

Distribution of newly settled western rock lobsters *Panulirus cygnus*

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ABSTRACT: Little is known about the biology of the post-plerulus stage (i.e. individuals < 25 mm carapace length) of the commercially valuable western rock (spiny) lobster *Panulirus cygnus*, and few have been found in the field. In the present study, the natural habitat of post-pleruli was discovered through intensive diving surveys. Additional studies of habitat preference were carried out using a variety of designs of artificial habitats and the response of the post-pleruli to transferral between shelters was evaluated. Post-plerulus *P. cygnus* were found to shelter in small holes on the face, in ledges and in caves on coastal limestone reefs. They apparently preferred shelters with additional cover, typically seagrass and/or algae. Movement between shelters appeared common because 50 % of monitored shelters were occupied for only a single day. Post-pleruli occurred in groups of up to 100 individuals, although 75 % were solitary. There was a trend for larger post-pleruli to be gregarious. Two designs of artificial shelter were successfully utilised by post-pleruli: those made of 'Tanikalon' which resembled algae or seagrass, and those that consisted of holes in limestone blocks covered by seagrass. In transferral experiments, at least 50 % of post-pleruli refused to enter or remain in new shelters after transfer from their previous shelters. This may be influenced by the method of release. Discovery of the natural habitat of post-plerulus *P. cygnus* means that it is now possible to study other aspects of their biology and population dynamics. Results of the transfer experiments indicate that future research is needed to determine the best release method to minimise rejection of new shelters. The successful utilisation of artificial habitats suggests that these habitats may have potential to enhance the survival of post-pleruli in areas where shelter is limited.

INTRODUCTION

Because of the commercial importance of the western (spiny) rock lobster *Panulirus cygnus* George, its biology and population dynamics have been intensively studied (e.g. Sheard 1962, Chittleborough 1970, Chittleborough & Phillips 1975, 1979, Morgan 1979, Joll 1982, Phillips et al. 1984, Phillips 1986, Jernakoff et al. 1987). After a planktonic life of 9 to 11 mo the phyllosoma larvae metamorphose offshore into pueruli (Chittleborough & Thomas 1969). The pueruli swim to the coast to areas where limestone reefs are abundant (Chittleborough & Phillips 1975) and peak settlement is between September to February each year (Phillips 1986). After settlement the pueruli acquire dark pigmentation and moult within a few days into post-pleruli juveniles which are between 7.5 and 9 mm

carapace length (CL) (Phillips 1972). Juvenile lobsters, 2 to 5 yr old, inhabit the coastal areas, living in dens which are usually caves or ledges in the limestone reefs (Cobb 1981). When the lobsters are between 4 and 6 yr old, they move offshore after the spring moult, to adult habitats in depths of 30 to 150 m (Morgan et al. 1982).

Although the stages of the life cycle have been identified, the post-plerulus stage has rarely been found in its natural habitat despite numerous attempts. These have included electrofishing (Phillips & Scolaro 1980), baited traps, beam trawls and ad hoc searching by divers (B. Phillips, CSIRO Marine Laboratories, pers. comm.). The successful use of artificial seaweed collectors to collect pueruli and post-pleruli (Phillips 1972) means, however, that limited information on their biology is available – for example the post-pleruli of *Panulirus cygnus* are cryptically coloured with a pattern similar to post-pleruli of other panulirid species [e.g. *P. interruptus* (Randall): Engle 1979; *P. argus* (Latrielle): Lewis et al. 1952, Andree 1981, Marx & Herrnkind 1985a,b]. From the results of laboratory

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studies, Phillips et al. (1977) suggested that post-pueruli of *P. cygnus* are probably solitary, living in shallow coastal seagrass beds, and that at about 25 mm CL they become gregarious and move from the seagrass beds to the nursery reefs.

The natural habitats of the post-pueruli of *Panulirus interruptus* and *P. argus*, unlike that of *P. cygnus*, have been described. Andree (1981), Marx (1983) and Herrnkind & Butler (1986) reported that the post-pueruli of *P. argus* in Florida, USA, are found in clumps of *Laurencia* spp. (red algae) and algal-covered rock rubble; they have also been found on algal-covered mangrove roots (Witham et al. 1964). The post-pueruli of *P. interruptus* in California, USA, live in *Phyllospadix* seagrass beds in predominantly rocky habitats with dense plant cover (Parker 1972, Serfling 1972, Engle 1979). The success in finding the habitats of post-pueruli of *P. argus* and *P. interruptus* was due to intensive searches by SCUBA divers (e.g. Serfling 1972, Engle 1979, Marx 1983). It has also led to studies of factors affecting their ecology e.g. food and shelter (Marx & Herrnkind 1985a). The lack of success in finding post-pueruli of *P. cygnus* in their natural habitat has made direct studies of their ecology and population dynamics impossible. The aim of the present study was, therefore, to redress the gaps in the knowledge of the natural habitat and habitat preference of post-puerulus *P. cygnus*. A related aspect of the study was to evaluate whether the lobsters can be successfully transferred between habitats. Chittleborough & Phillips (1975) suggested that transferral of individuals may be a way to increase the abundance of rock lobsters in areas of poor natural settlement. Various designs of artificial habitats were also evaluated to determine which if any artificial habitats are successfully utilised by post-pueruli. A methodical use of divers to search for *P. cygnus* in their natural habitat seemed appropriate in this study, given the successful use of divers in locating other species (e.g. Serfling 1972, Engle 1979, Marx 1983).

MATERIALS AND METHODS

Study site. The study was carried out at Seven Mile Beach in Western Australia (29° 08' S, 114° 54' E), a site in the centre of the geographical range of *Panulirus cygnus*. Pueruli and post-pueruli are regularly found at this site on floating artificial seaweed collectors (Phillips 1972) moored near patch reefs and seagrass in water 2 to 5 m deep. Limestone patch reefs and seagrass, interspersed with patches of sand and rock rubble, are found at Seven Mile Beach and are typical of the coastal areas where juvenile western rock lobsters are found (Fig. 1). The main habitat

features of the reefs are the tops, the reef face, caves and ledges.

The flat tops of the patch reefs are generally 1 to 2 m below the surface of the water except during low spring tides. Seagrasses, *Amphibolis antarctica* (Labill)

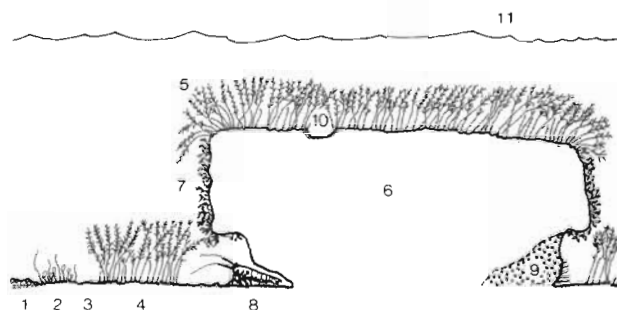


Fig. 1. Schematic diagram showing main habitat features in shallow coastal areas at Seven Mile Beach, Western Australia. 1 = rock rubble; 2 = *Heterozostera/Halophila* seagrass; 3 = sand; 4 = *Amphibolis* seagrass on the seabed; 5 = *Amphibolis* seagrass on the reef top; 6 = the limestone reef; 7 = the reef face with algal cover; 8 = a ledge sheltering a juvenile rock lobster; 9 = a cave; 10 = a patch of bare limestone reef; and 11 = the sea surface

Sond. & Asch. ex Asch. and *A. griffithii* (Black) den Hartog, usually cover the reef tops, although small patches of the reefs may be bare. Epiphytic coralline algae, sponges and non-coralline algae grow on the seagrasses and on patches on the reef devoid of seagrass (Fig. 1).

Some areas of the reef face are bare limestone, while other parts are covered by seagrass and algae. The face is usually either vertical, or slopes gently to the sea floor, and patches of large green algae (e.g. *Caulerpa* sp. and *Codium* sp.) may cover the entrance of ledges and caves.

Ledges are found on the face and at the base of the reefs and generally have a horizontal floor of bare limestone or sand (Fig. 1). They are usually between 1 cm and 1 m high, and up to several metres wide. They are open at the sides and have a sloping roof extending into the reef to a depth of about 1 m; there are often small ledges within larger ledges. Detritus periodically fills ledges and caves at the base of reefs (depending upon water movements).

Caves are similar to ledges except they are not open at the sides and usually extend into the reefs to a depth of up to 2 or 2.5 m (Fig. 1). There is probably less water movement and light in caves than in the ledges (P. Jernakoff pers. obs.). The roofs of caves, as of the ledges, are either bare limestone or covered by sponges, ascidians, bryozoans, tubeworms and epiphytic algae. Caves have a sand substratum and may have small ledges on their walls.

Seagrass beds consisting of either *Amphibolis antarctica* and *A. griffithii*, or *Heterozostera tasmanica* (Martens ex Asch.) den Hartog, and *Halophila ovalis* (Brown) Hooker, interspersed with patches of sand and small outcrops of algal-covered rock or rubble, separate the reefs (Fig. 1). The *A. antarctica* and *A. griffithii* canopy is dense and ca 40 cm tall. The canopy of *Heterozostera*/*Halophila* seagrasses, however, is sparse and no more than 10 cm high, and is often interspersed with various algae e.g. *Caulerpa* spp.

Post-pueruli surveys. Other species of post-pueruli have been found living in algal and seagrass habitats (Parker 1972, Serfling 1972, Engle 1979, Andree 1981, Marx 1983, Herrnkind & Butler 1986). Phillips et al. (1977) suggested that seagrass beds were the likely habitat of post-pueruli of *Panulirus cygnus*, and because seagrass beds are a dominant feature of the coastal areas of Western Australia, and are abundant at Seven Mile Beach, they were the first habitat searched. Various searching methods were used, some based on methods tried by other workers overseas (e.g. Sweat 1968, Engle 1979); beam trawls were not tried because this technique has proved unsuccessful in the past (B. Phillips, CSIRO Marine Laboratories, pers. comm.).

Seagrass beds were surveyed in October 1986 using modified 1 m² steel quadrats. Quadrats were constructed of a 40 cm high fence of flexible plastic mesh (1.5 × 3 mm mesh) supported by floats; the 15 cm wide bottom skirt was weighted with chain to prevent escape of post-pueruli around the bottom of the quadrat. A total of 136 quadrats were sampled. Quadrats were grouped in blocks of 4 for ease of sampling and to evaluate whether a sampling scale of 2 × 2 m was more appropriate than separate 1 m² quadrats. Twenty-nine blocks of 4 quadrats each were haphazardly placed in *Amphibolis* seagrass on the seabed, with another 5 blocks of 4 quadrats in *Amphibolis* seagrass growing on the top of 5 separate reefs. Because the post-pueruli are small and cryptic, 2 divers were used side by side to search each quadrat twice, once in a north-south and once in an east-west direction. This minimised the possibility of post-pueruli moving from one section of the quadrat to another and being missed by a single diver, and maximised the probability that all post-pueruli were counted.

Because *Amphibolis* seagrass beds are very thick, it is possible, even using the above sampling method, that post-pueruli may have been missed by the divers. To examine this possibility, the entire contents of 60 quadrats, 20 on the tops of reefs and 40 on the seabed, were removed (after searching) by cutting the seagrass stems and using a suction pump to suck the canopy, stems and sand substratum to a depth of about 2 cm into a plastic mesh bag (1.5 × 3 mm mesh). The samples were then taken ashore and searched. In addition,

fourteen 10 × 0.5 m, and one 6 × 0.5 m, transects were searched by divers without the use of fenced quadrats or suction pumps. During April 1987, 28 additional quadrats (12 on reef tops and 16 on the seabed) were searched and suctioned using the same methods used during October 1986.

Removal of the *Heterozostera* and *Halophila* canopy was unnecessary because these seagrass beds are very sparse (Fig. 1) and are easily searched. A total of 32 quadrats were searched in October 1986 by pairs of divers in the same way as previously described. Any post-pueruli could be easily seen by divers, who also probed the substratum in case post-pueruli were buried in the sand.

During November 1986, divers also systematically searched (without quadrats) a total of 40 m² of reef top, 55.5 m² of rock rubble and 87 m² of caves. The numbers and estimated size of post-pueruli were recorded. At this time, the sizes of lobsters were estimated in size classes of <10 mm, 10 to < 15 mm, 15 to < 20 mm, and 20 to < 25 mm CL.

Eleven reefs were searched during both February 1987 and March–April 1987. Seven of these reefs were sampled during both periods (i.e. 4 of the reefs sampled during March–April were different from those sampled in February). Habitats consisted of caves, ledges, the reef face, and *Amphibolis* growing on the reef top (see Fig. 1). The actual sizes of post-pueruli were estimated by divers who by this time had more experience in estimating the sizes of the lobsters. Preliminary checks indicated that the divers' estimates were generally within 2 mm of the measured carapace lengths. Density estimates (per m²) of caves, ledges and the reef face were made by divers using torches to assist in their search. As the areas searched were estimated and did not include the rugosity and microtopography of the reef surface, the real surface area searched is underestimated.

In addition to density surveys, the type of cover immediately adjacent to the shelter sites (hereafter called shelters) was recorded during November 1986. The occupancy rate of 52 marked shelters on 5 reefs was also followed for a period of 16 d during November 1986 by divers who observed whether or not the marked shelters were occupied on a daily basis.

Habitat preference experiments. To determine whether post-pueruli would accept artificial shelters, 4 designs of shelters (Fig. 2) were constructed to mimic either seagrass or holes in rocks, and were roughly based on designs used by Sweat (1968).

The first type of artificial shelter was a hollow concrete cylinder (70 mm diameter) with 12 holes (20 mm diameter). The ends of the cylinder were sealed with plastic mesh to allow water movement but exclude predatory octopi and fish (Fig. 2). The second type

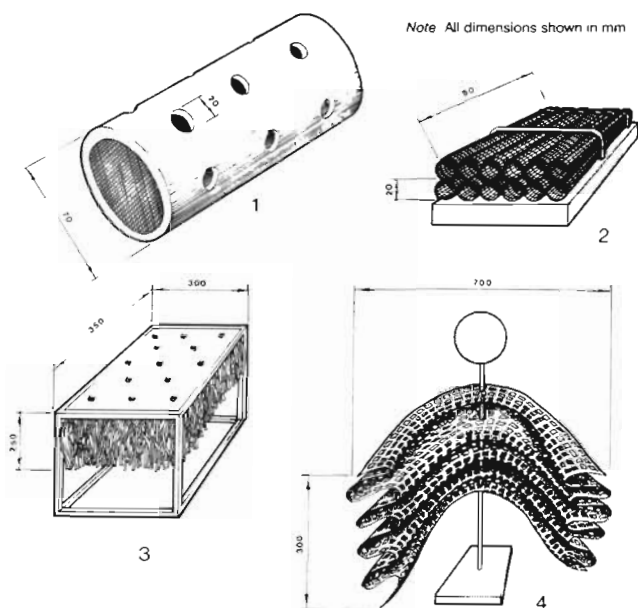


Fig. 2. Artificial shelters used at Seven Mile Beach. Type 1 is a concrete cylinder with 12 holes drilled in it; both ends are blocked with plastic mesh. Type 2 is a block of 12 PVC mesh cylinders clamped at one end and wired to a steel weight. Type 3 is a mat of 'Tanikalon' attached to a plastic sheet mounted on a steel frame. Type 4 is a concertina of fibre mesh on a rope suspended between a float and a steel weight

of artificial shelter was a block of 12 PVC mesh (1.5 × 3 mm mesh) cylinders, 20 mm diameter × 80 mm length, clamped at one end and strapped together on a flat steel anchor (Fig. 2). The third type consisted of a mat of 'Tanikalon' (Taniyama Chemical Industries Ltd. Okayama, Japan) synthetic fibres (350 × 300 × 250 mm) attached to a plastic sheet, as is used in puerulus collectors (Phillips 1972), mounted on a steel frame such that the fibres were hanging down (Fig. 2). The fourth type consisted of a concertina (ca 300 mm diameter × 700 mm long) of a fibre mesh, suspended on a rope between a float and flat steel anchor (Fig. 2).

Five of each of these types of shelters were haphazardly placed at 2 sites, 750 m apart within *Amphibolis*, during October 1986. The habitats were sampled for pueruli and post-puteruli in November 1986, February 1987 and March 1987. The concrete cylinders and PVC mesh cylinders were searched in situ by divers using torches to illuminate the shelters. The 'Tanikalon' and fibre mesh shelters were checked in situ and then carefully lifted onto a boat for more detailed sampling, after which the shelters were returned to their sites. No post-puteruli were ever observed by divers to flee these shelters during checking or removal of the shelters to the boat. The numbers

of pueruli and post-puteruli found in the artificial shelters and 5 control plots of *Amphibolis* (each ca 300 × 300 mm) at each site was recorded and the lobsters removed.

Preliminary observations in November 1986 indicated that 2 factors appeared to influence shelter preference: the size of shelter and the presence of immediately adjacent cover. An experiment using holes drilled in blocks of quarried local limestone was designed to test whether these factors significantly influenced the choice of shelter. Twelve blocks were used, each 60 cm long × 30 cm wide × 25 cm high. Holes of 8, 10, 12, or 14 mm diameter and either 25 or 50 mm deep were drilled in each block. The holes were drilled 100 mm apart over the sides of each block, with the size and diameter of holes randomly assigned within a grid. There were 4 replicates of each hole size and diameter per block (i.e. a total of 32 holes), thus these treatments tested for the effects of hole size and diameter on shelter preference of post-puteruli.

The effects of cover around the limestone block shelter was also tested by placing all of the 12 blocks in thick *Amphibolis* seagrass beds (6 blocks at one site and 6 at a second site 750 m away) and then cutting away the seagrass from 3 of the blocks at each site. In this way, all of the blocks were situated within seagrass beds but only half of the blocks were covered by seagrass; the other 6 blocks were bare.

The holes in the blocks were checked by divers with torches 5 times between 11 December 1986 and 21 November 1987. Presence and estimated size of post-puteruli were recorded and the lobsters were then removed and relocated away from the area.

Post-puteruli transferral experiments. Attempts to restock areas of poor natural settlement require a knowledge of how post-puteruli respond when transferred between habitats. In a series of studies, post-puteruli of < 15 mm CL were transferred between artificial shelters, from artificial to natural shelters, and between natural shelters. Their responses (i.e. whether they stayed or rejected their new shelters) were recorded.

It was found that some lobsters naturally vacated their shelters after only a single night (see 'Results'). Post-puteruli were observed to be active only at night, remaining within the shelters during the day (P. Jernakoff unpubl. data). It is possible that a shelter vacated by one individual may be reoccupied by another during the same night. Lobsters found in the same shelter on the following day could not, therefore, be identified as the same individual. Unfortunately, post-puteruli could not be individually marked because marking requires gripping them firmly. This often results in injury, because of their small size, and apparent stress as evidenced by their observed reluctance to

enter and remain in their shelters (see 'Results'). Consequently, comparisons of the shelter occupancy of transferred (disturbed) and control (undisturbed) lobsters provide somewhat ambiguous conclusions.

In the first experiment, 20 post-pueruli were individually transferred in clear plastic water-filled bottles from artificial seaweed collectors (Phillips 1972) to natural holes in the limestone reef, and 12 individuals were transferred to 14 mm diameter, 50 mm deep holes in limestone blocks (2 post-pueruli per block). The blocks (60 cm long \times 30 cm wide \times 25 cm high) had been placed in *Amphibolis* seagrass beds a month before, and were lightly colonised by epibenthos. Lobsters were observed for up to 1 h after release to determine whether they remained in their new shelters, and the shelters were checked in the morning of the following day to determine whether or not the shelters were occupied.

In the second experiment, the effect of transferral (disturbance) was examined by taking post-pueruli from natural shelters and returning them to the same shelters. Seventeen post-pueruli were taken from their individual shelters on a limestone reef by inserting a small length of wire between the body of the post-puerulus and the wall of the shelter and then tapping the side of the individual with the wire. This caused the post-puerulus to flee its shelter into a clear plastic water-filled bottle held over the entrance to the hole. Post-pueruli were released at their own shelters within 3 min of capture. Post-pueruli were released using 2 different techniques. In 8 cases, a bottle was held directly over the shelter so that the edge was in contact with the limestone reef; thus a post-puerulus could only stay in its bottle or re-enter its shelter until the bottle was removed (after about 3 min). In the other 9 cases, due to a misunderstanding between divers, the bottles were placed over the shelters at a 45° angle so that they did not seal with the substratum. In this case, post-pueruli could either go back into their shelters or move immediately into the surrounding seagrass. Animals and shelters, in addition to a control group of 15 undisturbed post-pueruli in natural shelters, were observed in an identical manner as in the first study.

The third experiment tested the effects of transferral (disturbance) of post-pueruli by taking them from their shelters in limestone blocks and then returning them to their own shelters. Divers took 8 out of the 16 post-pueruli that were naturally occupying holes in limestone blocks and then returned them to their own shelters within 3 min of capture. Post-pueruli were held in bottles and then released by holding the bottles at a 45° angle so that they had a choice of either re-entering the holes or escaping into the surrounding seagrass. The 8 transferred and 8 control lobsters and shelters were checked as previously described.

RESULTS

Post-pueruli surveys

During October 1986, no post-pueruli were found in seagrass beds during quadrat and transect sampling. In November 1986, 188 post-pueruli were found on reefs in caves ($n = 51$), ledges ($n = 110$) and on the reef face ($n = 27$). No lobsters were found sheltering in seagrass on reefs or in seagrass beds between the reefs. Most (60.1 %) of the post-pueruli were between 10 and 15 mm CL, while 23.4 % were < 10 mm, 10.1 % were between 15 and 20 mm, and 6.4 % were between 20 and 25 mm CL.

In February 1987 the areas searched consisted of 248 m² of caves, 701 m² of ledge, 489 m² of reef face and 622 m² of *Amphibolis*. In March–April 1987, the areas searched were 90 m² of cave, 373 m² of ledge, 277 m² of reef face and 791 m² of *Amphibolis*. No post-pueruli were found sheltering amongst *Amphibolis* during February 1987 and only 2 individuals were found in this habitat during March–April 1987; this habitat was excluded from statistical analyses.

A balanced, orthogonal analysis of variance (ANOVA) to determine whether the densities in the 3 habitats were independent of the particular reef being sampled was constrained because some habitats were absent on some patch reefs (e.g. not all reefs had caves). It was, however, possible to analyse a subset of the March–April 1987 density data on reefs with all 3 habitats present. In February 1987, the subset of data on reefs with all 3 habitats was too small to test statistically.

Analysis of a subset of the March–April 1987 data indicated no significant interaction in the density of post-pueruli in the 3 types of habitats and the reefs ($p = 0.89$, $df = 20,66$). Thus the effects of habitats were assumed to be independent of the effects of reef, therefore data from all reefs could be pooled to increase the power of the ANOVA to test for significant differences in the density of post-pueruli between habitats. Likewise, data from all habitats could be pooled to test whether reefs had significantly different densities. The independence of habitats and reefs was also assumed for February 1987, enabling separate analyses of reefs (pooling data from all habitats) and habitats (pooling data from all reefs).

In February 1987, there was no significant difference (ANOVA, $p = 0.98$, $df = 2,162$) in the densities of post-pueruli found on the reef face (mean = 0.57 ind. m⁻², $n = 56$), ledges (mean = 0.57 ind. m⁻², $n = 65$), or caves (mean = 0.64 ind. m⁻², $n = 44$). However, in March–April 1987 there were significant differences in the densities between habitats (ANOVA, $p = 0.01$, $df = 2,107$). The densities on the reef face (mean = 0.51 ind.

m^{-2} , $n = 38$) were significantly less than in caves (mean = $0.91 \text{ ind. } m^{-2}$, $n = 20$) which were significantly less than in ledges (mean = $1.36 \text{ ind. } m^{-2}$, $n = 52$; Student-Newman-Keuls [SNK] test, $p = 0.05$).

While the densities of post-pueruli on the reef face were similar during February 1987 and March–April 1987, the densities of post-pueruli in ledges and caves were higher in March–April 1987.

There was significant variation in the densities per m^2 of post-pueruli between reefs during the February sampling (ANOVA, $p < 0.01$, $df = 10,130$). The results of an SNK test ($p = 0.05$) indicated that the reefs could be split into 3 groups on the basis of their mean densities per m^2 . Reefs 45, 3, 29 and 35 (range = 0.09 to $0.20 \text{ ind. } m^{-2}$) had significantly lower densities than Reefs 5, 22, 21 and 17 (range = 0.42 to $0.47 \text{ ind. } m^{-2}$) which were lower than densities on Reefs 1s, 1n and 4 (range = 1.21 to $1.49 \text{ ind. } m^{-2}$). Reefs 1s, 1n and 4 were within 50 m of each other whereas the other 2 groups of reefs were interspersed. During March–April, there was no significant difference in the densities per m^2 (ANOVA, $p = 0.10$, $df = 10,88$). Mean reef densities for the 7 reefs sampled during both periods (Reefs 1s, 1n, 5, 21, 22, 29 and 45) were generally higher in March–April (range = 0.57 to $1.69 \text{ ind. } m^{-2}$) than in February (range = 0.09 to $1.49 \text{ ind. } m^{-2}$).

In February 1987, the sizes of post-pueruli in caves (mean size = 16.4 mm CL , $n = 107$) were not significantly different than those in ledges (mean size = 16.0 mm CL , $n = 249$), and both were significantly larger than those on the reef face (mean size = 14.6 mm CL , $n = 67$; ANOVA, $p < 0.01$, $df = 2,464$, and SNK test, $p = 0.05$). Analysis of the sizes of post-pueruli in March–April 1987 indicated that individuals in caves (mean size = 20.3 mm CL , $n = 51$) were significantly

larger than those of both ledges (mean size = 18.3 mm CL , $n = 254$) and the reef face (mean size = 18.4 mm CL , $n = 107$; ANOVA, $p < 0.01$, $df = 2,409$, and SNK test, $p = 0.05$). The sizes of post-pueruli had significantly increased between February 1987 and March–April 1987 (Kolmogorov Smirnov analyses, $p < 0.01$; caves, $D = 0.39$; ledges, $D = 0.21$; reef face, $D = 0.40$).

Cover around the shelter

Cover around shelters consisted mainly of *Amphibolis*, a range of algal species (see Appendix 1), or a combination of *Amphibolis* and algae. There were also small amounts of unidentified species of sponges (mainly in caves), and detritus (Fig. 3). Proportionally fewer post-pueruli $< 15 \text{ mm CL}$ were in bare shelters (Fig. 3), all of which were on ledges or in caves. No post-pueruli $< 10 \text{ mm CL}$ were found in shelters covered by detritus.

Fidelity to shelters

Most of the shelters were occupied by post-pueruli $< 15 \text{ mm CL}$. As the lobsters were not marked (because any disturbance might influence their fidelity to a shelter) it was not possible to be certain that occupants on the following day were the same individual. Approximately 50 % of shelters were occupied for 2 or more consecutive days and 20 % were occupied for more than 10 consecutive days (Fig. 4). Three shelters were occupied for at least 16 consecutive days, 2 for at least 15 consecutive days, 1 each for at least 10, 12 and 14 consecutive days.

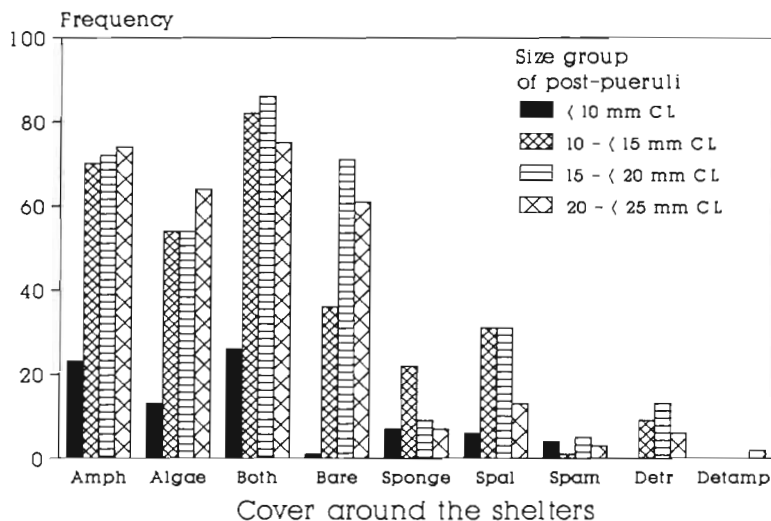


Fig. 3. Cover immediately adjacent to shelters at Seven Mile Beach. 'Amph': *Amphibolis*; 'Both': cover of both algae and *Amphibolis*; 'Bare': areas bare of cover; 'Spal': cover of both sponges and algae; 'Spam': cover of both sponges and *Amphibolis*; 'Detr': detritus; 'Detamp': cover of detritus and *Amphibolis*.

Gregariousness within shelters

Of the 265 post-pueruli, 75 % were solitary (Fig. 5). In 30 cases, lobsters were found in pairs, and on 8 occasions there were 10 or more post-pueruli in a group. The largest group had about 100 individuals in a small hole (0.25 m² surface area) in the reef face. Of these, 93 were captured and measured; 7 were juveniles between 25 and 31 mm CL, and the remainder were post-pueruli between 10 and 25 mm CL (Fig. 6). Although these data indicate that a range of sizes may occupy a single shelter, subsequent sampling by Fitzpatrick (CSIRO Marine Laboratories; see Fig. 7), using sampling methods identical to those in the present study, indicate that there is a trend for smaller post-pueruli to be solitary and larger animals to be gregarious.

Experiments on habitat preference

Of the 4 designs of artificial shelter (Fig. 2) post-pueruli were only found in those made of 'Tanikalon' which is used to make the artificial seaweed collectors. No post-pueruli were found in control plots of *Amphibolis*. A 2-factor ANOVA of the density of post-pueruli per 'Tanikalon' shelter indicated that there was no significant interaction between sites and sampling times ($p = 0.56$, $df = 2,24$). There were, however, significantly more post-pueruli per shelter ($p < 0.05$, $df = 2,24$) in March–April 1987 (mean = 1.34, $n = 10$) compared with February 1987 (mean = 1.01, $n = 10$), and more in February 1987 than in November 1986 (mean = 0.80, $n = 10$). Also significantly more post-pueruli ($p < 0.001$, $df = 1,24$) were found at 1 of the 2 sampling sites (Site 1 mean = 0.85, $n = 15$; Site 2 mean = 1.24, $n = 15$).

Limestone blocks

All 35 post-pueruli found in holes in the limestone blocks were between 7 and 12 mm CL (mean = 9.9 mm). Although this experiment was originally designed to be analysed by ANOVA (factors being times, sites, seagrass cover, hole size and hole depth) this analysis was unnecessary because of several clear-cut results. Post-pueruli preferred holes in blocks with seagrass cover compared to bare shelters ($n = 35$ with seagrass cover, $n = 0$ without cover). In addition, there was a strong preference for the deeper holes ($n = 34$ for 50 mm deep holes, $n = 1$ for 25 mm deep holes). There was no significant difference in the numbers of post-pueruli found between the 5 sampling times and the 2 sites (contingency table analysis, $G = 2.84$, $df = 4$, $p = 0.59$),

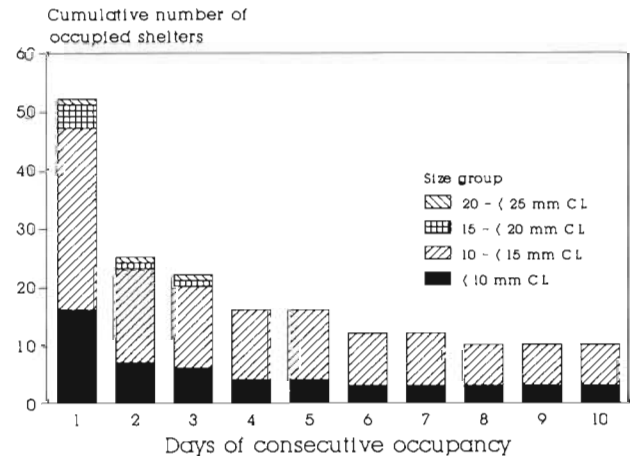


Fig. 4. *Panulirus cygnus*. Occupancy of natural shelters by size groups of post-pueruli at Seven Mile Beach during November 1986

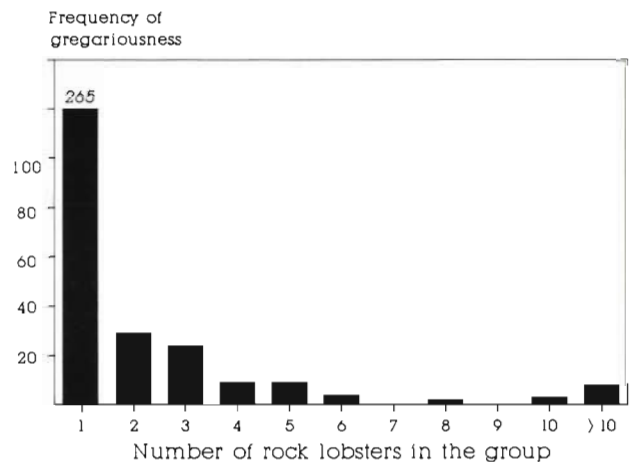


Fig. 5. *Panulirus cygnus*. Frequency of gregariousness of post-pueruli in natural shelters at Seven Mile Beach during February 1987

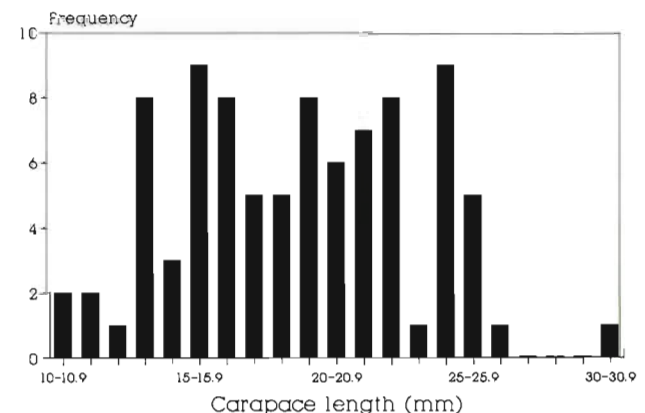


Fig. 6. *Panulirus cygnus*. Size range of 86 post-pueruli and 7 juveniles (greater than 25 mm CL) found together in one natural shelter at Seven Mile Beach during February 1987

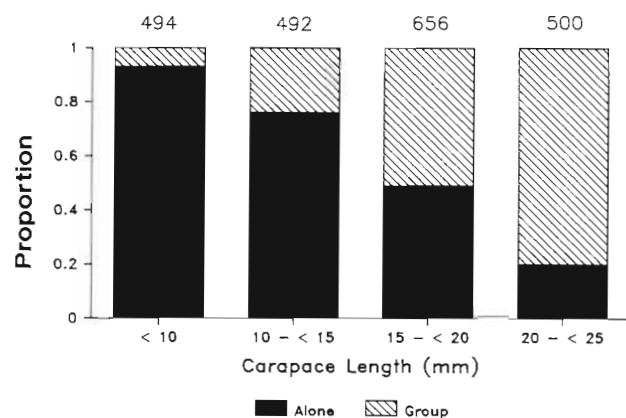


Fig. 7. *Panulirus cygnus*. Proportion of post-panulirus pueruli in groups or alone. Data are supplied by J. Fitzpatrick (CSIRO Marine Laboratories) and were collected at Seven Mile Beach in September 1988, November 1988, January 1989 and March 1989, pooled and then divided into 4 size classes. Numbers at the top of the histograms are the number of post-panulirus in each sample

and a total of 17 and 18 post-panulirus were recorded at the 2 sites respectively. The factor of hole size (diameter) was analysed by pooling the data over times, sites, seagrass cover and hole depth and regressing the diameter of the hole against the carapace length of the post-panulirus. The analysis is shown in Table 1 and indicates that there is a highly significant linear trend for smaller post-panulirus to be found in smaller holes.

Transferral of post-panulirus

Post-panulirus from the artificial collectors did not readily enter the natural shelters. Ten out of 20 eventually moved into the holes, tail first, after prodding by the divers. Four of these immediately walked out into the surrounding seagrass and one other left its hole 15 min later. A higher proportion of post-panulirus remained in holes in the limestone blocks compared with those transferred to natural shelters, in the first hour after

Table 1 *Panulirus cygnus*. Linear regression of the carapace length of post-panulirus against the hole diameter of shelters in limestone blocks. Carapace lengths are pooled over sampling times, sites and hole depth (34 individuals were in 50 mm deep holes and only 1 was in a 25 mm hole). The regression model assumes that there is more than one carapace length measurement for each hole size (Sokal & Rohlf 1981, p. 477)

Source of variation	SS	%	df	MS	F	p
Groups	20.11	31.48	3	6.70	4.75	<0.010
Linear	18.82	93.60	1	18.82	29.24	<0.001
Deviation	1.29	6.40	2	0.64	0.46	>0.05
Error	43.78	68.52	31	1.41		
Total	63.89					

$Y = 5.67 + 0.37X$ $R^2 = 0.94$

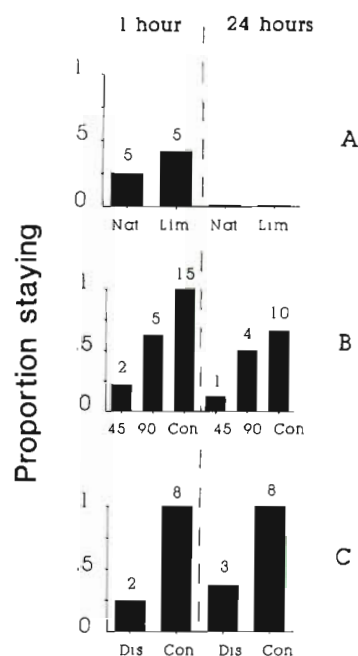


Fig. 8. *Panulirus cygnus*. Proportion of post-panulirus staying in shelters, 1 h and 24 h after transferral. (A) Results of transferring post-panulirus from artificial seaweed collectors to natural (Nat) or to artificial shelters in limestone blocks (Lim). Numbers on top of these and all other histograms in this figure refer to the number of post-panulirus remaining in shelters. (B) Results of transferring post-panulirus from their natural shelters and returning them by 2 different release methods, 45° (45) and 90° (90), compared with undisturbed control lobsters (Con). (C) Results of transferring/disturbing post-panulirus from their holes in limestone blocks (Dis) and returning them, compared with undisturbed controls (Con)

release, but all individuals were absent on the following day (Fig. 8A, Table 2).

In the second experiment, fewer post-panulirus released at 45° stayed within the first hour in their natural shelters compared with those released at 90°, and also with untransferred (undisturbed) control lobsters. The same trend was apparent on the following day (Fig. 8B, Table 2).

In the third experiment, 6 out of 8 transferred (dis-

Table 2. *Panulirus cygnus*. Results of transferral experiments with post-pueruli: Experiment 1 compared whether post-pueruli stay after being transferred from artificial collectors to either natural shelters or to artificial holes in limestone blocks. The response (stay/leave) was measured after 1 h and 24 h. Experiment 2 compared whether post-pueruli stay after being transferred from their natural shelters and returned to the same shelters, compared to those of undisturbed control post-pueruli in natural shelters. Two different release methods were used (release container held at 45° or at 90°; see text) and the response (stay/leave) was measured after 1 h and 24 h. Experiment 3 compared whether post-pueruli stay after being transferred from their own holes in limestone blocks and returned to their same holes compared with undisturbed control lobsters, and the response (stay/leave) was measured after 1 h and 24 h. All post-pueruli were transferred within 3 min of capture and all data were analysed by 3-factor loglinear G test contingency tables

Factors	df	G	p
Experiment 1			
Habitat × Time	1	0.19	>0.05
Time × Stay	1	304.23	<0.001
Habitat × Stay	1	305.67	<0.001
Habitat × Time × Stay	1	0.00	>0.05
Experiment 2			
Transfer × Time	2	1.62	>0.05
Transfer × Stay	2	249.83	<0.001
Time × Stay	1	245.00	<0.001
Transfer × Time × Stay	2	3.81	>0.05
Experiment 3			
Transfer × Time	1	0.11	>0.05
Transfer × Stay	1	108.01	<0.001
Time × Stay	1	103.77	<0.001
Transfer × Time × Stay	1	0.04	>0.05

turbed) post-pueruli left their holes in limestone blocks within 1 h. No control lobsters left during this time (Fig. 8C, Table 2). A similar trend was apparent on the following day but there were 3 individuals present in the 'disturbed' holes compared with 8 in the controls.

DISCUSSION

The post-pueruli of *Panulirus cygnus* were found in holes in the limestone reefs covered by seagrass and/or algae. Only 2 individuals were found in seagrass beds away from the reefs despite intensive sampling using suction pumps. Sweat (1968) used a variety of methods including vacuuming, pushnets and roller-frame trawls to find *P. argus* in seagrass beds and also failed to locate significant numbers of post-pueruli. The only consistently successful method of finding post-pueruli in their natural habitat has been by visual searching by divers (e.g. Serfling 1972, Engle 1979, Marx 1983).

The habitat of *Panulirus cygnus* at Seven Mile Beach, of holes in limestone reefs covered by seagrass, is different from that of some of the other post-pueruli in the genus. For example, *P. argus* is found predominantly in clumps of the red alga *Laurencia* (Marx & Herrnkind 1985b), although it has also been found in rock rubble (Andree 1981) and on mangrove roots (Witham et al. 1964). Post-pueruli of *P. interruptus*, however, are found in a range of habitats: shallow protected rock rubble and crevices, under boulders with an algal or seagrass covering and also in *Phyllospadix* seagrass beds (Parker 1972, Serfling 1972, Engle 1979). *P. japonicus* (von Seibold) has also been found in a range of habitats: algal clumps, rock crevices and holes in rocks and boulders (Yoshimura & Yamakawa 1988).

The difference in the habitats of the different species of post-pueruli may be species-specific, or may be a function of the type of shelter locally available; there were no *Laurencia* (Marx & Herrnkind 1985b) or boulders (Parker 1972, Yoshimura & Yamakawa 1988) at Seven Mile Beach. Although the habitat at Seven Mile Beach is typical of the coastal habitat where adult and juvenile *Panulirus cygnus* are found, the lobster also occurs at the Abrolhos Islands, ca 100 km off the coast of Western Australia. Abundant live coral grows in waters around the islands and post-pueruli have recently been discovered living amongst the plates of live coral and in cracks and crevices of algal covered coral (J. Fitzpatrick, CSIRO Marine Laboratories, unpubl. data).

During the present study, the numbers of post-pueruli of *Panulirus cygnus* at Seven Mile Beach in caves, ledges and the reef face changed with time from no significant difference between habitats during February 1987, to significantly more individuals found in ledges than in caves, and more in caves than in the reef face during March–April 1987. The change in habitat preference may reflect a change in behaviour; with increased size, the lobsters become more gregarious and move into the cave and ledge habitat of the juveniles. The mechanism causing gregariousness is unknown although conspecific odour has been suggested by Zimmer-Faust & Spanier (1987) to cause aggregation of juvenile *P. interruptus*.

The microtopography of the reef face, caves and ledges of coastal limestone reefs at Seven Mile Beach is characterised by a multitude of small holes, cracks and crevices with numerous and complex variations. Some of these habitats are occupied by post-pueruli whilst others, which appear to be suitable, and identical to occupied shelters, are unoccupied. It is, therefore, extremely difficult to identify what a post-pueruli perceives as a suitable shelter and to estimate the abundance of potential shelters. It is equally difficult to

determine the exact dimensions of the shelters including the microtopography. This problem was discussed by Caddy (1986) who suggested experimental approaches instead of measuring the fractal dimensions of the habitat. One such approach was to use artificial substrates with a fixed number of randomly placed holes of known dimensions over a range of discrete sizes. Caddy (1986) suggested that under equilibrium conditions, the proportion of holes of a given size which are occupied will be a function of the occupancy rate of naturally occurring holes of the same size, but more easily measured. The holes drilled in the limestone blocks, which provided a suitable habitat for *Panulirus cygnus*, may therefore be an important experimental tool for future research to overcome the problem of determining the shelter preference of the post-juvveniles in relation to shelter size.

On the limestone blocks, *Panulirus cygnus* preferred deeper holes and all individuals preferred blocks with a cover of *Amphibolis*. This suggests that the depth of hole and the cover of the shelter are important factors in habitat preference. In addition, there was a trend for smaller individuals to be associated with smaller holes. Most individuals found in natural shelters were in holes with only one entrance. It is not known whether they preferred a shelter with a single entrance or whether this type of habitat was more common, but Parker (1972) found that post-juvvenile *P. interruptus* also preferred shelters with a single entrance.

Of the other designs of shelter evaluated in the present study, only those constructed of 'Tanikalon' were occupied by the post-juvveniles of *Panulirus cygnus*. Floating collectors made of 'Tanikalon' (Phillips 1972) are also successful for collecting juveniles and post-juvveniles of *P. cygnus* (Phillips 1986). Post-juvveniles are also found when the collectors are moored on the seabed although in lower numbers (Phillips 1972). Similar stages of *P. argus* have also been collected on a different design of floating surface collector (Witham et al. 1964), although various designs of artificial habitat on the seabed have proved unsuccessful (Sweat 1968). Other designs of shelter which have proved successful with other species (e.g. those used by Witham et al. 1964 and Booth 1979) have been unsuccessfully tried with *P. cygnus* (B. Phillips, CSIRO Marine Laboratories, unpubl.). Although both the 'Tanikalon' habitats and holes in limestone blocks were successfully used by *P. cygnus*, they are very different designs of shelter. It may be possible for the 'Tanikalon' habitat to accommodate lobsters as they grow, unlike the fixed hole size in the limestone blocks. 'Tanikalon' habitats may therefore be a better design of shelter catering for a continuum of sizes and growth of post-juvveniles of *P. cygnus*.

Although some large groups of *Panulirus cygnus* (up

to about 100 individuals) were found in a single shelter, 75 % were solitary during sampling in February 1987. This value probably varies depending upon the size range of the lobsters (see Fig. 7) and therefore the time of year that sampling takes place. In comparison with other species, Yoshimura & Yamakawa (1988) reported that *P. japonicus* were solitary, although Herrnkind & Butler (1986) reported that post-juvveniles of *P. argus* sometimes occurred in groups.

Movement of *Panulirus cygnus* between shelters appeared to be common, as 50 % of the occupied shelters were vacated after only 1 d. It is not known where the lobsters went because they could not be individually marked and identified in other shelters. However, they may remain on the isolated patch reefs where there is shelter, because if they tried to move between reefs they would be exposed to a high risk of predation (Howard 1988). Howard (1988) found that predation by fish on the nursery reefs at Seven Mile Beach was concentrated on post-juvveniles between 8 and 15 mm CL. He estimated that fish predators annually remove thousands of lobsters per hectare and suggested that predation may be a major factor limiting the survival of *P. cygnus* on the nursery reefs.

In contrast to the movements of post-juvveniles of *Panulirus cygnus* between shelters, *P. japonicus* is reported to remain in the same shelters for up to 12 mo (Yoshimura & Yamakawa 1988), and Engle (1979) found that 381 out of 433 post-juvveniles of *P. interruptus* were recaptured in the same general area where they were first marked. *P. argus* was reported to move from shelters by Herrnkind & Butler (1986). These authors also found that between 26 and 83 % of post-juvveniles of *P. argus* dispersed overnight from algal clumps where they had been placed, although it is not known whether this dispersion from the shelters was as a result of transferral. In the case of *P. cygnus* the proportion remaining after transfer may be a function of the degree of disturbance (see Fig. 8B). The proportion of *P. cygnus* remaining after transfer by divers to their own or other shelters varied depending on the method of release. Post-juvveniles transferred from artificial collectors to what appeared to be ideal shelters did not stay, but moved off into the surrounding seagrass.

In the present study, post-juvveniles of *Panulirus cygnus* have been found in their natural habitat by the extensive use of divers. As a result, it was possible to investigate their habitat preference and behavioral patterns and future studies of their growth rate, feeding patterns and population dynamics are also possible. The rejection of shelters by post-juvveniles immediately after transferral may be a significant problem in areas of high natural predation. Further studies of transferral techniques could be of value in minimising such rejection. In experiments where post-juvveniles were allowed

to select artificial shelter without being transferred, 2 designs of artificial shelters, those made of 'Tanikalon' and the holes in limestone blocks with seagrass cover, were successfully utilised. This indicates that such habitats may be of value in enhancing the survival of post-juvéniles where natural shelter is limited.

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Appendix 1 Species of algae found as cover around shelters of post-juvéniles

Alga	Taxonomic authority
<i>Amphiroa anceps</i>	(Lamour) Decne.
<i>Botrycladia obvata</i>	(Sond.) Kylin
<i>Caulerpa cactoides</i>	(Turner) C.Ag.
<i>Caulerpa obscura</i>	Sonder
<i>Caulerpa racemosa</i>	(Turner) Bosse
<i>Caulerpa vesiculifera</i>	Harvey
<i>Corallina cuvieri</i>	Lamouroux
<i>Hypnea cervicornis</i>	J.Ag.
<i>Laurencia filiformis</i>	(C.Ag.) Harv.
<i>Lenormandia spectabilis</i>	Sonder
<i>Lobospora bicuspidata</i>	Aresch.
<i>Metagoniolithon stelliferum</i>	(Lamk.) Bosse
<i>Metamastophora flabellata</i>	(Sond.) Setchel
<i>Rhodymenia australis</i>	(Sond.) Harv.
<i>Struvea plumosa</i>	(Sond.) Harv.
<i>Zonaria turneriana</i>	J.Ag.

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