1.003	0.369	4
5	0.37	−0.983	0.301	6	0.22	−1.503	0.369	4	0.16	−1.848	0.369	4	0.53	−0.633	0.330	5
6	0.26	−1.345	0.330	5	0.31	−1.166	0.369	4	0.38	−0.977	0.369	4	0.18	−1.692	0.369	4
29	0.11	−2.170	0.330	5	0.43	−0.845	0.330	5	0.48	−0.730	0.330	5	0.49	−0.714	0.330	5
46	18.36	2.910	0.738	1	0.68	−0.386	0.426	3	0.45	−0.801	0.330	5	1.93	0.657	0.369	4
59	0.42	−0.863	0.426	3	0.63	−0.456	0.330	5	0.29	−1.222	0.369	4	0.39	−0.951	0.301	6
1s	0.61	−0.495	0.330	5	1.47	0.386	0.301	6	1.58	0.458	0.301	6	1.43	0.354	0.301	6
1n	0.17	−1.799	0.330	5	1.15	0.137	0.330	5	0.57	−0.562	0.330	5	0.77	−0.257	0.330	5
4	0.46	−0.767	0.369	4	0.46	−0.769	0.369	4	0.62	−0.445	0.369	4	0.43	−0.842	0.426	3
60	0.38	−0.976	0.330	5	0.49	−0.724	0.426	3	0.30	−1.200	0.369	4	0.22	−1.506	0.369	4
2	0.20	−1.633	0.369	4	0.39	−0.933	0.426	3	1.09	0.084	0.330	5	1.20	0.179	0.301	6
Pooled	0.32	−1.143	0.099	56	0.51	−0.669	0.099	56	0.50	−0.694	0.095	60	0.57	−0.556	0.095	61

Table 6: Mean density values from ANOVA on Cliff Head data. Table showsa (exponentiated), log. transformed means, standard errors of trans. means and numbers of observations.

	LEDGE				FACE				POOLED HABITATS			
	$\bar{X}$	Log.$\bar{X}$	SE	N	$\bar{X}$	Log.$\bar{X}$	SE	N	$\bar{X}$	Log.$\bar{X}$	SE	N
Transect B	0.36	-1.013	0.360	5	0.04	-3.155	0.403	4	0.14	-1.965	0.268	9
Transect C	0.30	-1.210	0.360	5	0.08	-2.470	0.360	5	0.16	-1.840	0.255	10
Transect D	0.43	-0.836	0.360	5	0.05	-3.012	0.403	4	0.16	-1.803	0.268	9
November	0.90	-0.107	0.375	3	0.05	-2.922	0.265	6	0.14	-1.984	0.216	9
January	0.24	-1.446	0.265	6	0.06	-2.767	0.325	4	0.14	-1.975	0.205	10
March	0.35	-1.049	0.265	6	0.06	-2.807	0.375	3	0.19	-1.635	0.216	9
1987/88	0.28	-1.278	0.216	9	0.04	-3.127	0.290	5	0.14	-1.938	0.174	14
1988/89	0.53	-0.632	0.265	6	0.07	-2.673	0.230	8	0.17	-1.798	0.174	14
Pooled	0.36	-1.020	0.168	15	0.06	-2.848	0.180	13	0.15	-1.868	0.123	28

Table 7: Density of newly settled post-pueruli (< 10 mm C.L.) on 13 reefs at Seven Mile Beach. The density of post-pueruli, pooled over divers and reefs, for each sampling period.

MONTH	HABITAT		
	Cave	Ledge	Face
September 1987	0.02	0.01	0.03
November 1987	0.04	0.08	0.18
January 1988	0.01	0.01	0.05
March 1988	0.02	0.01	0.01
September 1988	0.12	0.09	0.24
November 1988	0.22	0.29	0.49
January 1989	0.12	0.03	0.15
March 1989	0.00	0.02	0.04

Table 8: Transfer of post-pueruli between shelters. Post-pueruli were either transferred from one habitat (Original habitat) to the same or another habitat , or left undisturbed. Same = returned to the same shelter from which they were removed. * = post-pueruli were given the choice of entering shelter or escaping into the surrounding seagrass. The number of post-pueruli in the original habitat, and the number that were present the next day in the habitat to which they were transferred, are given.

Original Habitat ⟶ Habitat 2	No. in original hab.	No. present next day
Collector ⟶ Natural	20	0
Collector ⟶ Limestone	12	0
Natural ⟶ * Same	9	1
Natural ⟶ Same	9	6
Natural undisturbed	15	10
Limestone ⟶ * Same	8	3
Limestone undisturbed	8	8

Table 9: Error in visual estimation of lobster size. The mean difference between the estimated and measured sizes of post-pueruli (< 25 mm C.L.) and juveniles (≥ 25 mm C.L.). The means for each sample period, pooled means, standard deviations and the number of lobsters measured each month are given.

	POST-PUERULI			JUVENILES		
	Mean	S.D.	Number	Mean	S.D.	Number
March 1988	1.00	1.41	2	2.41	2.13	73
September 1988	0.63	0.81	16	2.44	2.06	32
November 1988	0.40	0.58	25	2.40	1.60	20
January 1989	1.00	1.26	11	2.95	1.69	21
March 1989	1.30	1.35	43	2.15	2.13	77
Pooled	0.92	1.05	97	2.38	2.03	223

Table 10: Post-puerulus foregut fullness vs moult stage. Post-pueruli, captured for diet analysis, with foreguts < 10 % full and with foreguts > 10 % full. The number of post-pueruli in each moult stage within these groups is given.

	FOREGUT < 10 % FULL	FOREGUT > 10 % FULL
PRE-MOULT	22	7
INTER-MOULT	18	33
POST-MOULT	5	6
TOTAL	45	46