#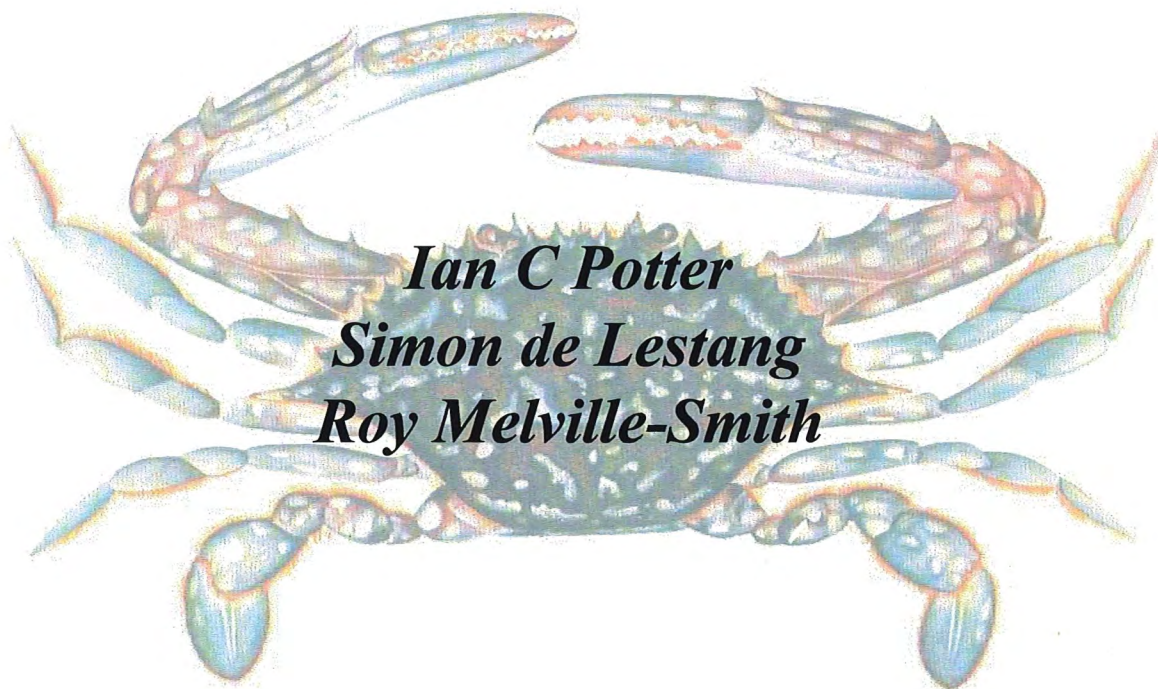 The collection of biological data required for management of the blue swimmer crab fishery in the central and lower west coasts of Australia

Ian C Potter
Simon de Lestang
Roy Melville-Smith

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The collection of biological data required for management of the blue swimmer crab fishery in the central and lower west coasts of Australia

Ian C Potter

Simon de Lestang

Roy Melville-Smith

Murdoch University Centre for Fish and Fisheries Research

Division of Science and Engineering

School of Biological Sciences and Biotechnology

Murdoch University

Murdoch Western Australia

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PRINCIPAL INVESTIGATOR: Prof. I. C. Potter
Centre for Fish and Fisheries Science
Division of Science and Engineering
Murdoch University
South Street, Murdoch University
Perth W.A. 6150
Telephone: 08 9360 2524   Fax: 08 9360 6303

OBJECTIVES:

1. The main overall objective for this study was to determine those biological parameters for the blue swimmer crab *Portunus pelagicus* in selected water bodies in south-western Australia and in Shark Bay that are crucial for undertaking the stock assessments that are necessary for developing management plans for this crustacean in these two regions.
2. Determine the habitat types occupied by blue swimmer crabs in the marine and estuarine environments in which this species is relatively abundant in south-western Australia and in Shark Bay, and the way in which the habitat requirements change with body size and state of maturity.
3. Determine the size and age compositions and growth rates of populations of blue swimmer crabs in different water bodies in south-western Australia (Leschenault Estuary, Koombana Bay, Peel-Harvey Estuary, Comet Bay and Cockburn Sound).
4. Determine the size and age compositions, growth rates, size at maturity and spawning period of blue swimmer crabs in Shark Bay and compare the resultant data with those obtained for the above four water bodies much further south.

NON-TECHNICAL SUMMARY:

Samples of the blue swimmer crab *Portunus pelagicus* were collected from nearshore and offshore waters in five water bodies in which this species is fished commercially and recreationally in Western Australia. These water bodies, which were sampled either monthly or bimonthly for at least two years, were the Leschenault Estuary, Koombana Bay, Peel-Harvey Estuary and Cockburn Sound on the lower west coast of Australia at latitudes between 32° and 33° S and Shark Bay on the central west coast of Australia at a latitude of about 25° S. The samples were used to obtain the following data for *P. pelagicus* in the above water bodies: (1) the size at first maturity, reproductive period and location of egg release; (2) the times of recruitment of the 0+ age class and also, in the case of estuaries, the times of emigration of older crabs into marine waters; (3) the types of habitats it occupies and how they change with body size and reproductive status and (4) the size and age compositions and growth rates.

Macroscopic and microscopic investigations of the characteristics of developing gonads led to the development of morphological criteria that could readily be used to assign each ovary and testis (+ vas deferens) to one of four maturity stages. These maturity stages enabled the phasing of reproduction and, in the case of males, the size at which sexual maturity was first attained, to be determined. Although ovigerous females, *i.e.* females with eggs beneath their abdomen, were found in estuaries, they were less abundant in these systems than in the marine environment. Female crabs leave estuaries as they become ovigerous and, together with those in the marine environment, release their eggs into marine waters where the resultant zoea develop. Spawning on the lower west coast occurs

predominantly between early spring and the middle of summer, whereas it takes place throughout the year in Shark Bay where water temperatures are consistently higher. The size (carapace width) at which female *P. pelagicus* typically reaches maturity in south-western Australia (*ca* 86 mm) was less than in Shark Bay (92 mm). The same type of differences between regions were found with male crabs.

The juveniles of blue swimmer crabs live on bare sandy substrates in protected nearshore, shallow waters until they reach a size equivalent to a carapace width of about 60 mm, when they move offshore into deeper waters and often into areas of sparse seagrass. The densities of blue swimmer crabs were far lower in Shark Bay than in any of the four water bodies on the lower west coast and they decline markedly in estuaries during winter as salinities fall precipitously due to massive increases in freshwater discharge.

Large numbers of 0+ recruits start appearing in nearshore, shallow waters as early as January in Cockburn Sound and February to March in the Peel-Harvey Estuary, but not until August in the Leschenault Estuary. Furthermore, the presence of few crabs with a carapace width less than 80 mm in Koombana Bay indicates that 0+ crabs are recruited into the Leschenault Estuary, rather than into Koombana Bay, the embayment into which this estuary discharges.

In estuaries and embayments in south-western Australia, *P. pelagicus* typically start to attain the minimum legal size for capture (127 mm) in late summer, when they are just over one year old. Most crabs have died, either through natural or fishing mortality, by the time they are about 20 months old. The growth rates of blue swimmer crabs in the Leschenault Estuary, Koombana Bay, Peel-Harvey Estuary and Cockburn Sound did not differ markedly. Since *P. pelagicus* spawns throughout the year in Shark Bay and individual crabs cannot be aged, it was not possible to derive a growth curve for the population in this embayment.

OUTCOMES ACHIEVED:

From a management perspective, this project has demonstrated that, although the sizes at first maturity varied amongst water bodies, they always lay well below the minimum legal size for capture. The optimal habitats required by crabs at different stages in their life cycle have been identified, thus providing managers with information on the likely consequences of anthropogenically-induced changes to the environment. Comparisons between the densities of crabs in Cockburn Sound in 2000 with those in the same water body in the early 1970s indicate that increased densities of crabs can lead to a reduction in growth rates. The development of reliable and readily applicable criteria for the stages in gonadal development has increased the precision with which various reproductive characteristics and trends can be determined. Consequently, managers can now be provided with precise and robust data for such characteristics as the size at first maturity and the spawning period and location. Finally, the growth parameters estimated in this project can be used, in combination with the reproductive data, to develop more appropriate fishery models for stock assessment.

Acknowledgments

Background

The fishery for *Portunus pelagicus* in Western Australia

The blue swimmer crab *Portunus pelagicus* is widely distributed throughout the Indo-West Pacific (Stephenson, 1962; Kailola *et al.*, 1993). This species generally lives in estuaries and relatively protected inshore marine waters and occupies areas ranging from near the shoreline to depths of at least 50 m. *Portunus pelagicus* supports commercial fisheries in numerous countries (*e.g.* India, Pakistan, Philippines, Java and Australia), with most of the catches being taken in water depths less than 25 m. In Australia, the commercial catches of the blue swimmer crab have been increasing rapidly, with annual catches in the mid 1990s reaching about 1700 tonnes (Kumar, 1997). The commercial fishery for blue swimmer crabs in Western Australia is the largest in Australia, with a catch of 673 tonnes and a beach price of approximately $3 million being recorded for the 1999/2000 financial year (Fisheries WA, Catch and Effort Statistics).

Activation of latent fishing effort in the Western Australian commercial fishery for blue swimmer crabs, as well as an extension of the fishery to previously unexploited or only lightly-fished areas of the coast, has led, in certain areas, to conflict between commercial fishers and the recreational users of this resource. Although there are currently no reliable figures for the recreational catches of crabs in

Western Australia, a survey of households showed that blue swimmer crabs are one of the most important recreational fishing species and that an estimated 76 000 people participated in the fishery in this state in 1986/87 (Anon., 1989). The results of recreational fishing surveys (*e.g.* Dybdahl, 1979; Sumner and Williamson, 1999) suggest that, in some years, recreational crab catches in certain areas of the fishery have been greater than those of commercial fishers. Since the size of the recreational fishery for blue swimmer crabs will almost certainly increase further in south-western Australia, there has been, in recent times, a move to buy out commercial licences in some important recreational fishing areas, such as the Leschenault and Peel-Harvey estuaries and Cockburn Sound. The greatest potential for the expansion of the commercial fishery for this species in Western Australia appears to lie in very large and remote marine embayments, such as Shark Bay, Nicol Bay, Onslow and Exmouth Gulf within which, this resource is only lightly exploited at the present time.

The expansion of the commercial fishery for *P. pelagicus* in Western Australia during recent years has been accompanied by a change in the method by which crabs are caught commercially. Until the early 1990s, most of the commercial catch was obtained using tangle nets, but in the last few years there has been a pronounced movement towards the use of traps. The change in gear, where it has been permitted to occur, has enabled individual commercially-licensed fishers to become more efficient. Analysis of commercial catch data for Cockburn Sound (Melville-Smith *et al.*, 1999) indicates that the shift from netting to trapping crabs has contributed significantly to the increase in commercial crab catches in this embayment. This type of shift in fishing method is likely to become widespread in the commercial fishery in Western Australia.

Further investigation of the commercial catch data maintained by Fisheries WA demonstrates that commercial catches of *P. pelagicus* in Cockburn Sound have increased markedly during the last 20 - 30 years. Unfortunately, the change from netting to trapping during the 1990s makes it difficult to derive comparable catch per unit effort (CPUE) data for the fishery over the last 20 - 30 years, and thus to obtain a clear indication as to whether the relative abundance of *P. pelagicus* has increased in Cockburn Sound. However, comparisons between the catches obtained by trawling with a research vessel in 1971 - 1973 and 2000 strongly indicate that the abundance of *P. pelagicus* in Cockburn Sound had become far greater by the later period (see Results). Earlier studies have demonstrated that increases in the densities of various

decapod species have been accompanied by significant declines in growth rate and the size at which sexual maturity is attained (Morrissy, 1975; Cobb, 1986; Polovina, 1988; Morrissy *et al.*, 1995).

Previous biological studies on *Portunus pelagicus* in Western Australia

Previous work on *Portunus pelagicus* has provided information on certain aspects of the biology of this species in two estuaries (Meagher, 1970, 1971; Potter *et al.*, 1983; FRDC Project 95/042; de Lestang *et al.*, 1999). The results of these studies demonstrate that the Leschenault and Peel-Harvey estuaries provide habitats that are important for *P. pelagicus* during the first 18 months of its life. They also show that female crabs first become ovigerous in early summer when they are about one year old and that soon after this time both sexes attain the minimum legal size for capture (127 mm carapace width).

The only published biological data on this species in the marine environment are those provided for catch rates, size-frequency distributions and prevalence of ovigerous (berried) females in the highly-protected marine embayments of Cockburn Sound (Penn, 1977) and Koombana Bay (Meagher, 1971) and on the diets of this species in more open waters (Edgar, 1990). The results of these studies implied that the zoea are released in marine waters. Furthermore, the distribution of the relatively small number of crabs recorded in the last of these studies indicated that, as this portunid increases in size in Western Australia, it moves from unvegetated areas in nearshore waters to either unvegetated or vegetated areas in more offshore and deeper waters.

From the above, it follows that the type of detailed biological data that are required to manage effectively the stocks of *P. pelagicus* in Western Australia, is limited. Furthermore, there are no data available on the growth rates, size at maturity and duration of the spawning period of *P. pelagicus* in embayments, such as Shark Bay, which are located nearly 1000 km to the north of Cockburn Sound, the most northerly water body in which the blue swimmer crab has been studied in Western Australia. Comparisons between the results of other studies on *P. pelagicus* at different latitudes (Smith 1982; Ingles & Braum, 1989; Reeby *et al.*, 1990; Sumpton *et al.*, 1994) suggest that the growth rates, size at first maturity and duration of the spawning period of this species will be greater in Shark Bay than in the water bodies on the lower west coast where *P. pelagicus* has previously been studied and within

which water temperatures are far lower. Clearly, this biological information will be of considerable importance in the future for managing *P. pelagicus* in the central and northern parts of Western Australia, where the commercial fishery for blue swimmer crabs is expanding.

Rationale for extending the proposed reproductive studies

During the course of this study, it became increasingly apparent that the methods typically used for exploring critical aspects of reproduction in *P. pelagicus* often varied and were far from optimal. This was particularly the case with the criteria employed for determining whether or not a male crab had reached the stage at which it could reproduce and had therefore become mature. Part of the present study thus focused on comparing the results obtained by the different methods used for determining whether a male crab was mature and, as a consequence of those comparisons, to a refinement of the most appropriate of those methods.

Presumably because it is difficult to distinguish between stages in the development of the gonads of male crabs, most estimates of the size at which male portunids reach maturity have utilised data derived from differences in the patterns of allometric growth of the appendages of immature and mature male crabs (*e.g.* Hartnoll, 1974; Reeby *et al.,* 1990; Muino *et al.*, 1999). However, this approach is time consuming and not very precise and is dependent on the requisite original appendage still being present. A few workers have shown that it is possible to use morphological criteria to categorise the gonads of male crabs according to their state of development, and to use the resultant stages to determine the size at which male crabs typically become mature (*e.g.* Meagher, 1971; Comeau & Conan, 1992). Sumpton & Smith (1994) proposed that a male crab can be considered to have become mature when its abdominal flap ceases to be tightly fixed to its cephalothorax. Although this method is applicable for elucidating whether female crabs are mature, it has not yet been demonstrated that the same criteria can be applied to determine whether male crabs have become mature.

In the case of teleost fishes, histological sections of subsamples of their ovaries are often examined to ensure that the appropriate stage is being assigned to the gonads on the basis of their macroscopic appearance (*e.g.* Chubb & Potter, 1984). Such an approach has only occasionally been adopted with portunids (*e.g.* Kumar *et al.*, 1999). It was therefore decided that it would be desirable to extend the present

study to validate that the criteria adopted for the macroscopic staging of ovaries were appropriate.

Since moulting and the loss and regrowth of limbs each lead to a change in the body weight of decapods and therefore also in their gonadosomatic index (GSI), Kamiguchi (1971) decided, in the case of the lobster *Palaemon puacidens*, to express the gonad weight of each individual as a percentage of its body volume (gonadovolumetric index - GVI), rather than as a percentage of its body weight. We agree with this view and have thus adopted a similar approach for examining the trends exhibited by the relative size of the gonads of female and male crabs throughout the year.

Need

There is a critical need to develop a management policy for the blue swimmer crab fishery in Western Australia, that is based on sound biological data for this species in a range of environments in this state. Since the environments in which blue swimmer crabs are caught in Western Australia are unique, it is essential that detailed biological data of this species are collected specifically for these waters. The type of biological data that are required include information on the habitat requirements, size and age compositions, growth and reproductive biology of this species. Reliable data on some of these aspects (size and age compositions and reproductive biology) are essentially confined to those obtained for the Leschenault Estuary, Koombana Bay, Peel-Harvey Estuary and to those derived from catches obtained in Cockburn Sound, using a trawl net with a large mesh (Meagher, 1971; Penn, 1977; Potter *et al.*, 1983; FRDC project 95/042). From a comparison of data in these latter studies, it would appear that crabs grow to a larger size or live longer in marine waters than in estuaries. There is thus an urgent need to obtain more precise information on the biology of blue swimmer crabs in a range of environments in south-western Australia.

There are no biological data for blue swimmer crabs in Shark Bay, where the fishery is developing and appears to have considerable potential. Shark Bay is located at a far more northern latitude and is thus far warmer than the Peel-Harvey Estuary and Cockburn Sound. Furthermore, there are essentially no estuaries near Shark Bay, which means that the type of area, which is often used as a nursery ground, is not available to this portunid in the region of Shark Bay. The presence of far warmer

temperatures in Shark Bay, which will presumably influence the feeding activity, growth and reproductive biology of this species (see *e.g.* Hill, 1980; Sukumaran & Neelakantan, 1996), together with the type of environment found in that region, mean that it would be inappropriate to extrapolate from the results of studies further south in temperate Western Australia, or indeed from elsewhere in Australia.

It should be noted that the biological data produced by this proposal will complement a separate study of the dynamics of the fishery (both commercial and recreational) and exploitation of the series of stocks which contribute to the catch of blue swimmer crabs in Western Australia (FRDC project 97/121).

Objectives

- The main overall objective for this study was to determine those biological parameters for the blue swimmer crab *Portunus pelagicus* in selected water bodies in south-western Australia and in Shark Bay that are crucial for undertaking the stock assessments that are necessary for developing management plans for this crustacean in these two regions.

- Determine the habitat types occupied by blue swimmer crabs in the marine and estuarine environments in which this species is relatively abundant in south-western Australia and in Shark Bay, and the way in which the habitat requirements change with body size and state of maturity.

- Determine the size and age compositions and growth rates of populations of blue swimmer crabs in different water bodies in south-western Australia (Leschenault Estuary, Koombana Bay, Peel-Harvey Estuary, Comet Bay and Cockburn Sound).

- Determine the size and age compositions, growth rates, size at maturity and spawning period of blue swimmer crabs in Shark Bay and compare the resultant data with those obtained for the above four water bodies much further south.

Methods

Sampling localities and routine sampling regime

The following account provides a description of the water bodies in which *Portunus pelagicus* was routinely sampled and the sampling regime (sites and sampling methods) adopted in each of those water bodies.

Leschenault Estuary and Koombana Bay

The Leschenault Estuary and Koombana Bay are located *ca* 125 km south of the city of Perth (Fig. 1). The Leschenault Estuary, which is a permanently open microtidal estuary, consists of a large lagoonal-like basin that covers an area of *ca* 63 km² and rarely exceeds 2 m in depth. The outer edge of this basin is surrounded by a shallow ($\leq$ 0.5 m) fringing platform. The substrate of the basin consists of silt and sand which, in places, is covered by dense seagrass beds of *Halophila ovalis* and *Ruppia megacarpa* (Meagher, 1971). The estuary basin lies parallel to the coast and is separated from the Indian Ocean by a narrow ($\leq$ 1.5 km) sand dune system, the Leschenault Peninsula (Fig. 2). The Collie River discharges into the south-eastern end of this basin, opposite the point where the entrance channel of the estuary opens into Koombana Bay and the sea.

Koombana Bay is the only relatively enclosed and sheltered marine embayment along the approximately 200 km of coastline between Warnbro Sound and Cape Naturaliste (Fig. 2). Koombana Bay occupies an area of *ca* 3.5 km² and has a maximum depth of *ca* 13 m.

Portunus pelagicus was collected during the day from the Leschenault Estuary and Koombana Bay for 28 consecutive months (Table 1). Sampling was carried out at three nearshore, shallow sites and five offshore, deeper sites in both the middle and lower regions of the basin of the Leschenault Estuary and at three nearshore, shallow sites and six offshore, deeper sites in Koombana Bay (Fig. 2).

Leschenault Estuary and Koombana Bay were sampled using two seine nets of different size and an otter trawl and lines of four crab traps. A 21.5 m seine net was employed in the three nearshore, shallow sites in both the middle and lower regions of the basin of the Leschenault Estuary and in three of the sheltered nearshore, shallow sites in Koombana Bay. The water depths at each of these sites ranged from 0.5 to

1.5 m. The same three nearshore, shallow sites in Koombana Bay were also sampled with a 102.5 m seine net. An otter trawl and crab traps were employed to sample the five offshore, deeper sites in both the middle and lower regions of the basin of the Leschenault Estuary, where the depths ranged from 2 to 3.5 m, and the six offshore, deeper waters of Koombana Bay, where the depths ranged from 9 to 14 m.

Note that each of the sampling sites in the Leschenault Estuary and Koombana Bay and in the three other water bodies (Peel-Harvey Estuary, Cockburn Sound and Shark Bay) were randomly selected.

Peel-Harvey Estuary

The Peel-Harvey Estuary is located *ca* 55 km south of the city of Perth (Fig. 1). The two large and shallow basins of the Peel-Harvey Estuary, *i.e.* Peel Inlet and Harvey Estuary, are supplied by three tributaries, namely the Serpentine, Murray and Harvey rivers (Fig. 3). The Peel-Harvey Estuary is connected to the Indian Ocean via the natural Mandurah Entrance Channel, which is located at the northern end of Peel Inlet and opens into Comet Bay, and by the artificial Dawesville Channel, which connects the northern end of the Harvey Estuary with the ocean. The Mandurah Entrance Channel is *ca* 5 km long and 250 m wide and is relatively shallow (< 3 m), while the Dawesville Channel, which was opened in April 1994, is 2.5 km long and 200 m wide and ranges in depth from 4.5 to 6.4 m (Anon. 1996; Bradby, 1997).

The Peel Inlet, which is essentially circular, covers an area of *ca* 75 km^2 and never exceeds 2.5 m in depth (Fig. 3). More than half of this inlet comprises wide and shallow fringing banks, large areas of which become exposed under certain conditions (Hodgkin *et al.,* 1980; McComb *et al.,* 1981; Rose, 1994). The Serpentine and Murray rivers discharge into the Yunderup delta on the north-eastern side of Peel Inlet (Fig. 3).

The Harvey Estuary is an elongate, shallow basin (< 2.5 m deep), that is *ca* 20 km long, 2.5 km wide and covers an area of *ca* 56 km^2 (Fig. 3). The northern end of this estuary is joined to the Peel Inlet by the Grey Channel, a shallow 2 km long channel. As is now the case with the Mandurah Channel, the Grey Channel is kept open by regular dredging. The Harvey River discharges into an extensive shallow delta at the southern end of the Harvey Estuary (Hesp, 1984).

Portunus pelagicus was collected from the Peel-Harvey Estuary using 10.5, 21.5 and 102.5 m seine nets and the otter trawl and crab traps at four weekly intervals for 36 months (Table 1). The 10.5 and 21.5 m seine nets were both used to sample the three sites in nearshore, shallow waters (< 0.5 m) of the Mandurah Entrance Channel, western Peel Inlet, eastern Peel Inlet, Serpentine River, northern Harvey Estuary and southern Harvey Estuary. The 102.5 m seine net was used to sample two sites in nearshore, shallow waters (< 0.5 m) of the western Peel Inlet, eastern Peel Inlet, northern Harvey Estuary and southern Harvey Estuary. The otter trawl was not used in offshore, deeper waters (2 to 3.5 m) of the basins of the Peel Inlet and Harvey estuary as these waters contained large accumulations of macroalgae, or in the offshore, deeper waters of the Serpentine River as this contained numerous fallen trees. A line of four crab traps was used to sample the two sites in offshore, deeper waters in each of the western Peel Inlet, eastern Peel Inlet, northern Harvey Estuary and southern Harvey Estuary (Fig. 3). Heavy boat traffic and fallen trees made it impractical to use traps to sample crabs in the Mandurah Entrance Channel and Serpentine River, respectively.

Note that the presence of steeply sloping banks and very strong tidal flow within the Dawesville Channel prevented the use of either seine nets, otter trawls or traps in this artificial channel. Thus, in the present study, the characteristics of blue swimmer crabs in the Dawesville Channel are considered to be represented by those caught in the northern-most end of the Harvey Estuary, just inside the innermost entrance of this channel. Thus, subsequently in this report, the term entrance channel encompasses the three 21.5 m seine net, three 102.5 m seine net and three otter trawl sampling sites in the Mandurah Entrance Channel and the three 21.5 m seine net, one 102.5 m seine net, three otter trawl and one crab trap sampling site in the northern part of the Harvey Estuary.

Cockburn Sound

Cockburn Sound, which is located *ca* 20 km to the south of the city of Perth, covers an area of *ca* 100 km^2 (Fig. 4). The shallow and fringing waters of this protected marine embayment, which expand outwards to form the expansive Southern Flats (2 – 4 m deep) in the south-west and the Parmelia and Success banks (4 – 6 m deep) in the north, surround a large basin, in which the water depths range from 17 to

24 m. The above banks are covered by dense beds of the seagrasses *Posidonia sinuosa*, *Posidonia australis* and *Amphibolis antarctica*, whereas the substrate in the deep basin consists mainly of unvegetated bare sand and silt. The seagrass beds have helped stabilise the substrate and promoted sediment accumulation, thereby restricting the movement of water into Cockburn Sound and producing a lagoonal-like marine embayment (Hutchinson & Moore, 1979).

Since no rivers discharge into Cockburn Sound, the input of freshwater into this embayment is restricted to that derived from rainfall and groundwater and storm-drain discharge (Hutchinson & Moore, 1979). As a consequence, the salinities in Cockburn Sound remain close to full strength seawater (35 ‰) for much of the year.

Portunus pelagicus was collected in 24 consecutive months from five regions of Cockburn Sound (Table 1; Fig. 4). In Mangles Bay in the south-western corner of Cockburn Sound, sampling was undertaken at three sites in nearshore, shallow waters (< 1.5 m) using the 21.5 m long seine net, and at three sites in slightly more offshore waters (< 2 m) using the otter trawl. The otter trawl was also used to obtain *P. pelagicus* from three sites in offshore, shallow waters of the Southern Flats (< 3 m) and from three sites in offshore, deeper waters of each of the northern deep, middle deep and southern deep regions of Cockburn Sound (Fig. 4).

Shark Bay

Shark Bay, which is located *ca* 800 km north of the city of Perth, covers an area of *ca* 13 000 km^2, making it the largest marine embayment in Australia (Francesconi & Clayton, 1996). It is divided into western and eastern gulfs by the Peron Peninsula (Fig. 5). The substrate of large areas of the relatively shallow water (< 5 m) in the two gulfs are covered by substantial beds of seagrass. Indeed, the seagrass beds in Shark Bay cover an area as great as *ca* 4000 km^2 and contain 12 species, which represents the greatest coverage and diversity of seagrasses reported for any water body anywhere in the world (Walker, 1985). The dominant species of seagrass, *Amphibolis antarctica*, contributes *ca* 90% to the total cover by seagrass.

Shark Bay receives little freshwater input, undergoes limited exchange of water with the ocean and is subject to high evaporation rates. As a result, salinities in much of the embayment exceed that of full strength seawater and form a gradient that increases from the top to the bottom of each gulf (Hagan & Logan, 1974).

Portunus pelagicus was collected from four regions in Shark Bay, *i.e.* Herald Bight, Denham, Monkey Mia and Nanga Bay, at bimonthly intervals during 24 consecutive months (Table 1). Three unvegetated sites in nearshore, shallow waters (< 1.5 m) of each of these regions were sampled using the 21.5 m and 102.5 m seine nets. In each region, three unvegetated sites and three adjacent seagrass sites in slightly further offshore, shallow waters (2 – 4 m) were sampled using the otter trawl (Fig. 5). The otter trawl was also used to sample three sites in offshore, deeper waters (10 – 14 m) that were moderately vegetated at Denham and Nanga Bay and unvegetated at Herald Bight and Monkey Mia (Fig. 5). The lines of crabs traps were also used to obtain crabs from two sites in slightly offshore, shallow waters and two sites in offshore, deeper waters of each region.

The sites used for sampling crabs in Shark Bay were selected on the basis that commercial and recreational crab fishers reported that they were regions where they fished.

Sampling equipment

The 10.5 m long seine net consisted of two 4.5 m long wings, each comprising 6 mm mesh, and a 1.5 m long pocket made of 3 mm mesh. The net, which fished to a maximum depth of 1.5 m, was trawled by hand along the shallow banks for 5 min. The distance covered by each trawl was recorded and ranged from 75 to 130 m, the precise distance depending on the strength of water current and the composition of the substrate.

The 21.5 m seine net consisted of two 10 m long wings and a 1.5 m bunt. Each wing consisted of a 6 m long panel of 9 mm mesh and a 4 m panel of 3 mm mesh. The 1.5 m bunt had a mesh of 3 mm. The net fished to a depth of 1.5 m and covered an area of *ca* 116 m^2. The net was carried out from the beach for *ca* 10 m and then extended parallel to the shoreline, after which it was dragged shorewards and on to the beach.

The 102.5 m seine net consisted of two 50 m long wings and a 2.5 m bunt. Each wing consisted of a 44.5 m long panel made of 25 mm mesh and a 5.5 m long panel of 13 mm mesh. The bunt consisted of 9.5 mm mesh. The net was 1.8m high and, during each seine, covered an area of *ca* 1670 m^2. The net was laid in a semi-circle from the bow of a boat until fully extended and then rapidly pulled on to the beach.

The number of crabs in each seine net sample was converted to a density, *i.e.* number of crabs 100 m^{-2}.

The otter trawl net (small 'tri-net'), which was 2.6 m wide (effective fishing width), 0.5 m high and 5 m long, consisted of 51 mm mesh in the wings and 25 mm mesh in the bunt. The bridle length was 13 m, while the warp length was varied in relation to water depth, according to the equation warp length = water depth x 4. The otter trawl net was towed at a speed of *ca* 3.5 km h^{-1} for between 150 and 500 m, the distance covered was recorded and depended on the type of substrate and the volume of seagrass retained in the net. The number of crabs in each sample was converted to a density, *i.e.* number of crabs 1000 m^{-2}.

The crab traps, which were the same as those employed by the majority of professional fishers who target *Portunus pelagicus* in Western Australia, were *ca* 630 mm high and 1000 mm in diameter and contained 76 mm mesh. The traps were joined together in four lines of four, with each trap being separated by a distance of 15 m. The traps were baited with fish and set for *ca* 24 h. The number of crabs in each sample was expressed as a catch per unit effort, *i.e.* number of crabs trap^{-1} 24 h^{-1}.

Table 1 Regimes employed to sample *Portunus pelagicus* in five water bodies in which this species is fished commercially and recreationally in Western Australia.

	Leschenault Estuary	Koombana Bay	Peel-Harvey Estuary	Cockburn Sound	Shark Bay
Methods	21.5 m seine net	21.5 m seine net	10.5 m seine net	21.5 m seine net	21.5 m seine net
	Crab traps	102.5 m seine net	102.5 m seine net	Otter trawl	102.5 m seine net
	Otter trawl	Crab traps	Crab traps		Crab traps
		Otter trawl			Otter trawl
Water depth (m)	<1 – 3	<1 – 9	<1 – 3	<1 – 23	<1 – 14
Regions	2	2	6	5	4
Sampling Frequency	Monthly	Monthly	Monthly	Monthly	Bimonthly
Duration	28 months	28 months	36 months	24 months	24 months

Sampling with a commercial trawler

A commercial trawler was used to obtain samples that would provide data on the densities, size compositions, age and growth and certain reproductive characteristics of *Portunus pelagicus* during recent times and which would be

comparable with those recorded by Penn (1977) during the early 1970s. Thus, this commercial trawl was used seasonally between the summer and spring of 2000 to sample the same six randomly-selected sites in the northern half of Cockburn Sound as were sampled monthly by Penn (1977) between August 1971 and January 1973. Comparisons between the two periods utilised the data for the months in which sampling was undertaken in the latter period, *i.e.* 2000.

The trawl net used by the commercial trawler during the 1970s possessed wings constructed of 51 mm mesh and a cod end of 45 mm mesh. A tickler chain was hung below the footrope. The effective fishing width and height of the net were *ca* 12 m and 1 m, respectively. This net was towed for a period of *ca* 30 min at a speed of *ca* 6.4 km h^{-1} (Penn, 1977). The two nets, that were used in tandem by the commercial trawler during the 1990s, each comprised wings made of 51 mm mesh and a cod end of 45 mm mesh. The effective fishing width and height of each net was *ca* 8 m and 1 m, respectively. These nets were towed for *ca* 20 min at a speed of *ca* 4.6 km h^{-1}. The trawl net employed by the smaller trawl vessel in the 1990s consisted of 51 mm mesh in the wings and 25 mm mesh in the cod end and was towed for 500 m at a speed of *ca* 3.5 km h^{-1}.

The number of crabs caught in each replicate trawl on each sampling occasion in the 1970s has been recorded in Fisheries WA data files as a mean catch rate for each sampling occasion, *i.e.* mean number of crabs caught h^{-1}. The mean catch rate was then used, in conjunction with the area covered per hour of trawling, to calculate the mean density, *i.e.* number of crabs 1000 m^{-2}.

In the case of samples collected by both the commercial and smaller trawler in the 1990s, the number of crabs caught and the area covered during each replicate trawl on each sampling occasion were used to calculate the density of crabs in the area trawled, *i.e.* number of crabs 1000 m^{-2}. The values for each replicate sample were then used to calculate the mean density ± 1 SE on each sampling occasion.

Measurements

The water temperature (^{o}C) and salinity (‰) near the bottom of the water column at each site in nearshore, shallow waters (< 1.5 m) and at the surface and bottom of the water column at each site in offshore, deeper waters were recorded. The water depth at each site was also measured.

The carapace width (CW) of each crab, *i.e.* the distance between the tips of the two lateral spines of the carapace, was measured to the nearest 1 mm. The wet weight of each crab was recorded to the nearest 0.1g.

In the case of female *Portunus pelagicus*, the abdomen is triangular and firmly attached to the cephalothorax in the juvenile, whereas it is almost circular and free in the adult. These differences can be used to determine whether an individual female crab has undergone a pubertal moult and thus attained maturity (Van Engel, 1958; Ingles & Braum, 1989). The carapace width at which 50% of crabs undergo a pubertal moult will therefore correspond to the CW_{50} at first maturity. Although the shape of the abdominal flap can be used to distinguish the sex of crabs with a CW > *ca* 30 mm, it cannot be used to sex smaller crabs. The smaller crabs were thus sexed by using a dissecting microscope to ascertain whether or not their pleopods bore setae and were thus either females or males. A record was kept of any ovigerous females and whether the spermathecae of females were enlarged and pear-shaped, and thus indicating that copulation had recently occurred (Bawab & El-Sherief, 1988, 1989).

Relationship between reproductive variables and moulting and the environment.

The frequency of occurrence of moulting crabs and female crabs amongst all crabs and of ovigerous female crabs amongst female adult crabs in three different water depths (Cockburn Sound), in three regions of an estuary (Peel-Harvey Estuary) and between an estuary (Leschenault Estuary) and an adjacent coastal marine embayment (Koombana Bay) were compared using a chi-square test.

Age and growth

Seasonal growth curves were fitted to the size-frequency data recorded for both female and male crabs from the Leschenault Estuary / Koombana Bay, Peel-Harvey Estuary, Cockburn Sound and Shark Bay. The seasonal growth curve fitted to the data was

$$CW_t = CW_\infty \left\{ 1 - \exp \left[-\left\{ K(t - t_0) + \frac{CK}{2\pi} \sin 2\pi(t - t_s) - \frac{CK}{2\pi} \sin 2\pi(t_0 - t_s) \right\} \right] \right\},$$

where CW_t is the estimated carapace width at age t years, CW_∞ is the asymptotic carapace width, K is the curvature parameter, t_0 is the theoretical age at which the

estimated carapace width is zero, C (where $0 \leq C \leq 1$) determines the relative amplitude of the seasonal oscillation and t_s (where $0 \leq t_s \leq 1$) determines the phase of the seasonal oscillation with respect to t_0. This modified form of the von Bertalanffy growth curve was developed by Hoenig and Choudary Hanumara (1982) and independently by Somers (1988) (as cited by Pauly et al., 1992).

The size frequency data were assumed to represent a mixture of 0+ and 1+ crabs, where the component distributions were assumed to be normally distributed with a common variance, s^2. The mean of each component distribution was taken to be the value estimated from the seasonal growth curve. The proportions of each component present within the carapace width frequency data varied among months and was written as $p_{k,m}$, where k represents the component ($1 \leq k \leq n_{comp}$) and m represents the calendar month.

If $\hat{L}_{j,k}$ represents the expected carapace width of the j th crab, sampled in month m_j and estimated from the seasonal growth curve under the assumption that the crab is a member of the k th component (thus, in combination with the birth data determined from trends in spawning females, determining its age), then the value of the probability distribution function for the observed carapace width, L_j, is $f_{j,k}$, where

$$f_{j,k} = \frac{1}{\sqrt{2\pi s^2}} \exp\left[-\left(L_j - \hat{L}_{j,k} \right)^2 / \left(2s^2 \right) \right].$$

The log-likelihood of the j th observation may be written as

$$\lambda_j = \sum_{k=1}^{n_{comp}} z_{j,k} \log\left(f_{j,k} \right)$$

where

$$z_{j,k} = \frac{p_{k,m_j} f_{j,k}}{\sum_{k=1}^{n_{comp}} p_{k,m_j} f_{j,k}}.$$

The overall log-likelihood was calculated for the n observations for each sex within each region as

$$\lambda = \sum_{j=1}^{n} \lambda_j .$$

The parameters of the seasonal growth curve and the monthly proportions within the 0+ component distribution were estimated by maximising this log-likelihood using AD Model Builder (Otter Software, Inc.).

For the Peel Harvey, an additional cohort was present in April and May and as a consequence an alternative method was used. The size distributions within each month for each sex for crabs from the Peel Harvey Estuary were considered to be a mixture of one to three component normal distributions. These component distributions were estimated by fitting an appropriate mixture to the observed size distributions. From the means of the resulting component distributions, a selection was made of those that best described the growth of the crabs in this estuary. A seasonal growth model of the form described above was fitted by least squares to the selected monthly mean carapace widths.

Timing of reproduction

The gonads were removed from at least 30 females and 30 males, collected from each of the five water bodies on each sampling occasion, and weighed to the nearest 0.01g. The gonadovolumetric index (GVI) of each of these crabs was calculated using the equation $(W/CW^3) \times 10^6$, where W = wet weight of the gonad and CW = carapace width of the crab (Aiken & Waddy, 1980).

The gonads of at least 50 female and 50 male crabs, collected from the Peel-Harvey Estuary, Cockburn Sound and Shark Bay on each sampling occasion, were dissected out and assigned a maturity stage based on a combination of both macroscopic and histological characteristics (see Tables 3 & 4 in Results). The characteristics of these stages represent cumulative modifications of those employed for various species of decapod (Meagher, 1971; Bawab & El-Sherief, 1988; Bauer & Lin, 1994; Sumpton et al., 1994; Minagaw & Sano, 1997; Kumar et al., 1999).

For the purposes of histology, the posterior lobe of the left ovary and the mid region of the left vas deferens were removed from female and male crabs, respectively, covering a wide size range and a full range of maturity stages. They were fixed in 4% glutaraldehyde in 0.025M phosphate buffer (pH 7.0) for 24h, dehydrated in a series of increasing concentrations of ethanols and embedded in

paraffin wax. NB. The 4% glutaraldehyde was used as the fixative because traditional fixatives, *i.e.* Bouin's fixative and 5% formaldehyde, did not fix the gonadal tissue of *Portunus pelagicus* sufficiently well for the preparation of satisfactory histological sections. Transverse sections of the above gonadal tissues were cut at 6 μm and stained with Mallory's trichrome. The longest and shortest diameters of 30 randomly-selected oocytes, which were sectioned through the nucleus, were measured to the nearest 5 μm. The mean of these measurements for each oocyte was then calculated. This approximates to the diameter of the oocyte.

Size of female crabs at maturity

The size at which 50% of the female crabs reach sexual maturity (CW_{50}) was determined from data obtained for a wide size range of female crabs in which each crab had been recorded as either having not undergone or having undergone a pubertal moult and thus had reached the size at which it was mature (adult).

The size at first maturity of crabs is typically calculated by fitting a logistic curve to the proportion of mature crabs within each size class in order to determine the parameters of the relationship, $CW_{50,k}$ and $CW_{95,k}$. However, such grouping introduces error as all crabs within each size class are assumed to have a size equal to that of the class midpoint. To overcome this problem, the blue swimmer crab data were not classified into width classes but were treated as individual outcomes of a set of binomial trials.

The determination of the maturity status of a female crab drawn from a population of crabs may be considered to be a binomial trial, where the probability of success is taken as the probability that the crab is mature. For a sample of female crabs from assemblage k, the probability that the j th crab is mature is calculated from the logistic function as:

$$p_{j,k} = \frac{1}{1 + \exp\left[-\ln(19)\frac{\left(CW_{j,k} - CW_{50,k}\right)}{\left(CW_{95,k} - CW_{50,k}\right)}\right]},$$

where $CW_{j,k}$ is the observed carapace width of the crab and $CW_{50,k}$ and $CW_{95,k}$ are the carapace widths at which 50% and 95%, respectively, of the female crabs in the assemblage are mature.

A variable, $X_{j,k}$, was created and set to 1 if the j th crab from assemblage k was mature and 0 if it was immature. The likelihood of the j th observation was then defined as

$$L_{j,k} = p_{j,k}^{X_{j,k}} \left(1 - p_{j,k}\right)^{1 - X_{j,k}}.$$

From this, the log-likelihood of the sample data from assemblage k was calculated as

$$\lambda_k = \sum_{j=1}^{n_k} \left[X_{j,k} \ln\left(p_{j,k}\right) + \left(1 - X_{j,k}\right) \ln\left(1 - p_{j,k}\right) \right]$$

where n_k is the number of observations in the sample from this assemblage. The parameters of the logistic equation were estimated by maximising the log-likelihood using the Microsoft Excel routine, Solver. The sample data from the assemblage were randomly resampled and analysed to create 100 sets of bootstrap estimates of the parameters and estimates of the probability of maturity at a set of carapace widths covering the range of observed data. Estimates of the 95% confidence intervals for the parameters and of the estimated probability of maturity at each specified carapace width were taken as the 2.5 and 97.5 percentiles of the table of results from this analysis. The point estimate of each parameter and of each probability of maturity at the specified carapace width were taken as the medians of the bootstrap estimates.

The resulting confidence intervals of the probability of maturity at each specified carapace width represent the 95% confidence limits for the expected (mean) value. The precision of the point estimate reflects both the total number and the carapace width distribution of the crabs that were sampled. As expected from probability theory, when sample size is large, the resulting estimate of the mean probability at a specific carapace width will be relatively precise as the information from the entire data set contributes to the fitted logistic curve. In contrast, the confidence limits for the observed proportion of mature crabs within each carapace width class will reflect only the total number of crabs that were sampled for that carapace width class; no information is drawn from other carapace width classes over the range of carapace widths that were sampled.

The maturity-carapace width relationships for data from different assemblages were compared using a likelihood ratio test. The data for two assemblages ($k=1$ and

2) were analysed simultaneously. The log-likelihood for the combined data set was calculated as

$$\lambda = \lambda_1 + \lambda_2.$$

The null hypothesis, ω, was that the maturity-carapace width relationships for the data from the two assemblages could be described by logistic equations with q linear constraints on the parameters, such as $CW_{50,1} = CW_{50,2}$ and $CW_{95,1} = CW_{95,2}$. The alternative hypothesis, Ω, was that the parameters $CW_{50,1}$, $CW_{50,2}$, $CW_{95,1}$ and $CW_{95,2}$ were distinct, i.e. the maturity-carapace width relationships were different. The log-likelihood was calculated for the combined sample data set for the null hypothesis and for the alternative hypothesis as λ_ω and λ_Ω, respectively. The test statistic for the likelihood ratio test was calculated as $2(\lambda_\Omega - \lambda_\omega)$. The null hypothesis was rejected at the α level of significance when the test statistic exceeded $\chi^2_\alpha(q)$ (Cerrato, 1990). Hypotheses tested were that (a) $CW_{50,1} = CW_{50,2}$; (b) $CW_{95,1} = CW_{95,2}$; and (c) $CW_{50,1} = CW_{50,2}$ and $CW_{95,1} = CW_{95,2}$.

Size of male crabs at maturity

It is far more difficult to determine whether a male than a female crab has attained maturity. Consequently, the results obtained using different criteria as to whether a male crab has reached maturity (macroscopic staging of gonads, changes in allometric growth and the tightness of the abdominal flap) have been compared (see Introduction for further background information).

Macroscopic staging of gonads

Male crabs with stage I (immature) and stage II (early development) "gonads" were considered not yet to have reached maturity, i.e. they were immature, while those with stage III (late development) and stage IV (fully mature) "gonads" were considered to be mature (see Table 3 in Results). For a sample of male crabs from assemblage k, the probability that the jth crab is mature (stages III and IV) is calculated from a logistic function, using the analysis described above for female crabs.

Allometric growth method

Male crabs were separated into three categories, namely (i) those that were small (CW < 60 mm) and thus below the minimum size at which maturity is usually reached in other populations of blue swimmer crabs, *i.e.* they were juveniles, (ii) those that were large (CW > 120 mm) and were thus of a size that would be expected to have reached maturity, *i.e.* they were adults, and (iii) those in which the carapace widths lay between 60 and 120 mm and would thus constitute either juveniles or adults. The choice of the above three categories of carapace widths was based on the sizes recorded for juveniles and adults in different populations of blue swimmer crabs by Meagher (1971), Ingles & Braum (1989), Reeby *et al.* (1990) and Potter & de Lestang (2000). The lengths of the dorsal surface of the propodus of the largest chela were plotted against the respective carapace widths of male crabs belonging to the first and second of these categories. Regression lines were fitted by the least sum of squares method to these two data sets, assuming $CP = mCW + b$, where CP is the length of the chela propodus, CW is the carapace width and m and b are constants. The next step involved determining whether the point representing the relationship between the CP and CW of each crab was closer to the regression lines for these two variables for juvenile crabs or for adult crabs, as defined above. Each crab was then re-classified as juvenile or adult depending on the distances from the respective lines. These two lines were then fitted iteratively to the sets of reclassified points until convergence was achieved. The point at which the lines intersect was then assumed to provide a close approximation of the carapace width at which there is a pronounced change in the pattern of growth of the largest chela, a feature which, in male crabs, is associated with its pubertal moult (Ingles & Braum, 1989; Reeby *et al.*, 1990). The final regression lines were used to classify the crabs as juvenile or adult. The size at which 50 % of the male crabs first become mature was calculated from the logistic curve fitted to the proportions of adult crabs in these data, as described above for female crabs.

Abdominal tightness

The abdomen of a juvenile male crab is tightly fixed to the ventral surface of its cephalothorax, while that of an adult crab hangs free or is held in place through the presence of two notches (Van Engel, 1958; Sumpton *et al.*, 1994). The carapace

width at which the abdomens of 50% of the male crabs first became loosely fixed was calculated from the logistic curve fitted to the proportions of crabs with loosely fixed abdomens, as described above for female crabs.

Tagging of *Portunus pelagicus* in Cockburn Sound

The individuals of three groups of 1000 undamaged intermoult crabs, incorporating both sexes and covering a wide size range, were each tagged with Hallprint TBA-1 t-bar tags, using one of the following three methods.

(i)   The insertion of a standard (13 mm) stem-length and a fine (1 mm) filament and anchor, through the suture line between the posterior edge of the carapace and the anterior edge of the abdomen.

(ii)   The insertion of a short (13 mm) stem-length and a fine (1 mm) filament and anchor in the same anatomical position as in (i) above.

(iii)   The insertion of a short stem-length and a fine filament and anchor, through the epimeral suture line.

All crabs were immediately returned to the water in their original location of capture. A reward of a $2 "scratch'n'win" ticket was supplied for all returns.

Results/Discussion

Environmental variables

Water temperatures

On the basis of pooled data for different years of sampling, the mean monthly water temperatures at the bottom of the water column in the Leschenault Estuary, Peel-Harvey Estuary, Cockburn Sound and Shark Bay each followed the same trends, with values rising to a maximum in mid to late summer and declining to a minimum in mid winter (Fig. 6). [Note that since water temperatures in Koombana Bay were essentially the same as those in Leschenault Estuary, they have not been included in Fig. 6] However, in each of the six months that Shark Bay was sampled, the mean water temperature was greater in that embayment than in the other four water bodies. Thus, for example, while the maximum mean monthly water temperature was *ca* 27°C in Shark Bay, it never reached 25°C in any of the other water bodies (Fig. 6). Likewise, the minimum monthly water temperature was greater in Shark Bay (*ca* 19°C) than in either Cockburn Sound (16°C) or the Leschenault and Peel-Harvey estuaries (*ca* 12-13°C). While the mean water temperatures in the Leschenault and Peel-Harvey estuaries in each month were similar, they were less than in Cockburn Sound in eight of the twelve months of the year.

Salinity

Mean monthly salinities at the bottom of the water column, utilising pooled data for the different years, ranged only from 34.4 to 36.7 ‰ in Cockburn Sound and from 40.0 to 41.8 ‰ in Shark Bay (Fig. 7). While the mean bottom salinities in Koombana Bay ranged only from 34.7 to 38.4 ‰ in ten of the twelve months, it did decline to 28.5 ‰ in September, as a result of heavy freshwater discharge from the Collie River. In contrast, salinities at the bottom of the water column in both the Leschenault and Peel-Harvey estuaries fell markedly from values close to full strength sea water during the summer and autumn to as low as 20.9 ‰ in the former estuary and 11.5 ‰ in the latter estuary in August (Fig. 7).

Densities of *Portunus pelagicus* in different water bodies

Leschenault Estuary and Koombana Bay

Based on data derived from seine netting over two years, the mean monthly densities of crabs in nearshore, shallow waters (< 1.5 m) of the Leschenault Estuary declined progressively from *ca* 9.5 crabs 100m^{-2} in January to *ca* 0.1 crabs 100m^{-2} in July (Fig. 8). No crabs were caught in August or September of any year. The densities subsequently rose from *ca* 1 crab 100m^{-2} in October to over 2.8 crabs 100m^{-2} in November and December (Fig. 8).

The mean monthly densities in nearshore, shallow waters (< 1.5 m) of Koombana Bay, into which the Leschenault Estuary discharges, exhibited the reverse trend to that just described for that estuary. Thus, while substantial numbers of crabs were caught in August to October, very few or no crabs were caught in each of the other months of the year (Fig. 8).

The trends exhibited by the densities of crabs in offshore waters (2-3 m) of the Leschenault Estuary, derived from data obtained from samples collected by otter trawling, parallel, to a certain degree, those described above for the nearshore, shallow waters of this estuary (*cf.* Figs 8, 9). Thus, densities remained between *ca* 1.5 and 5 crabs 100m^{-2} from January to June and then declined to less than 0.9 crabs 100m^{-2} between July and September, before rising to over 14 crabs 100m^{-2} in November and December (Fig. 9).

The mean monthly densities in offshore, deeper waters of Koombana Bay varied less markedly during the year than those in the nearshore, shallow waters of this embayment and in both the nearshore, shallow and offshore, deeper waters of the Leschenault Estuary (*cf.* Figs 8, 9). However, while the densities of crabs in offshore, deeper waters of Koombana Bay ranged between 3.4 and 7.4 crabs 100m^{-2} between January and August and in December, they never exceeded 1.7 crabs 100m^{-2} between September and November (Fig. 9).

Peel-Harvey Estuary

Seine netting in nearshore, shallow waters (< 1.5 m) of the Peel-Harvey Estuary during July and August yielded few crabs in the entrance channel regions (Mandurah Entrance Channel and northern Harvey Estuary – see Methods) and also the basins and no crabs in the Serpentine River (Fig. 10). The mean monthly densities

in nearshore, shallow waters subsequently peaked in September in the entrance channel regions, in October in the basins and in December in the Serpentine River. Densities in each region subsequently declined and then remained relatively constant until May or June (Fig. 10).

Cockburn Sound

The mean monthly densities in nearshore, shallow waters of Mangles Bay ($<$ 1.5 m), which is located at the southern end of Cockburn Sound (Fig. 4), based on data derived from samples collected by monthly seine netting over two years, declined progressively from *ca* 4 crabs 100m^{-2} in January to *ca* 0.4 crabs 100m^{-2} in April (Fig. 11). Densities remained at between 0.2 and 0.5 crabs 100m^{-2} from May to September and then rose to *ca* 4.5 crabs 100m^{-2} in October and remained above 0.8 crabs 100m^{-2} in November and December (Fig. 11).

The monthly trends exhibited by the densities in slightly deeper waters ($<$ 3 m) in Mangles Bay, based on data derived from samples collected by otter trawling over two years, were broadly similar to those just described for slightly shallower waters in this region (*cf.* Figs 11, 12). The mean monthly densities of crabs in Mangles Bay, the shallowest site sampled by otter trawling in Cockburn Sound, declined progressively from between 2 and 4 crabs 100m^{-2} in January to March to *ca* 0.2 crabs 100m^{-2} in June (Fig. 12). No crabs were caught in Mangles Bay in either July or August. Mean monthly densities subsequently rose progressively from only 0.1 crabs 100m^{-2} in September to *ca* 3.5 crabs 100m^{-2} in December (Fig. 12).

Although crabs were obtained by otter trawling on the Southern Flats (2 – 4 m) and in deeper waters of the middle and northern regions of Cockburn Sound (17 – 25 m), they were never caught in large numbers in any of these three regions (Fig. 12). Furthermore, the mean monthly densities in these three regions, based on data derived from otter trawl samples, did not change consistently during the year. In contrast, the overall catch of crabs obtained by trawling in the deep waters of the southern region of Cockburn Sound (19 – 22 m) was far greater than from the Southern Flats and the deeper waters of the northern and middle regions of Cockburn Sound. Moreover, the densities in the southern deep waters did undergo conspicuous changes throughout the year and these were essentially the opposite of those recorded in nearshore waters of Mangles Bay. Thus, the mean monthly densities in the

southern deep waters rose from *ca* 0.9 crabs 100 m^{-2} in January and February to *ca* 3.6 crabs 100 m^{-2} in May and, apart from in July, remained above 1.7 crabs 100 m^{-2} between June and September, with the mean density in the latter month (5.1 crabs 100 m^{-2}) being the highest recorded during the year. Densities subsequently declined progressively to 1.4 crabs 100 m^{-2} in December (Fig. 12).

Shark Bay

The number of crabs caught by seine netting in the four sampling regions in Shark Bay was low (Fig. 13).

Although crabs were caught by otter trawling over bare sand and in seagrass in nearshore shallow waters (2 – 4 m) at Denham and Nanga Bay in the western gulf on each sampling occasion, the catches in these waters were always low. While a greater number of crabs were caught by otter trawling at Herald Bight and Monkey Mia in the eastern gulf, the densities of crabs at these two localities were still relatively low (Fig. 14).

Since very few crabs were caught by otter trawling in offshore, deeper waters at both Denham and Nanga Bay in the Western Gulf and at Herald Bight and Monkey Mia in the Eastern Gulf, the mean densities of crabs in these waters is not presented.

Size distribution by habitat

The size range of crabs caught in nearshore, shallow waters (< 2 m), intermediate water depths further offshore (3 – 5 m) and in offshore, deeper waters (17 – 25 m) in Cockburn Sound were similar, with the carapace widths of the vast majority of crabs in each of these three water depths lying between 40 and 160 mm (Fig. 15). However, the size distributions of the crabs in these three water depths varied. Thus, the modal size class in the size distribution in shallow waters lay at 60 – 69 mm and was skewed markedly to the left, while those of crabs in both intermediate and deeper waters lay at 90 - 99 mm and were not skewed (Fig. 15).

The size distributions of crabs caught over sand and in seagrass in nearshore, shallow waters (2 – 4 m) in Shark Bay differed markedly (Fig. 16). Thus, while the size distribution of crabs in seagrass was essentially unimodal (modal carapace width = 110 – 119 mm) and with most crabs having carapace widths greater than 80 mm,

that of crabs caught over bare sand tended to be bimodal and contained a substantial number of crabs with carapace widths less than 60 mm (Fig. 16).

Although the number of crabs caught over sand in nearshore, shallow waters of Shark Bay during the day was low (35), despite extensive sampling over two years, the size data obtained were still sufficient to indicate that the size distribution of crabs over sand during the day did not differ conspicuously from that over sand at night (Fig. 17). Likewise, there was no evidence that the size of crabs in nearshore seagrass habitats differed between day and night. Indeed, the modal carapace width during both the day and night was 110 – 119 mm (Fig. 17).

Relationship between reproductive variables and moulting and the environment

In Cockburn Sound, the proportions of crabs found to be moulting were essentially the same in shallow, intermediate and deep water depths ($p > 0.05$) (Fig. 18). The ratio of female to male crabs was close to parity in water depths < 2 m and > 17 m, but well below parity in water depths $3 - 5$ m ($p < 0.05$). However, the proportions of ovigerous female crabs amongst all adult female crabs in water depths of $3 - 5$ m (*ca* 20 %) and > 10 m (*ca* 15 %), were significantly greater ($p < 0.05$) than those recorded in water depths of *ca* 1 - 2 m, *i.e.* 0.3 % (Fig. 18).

In the Peel-Harvey Estuary, the proportion of moulting crabs caught in the entrance channels (28 %) was significantly greater ($p < 0.05$) than in the basins (17.5%) and the river (16.7 %) (Fig. 19). The proportion of female crabs caught in the entrance channels (51.3 %) was also significantly greater ($p < 0.05$) than in the basins (38.1 %) and river (33.3 %). The proportion of ovigerous female crabs amongst all adult crabs in the entrance channels (7.5 %) and basins (3.3 %) was significantly different ($p < 0.01$) (Fig. 19). No ovigerous crabs were caught in the river.

The proportions of moulting crabs amongst all crabs were significantly greater ($p < 0.01$) in the Leschenault Estuary (8.8 %) than in Koombana Bay (4.0 %) (Fig. 19). However, the reverse trend pertained with the proportions of female crabs amongst all crabs (61.4 % in Koombana Bay and 42.7 % in the Leschenault Estuary) and of ovigerous females amongst all adult female crabs (11.9 % in Koombana Bay and 1.6 % in the Leschenault Estuary) ($p < 0.01$).

Size and age compositions

Leschenault Estuary and Koombana Bay

The new 0+ age class became recruited into the Leschenault Estuary in April (Fig. 20). However, the numbers of these small crabs were very low in this and the ensuing months and did not start to increase until August, at which time their modal carapace width had reached 40 – 49 mm. However, the size of the members of this 0+ age class cohort ranged widely between August and November and there were indications that it may have been represented by two cohorts (Fig. 20). This view is based on the fact that there was some evidence of bimodality in the size distribution for September and November and the modal carapace width class for September was 30 – 59 mm and thus far smaller than the 90 – 119 mm recorded in November. By December, the modal carapace width class of this cohort, now early 1+, lay at 100 – 109 mm and remained at this value in four of the next six months. The number of crabs in the Leschenault Estuary declined markedly after May (Fig. 20).

Although a few small crabs were caught in Koombana Bay between May and September, the carapace widths of the vast majority of crabs in this embayment were greater than 80 mm.

Peel-Harvey Estuary

In contrast to the situation in the Leschenault Estuary, the 0+ age class was recruited into the Peel-Harvey Estuary at an earlier time and in far more substantial numbers during the early months of the recruitment period (Fig. 21). However, substantial numbers of crabs did not start appearing in the entrance channels until January or February. Furthermore, on the basis of the data for the entrance channels, it had become evident that by March two cohorts of 0+ crabs had entered the Peel-Harvey Estuary (Fig. 21). Thus, the modal carapace width class of the cohort that entered the estuary first had reached 60 – 69 mm by March and 80 – 89 mm in April to June, whereas the second 0+ cohort was represented by crabs with carapace widths as small as 10 – 19 mm in each month between February and September (Fig. 21). However, this second cohort was only well represented in April and May. Furthermore, and in contrast to the trends exhibited by the numbers of the older 0+ age cohort, the relative abundance of the younger 0+ cohort declined over the next three months.

The modal carapace width class of the main 0+ age class increased from 80 –
89 mm in June to 90 – 99 mm in October. The modal carapace width class of the
corresponding cohort, now early 1+, had reached 110 – 119 mm by December and
120 – 129 mm by March and May (Fig. 21). The numbers of the 1+ age class
declined after the latter month.

The trends exhibited by the size distributions for blue swimmer crabs in the
basins of the Peel-Harvey Estuary essentially parallelled those just described for the
entrance channels. However, the abundance of the younger of the two 0+ age classes
remained relatively higher for a longer period, *i.e.* until October (Fig. 21). Yet, this
cohort was clearly not well represented in subsequent months.

The size-frequency distributions of blue swimmer crabs in the lower reaches
of the Serpentine River demonstrate that substantial numbers of late 0+ and 1+ crabs
are present in this part of the lower estuary between November and February and that
0+ crabs are also relatively abundant there between February and May (Fig. 22). No
crabs or only a very few crabs were caught in the Serpentine River between June and
August (Fig. 22).

Cockburn Sound

The samples collected from shallow waters (< 2.5 m) in Mangles Bay in the
south-western corner of Cockburn Sound in January, February and April, contained
two discrete size groups (Fig. 23). The modal carapace width of the cohort of
smallest crabs, which corresponded to the new 0+ recruits, increased from 40 –
49 mm in January to 50 – 59 mm in April. The modal size class of the second cohort,
which presumably comprised, at least mainly, members of the 1+ age class, increased
from 90 – 99 mm in January to 120 – 139 mm in April (Fig. 23). Few or no crabs
were caught between May and September. The carapace widths of the vast majority
of crabs caught in October and November, which presumably corresponded to crabs
that were approximately 1 year old, lay between 50 and 80 mm.

The new 0+ recruits were first caught in the southern deep region of Cockburn
Sound in February, but only in very low numbers (Fig. 24). The samples collected in
March, April and May were each bimodal and, as in the shallows of Mangles Bay
(Fig. 23), represented the 0+ and at least predominantly 1+ age classes. The cohort of
smaller crabs could be readily traced through the sequential size-frequency
distributions until November, when they had reached the end of the first year of life

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(Fig. 24). The size distributions of the 1+ cohort were clearly distinguishable in the size-frequency histograms for January and February and, as mentioned above, also in March, April and May. The numbers of these older crabs declined markedly after the latter month.

The size-frequency distributions for crabs in the southern flats region of Cockburn Sound did not display any clear change throughout the year, which is presumably partly due to the fact that the monthly sample sizes were relatively small and that few members of the 0+ age class with a carapace width < 80 mm were caught (Fig. 24).

The trends exhibited during the year by the size-frequency distributions for *P. pelagicus* in the northern deep and middle deep regions of Cockburn Sound were consistent with those described above for the southern deep region of this embayment (*cf.* Figs 24, 25). However, it is noteworthy that the first substantial influx of new 0+ recruits into the middle deep region occurred in March, and thus in the same month as in the southern deep region, whereas substantial numbers of young 0+ recruits did not start appearing in samples from the northern deep region until May (Fig. 25).

Shark Bay

Small crabs, *i.e.* those with a carapace width > 20 mm, were found in each of the bimonthly samples collected throughout the year in Shark Bay (Fig. 26). Neither the distributions nor the modal classes of the carapace widths of the different size groups showed any obvious pattern of change in the sequential size-frequency distributions of blue swimmer crabs in Shark Bay (Fig. 26).

Growth

Since blue swimmer crabs spawn throughout the year in Shark bay and there were thus no consistent trends exhibited by the modes in the size frequency data for this species, and as individual crabs could not be aged, it was not possible to fit growth models to the size data for this region. In contrast, blue swimmer crabs typically spawn during a restricted time of the year (early spring to mid summer) on the lower west coast of Australia. Estimates of the carapace width at age for crabs in estuaries and marine embayments in this region were derived from the growth curves for those age classes whose carapace widths were detectable in the size frequency distributions for sequential samples. Since these estimates were derived from modal

progression analysis, they are less precise than those that may be obtained from size at age data. The estimates for the growth rates of crabs did not vary markedly between water bodies on the south-west coast of Australia (Fig. 27). Thus, the carapace width at age 1, the age at which spawning first occurs, was similar in these regions. Estimates for the growth parameters are presented in Appendix 3.

Reproduction

Size at sexual maturity

The carapace widths of the smallest female crab that was found to have reached maturity, *i.e.* had undergone its pubertal moult, ranged from 61 mm in both the Peel-Harvey Estuary and Shark Bay to 90 mm in the Leschenault Estuary. The estimates for the CW_{50}s for female crabs in each of these five systems, which ranged from 86.2 mm in Cockburn Sound to 98.2 mm in the Leschenault Estuary (Table 2, Fig. 28), were significantly different ($p < 0.05$) from each other in each pair-wise comparison apart from that for Koombana Bay *vs* Cockburn Sound.

Table 2. Carapace widths at which 50% of female and male *Portunus pelagicus* first reach maturity (CW_{50}) and their 95% confidence intervals (*CI*) in five water bodies in Western Australia.

	Leschenault Estuary	Koombana Bay	Peel-Harvey Estuary	Cockburn Sound	Shark Bay
CW_{50} (mm)					
Females	**98.2**	**87.3**	**95.2**	**86.2**	**92.4**
95% CI (Lower)	*95.7*	*80.8*	*94.1*	*85.2*	*96.3*
95% CI (Upper)	*100.4*	*90.9*	*96.7*	*87.9*	*87.4*
Males	**91.9**	**92.8**	**94.2**	**96.8**	**115.1**
95% CI (Lower)	*83.2*	*85.3*	*91.5*	*93.4*	*109.5*
95% CI (Upper)	*100.4*	*100.6*	*97.4*	*100.0*	*119.3*

The use of the "allometric method" (see Material and Methods) for estimating the CW_{50}s of male crabs yielded values ranging from 91.9 mm in the Peel-Harvey Estuary to 115.1 mm in Shark Bay (Table 2, Fig. 29). The CW_{50}s for male crabs in the four water bodies located on the south western coast of Australia did not differ significantly among each other, but all differed significantly ($p < 0.05$) from that recorded for male crabs in Shark Bay.

The CW_{50} of male crabs at the "time" when the abdomen ceases to be tightly attached to the cephalothorax, which is regarded by Sumpton & Potter (1984) as implying that sexual maturity has been attained, was also calculated for male crabs in

Cockburn Sound and Shark Bay. The resultant CW_{50}s for these data for male crabs in these two water bodies, 72.1 and 76.2 mm, respectively, were significantly different ($p < 0.05$).

Macroscopic and histological gonad staging

Close macroscopic examination of the gonads of a large number of female *Portunus pelagicus*, that covered a wide size range, showed that the ovaries of this species could readily be separated into four main developmental stages (I – IV), which have been termed immature, early development, late development and mature (Table 3, Fig. 30).

Table 3. Morphological characteristics of sequential macroscopic stages in the development of the ovaries of *Portunus pelagicus* and the types of oocytes in the corresponding stages. Mean diameters are provided for the different stages in oocyte development. GVI = gonadovolumetric index.

Maturity stage	Macroscopic appearance of ovary	Types of oocytes
I Immature	Relatively small (mean GVI = 0.33), flattened and off white to ivory in colour. Anterior region is small, and does not displace the hepatopancreas. The central 'H' shaped region, located in the gastric region, is lightly joined to the dorsal surface of the spermathecae. The posterior section, located in the cardiac and intestinal regions, form two parallel lines.	Loosely packed oocytes, comprising oogonia (5 μm) and, to a lesser extent, chromatin nucleolar oocytes (10 μm) and perinucleolar oocytes (30 μm) (Fig. 30).
II Early development	Obviously larger than stage I ovaries (mean GVI = 0.87), pale yellow, oval in cross section and slightly nodulated. The anterior region marginally displaces the hepatopancreas and the central region envelops the dorsal surface of the spermathecae, while the two lobes of the posterior region are starting to become convoluted.	Loosely packed oogonia, and chromatin nucleolar, late perinucleolar and yolk-vesicle oocytes (90 μm) (Fig. 30).
III Late development	Large (mean GVI = 2.66), yellow and nodulated. Anterior region displaces the hepatopancreas, while the central and posterior regions occupy almost all of the space in the gastric, posterior and intestinal cavities. Most of the spermathecae are enveloped by ovarian tissue.	Early yolk-granule oocytes (130 μm), surround small areas of early stage oocytes (Fig. 30).
IV Fully Mature	Very large (mean GVI = 5.83), deep yellow to orange and highly nodulated. Hepatopancreas is now completely displaced from its former position by the anterior region of the ovary. The gastric, posterior and intestinal cavities are completely filled by the "swollen" central and posterior sections of the ovary. The spermathecae are totally enveloped by the ovary.	Advanced oocytes all at the late yolk-granule stage (250 μm) (Fig. 30).

As with female crabs, the gonads of male crabs could also be readily divided into four stages, which in this case are termed immature, prepubertal, mature and mature-mating (Table 4, Fig. 31).

The distribution of mature testes amongst different sized male crabs was used to determine the CW_{50}s of male crabs in the Leschenault Estuary, Peel-Harvey Estuary, Cockburn Sound and Shark Bay to ascertain whether the CW_{50}s derived using these data were similar to those obtained using the "allometric method" (see earlier), the approach typically employed for this purpose in male crabs (Sukumaran & Neelakantan, 1996). Note that the development of the criteria for the gonad stages of male crabs occurred relatively late in this project and thus prevented their use for determining the CW_{50} for male crabs in Koombana Bay. The CW_{50}s of male crabs at first maturity in the Leschenault Estuary, Peel-Harvey Estuary, Cockburn Sound and

Shark Bay, derived using gonadal stages, were 88.8, 86.6, 89.7 and 96.5 mm, respectively (Fig. 33). The values for the CW_{50}s for male crabs in the three southern water bodies were not significantly different, but all differed significantly from that determined for Shark Bay ($p < 0.05$).

Table 4. Morphological characteristics of sequential stages in the development of the testes / vas deferens of *Portunus pelagicus* and the location of spermatophores in the corresponding stages. Mean gonadovolumetric index (GVI) is given for testes alone in stage I and for testes and vas deferens together in stages II – IV.

Maturity stage	External appearance of testes and vas deferens	Histological appearance of testes and vas deferens
I Immature	Testes very small and white. Vas deferens not detectable macroscopically. Mean GVI = 0.12.	Spermatophores present in testes (Fig. 31).
II Prepubertal	Testes white and becoming enlarged. Vas deferens straight and opaque. Mean GVI = 0.36.	Spermatophores present in testes, but absent in vas deferens.
III Mature	Testes white and enlarged. Vas deferens enlarged and convoluted but still opaque. Mean GVI = 1.70	Spermatophores present in testes and anterior and middle regions of vas deferens.
IV Mature mating	Although testes have a similar appearance to those of previous stage, the vas deferens have become far thicker, more convoluted and a "milky" white. Mean GVI = 1.85.	Spermatophores present in testes and anterior, middle and posterior sections of vas deferens.

Trends exhibited by gonadovolumetric indices and proportions of ovigerous females.

The mean monthly gonadovolumetric index (GVI) of mature female crabs rose to a sharp peak of over 3 in October in Koombana Bay and in September in Cockburn Sound and there was an indication of a second minor peak in November in the second of those two embayments (Fig. 34). In contrast, the mean monthly GVIs for mature female crabs in the Leschenault and Peel-Harvey estuaries did not undergo similar pronounced rises at any time of the year and were always < 1.5. Unlike the situation in Koombana Bay and Cockburn Sound, the mean monthly GVI of mature female crabs in Shark Bay did not peak sharply at any time during the year and was always > 1.3 (Fig. 34).

In the case of male crabs, the mean monthly GVIs always remained below 1 and showed no tendency to produce a conspicuous peak at any time of the year (Fig. 34).

Although the monthly proportions of ovigerous female crabs to all adult females were relatively lower, *i.e.* < 10%, in the Leschenault and Peel-Harvey estuaries than in Koombana Bay and Cockburn Sound, the prevalence of ovigerous females in each system was greatest between mid spring and mid summer (Fig. 34). The monthly proportions of ovigerous females in Shark Bay were low in every month sampled and displayed no seasonal trends (Fig. 34).

Trends exhibited by gonadal stages

Ovarian stages I, II and III were found throughout the year in adult female crabs caught in Cockburn Sound (Fig. 35). No female crabs with stage IV ovaries were found in April or May. The prevalence of adult female crabs with stage IV ovaries increased from a very low level of 4.5 % in June to reach a peak of 52.8 % in September and subsequently declined sequentially from 22.9 % in November to a very low level in March (Fig. 35).

Virtually all of the testes/vas deferens of male crabs in Cockburn Sound, for which the carapace width exceeded the CW_{95} at first maturity, were at stage III (Fig. 35). There were however a few male crabs with stage IV gonads in February, March, June and September.

In contrast to the situation in Cockburn Sound, females with stage IV gonads were found throughout the year in Shark Bay (data not shown).

Trends exhibited by oocyte development

In the ovaries of *P. pelagicus* in Cockburn Sound, large numbers of oogonia, together with some small chromatin nucleolar oocytes, produced a well defined modal diameter class of 0 – 10 μm (Fig. 36). These two stages in oocyte development, which were found in ovaries at all subsequent stages in development, constituted, together with perinucleolar oocytes, the only types of oocyte found in stage I ovaries (Figs 30, 36). The maximum diameter class of oocytes in histological sections of ovaries increased from 90 – 94.9 μm in stage I to 120 – 124 μm in stage II, 160 – 164 μm in stage III and 275 – 279 μm in stage IV. The larger oocytes in stage II ovaries belonged exclusively to the yolk vesicle stage. By stage III, the distribution of the oocyte diameters had become essentially bimodal, with the modal diameter class of the larger oocytes, which represented predominantly the early yolk granule stage,

lying at 130 – 139 μm. The corresponding cohort of larger oocytes in stage IV ovaries, which are now almost exclusively at the yolk granule stage (Fig. 30), range in diameter from 190 to 279 μm and have a modal diameter class of 250 – 254 μm (Fig. 36).

The diameter of the bright orange fertilised eggs, which had recently been extruded and were attached to the pleopods, ranged from 235 to 324 μm (Fig. 36). The more developed grey eggs, that were still attached to the pleopods, exceeded 320 μm in diameter, and were thus larger than the above recently extruded yellow eggs (Fig. 36).

The ovary of a crab that had only very recently extruded its eggs contained large numbers of post-ovulatory follicles and the occasional residual fully mature egg (Figs 30, 36). In April and May, after the completion of the spawning season, the ovaries of female crabs that had undergone a pubertal moult contained some areas which were dominated by oogonia and chromatin nucleolar oocytes and others which contained advanced oocytes (yolk vesicle and yolk granule oocytes) that were undergoing atresia (Fig. 30).

Size and time of sexual maturation of Portunus pelagicus

The carapace-width frequency distributions for female crabs in Cockburn Sound, utilising the data obtained by trawling and seine netting and for all regions, indicate that two size classes are present in January (Fig. 37). The modal class for the carapace widths of the first of these groups, which is skewed to the left, is 20 – 29 mm, while that of the second is 100 – 119 mm (Fig. 37). The first group corresponds to the first of the 0+ recruits, which are the product of spawning in Cockburn Sound between September and January. It is particularly noteworthy that some of the smaller crabs in the second group have not yet undergone a pubertal moult. However, by April and May, the vast majority or all of the group of larger crabs had undergone a pubertal moult and thus become mature, *i.e.* adult (Fig. 37). If one assumes that the second group almost exclusively comprises crabs that belong to the 1+ age class, it then follows that, by the time crabs are just over 1 year old, they will have undergone a pubertal moult. However, some of the larger crabs of the first and presumably 0+ age class had undergone a pubertal moult by May, *i.e.* when they are presumably about six months old (Fig. 37).

The above trends for female crabs in Cockburn Sound are essentially paralleled by those of male crabs (Fig. 37). However, it is evident that the numbers of the 1+ age class of female crabs declined much less rapidly between January and May than was the case with male crabs (Fig. 37). This is presumably due to the fact that the law requires that females that are ovigerous have to be returned to the water.

Influence of size and time on reproduction

The prevalence of stage III and stage IV ovaries in crabs caught in Cockburn Sound with a carapace width > 115 mm was very high between August and October and to a slightly lesser extent in June, July and November (Fig. 38). In contrast the prevalence of stage III and stage IV gonads in crabs with a carapace width < 115 mm, was high only in September. For this reason, the prevalence of recently-copulated and spawning crabs and the gonadovolumetric indices were calculated separately for crabs < 115 mm and ≥ 115 mm (Fig. 39).

The mean monthly values for the prevalence in Cockburn Sound of recently-copulated female crabs amongst all adult female crabs rose, in the case of the smaller crabs, *i.e.* < 115 mm, from 36 % in January to 50 % in March and then declined slowly to 0 % in August (Fig. 39). During the next four months it slowly increased to 14 %. Although the prevalence of recently-copulated larger crabs, *i.e.* ≥ 115 mm, followed a similar trend, it reached a higher peak, *i.e.* 58 %, before declining to very low levels, *i.e.* < 6 %, in every ensuing month except December (Fig. 39).

The mean monthly GVIs of small and large adult female crabs followed similar trends and reached pronounced peaks in September (Fig. 39). However, the mean GVIs for the larger crabs in each month were almost invariably greater than those for the smaller crabs in the corresponding months.

The mean monthly values for the prevalence of the larger and smaller ovigerous female crabs amongst all adult female crabs in Cockburn Sound followed similar trends, rising sharply after August to reach their highest level between October and December and then declining sharply to their minimum levels in February (Fig. 39). As with the GVIs, the mean values for the larger crabs in each month were almost invariably greater than those for the smaller crabs in the corresponding months (Fig. 39).

Discussion of reproductive biology

The use of histological sections of the ovaries and testes/vas deferens of *P. pelagicus* confirmed that the criteria used for macroscopic staging of the gonads of this species were appropriate. Thus, our macroscopic criteria could be employed with confidence to elucidate crucial aspects of the reproductive biology of *P. pelagicus*. For example, the use of such staging for females enabled the main spawning period to be determined and demonstrated that the spawning period was much shorter in small than large crabs. More importantly, the development of reliable staging criteria for males provided a good basis for estimating, through the use of the prevalence of adult (mature) crabs, the CW_{50} for this sex at maturity. The conclusion that this approach is valid is based on the precision with which it enabled the CW_{50} to be determined. Furthermore, the precision using this method is far greater than that achieved through employing data derived from differences in the pattern of growth of the chelipeds of juvenile and adult crabs, an approach that has frequently been employed for decapods (Hartnoll, 1974; Reeby *et al.,* 1990; Sukumaran & Neelakantan, 1996; Muino *et al.,* 1999; Potter & de Lestang, 2000). Moreover, the values obtained for the CW_{50} of males, using data obtained from gonadal staging, and also using the allometric method, were markedly higher than those derived using the tightness of the abdominal flap as a presumed indicator of whether a crab has reached maturity (Sumpton *et al.,* 1994). An examination of male crabs at the time when the abdominal flap became loosely attached demonstrated that, at this time, the gonads were still only at stage I in their development. Thus, in contrast to the situation in females, the loosening of the abdominal flap represents the time when a prepubertal and not a pubertal moult occurs.

There are a number of reasons why the use of gonadal stages provides a better basis for estimating the CW_{50} of male crabs at first maturity than is the case with data derived using the allometric method. (1) The staging of the development of the gonads of a male crab can be used directly to determine whether a male crab is mature. In contrast, the categorisation of whether each of the critical medium size crabs are mature, based on derivations from differences in the pattern of growth of small and large crabs, represents an indirect and not very precise method. (2) The use of gonadal stages does not require as large a number of individuals to obtain a reliable CW_{50}. In this context, the presence of a far greater scatter of the points for the construction of the logistic curve for male crabs from the Leschenault Estuary using

the allometric method, than was the case with male crabs from the Peel-Harvey Estuary or Cockburn Sound employing the same method (Fig. 29), can be related directly to the relatively smaller number of immature crabs that were caught in this estuary. (3) Since the allometric method relies on the appropriate limb being retained, any undetected damage to such limbs can lead to the incorrect classification of a crab as either mature or immature. The far wider scatter of the points for the proportions of male crabs that were adult in each size class for crabs in Shark Bay (Fig. 29), based on allometric data, than was the case for the Peel-Harvey Estuary and Cockburn Sound was attributable to the far greater damage caused to the limbs of crabs in that large and more northern embayment and which are presumably due to attacks from predators.

Our data demonstrate that estimates of the CW_{50} for the attainment of maturity in female crabs in south-western Australia are greater when plotting the logistic curve using the proportion of adult females in estuaries than when applying the same approach for data obtained for marine embayments. The greater CW_{50}s for female crabs in estuaries is due to the fact that, prior to spawning, female crabs emigrate out of estuaries into marine waters and, as a consequence, the proportion of mature female crabs in estuaries is reduced. This change thus results in a shift to the right of the logistic curve, when it is based on data for crabs in estuaries, and thus accounts for the relatively high value for the resultant CW_{50}. This point needs to be born in mind when developing management plans that are based on the relationship between the minimum legal size for capture and the size at first maturity.

Results of tagging experiments

Although tagged crabs were released randomly throughout Cockburn Sound, the vast majority of recaptured tagged crabs were caught in a region approximately two-thirds of the way towards the southern and bottom end of Cockburn Sound. While most of the crabs had travelled less than 2 km from their point of release, a few crabs had travelled 6 to 8 km and two crabs had even travelled > 10 km (Fig. 40).

Most of the tagged crabs travelled relatively short distances from their point of release and there does not appear to be any marked tendency for any tagged crabs to move in any particular direction (Fig. 41). However, it should be noted that the distribution of the fishing effort will have affected the distribution of the recaptured crabs.

The recapture rate of crabs tagged in three different ways did not differ significantly (p > 0.05) (Fig. 42). However, the prevalence of crabs in which the carapace width had increased by at least 5 % was significantly greater in the case of crabs tagged with a short tag in the branchial region than those tagged with either a short or long tag in the abdominal region (Fig. 42).

The preliminary results of tagging experiments, currently being carried out on *P. pelagicus* using a cryogenic method developed for coconut crabs by Fletcher *et al.* (1989) are proving very encouraging and will almost certainly prove to be more effective than spaghetti tags.

Comparisons between the assemblages of *Portunus pelagicus* in Cockburn Sound in the early 1970s and late 1990s.

The mean density of *Portunus pelagicus* in each season between the summer of 2000 and spring of 2000 was between 2.7 and 16 times greater than in the corresponding season in the period between the winter of 1971 and summer of 1972/1973 (Fig. 43). [Note that the mean seasonal densities for the 1970s are based on data for two years.] The minimum and maximum mean seasonal densities in 2000 ranged from *ca* 9000 crabs 1000 m^{-2} in the summer and autumn to 39198 crabs 1000 m^{-2} in winter and in the early 1970s from only 1054 crabs 1000 m^{-2} in spring to just 5013 crabs 1000 m^{-2} in winter (Fig. 43).

The distributions of the carapace widths of both female and male *P. pelagicus* were both conspicuously unimodal in the summer of 2000 and the same was true for the males in that season in the early 1970s (Fig. 44). While the distributions of the carapace widths of females in the summer of the early 1970s was bimodal, the modal size class of the predominant group was well defined, and the contribution made by the individuals that comprised the other group, which consisted of the largest crabs, was small.

The distribution and modal class of the carapace widths of the female and even more particularly male crabs caught in the summer of 2000 were located to the left of those for the early 1970s (Fig. 44). Thus, the modal carapace width for females and males in that season were 120 - 129 mm and 130 - 139 mm, respectively, in summer 2000 compared with 150 - 159 mm and 150 - 159 mm, respectively, in the early 1970s.

The 0+ age class first appeared in autumn, when, for example, in the case of both females and males in 2000, it was represented by a modal width class of 70 – 79 mm (Fig. 44). The second group in that season clearly corresponded to the group that has just been described for summer. Furthermore, the distribution and modal class for the carapace widths of both females and males in the autumn of 2000 were likewise located further to the left than those for the corresponding sexes in the autumn of the early 1970s (Fig. 44). Although the modal carapace width classes of the 0+ age class of females and males in the winter of both 2000 and the early 1970s were identical, i.e. 100 – 110 mm, they had become, by the spring, in the case of both sexes, greater during the early 1970s than in 2000 (Fig. 44).

It is recognised that the above size-frequency data for the second of the two periods were restricted to only one year, i.e. 2000. Thus, the monthly size-frequency data obtained using samples collected by a smaller trawl vessel for two years, i.e. May to April in 1998/99 and 1999/2000, were each pooled according to month to ascertain whether the size compositions of P. pelagicus caught by the small trawl vessel were similar to those obtained with the commercial trawl vessel and could thus be used to determine whether the size composition data for 2000 were typical of the late 1990s and 2000 (Fig. 45). Since the distributions of the modal carapace-width classes for both female and male crabs caught by the small trawl vessel in each corresponding season in each of these two 12 month periods were essentially the same (data not shown), and similar to those caught by the commercial trawl vessel in 2000, the growth rates in 1998, 1999 and 2000 were presumably likewise similar. Comparisons between the size compositions of P. pelagicus in the samples collected seasonally by the commercial trawler in different years in the early 1970s also failed to find any conspicuous differences between the size compositions in corresponding seasons in those years (data not shown).

Reproductive biology

The percentage contributions of ovigerous female P. pelagicus to the numbers of crabs in trawl samples collected in May, June and July of 1998/2000 were low, i.e. < 5 %, but then rose to 10 % in August and to a maximum of 55.4 % in October (Fig. 46). They subsequently declined sequentially to 33 % in December and 7 % in February and then to zero in March and April. Although the percentage of ovigerous female crabs attained their peak slightly later in the early 1970s, i.e. November vs

October, they clearly exhibited similar monthly trends in that period to those just described for 1998/2000 (Fig. 46).

The values for the modal and mean carapace widths of ovigerous female crabs in 1998 – 2000, *i.e* 110 – 119 and 119.2 mm, respectively, were less than in 1971 – 1973, *i.e.* 120 – 129 and 138.7 mm, respectively (Fig. 47). The means for the two periods were significantly different ($p < 0.05$). The above differences between periods reflected differences in the size distributions. Thus, for example, the minimum and maximum carapace widths of *P. pelagicus* in 1971 – 1973 were greater by approximately 20 and 30 mm, respectively, than was the case in 1998 – 2000 (Fig. 47).

Growth

Estimates of carapace width at age for crabs sampled in Cockburn Sound in the early 1970s and 2000 differed markedly (Fig. 48). For those months in which an age class was well represented in the samples, that age class attained a greater average size in the earlier period. Thus, the mean carapace width at age 1, the age at which spawning first occurs, was greater in the early 1970s and the estimated asymptotic carapace width of crabs in this period was 30 and 80 % greater for females and males, respectively, in the earlier period (Fig. 48). Furthermore, on average, crabs would have attained the minimum legal size for capture a few months earlier in the early 1970s. Estimates for the growth parameters are presented in Appendix 3.

Benefits

The various biological parameters determined for *P. pelagicus* during this project will be used by Fisheries WA to assess existing fisheries data and to develop more appropriate stock assessment models that will enable the management plans of this important resource to be refined. The dissemination of information on the biology of *P. pelagicus* to commercial and recreational fishers will enable those fishers to understand the rationale for any measures that are developed to help conserve this species. The techniques developed and refined during this study will be applicable and of value in studies of other morphologically similar crustaceans and, in some cases, also fishes.

Further Development

While we now have a good understanding of the juvenile and adult phases in the life cycle of *Portunus pelagicus* in estuaries and marine waters, we have little information on the way in which the zoea are dispersed and the megalopae are recruited into nursery areas. Such information would be invaluable for refining management plans for blue swimmer crabs. Furthermore, appropriate methods of tagging blue swimmer crabs will need to be developed to allow determination of the growth parameters of crabs in fisheries such as Shark Bay, where spawning occurs throughout the year.

Conclusions

The following account of the conclusions and outcomes of this project are based on studies of the blue swimmer crab in two estuaries (Leschenault and Peel-Harvey estuaries) and two embayments (Koombana Bay and Cockburn Sound) on the lower west coast of Australia and in a large embayment (Shark Bay) on the central west coast of Australia. The project has successfully achieved its objectives.

Objective 1. *Determine aspects of reproductive biology relevant for management.*

The reproductive biology of *P. pelagicus* is influenced by whether this species is living in an estuary or an embayment and whether it is occupying water bodies on the lower west coast or in more northern regions, *i.e.* Shark Bay, where water temperatures are appreciably higher. Although ovigerous female crabs are found in estuaries, their prevalence is far less in these systems than in protected coastal embayments. Furthermore, ovigerous crabs migrate out of estuaries into coastal marine waters where, together with the resident ovigerous females, they release their eggs just prior to their hatching. The spawning period, which is considered as corresponding to the period during which the vast majority of the ovigerous females are found, extends from early spring to mid summer on the lower west coast of Australia. In contrast, spawning occurs throughout the year in Shark Bay, presumably reflecting the influence of the higher water temperatures in this embayment.

The sizes at which females typically first reach maturity (CW_{50}) in the five water bodies were almost invariably significantly different from each other. Estimates of the CW_{50} for female crabs in the Leschenault and Peel-Harvey estuaries were about 10 mm greater than those for female crabs in Koombana Bay and Cockburn Sound. The greater CW_{50}s for female crabs in estuaries reflect the influence on the logistic curve of the reduction in the numbers of adult females that is brought about by the emigration of ovigerous females. This study shows that the stages in maturation of the male gonads (testes & vas deferens) can be readily distinguished morphologically and that such data provide a better basis for estimating the size at first maturity of male crabs than those most frequently used in the past. The CW_{50} for males in Shark Bay was significantly greater than those in the Peel-Harvey Estuary and Cockburn Sound, possibly as a result of the warmer water temperatures inducing a faster growth rate.

Objective 2. *Determine habitats, recruitment times and movements*

The small juveniles of *Portunus pelagicus* live on bare sandy substrates in protected nearshore, shallow waters. When their carapace width has reached about 60 mm, the juvenile crabs show a marked tendency to move offshore into deeper waters and often into areas of relatively sparse seagrass if such vegetation is present. The densities of *P. pelagicus* were far lower in Shark Bay than in any of the four water bodies on the lower west coast and, in estuaries, they decline markedly in

winter as salinities fall precipitously as a result of massive increases in fresh water discharge.

The timing of recruitment into the four water bodies in south-western Australia varies markedly. Thus, appreciable numbers of small 0+ recruits start appearing in nearshore, shallow waters as early as January in Cockburn Sound and February to March in the Peel-Harvey Estuary, but not until August in the Leschenault Estuary. Furthermore, the presence of few small crabs, *i.e.* < 80 mm CW, in the samples from Koombana Bay, into which the Leschenault Estuary discharges, indicates that, in this region, the 0+ crabs are recruited into the estuary rather than adjacent marine waters.

The tagging and release of large *P. pelagicus* within Cockburn Sound indicate that, while many of these crabs remained within 2 km of their point of release and particularly when they were released towards the southern region of this embayment, some crabs did move more than 6 km. However, since only a very small proportion of tagged crabs apparently moulted, the use of spaghetti tags would appear to have limited value for determining growth rates of *P. pelagicus*.

Objective 3. *Determine size and age compositions and growth rates.*

In estuaries and embayments in south-western Australia, *P. pelagicus* typically start to attain minimum legal size of capture (127 mm) in late summer, when they are just over one year old, and most have either died through natural or fishing mortality by the time they are about 20 months old. The growth rates of this species in the water bodies sampled on the lower west coast of Australia did not differ markedly. Since *P. pelagicus* spawns throughout the year in Shark Bay and individual crabs cannot be aged, it was not possible to derive a growth curve for the population in this embayment.

Management implications

(i)   The habitats occupied by *P. pelagicus* in estuaries and embayments have been identified, thereby facilitating their appropriate management and conservation.

(ii)   Densities of *P. pelagicus* vary amongst water bodies, being particularly low in Shark Bay, and they undergo greater seasonal changes in estuaries than embayments.

(iii)   Data for Cockburn Sound indicate that increased densities and/or environmental changes can lead to significant reductions in growth rates.

(iv)   Timing of juvenile recruitment varies markedly between water bodies.

(v)   Size at maturity of both sexes varies significantly amongst water bodies, but is always well below the minimal legal size for capture.

(vi)   Results from the growth and reproduction studies enable better assessment and management.

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Appendix 1: Intellectual Property

N/A

Appendix 2: Staff

The following researchers, at the Murdoch University Centre of Fish and Fisheries Research contributed to this report:

Principal Investigator: Ian C. Potter

Research Assistant: Simon de Lestang

Casual Research Assistant: David V. Fairclough

Appendix 3: Growth parameters

Estimates of the growth parameters for *Portunus pelagicus* from the Leschenault Estuary/Koombana Bay, Peel-Harvey Estuary and Cockburn Sound in the late 1990s and from Cockburn Sound in the early 1970s.

	Leschenault Estuary/ Koombana Bay		Peel-Harvey Estuary		Cockburn Sound (1998 – 2000)		Cockburn Sound (1971 – 1973)	
	Female	Male	Female	Male	Female	Male	Female	Male
Birth date	Dec. 1	Dec. 1	Dec. 1	Dec. 1	Nov. 1	Nov. 1	Nov. 1	Nov. 1
CW_∞	124.7	119.1	140.5	127.4	161.3	166.0	215.4	305.0
K	2.67	3.11	1.66	1.90	1.01	0.98	0.62	0.36
t_0	0.25	0.25	0.06	0.031	0.1	0.11	-0.25	-0.25
C	1	1	-0.861	-0.591	1	0.96	1	1
t_s	0.57	0.54	0.17	0.28	0.76	0.7818	0.55	0.57
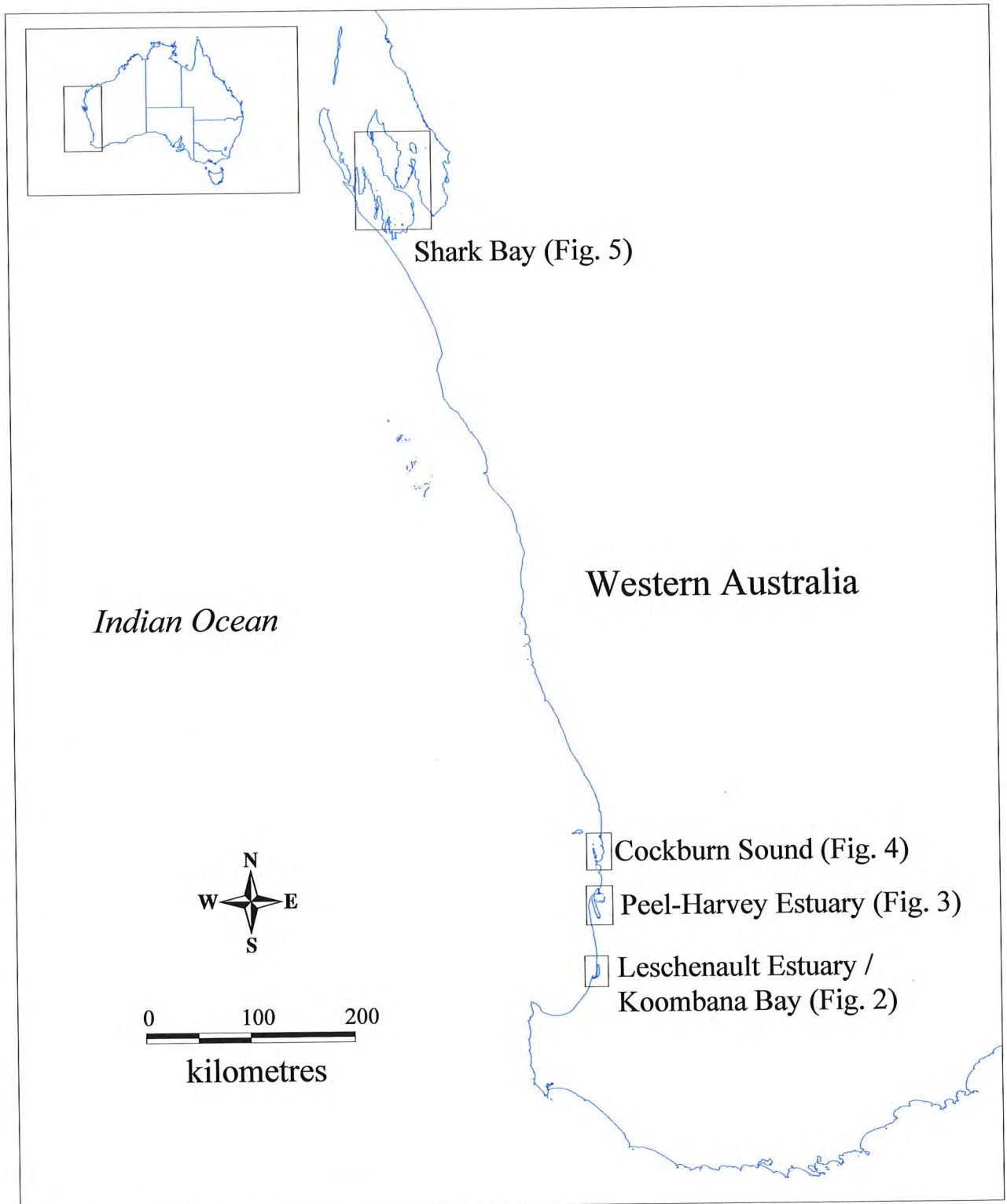
Figure 1. Map showing the locations of the five water bodies in which blue swimmer crabs were sampled on the west coast of Australia. Inset: map of Australia showing location (box) of sampling region.
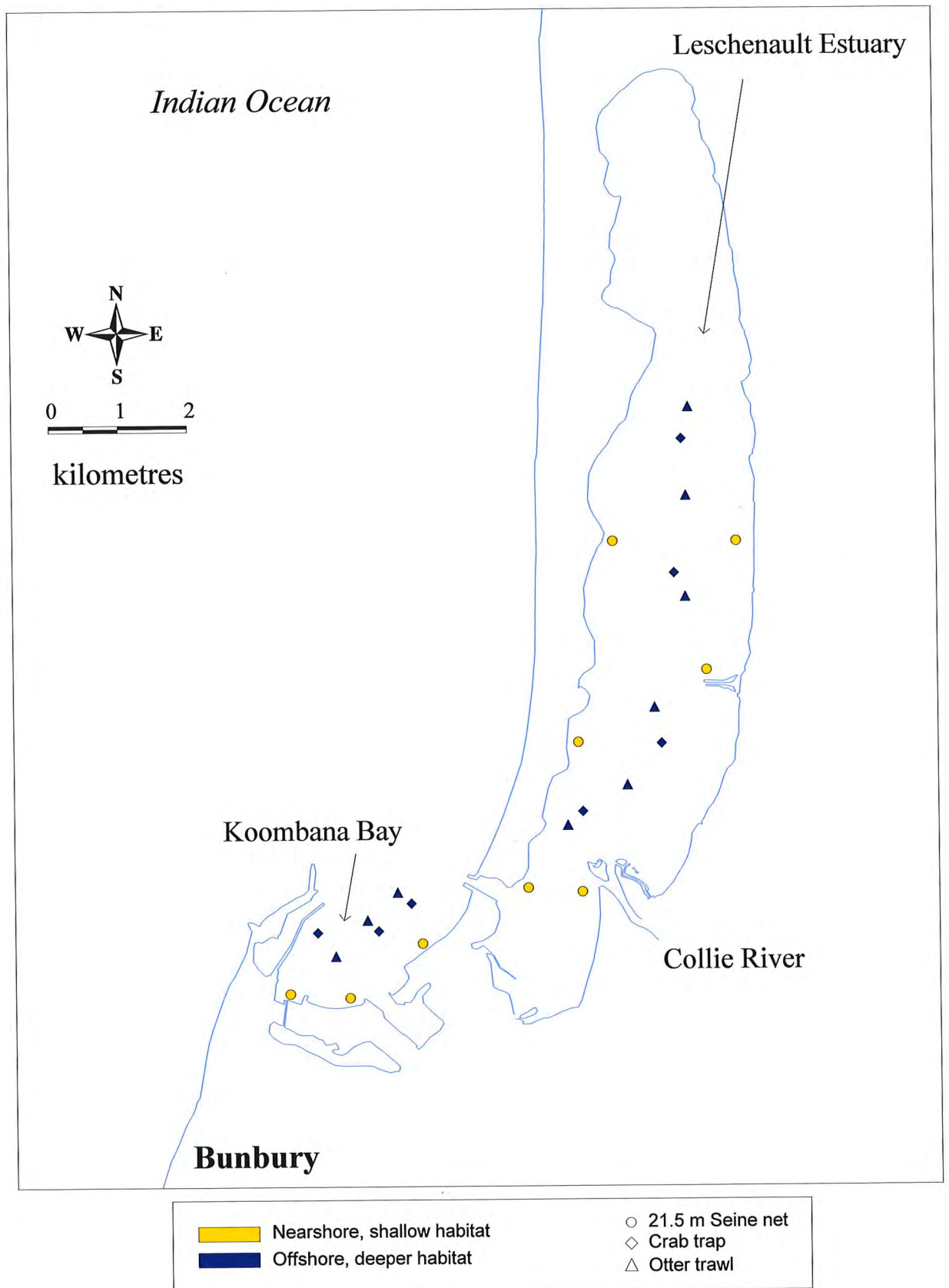
Figure 2. Map showing the location of the sites in the Leschenault Estuary and Koombana Bay at which blue swimmer crabs were sampled by seine netting, crab trapping and otter trawling.
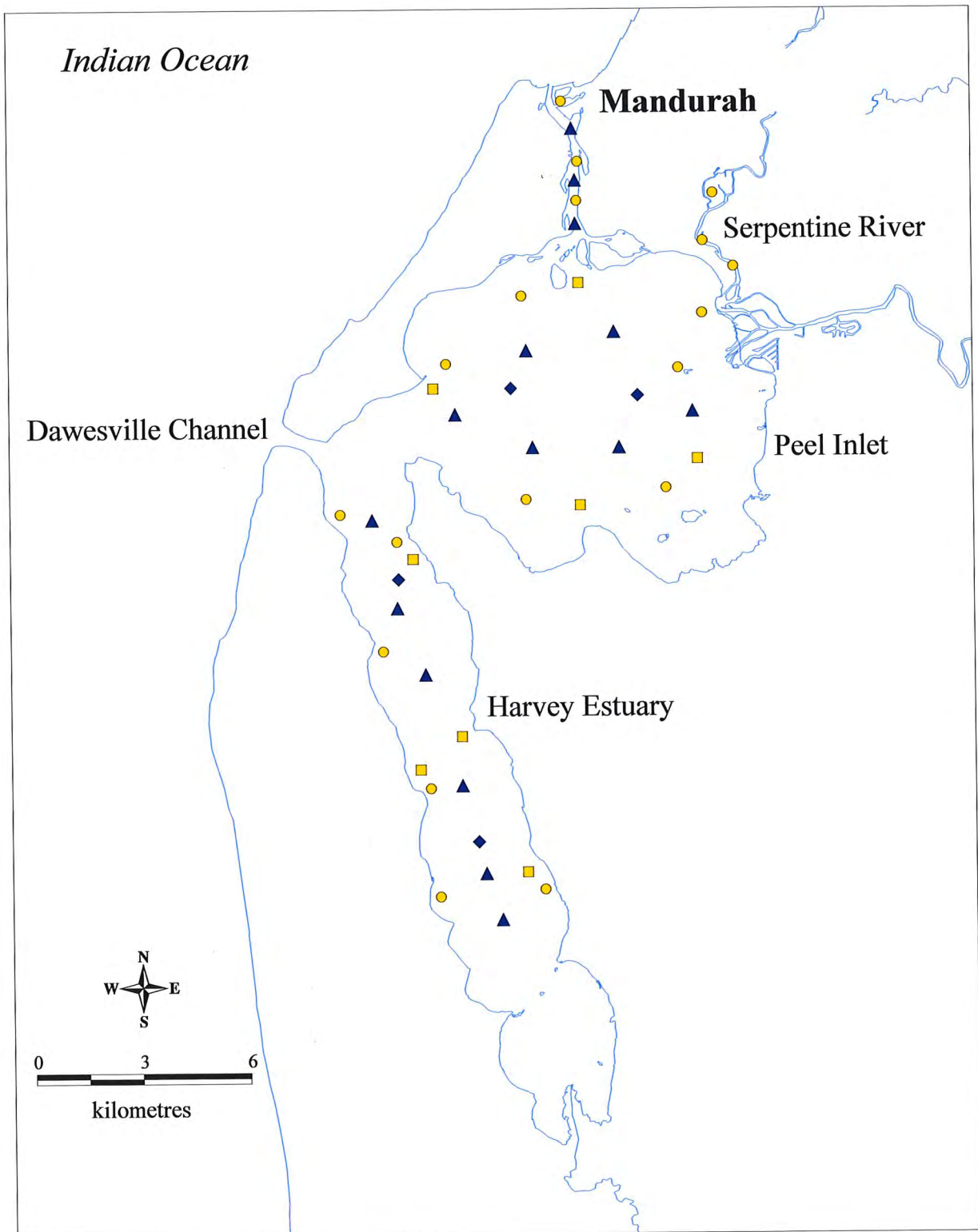
Figure 3. Map showing the location of the sites in the Peel-Harvey Estuary at which blue swimmer crabs were sampled by seine netting, crab trapping and otter trawling.
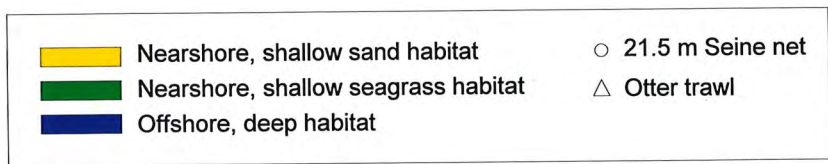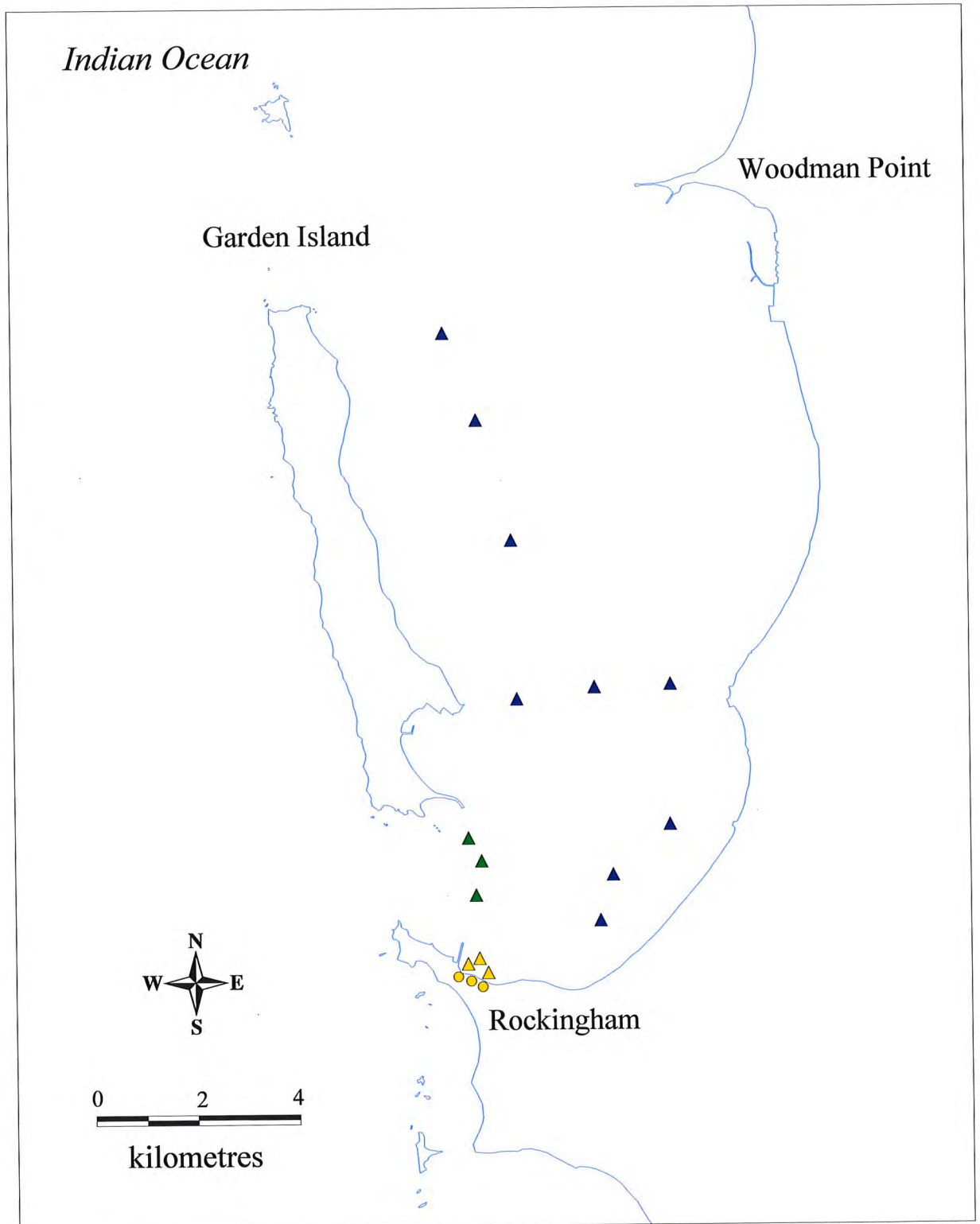
Figure 4. Map showing the location of the sites in Cockburn Sound at which blue swimmer crabs were sampled by seine netting and otter trawling.
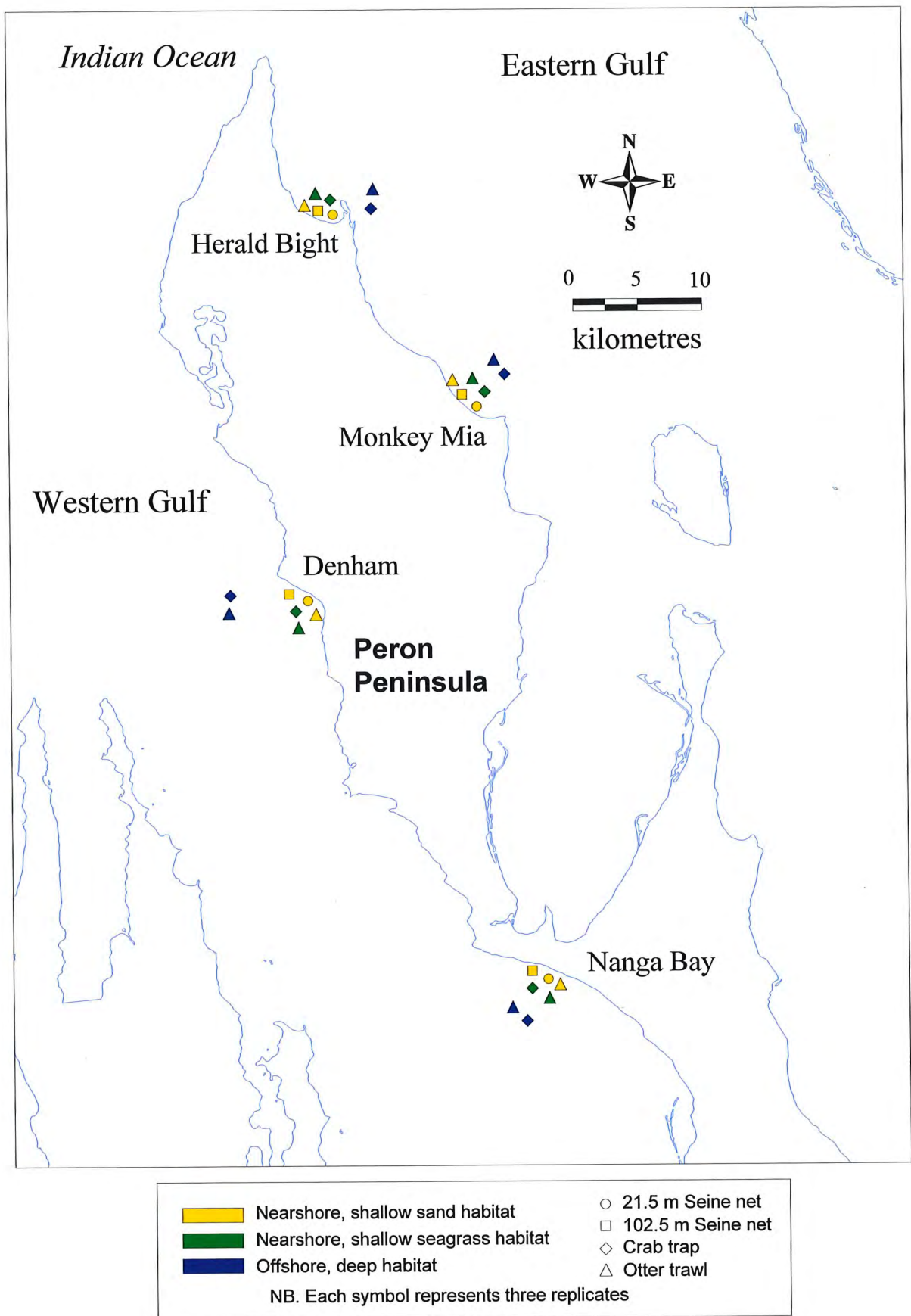
Figure 5. Map showing the location of the sites in Shark Bay at which blue swimmer crabs were sampled by seine netting, crab trapping and otter trawling.
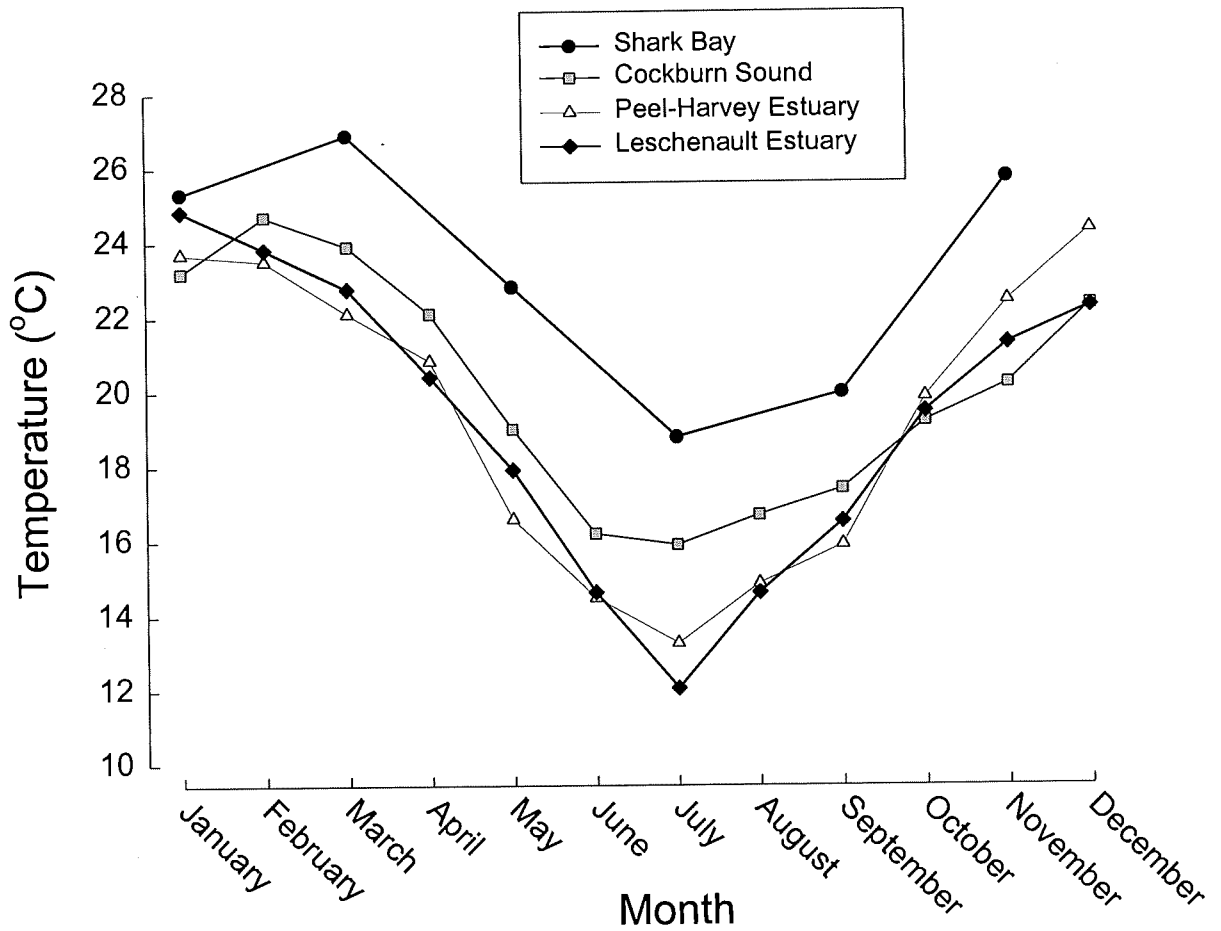
Figure 6. Mean monthly water temperatures for sites in the Leschenault Estuary, Peel-Harvey Estuary, Cockburn Sound and Shark Bay. NB. Water temperatures in Koombana Bay were essentially the same as those in the Leschenault Estuary. Mean monthly water temperatures in each water body are derived from pooled data for at least two years.
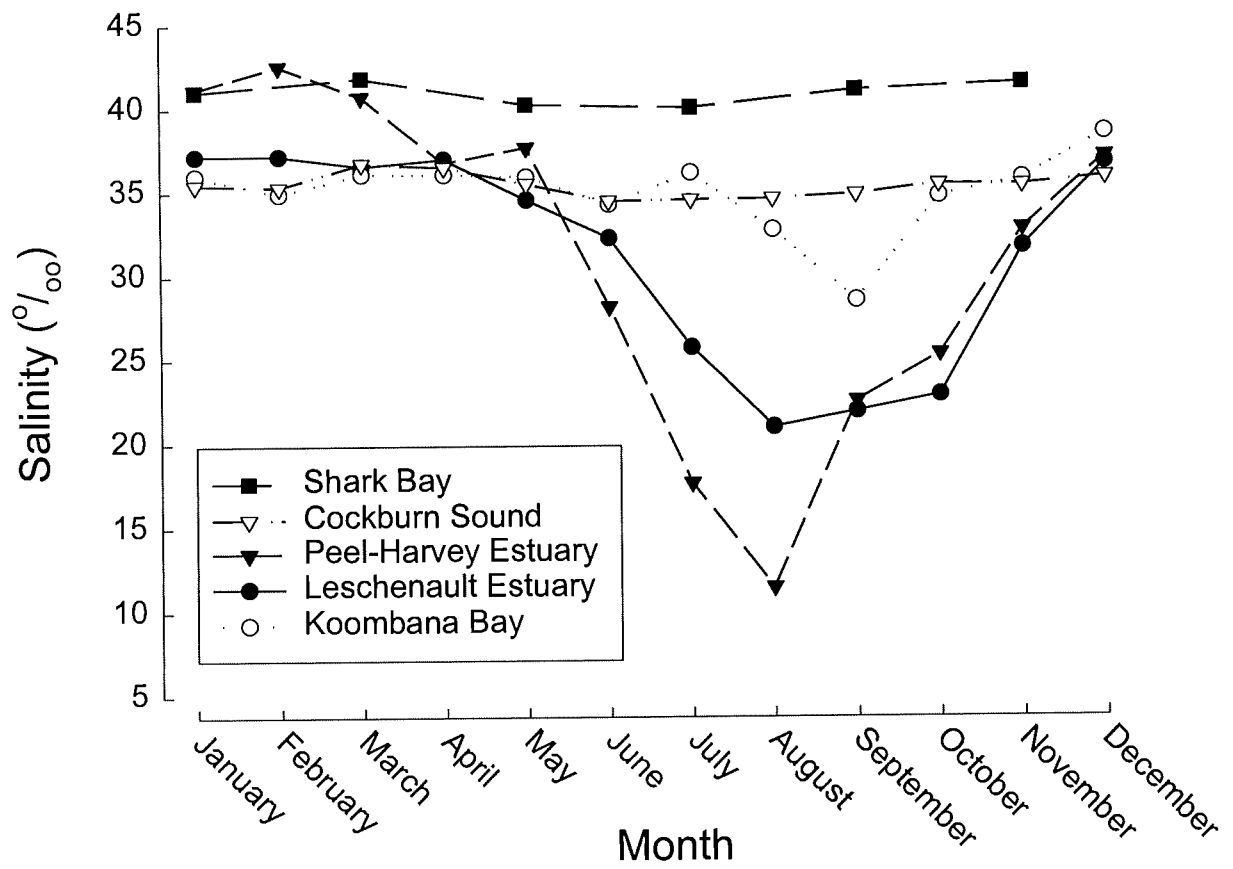
Figure 7. Mean monthly salinities at the bottom of the water column for sites in the five water bodies sampled on the west coast of Australia. Mean monthly salinities in each water body are derived from pooled data for at least two years.

Leschenault Estuary
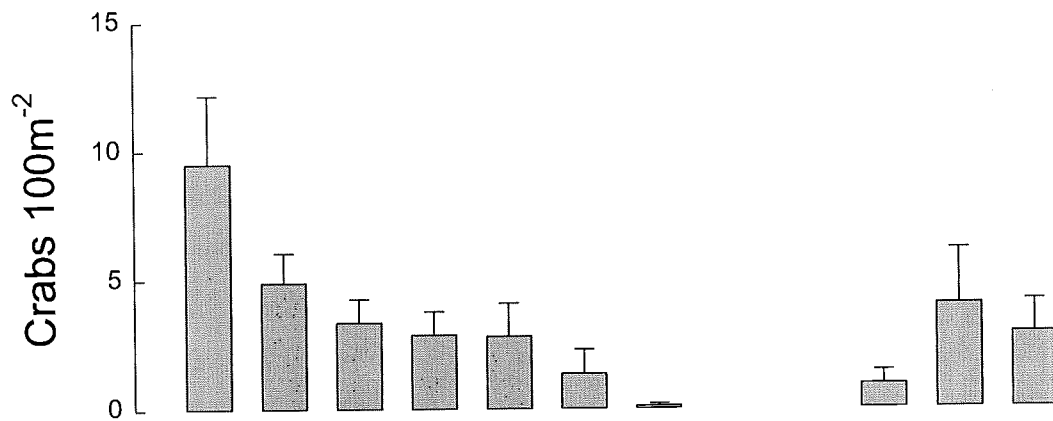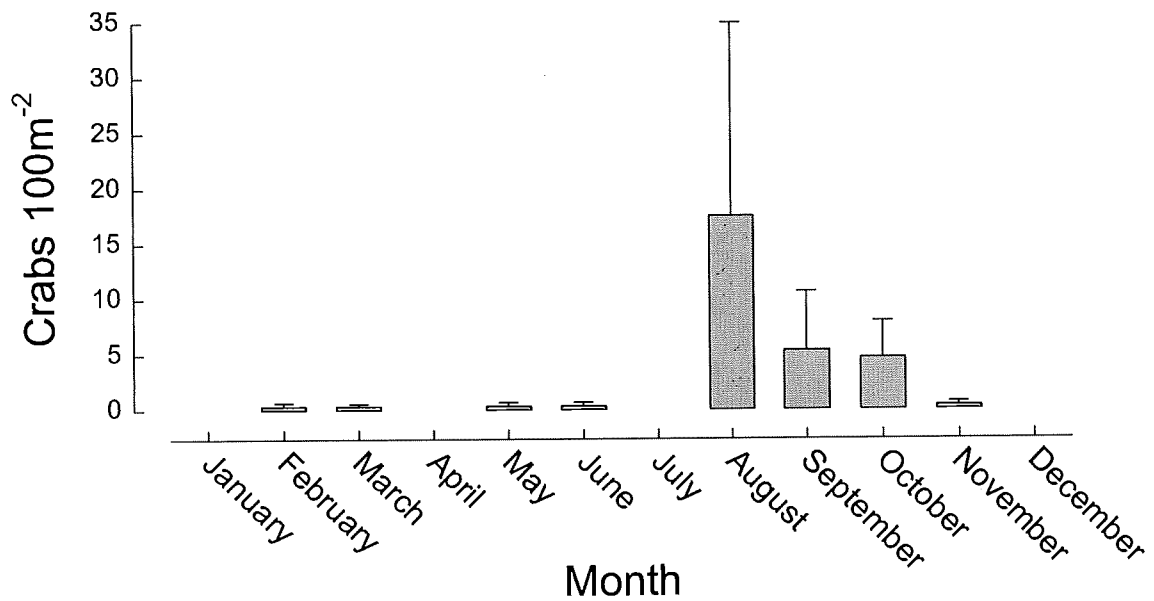
Koombana Bay

Figure 8. Mean monthly densities + 1 S.E. for *Portunus pelagicus* in nearshore, shallow waters of the Leschenault Estuary and Koombana Bay, derived from catches obtained by seine netting during the day. In this Figure and Figs 9 – 14, the mean monthly densities in each water body were calculated using monthly data for at least two years.
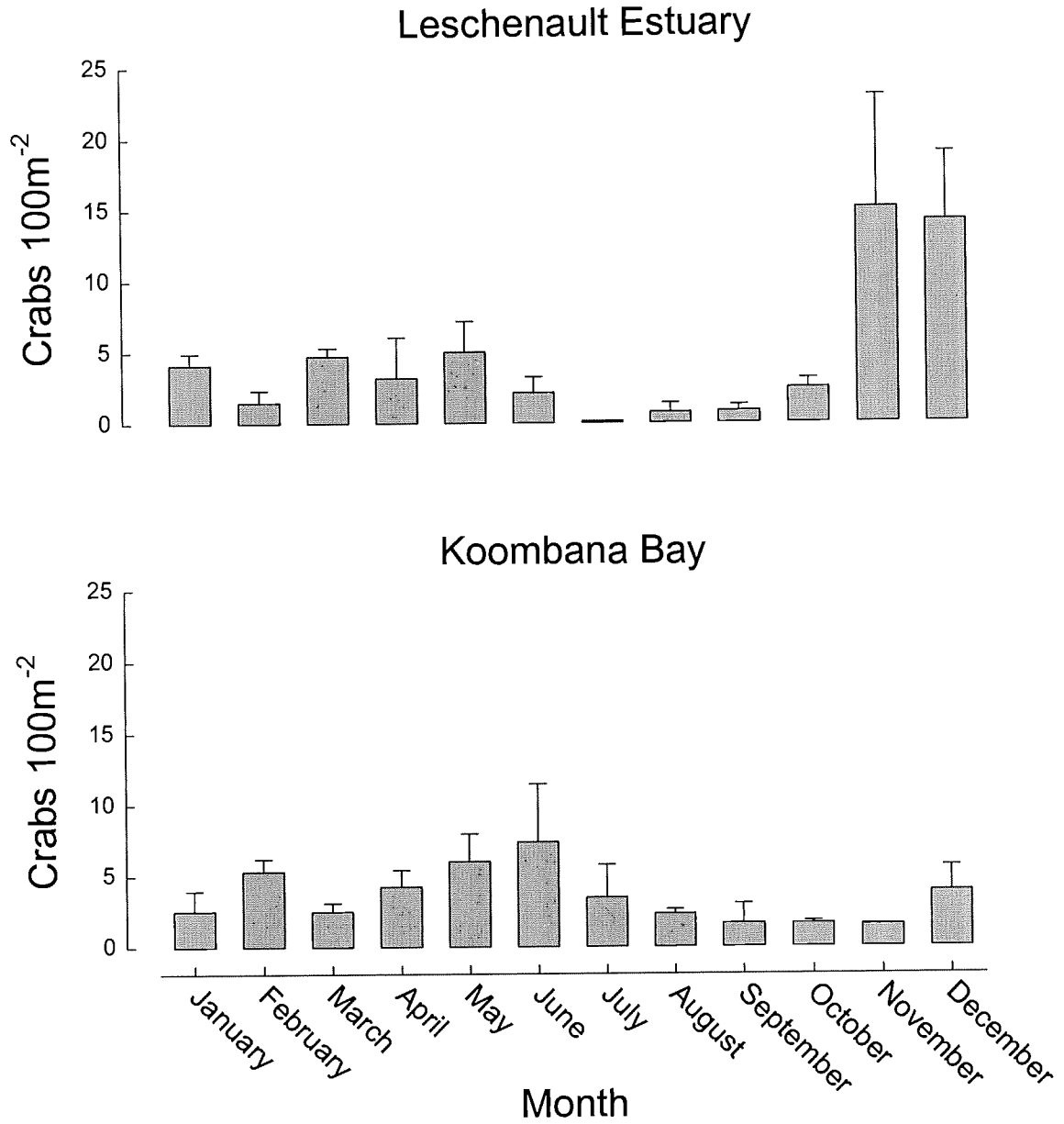
Figure 9. Mean monthly densities + 1 S.E. for *Portunus pelagicus* in offshore, deeper waters of the Leschenault Estuary and Koombana Bay, derived from catches obtained by otter trawling during the day.
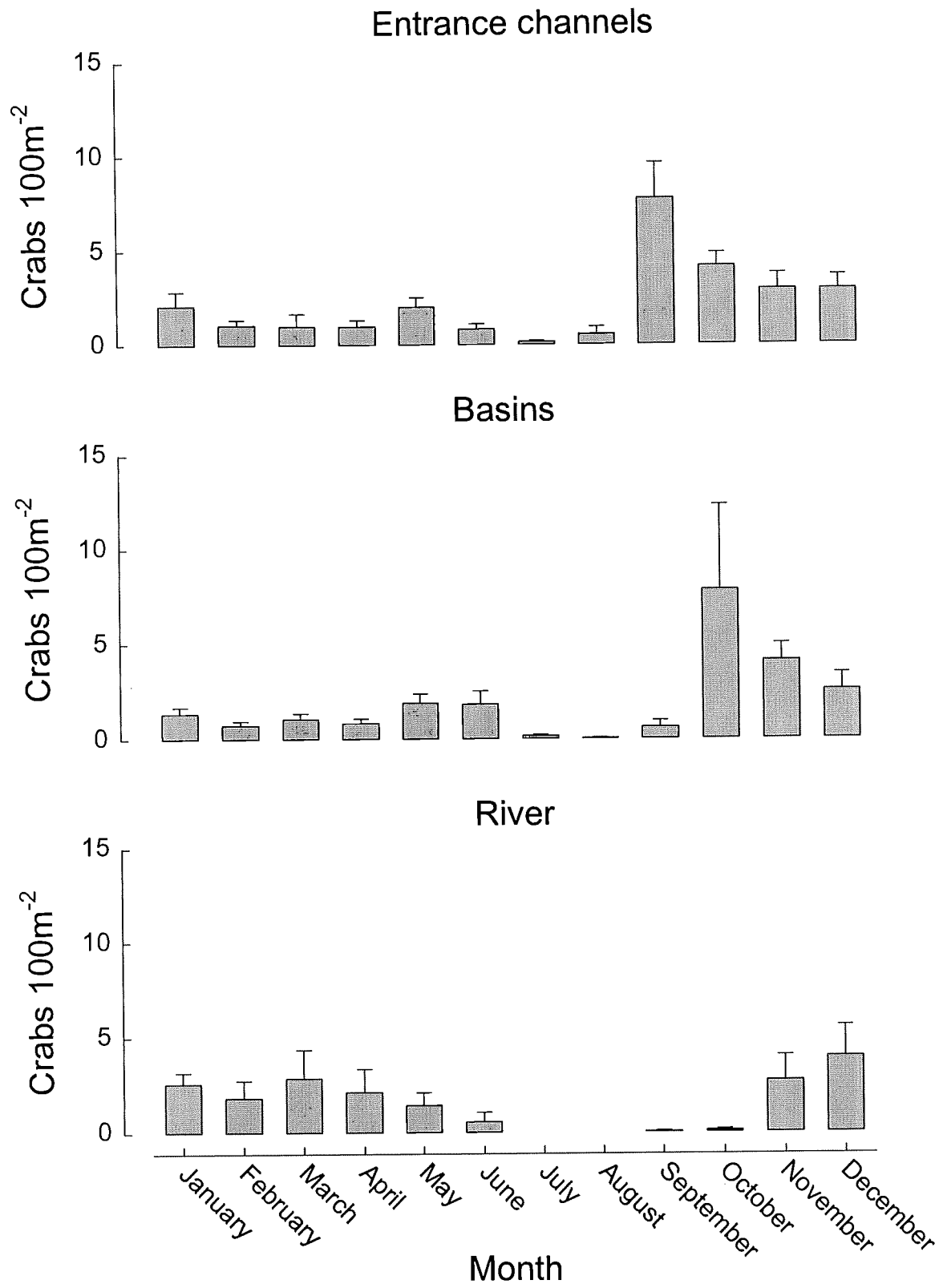
Figure 10. Mean monthly densities + 1 S.E. for *Portunus pelagicus* in nearshore, shallow waters of the three main regions of the Peel-Harvey Estuary, derived from catches obtained by seine netting during the day and night.
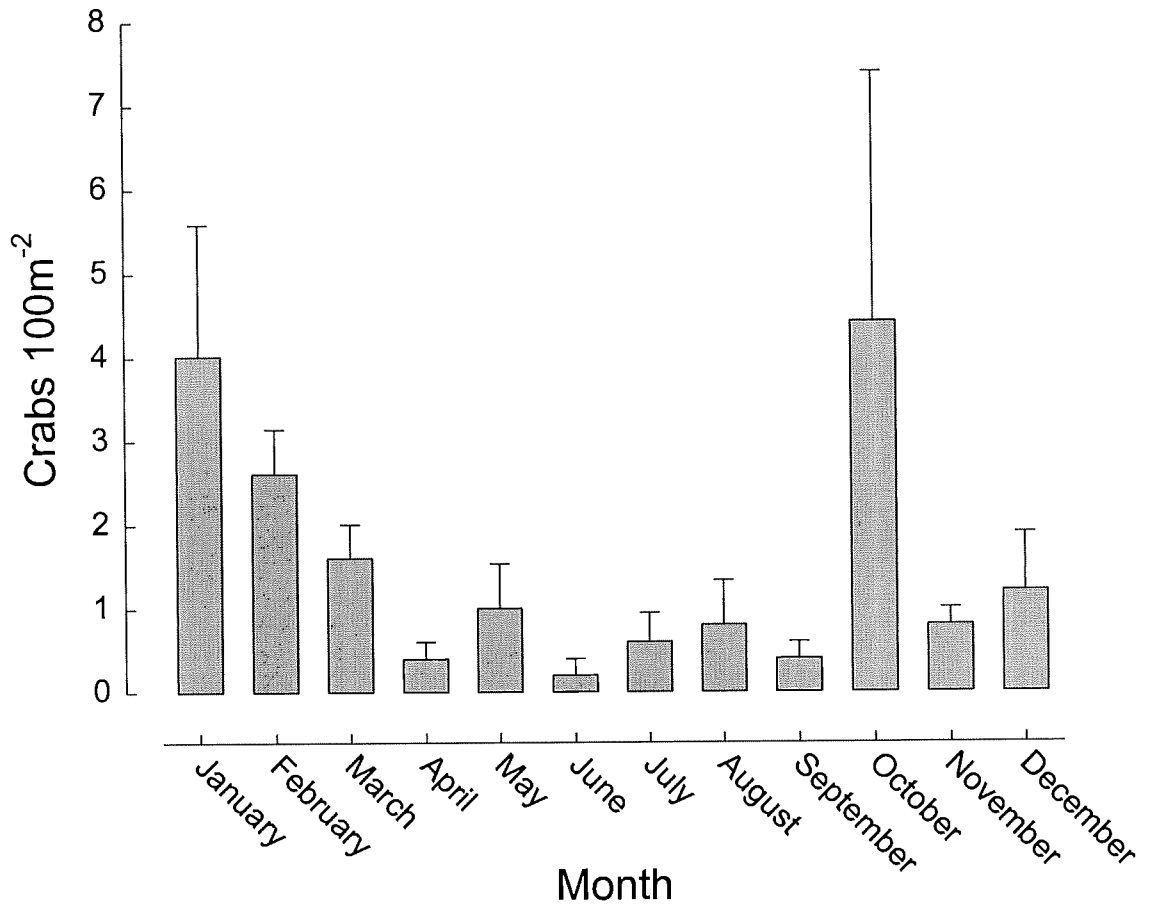
Figure 11. Mean monthly densities + 1 S.E. for *Portunus pelagicus* in nearshore, shallow waters of Mangles Bay in the south-western corner of Cockburn Sound (Fig. 4), derived from catches obtained by seine netting during the day.
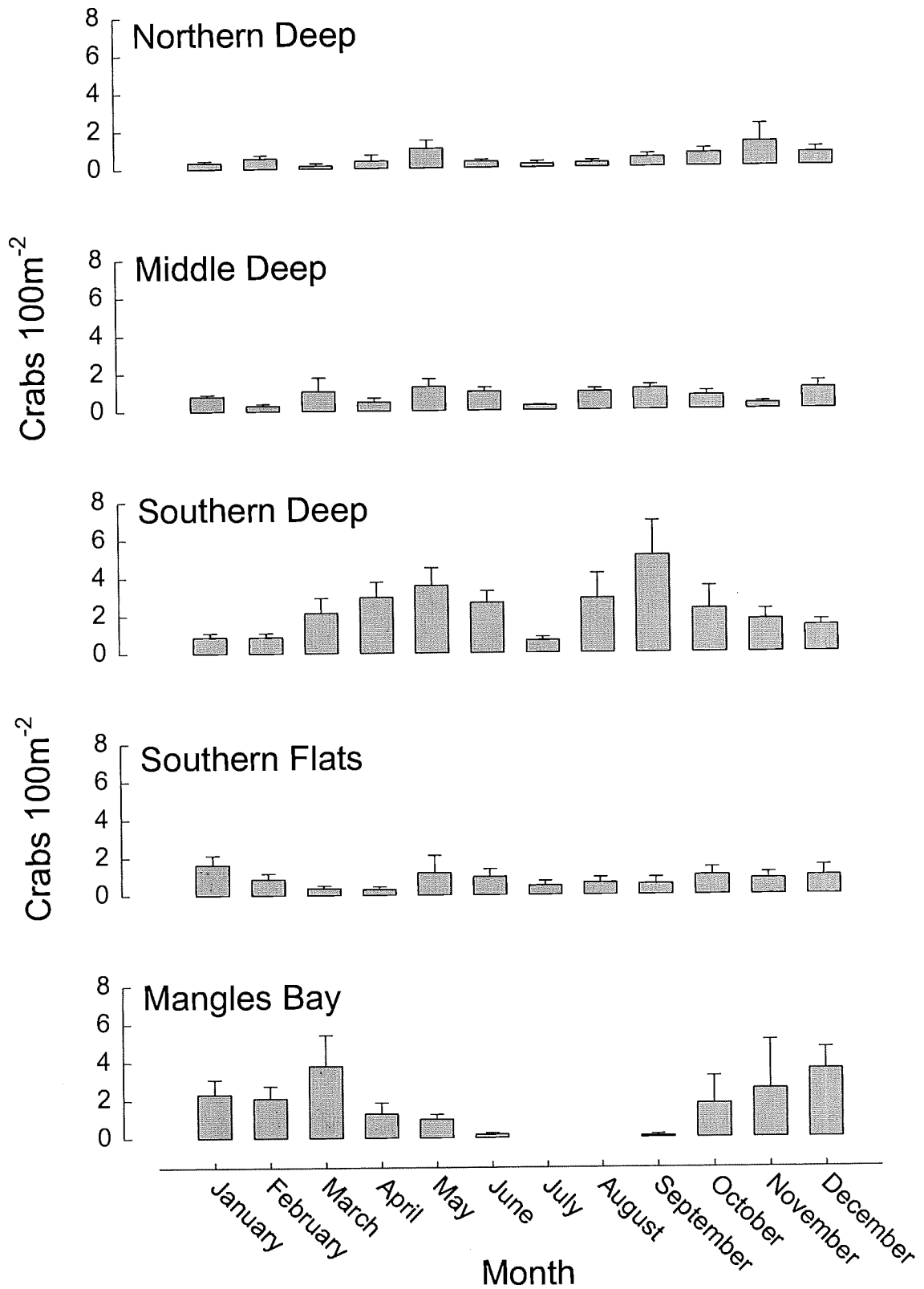
Figure 12. Mean monthly densities + 1 S.E. for *Portunus pelagicus* in offshore waters at five sites in Cockburn Sound, derived from catches obtained by otter trawling during the day.
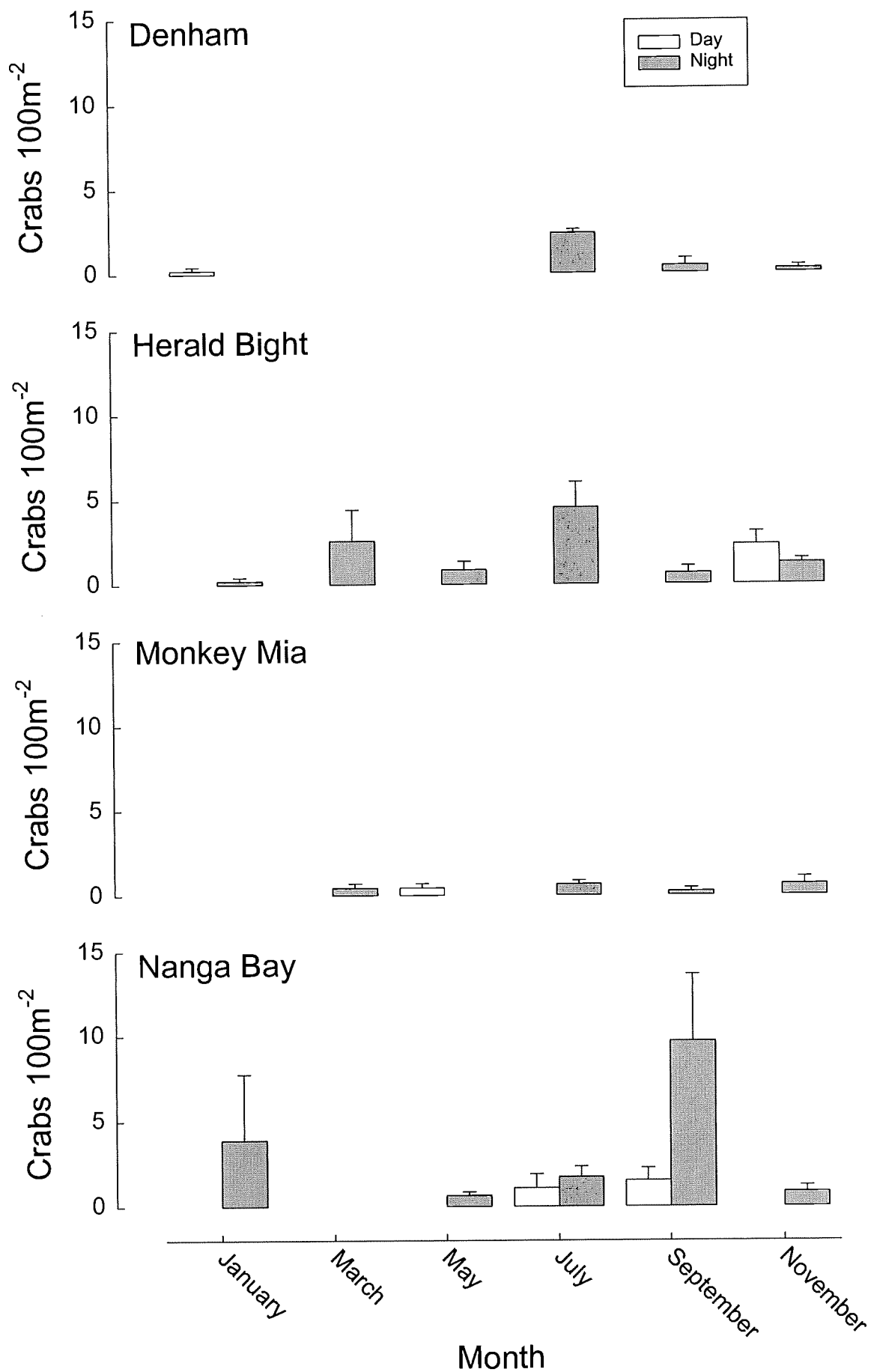
Figure 13. Mean densities + 1 S.E. for *Portunus pelagicus* in nearshore, shallow waters at the four sampling sites in Shark Bay, derived from catches obtained by seine netting during the day and night in alternate months over two years.
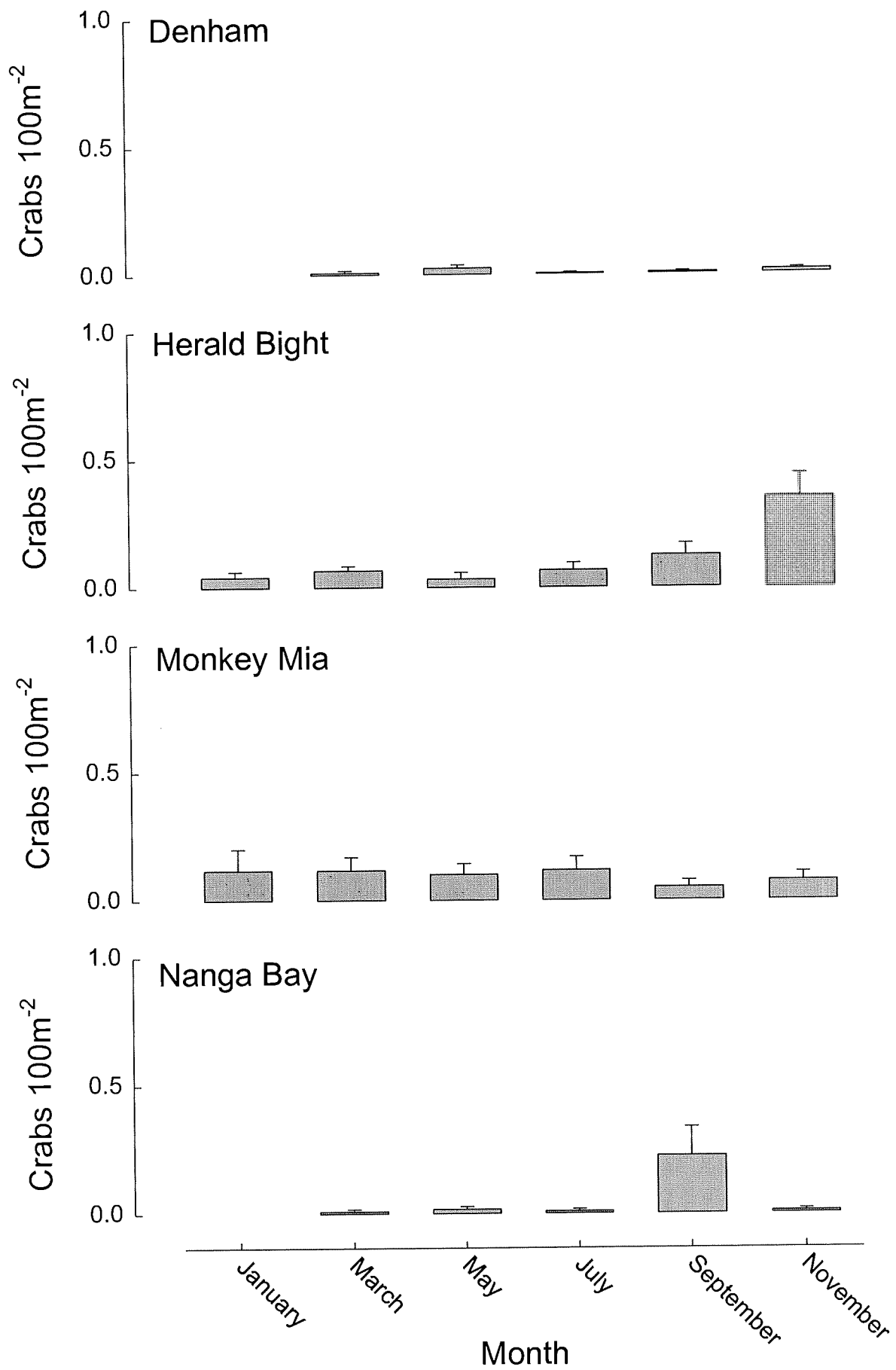
Figure 14. Mean monthly densities + 1 S.E. for *Portunus pelagicus* in offshore, deeper waters in Shark Bay, derived from catches obtained by otter trawling during the day.
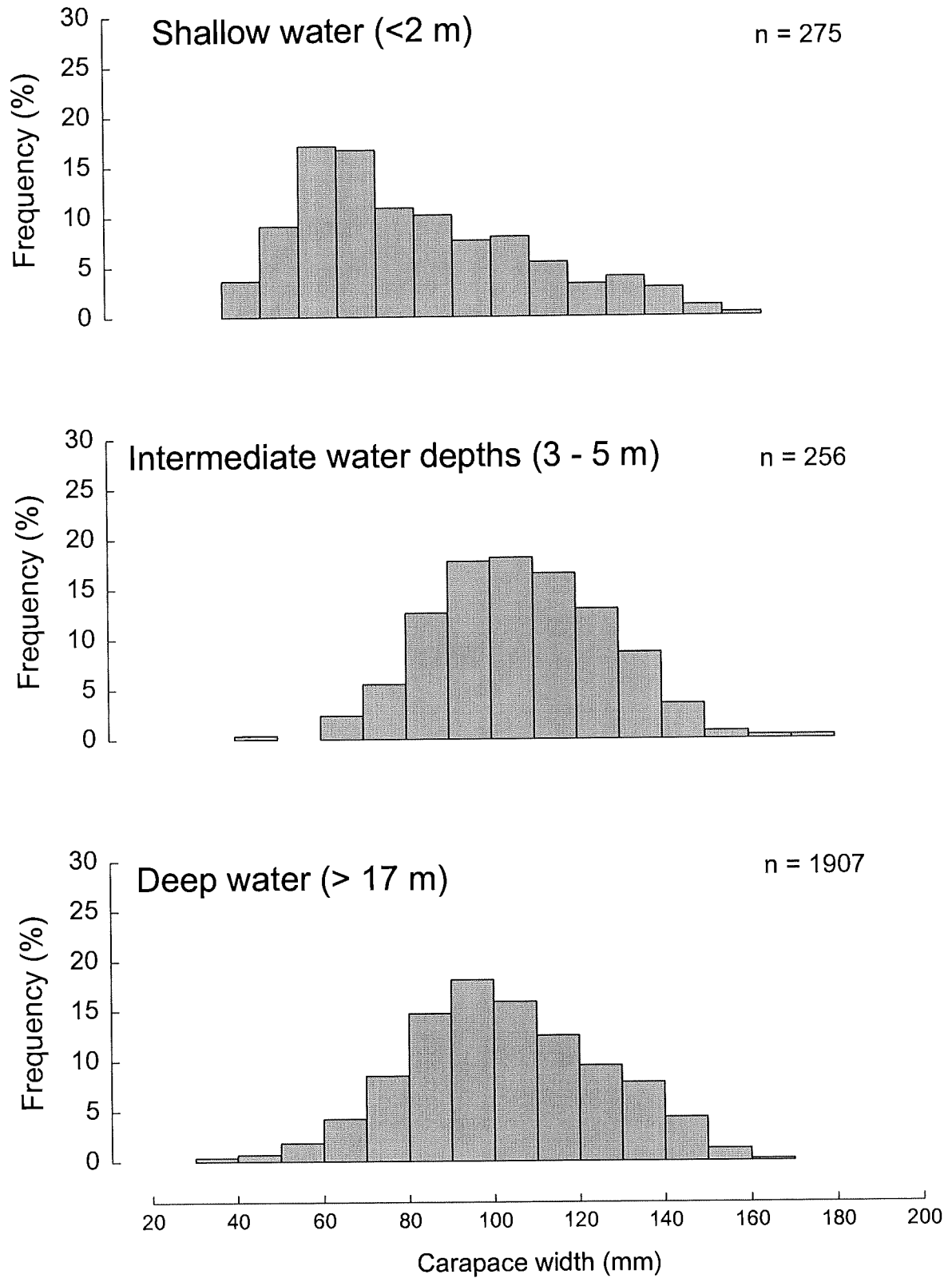
Figure 15. Size-frequency distributions of *Portunus pelagicus* caught in three water depths in Cockburn Sound by otter trawling. n = number of crabs caught.
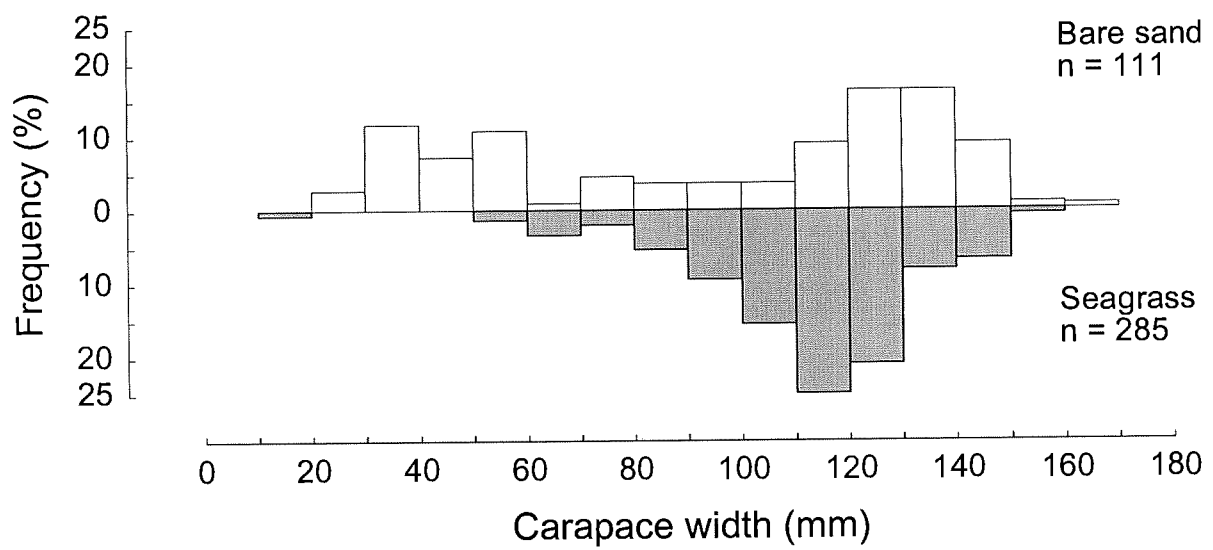
Figure 16. Size-frequency distributions of *Portunus pelagicus* caught by otter trawling over sand and in seagrass in each of the four regions sampled in Shark Bay. n = number of crabs caught.
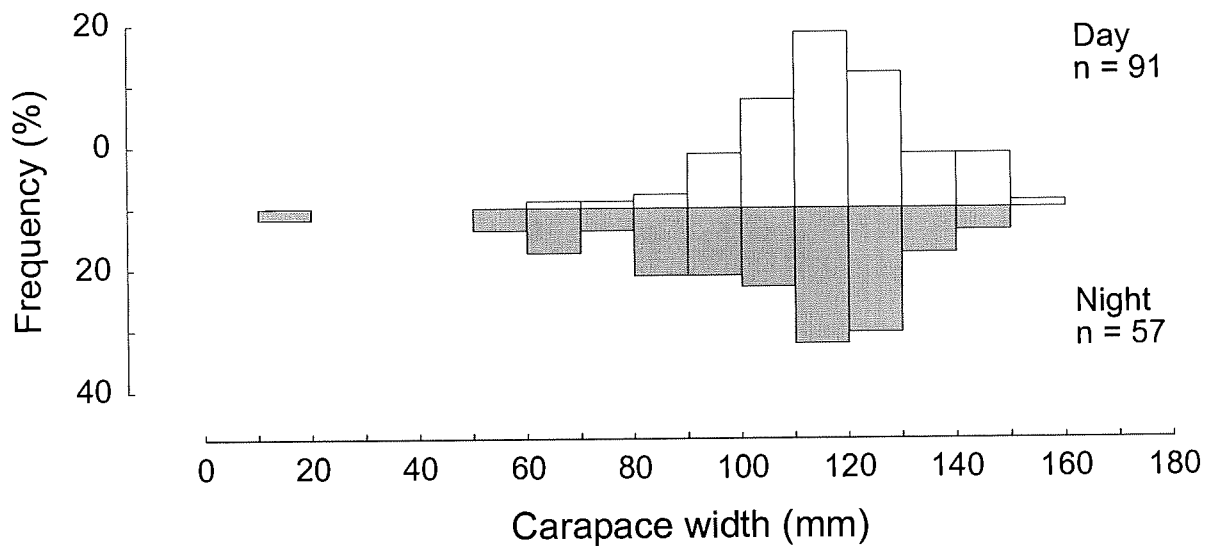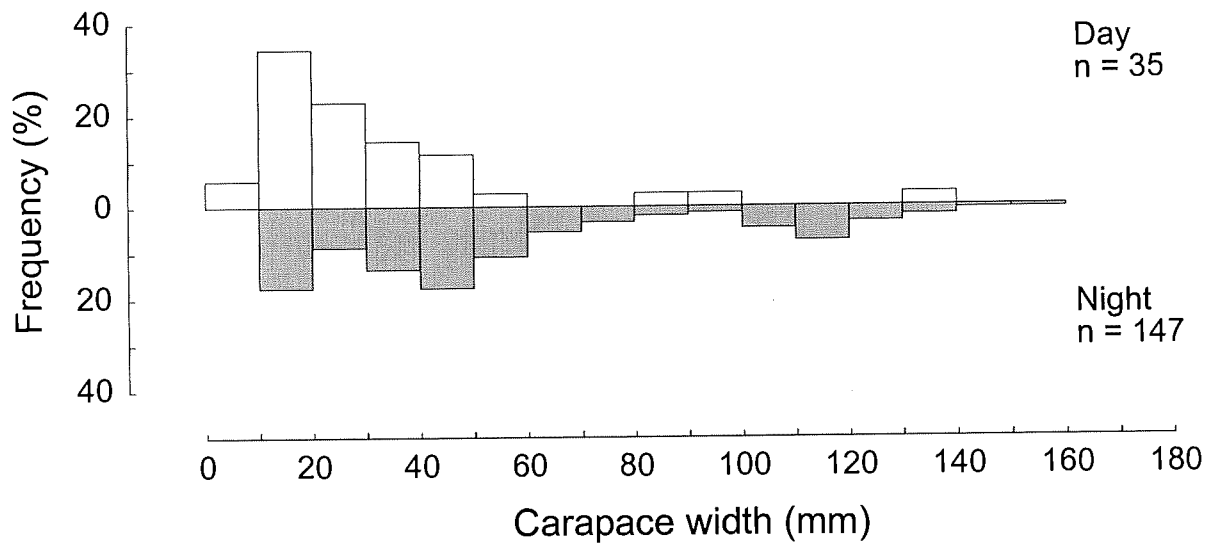
Figure 17. Size-frequency distributions of *Portunus pelagicus* caught during the day and night over bare sand (above) and in seagrass (below) in Shark Bay. N.B. Densities over sand were derived from catches obtained by seine netting in all four sampling regions, while densities in seagrass were derived from catches obtained by otter trawling at Monkey Mia. n = number of crabs caught.
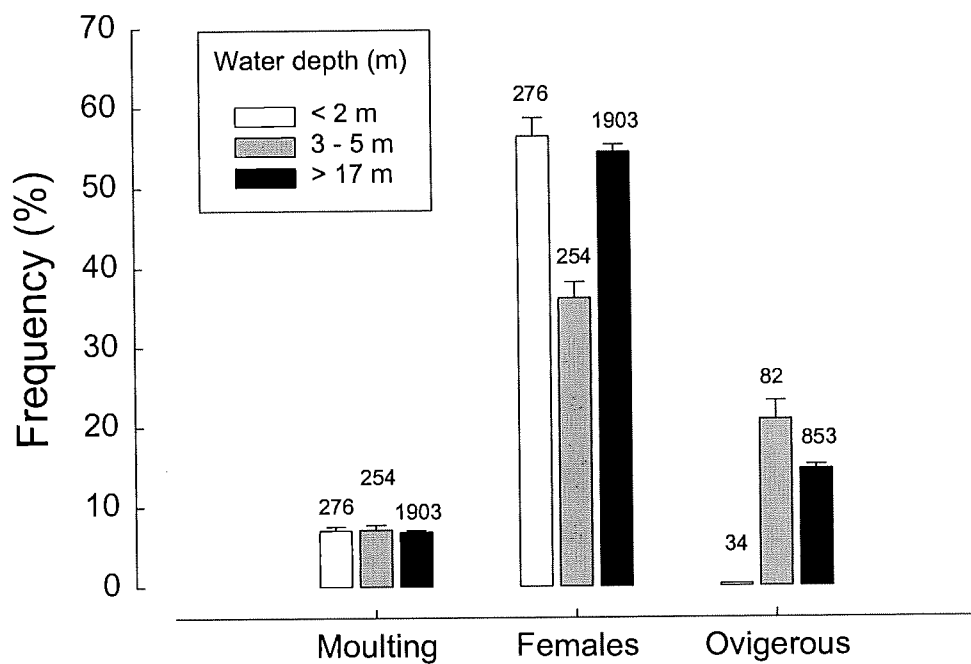
Figure 18. Frequency of occurrence + 95% C.I. of moulting crabs, of female crabs amongst all crabs and of ovigerous female crabs amongst all adult female crabs, derived from data obtained from catches taken by otter trawling in three water depths in Cockburn Sound.
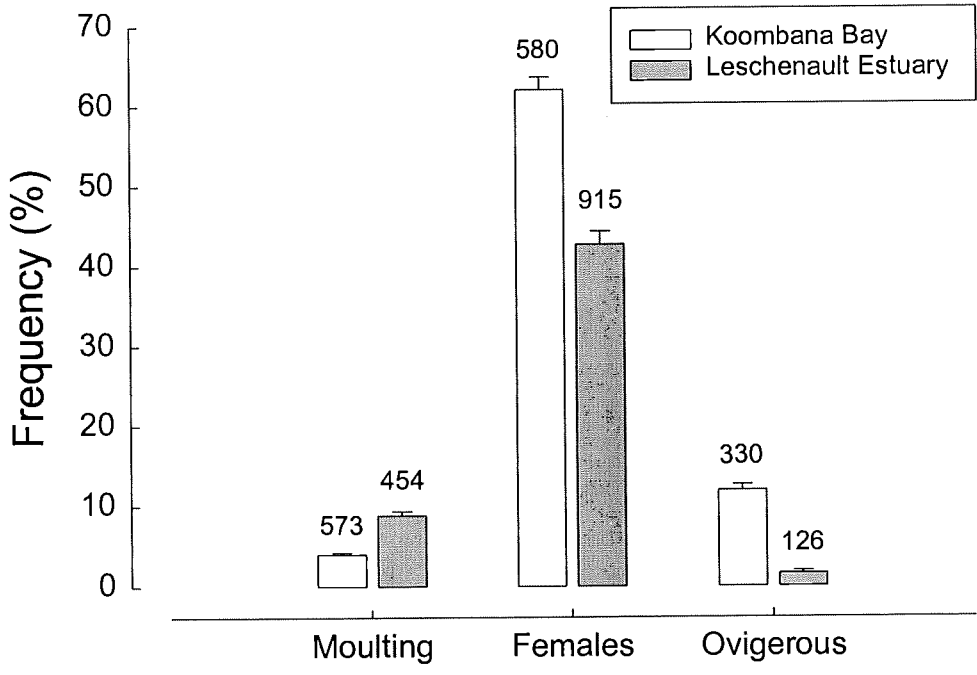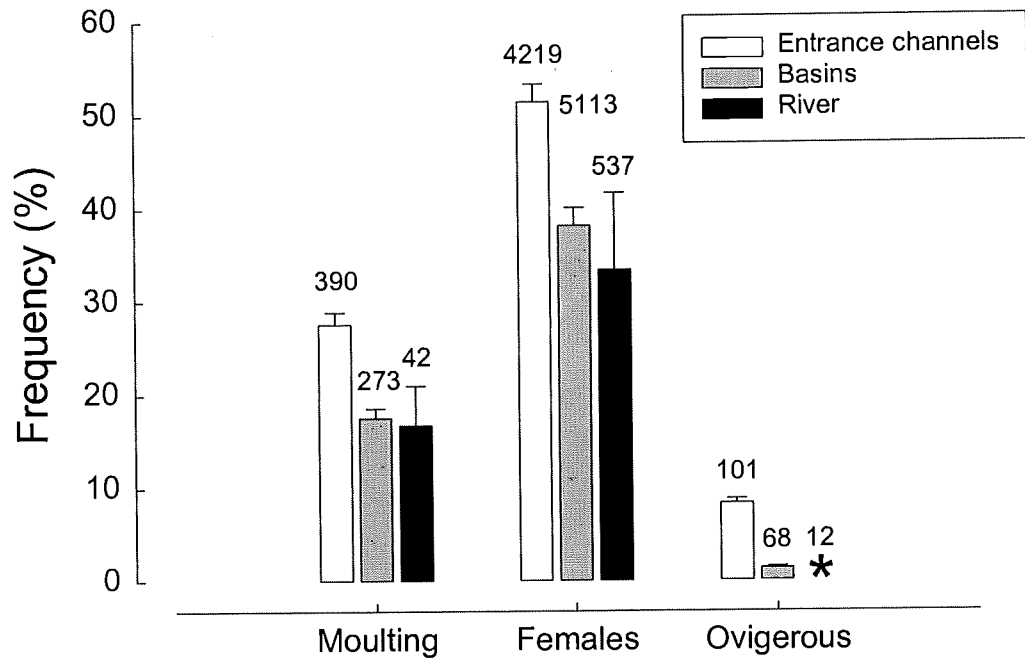
Figure 19. Frequency of occurrence + 95% C.I. of moulting crabs, female
crabs amongst all crabs and of ovigerous female crabs amongst
adult female crabs in catches obtained by seine netting in three
different regions of the Peel-Harvey Estuary (above) and in the
Leschenault Estuary and Koombana Bay (below). * = zero
value.
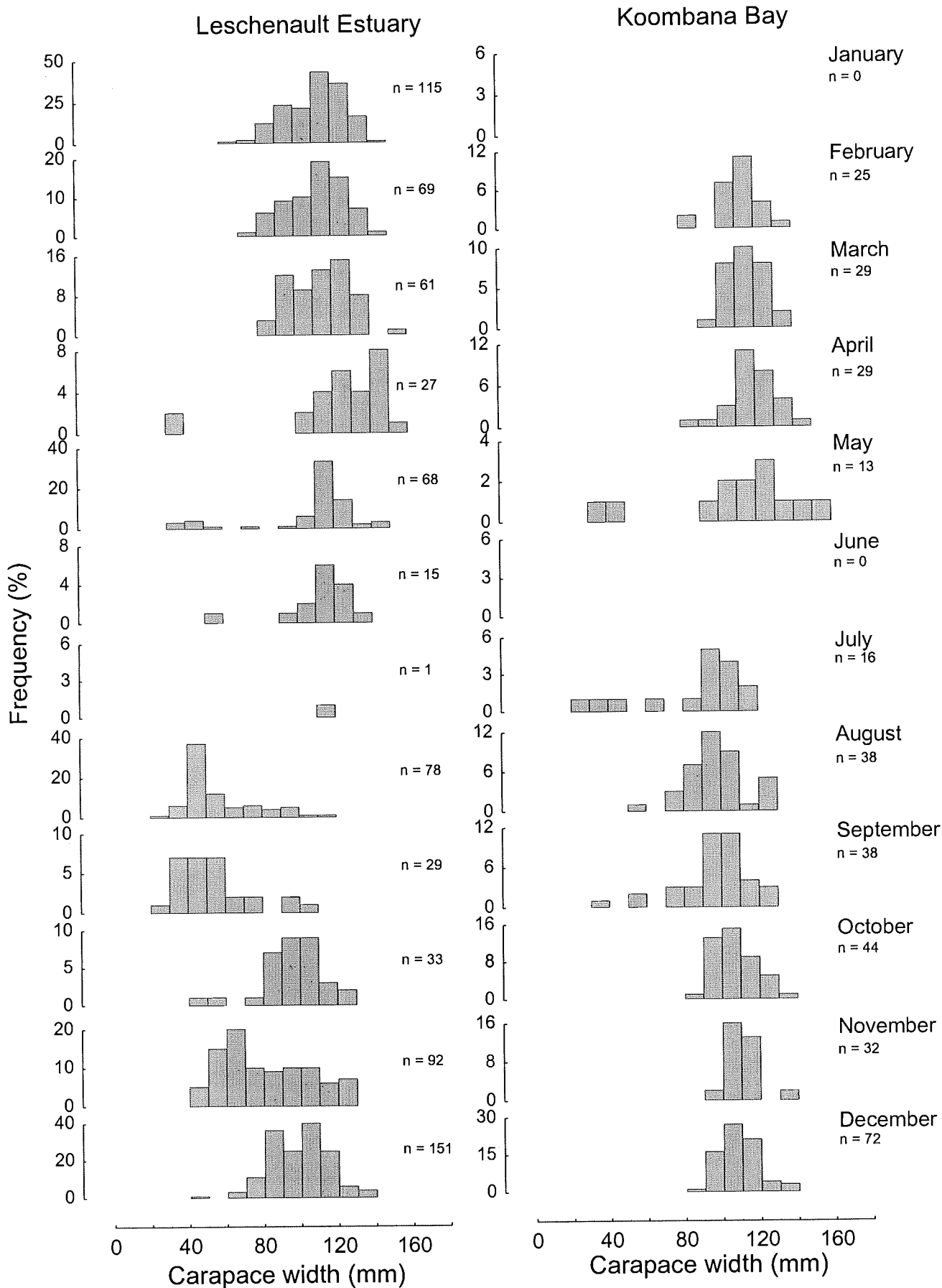
Figure 20. Size-frequency distributions for *Portunus pelagicus* caught by seine netting and otter trawling in the Leschenault Estuary and Koombana Bay. In this Figure and Figs 21 – 26, the monthly size frequencies in each water body were calculated using monthly data for at least two years and n = number of crabs caught.
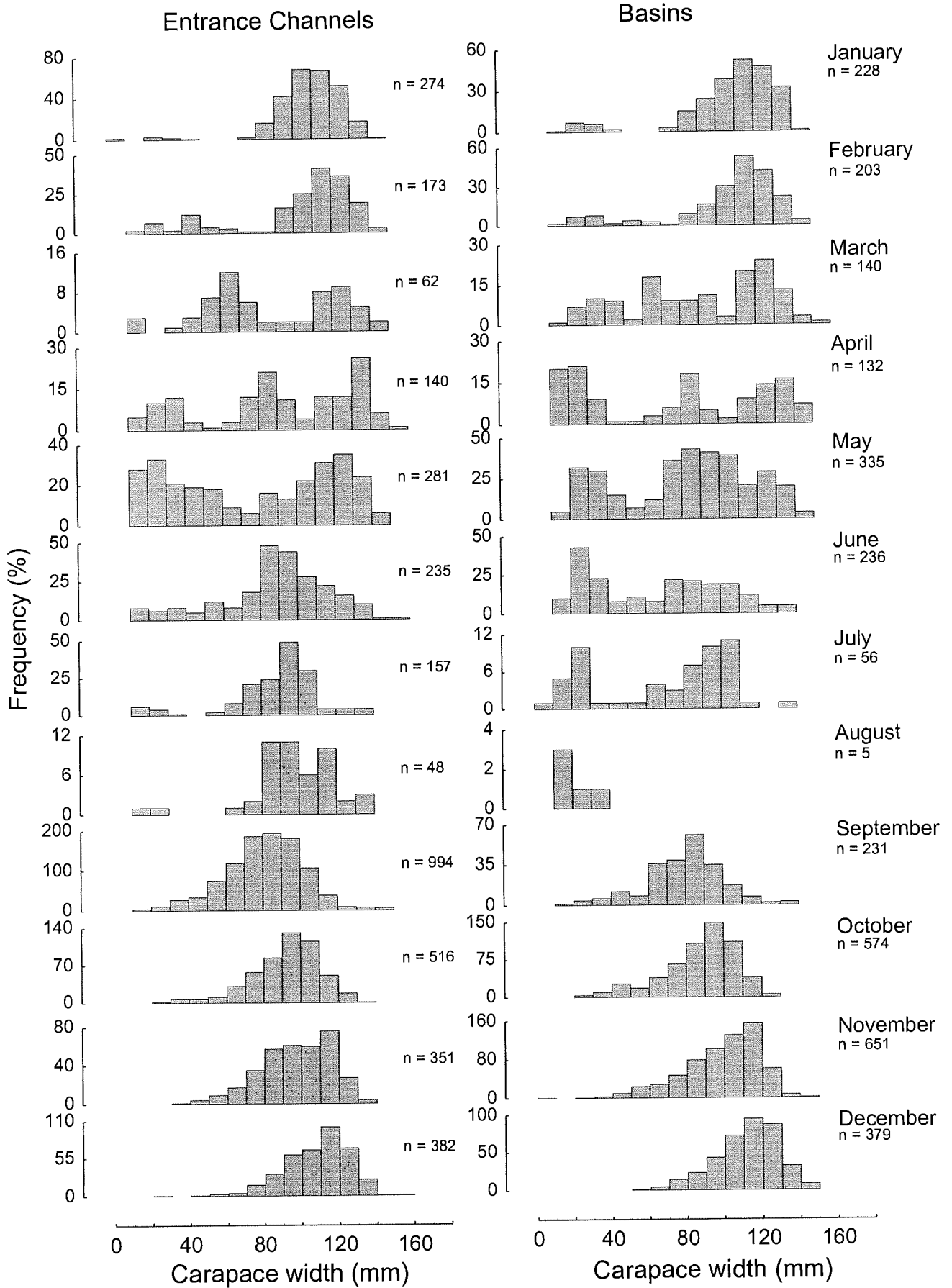
Figure 21. Size-frequency distributions for *Portunus pelagicus* caught by seine netting and otter trawling in the entrance channels and basins of the Peel-Harvey Estuary.
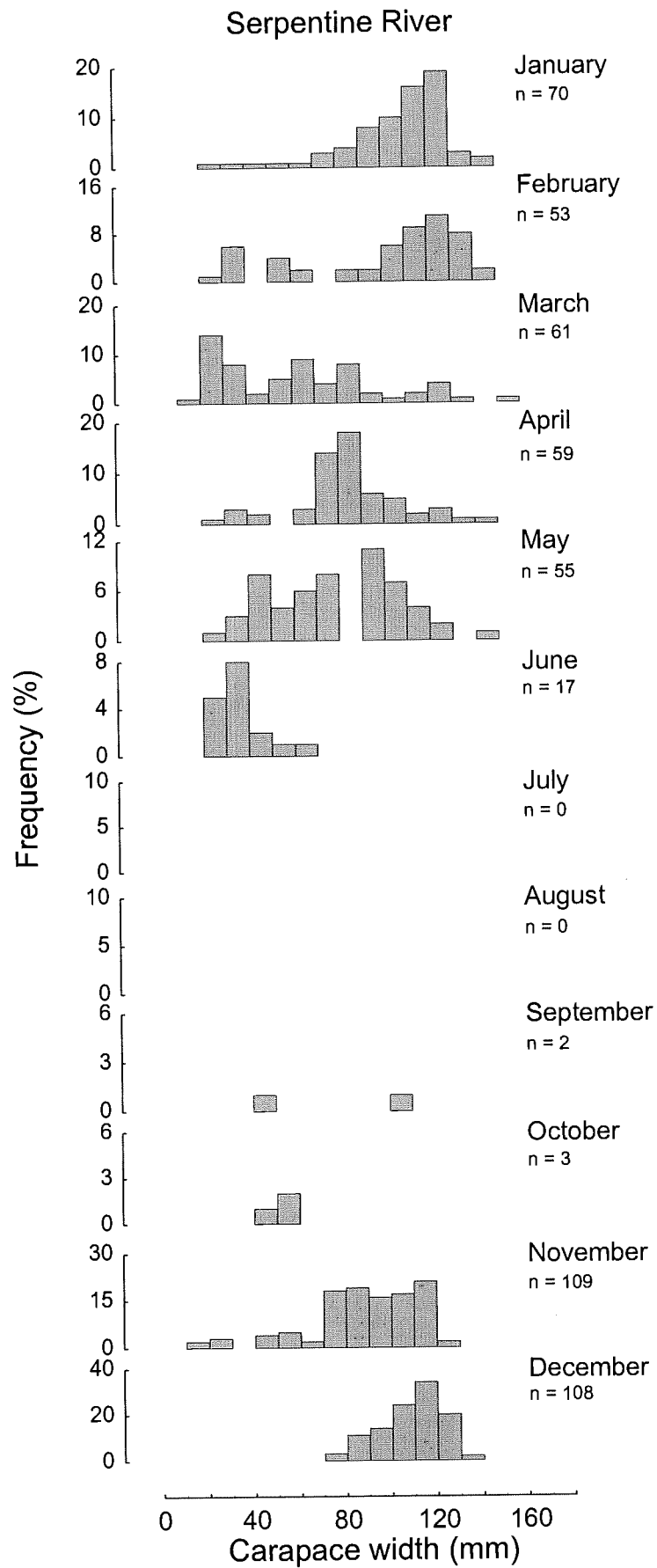
Figure 22. Size-frequency distributions for *Portunus pelagicus* caught by seine netting and otter trawling in the Serpentine River of the Peel-Harvey Estuary.
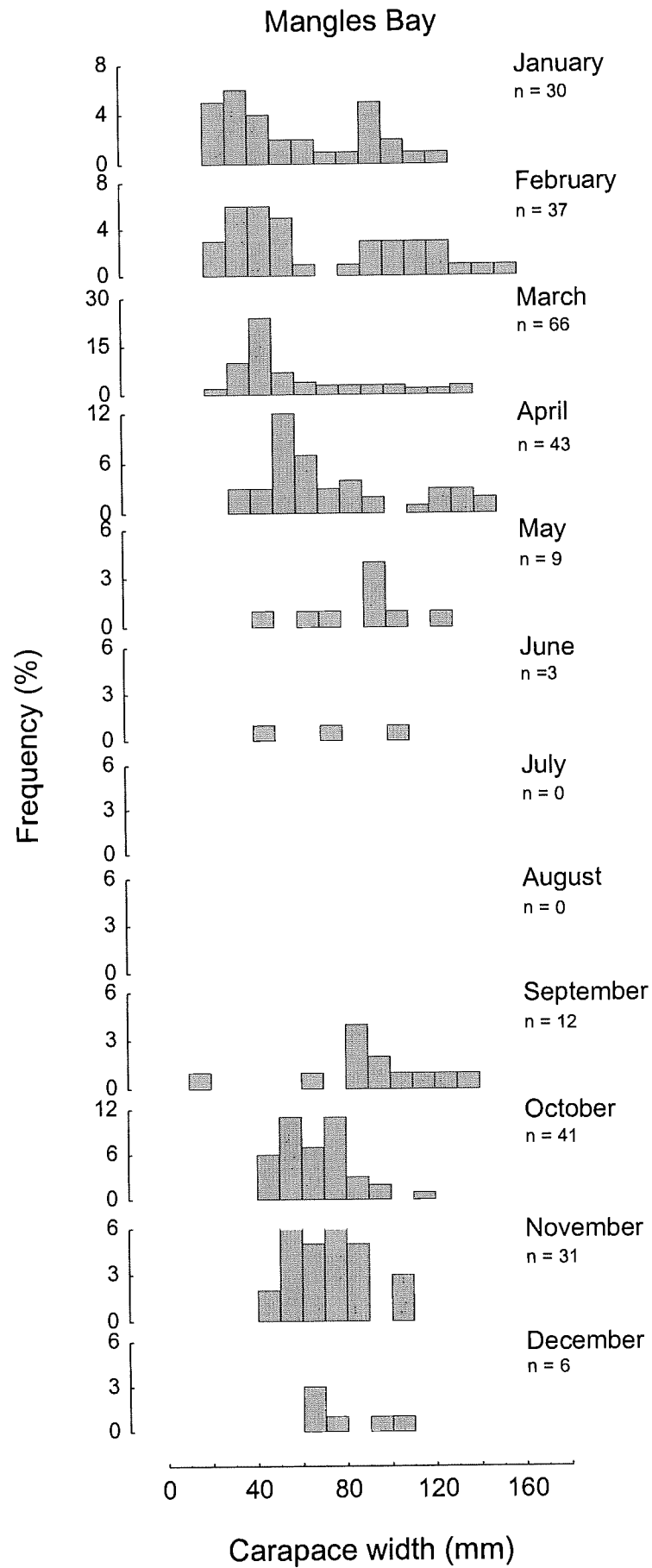
Mangles Bay

Figure 23. Size-frequency distributions for *Portunus pelagicus* caught by seine netting and otter trawling in shallow waters (< 2.5 m) in the Mangles Bay region of Cockburn Sound.
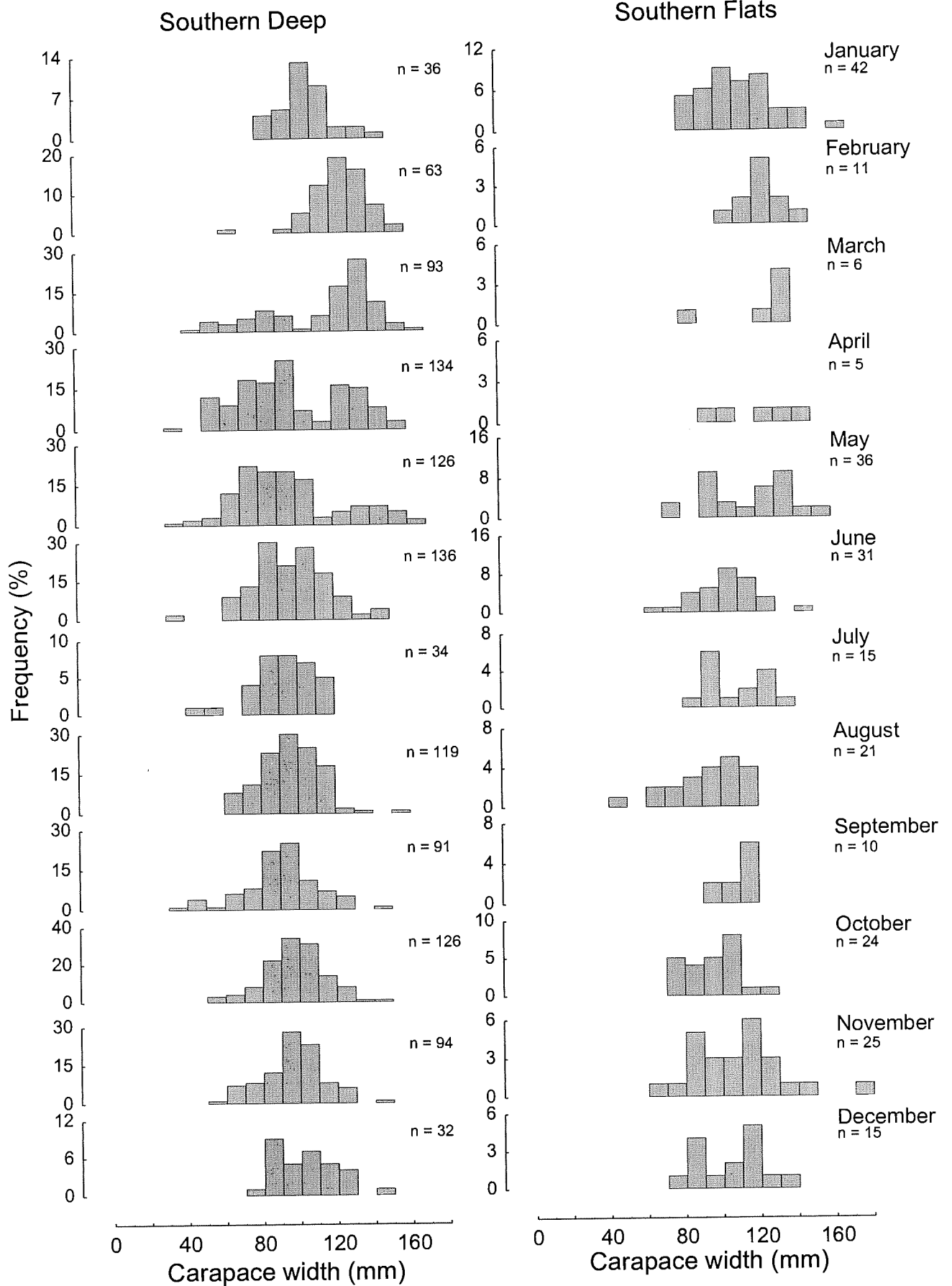
Figure 24. Size-frequency distributions for *Portunus pelagicus* caught by otter trawling in the southern deep and southern flats regions of Cockburn Sound.
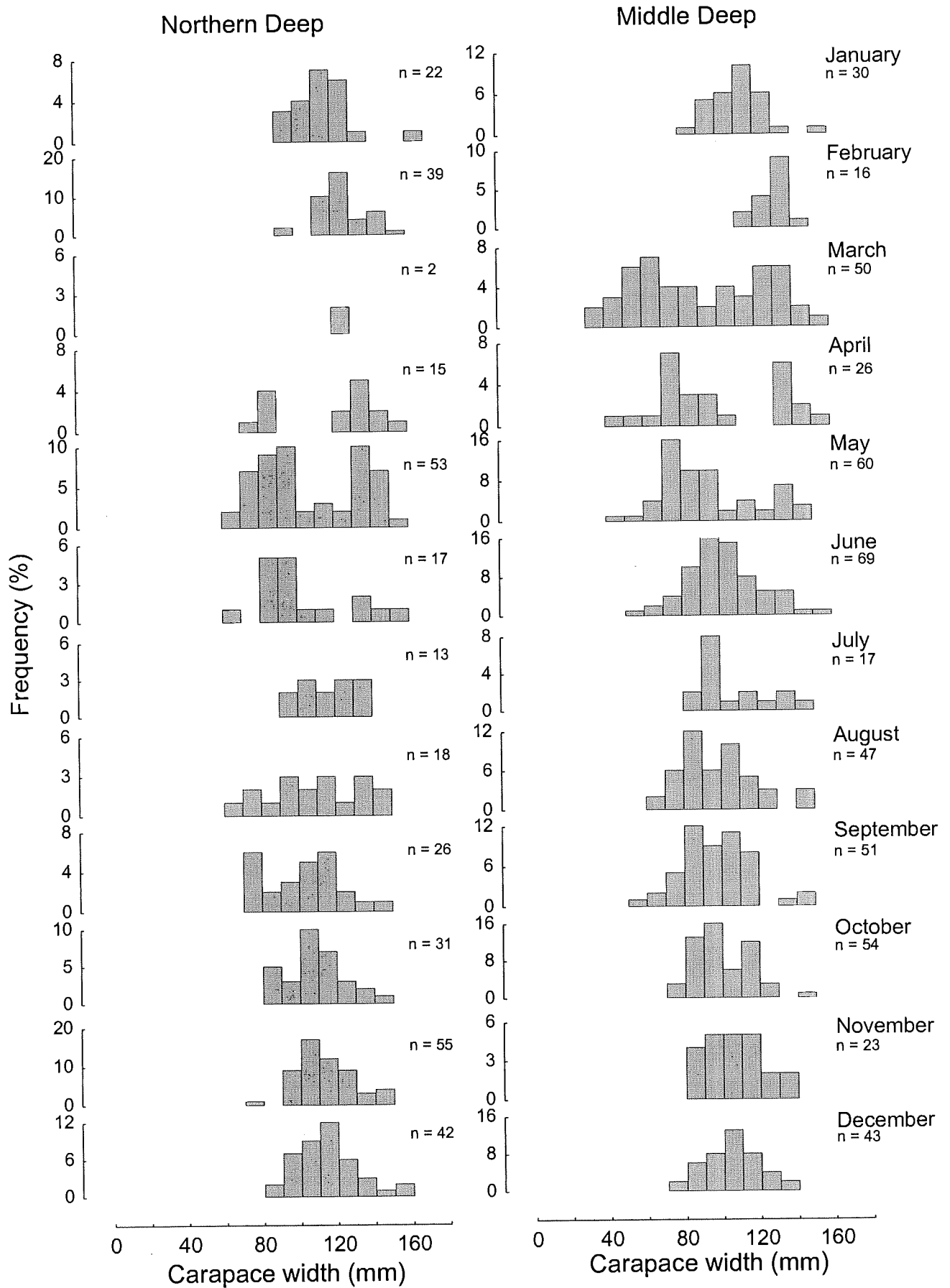
Figure 25. Size-frequency distributions for *Portunus pelagicus* caught by otter trawling in the northern deep and middle deep regions of Cockburn Sound.
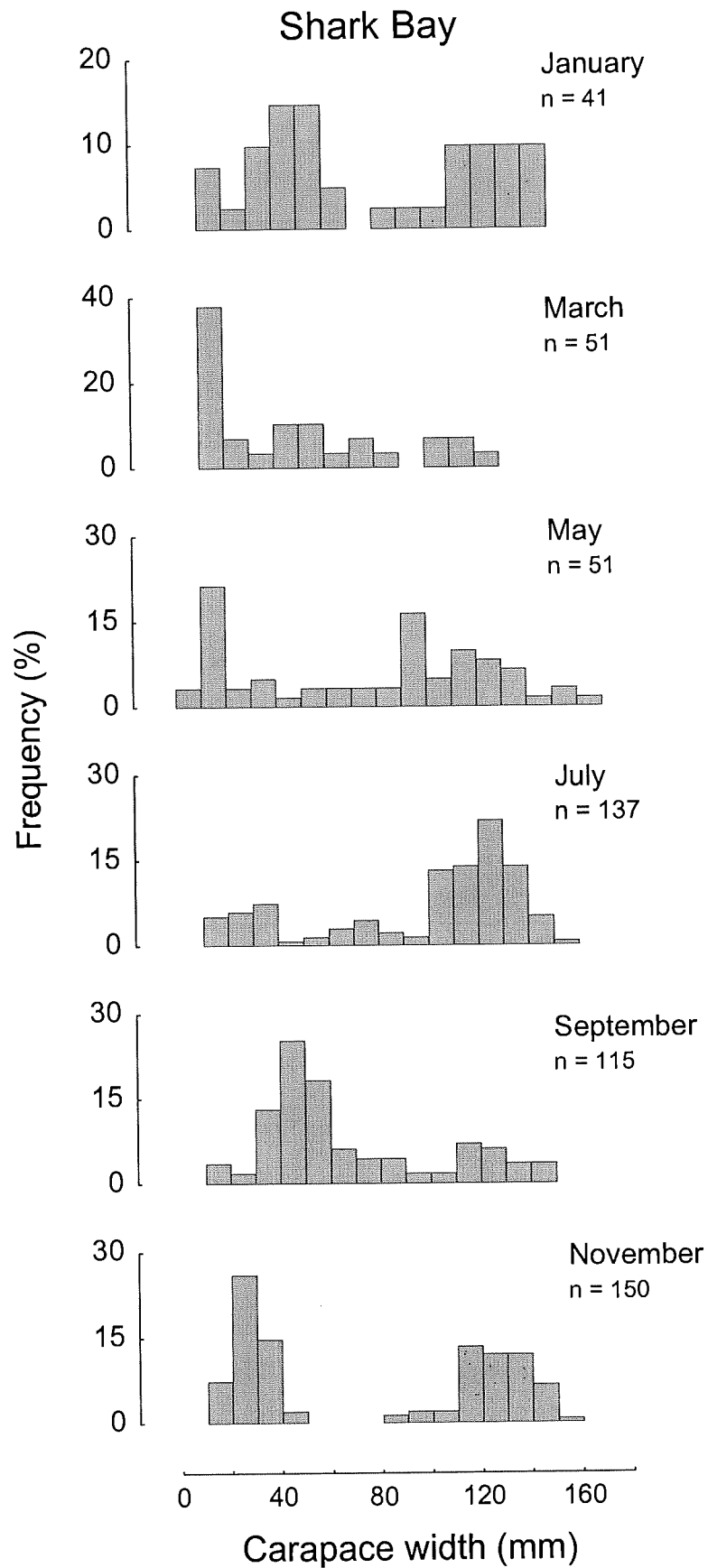
Figure 26. Size-frequency distributions for *Portunus pelagicus* caught by seine netting and otter trawling in the four regions of Shark Bay.
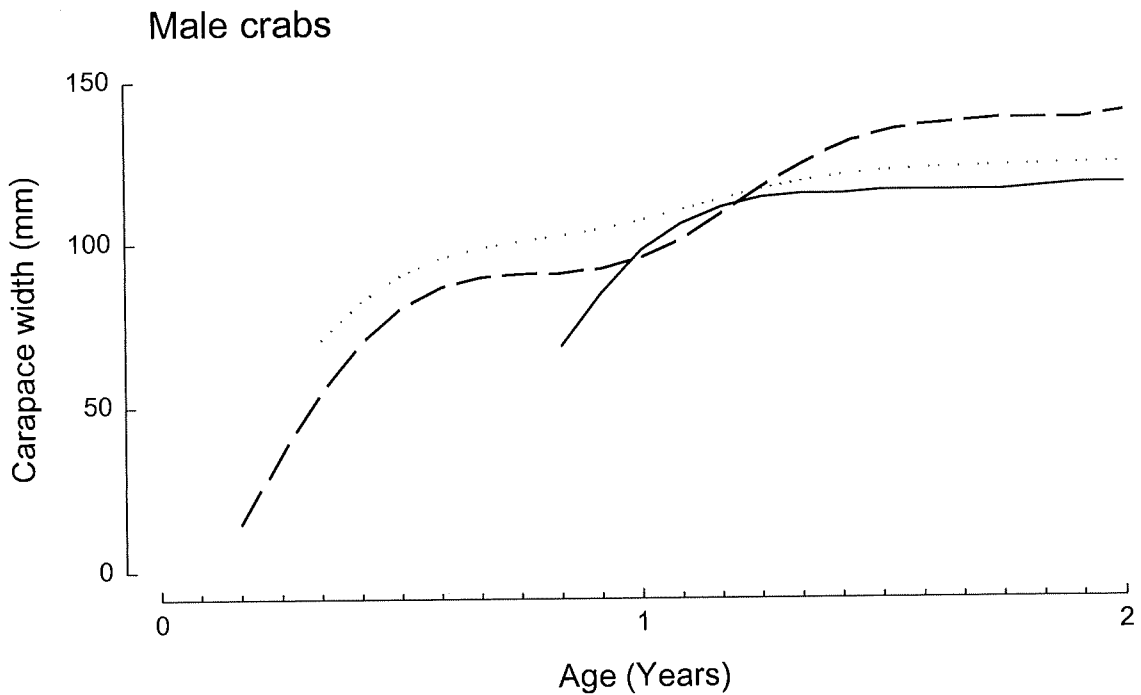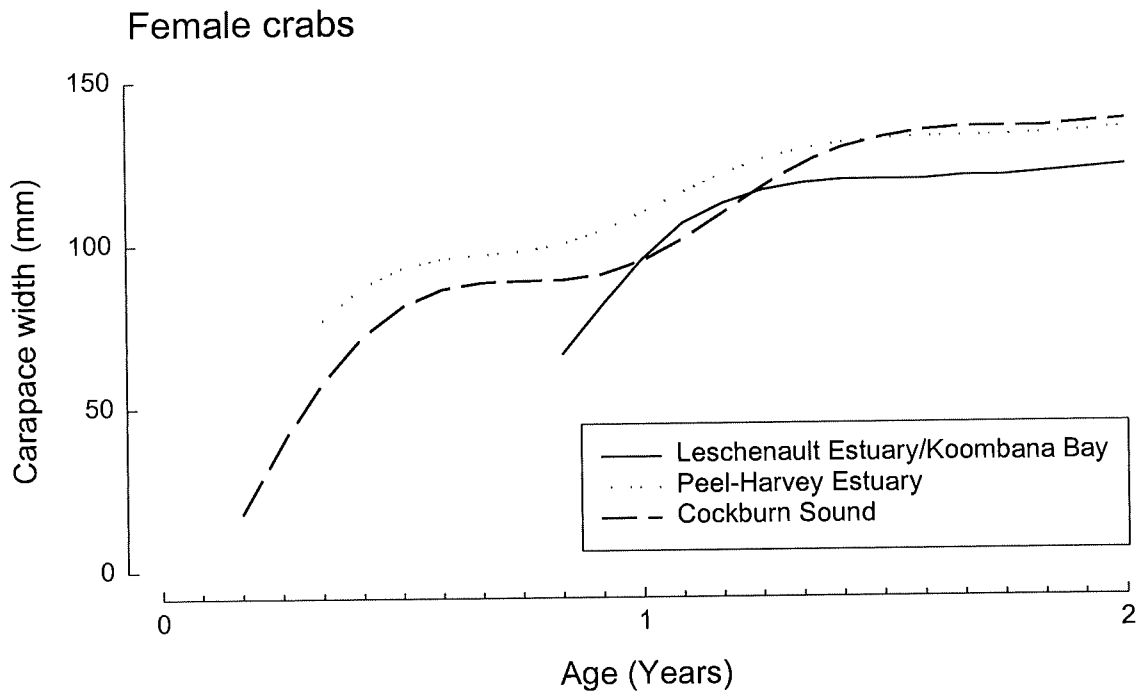
Figure 27. Estimated carapace width at age of female and male *Portunus pelagicus* in the Leschenault Estuary/Koombana Bay, the Peel-Harvey Estuary and Cockburn Sound, derived from analysis of the progression of modal carapace widths in sequential monthly samples.
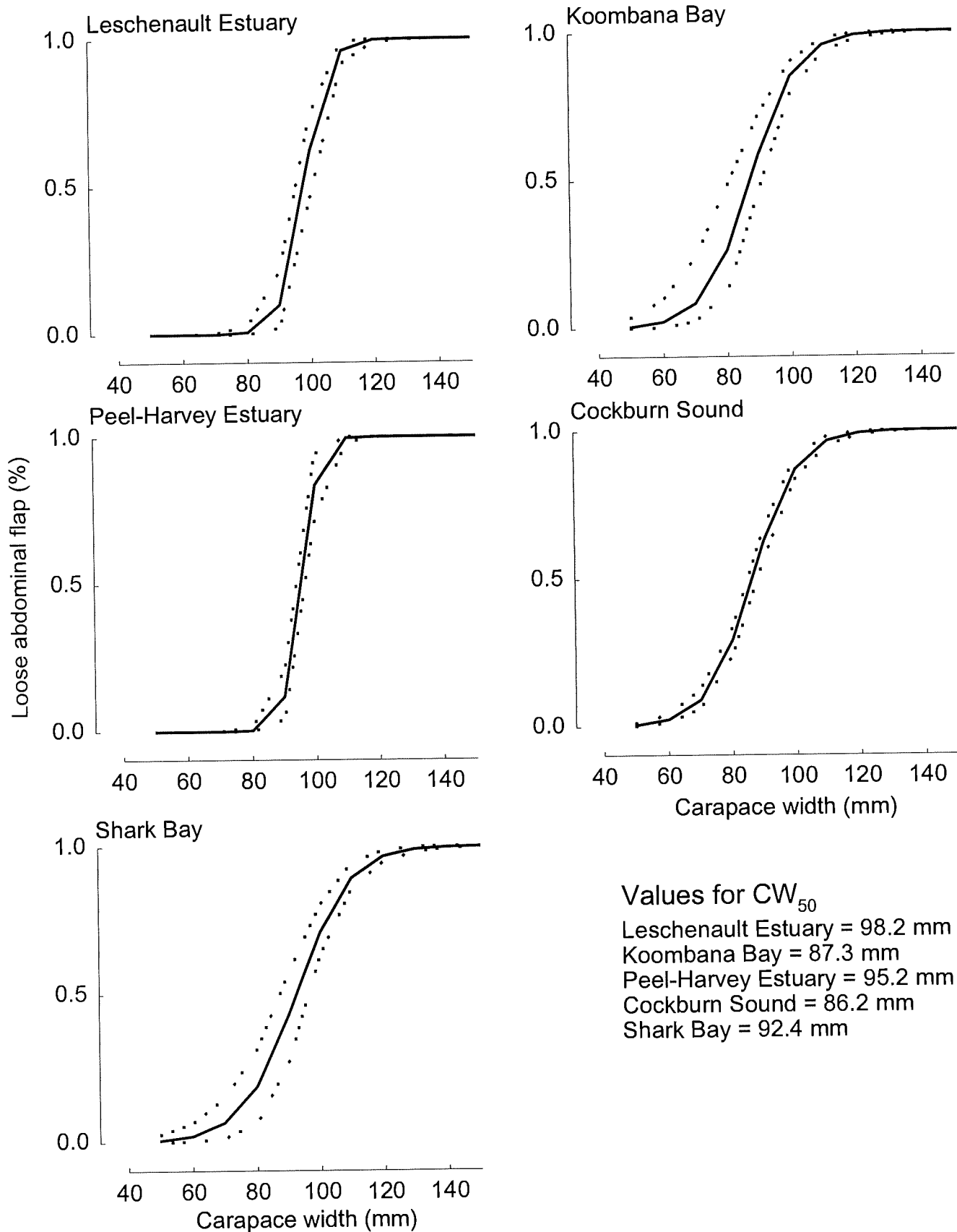
Figure 28. Percentage contributions of adult females, as reflected by the presence of a loose abdominal flap, in the five water bodies sampled in Western Australia. The logistic curve (continuous line) and the 95% confidence limits for that curve (dotted line) were fitted to data for individual female crabs.

Values for CW$_{50}$

Leschenault Estuary = 92.9 mm
Koombana Bay = 92.8 mm
Peel-Harvey Estuary = 94.2 mm
Cockburn Sound = 96.8 mm
Shark Bay = 115.1 mm
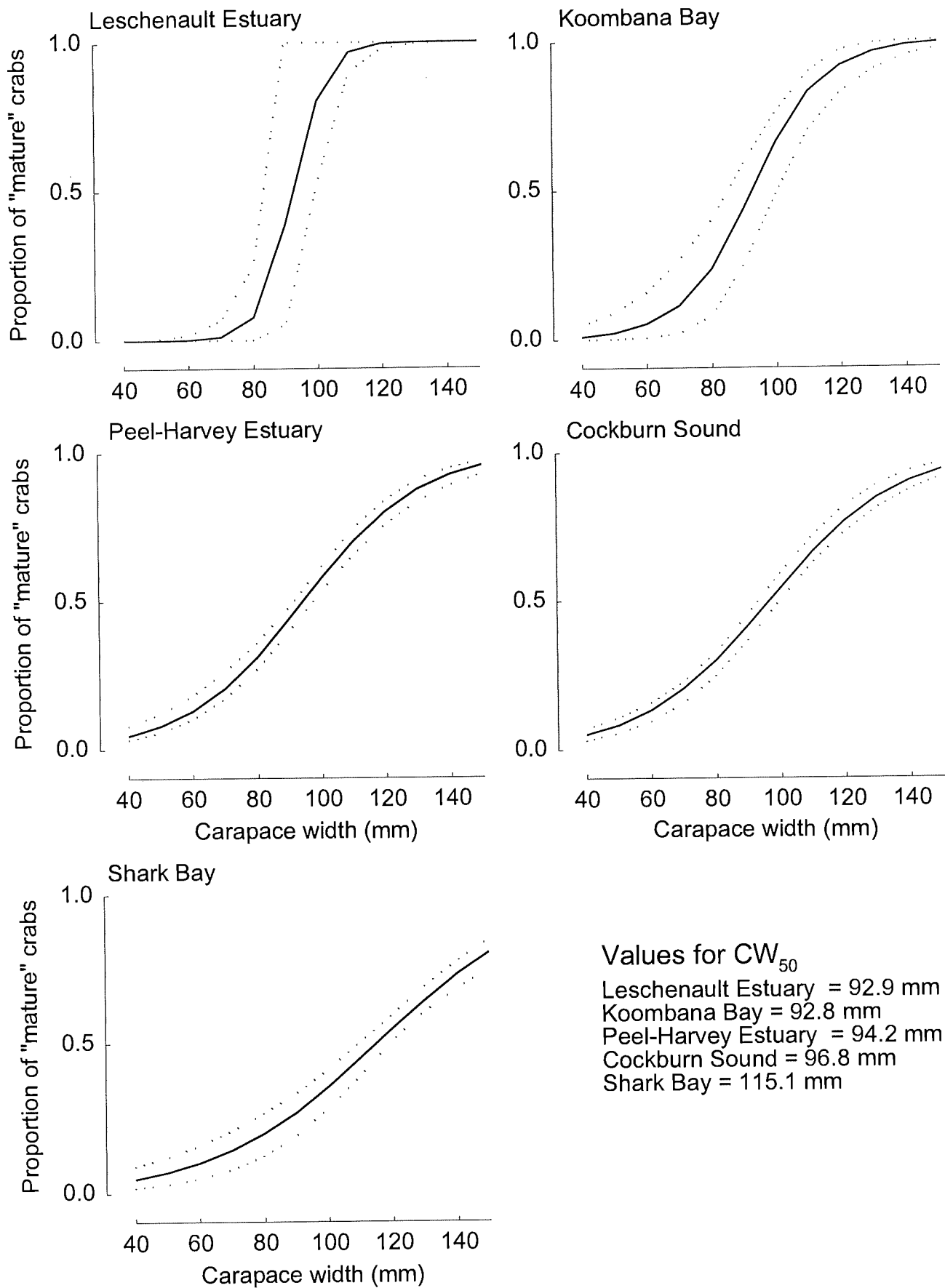
Figure 29. Percentage contributions of mature male crabs, as reflected by the changes in the pattern of allometric growth in the Leschenault Estuary, Koombana Bay, Peel-Harvey Estuary, Cockburn Sound and Shark Bay. The logistic curve (continuous line) and the 95% confidence limits for that curve (dotted lines) were fitted to data for individual male crabs.
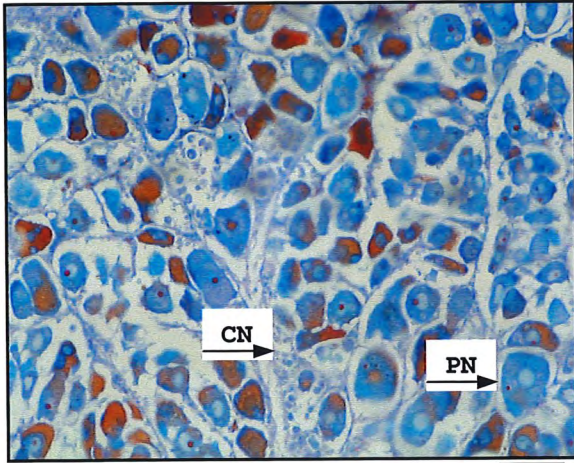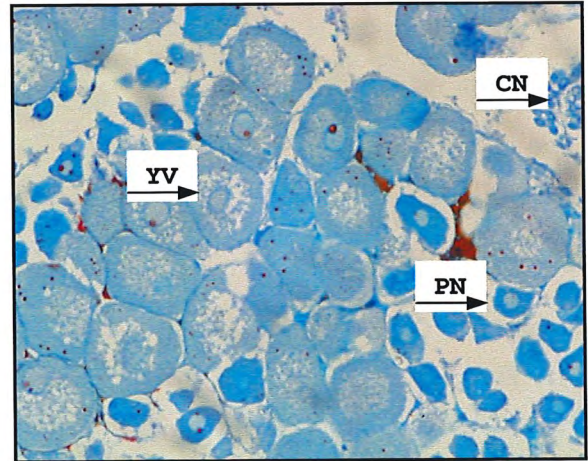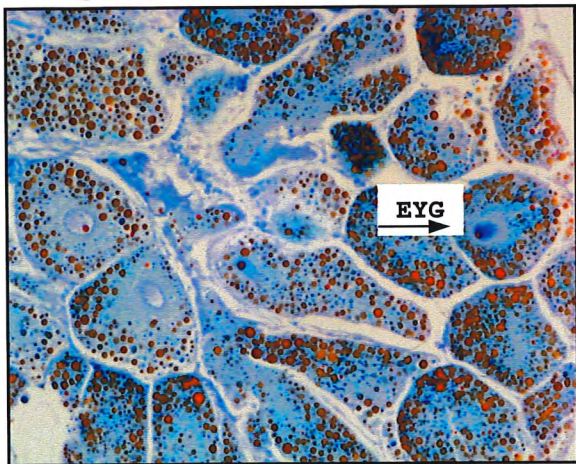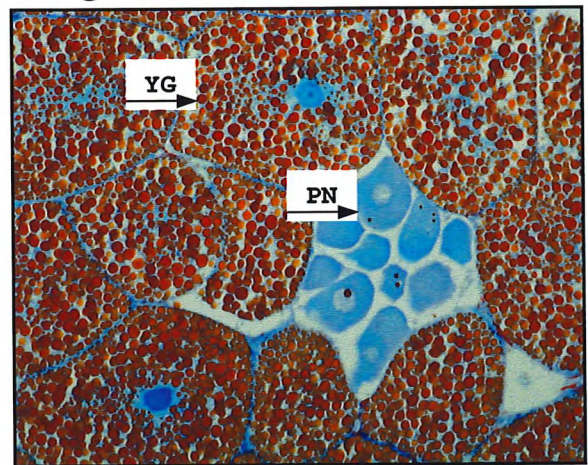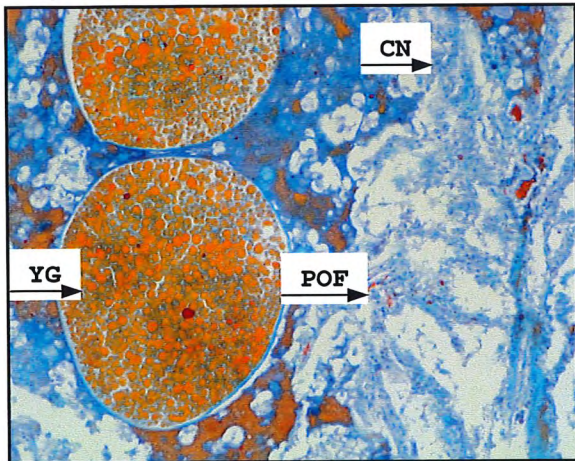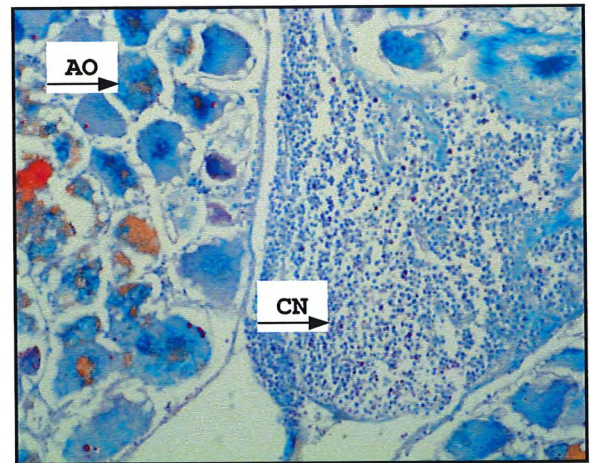
Figure 30. Histological sections of ovaries of *Portunus pelagicus* at stages I - IV and during spawning and while oocytes are undergoing artresia after the completion of spawning. Sections stained using Mallory's trichrome. **CN** = chromatin nucleolar oocyte, **PN** = perinucleolar oocyte, **YV** = yolk vesicle oocyte, **YG** = yolk granule oocyte, **POF** = post ovulatory oocyte, **AO** = atretic oocyte.

Testes
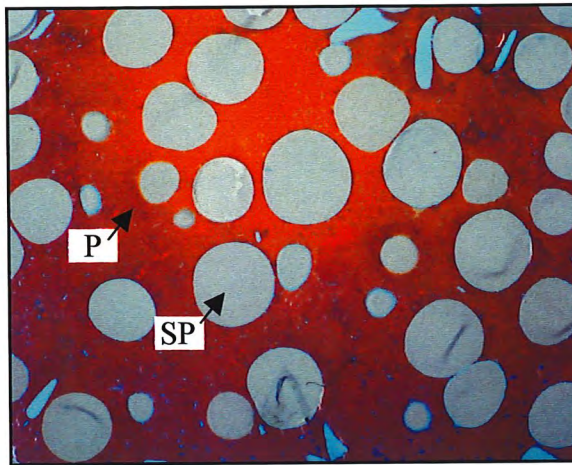
100 µm

Immature vas deferen

100 µm

Mature vas deferen
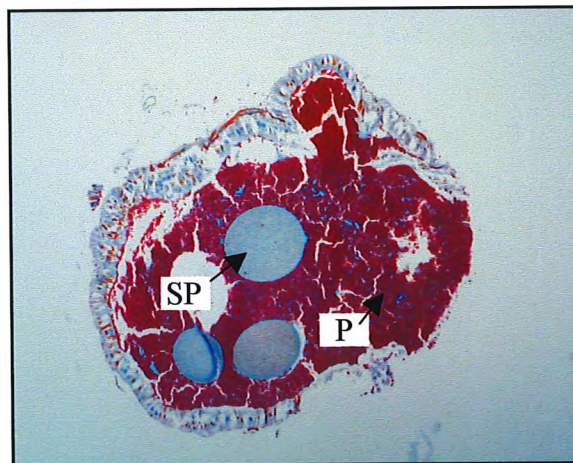
100 µm

Figure 31. Histological sections of the testes and immature and mature vas deferens of *Portunus pelagicus.* The histological appearance of the testes remains similar in all stages of development and the appearance of the vas deferens remains the same in gonadal stages III and IV. Sections stained using Mallory's trichrome. **SP** = spermatophores, **P** = Seminal plasma.

(a) Gonad staging — Proportion of crabs with mature gonads vs Carapace width (mm)

(b) Allometric Analysis — Proportion of "mature" crabs vs Carapace width (mm)

(c) Abdominal tightness — Loose abdominal flap (%) vs Carapace width (mm)

Values for CW_{50}

Macroscopic gonad method = 89.7 mm
Allometric method = 96.8 mm
Abdominal tightness method = 72.1 mm
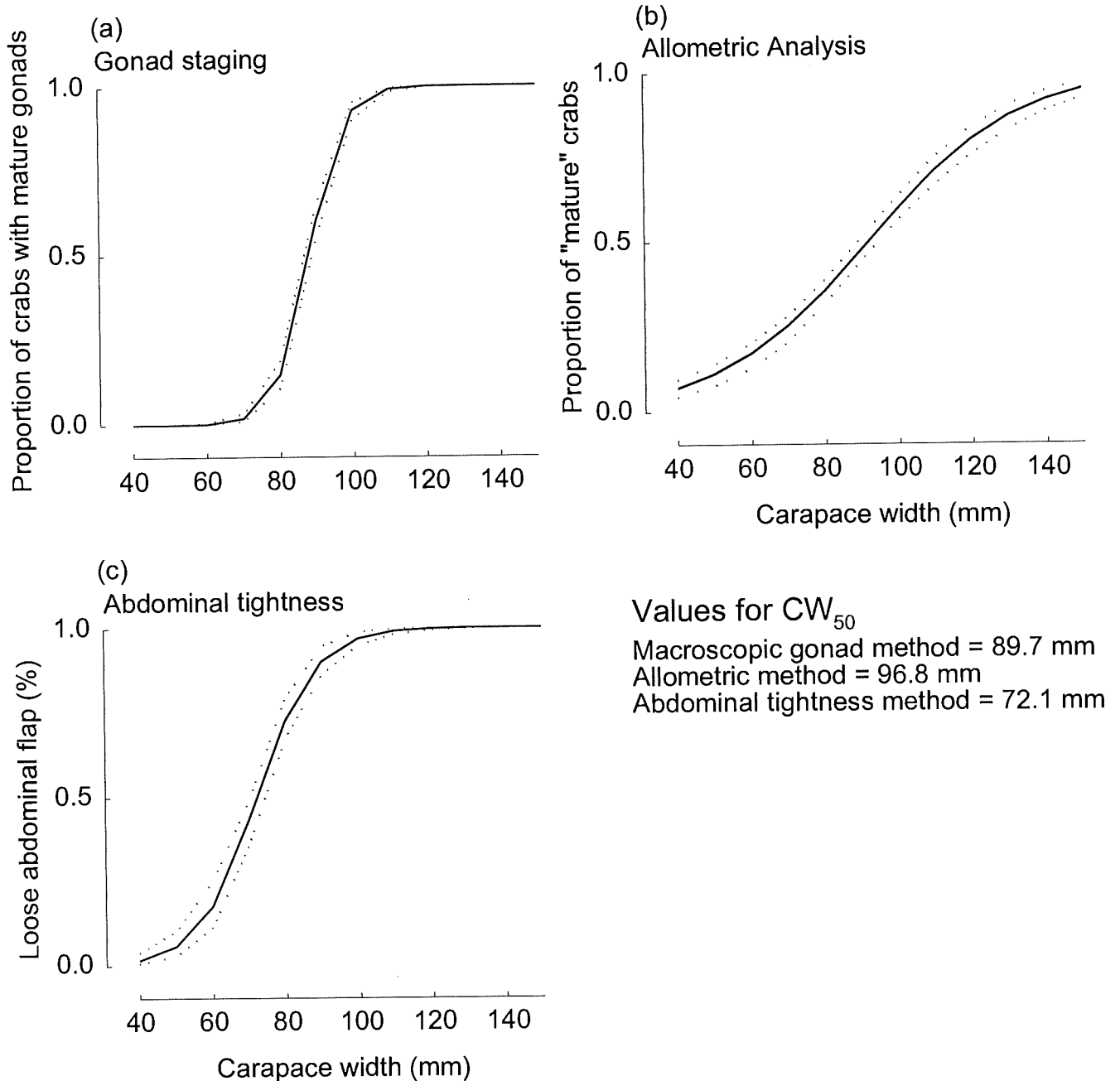
Figure 32. Percentage contributions of males which, in Cockburn Sound, were considered to have reached maturity on the basis of (a) their gonadal stage and (b) changes in the pattern of allometric growth of the dorsal propodus of the right cheliped. (c) shows the corresponding frequencies of occurrence of male crabs with loosely fixed abdominal flaps. The logistic curve (continuous line) and the 95% confidence limits (dotted line) were fitted to data for individual male crabs.
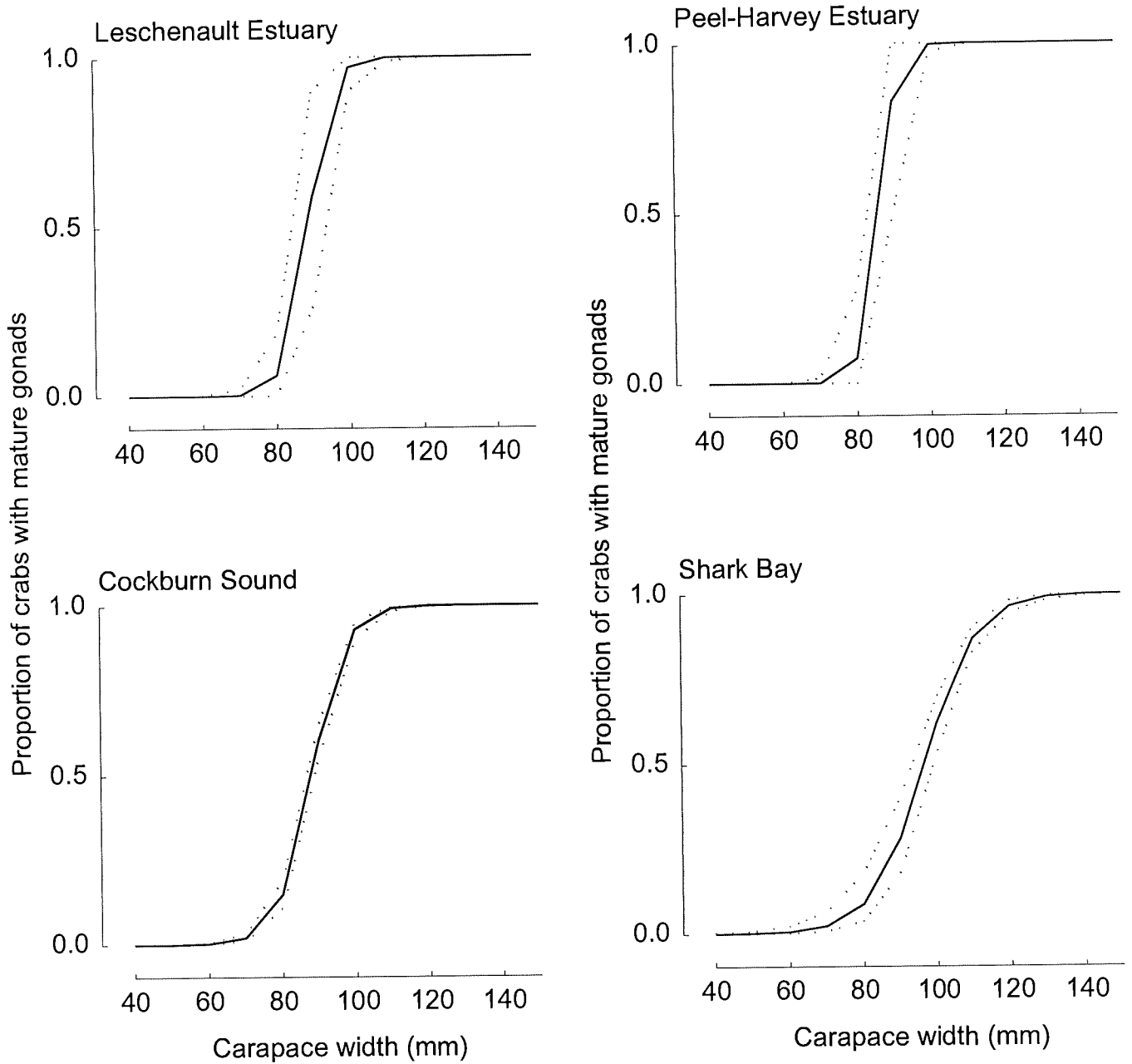
Values for CW_{50}

Leschenault Estuary = 88.8 mm
Peel - Harvey Estuary = 86.6 mm
Cockburn Sound = 89.7 mm
Shark Bay = 96.5 mm

Figure 33. Percentage contributions of mature male crabs, as reflected by the presence of mature gonads in the Leschenault Estuary, Peel-Harvey Estuary, Cockburn Sound and Shark Bay. The logistic curve (continuous line) and the 95% confidence limits for that curve (dotted line) were fitted to data for individual male crabs.
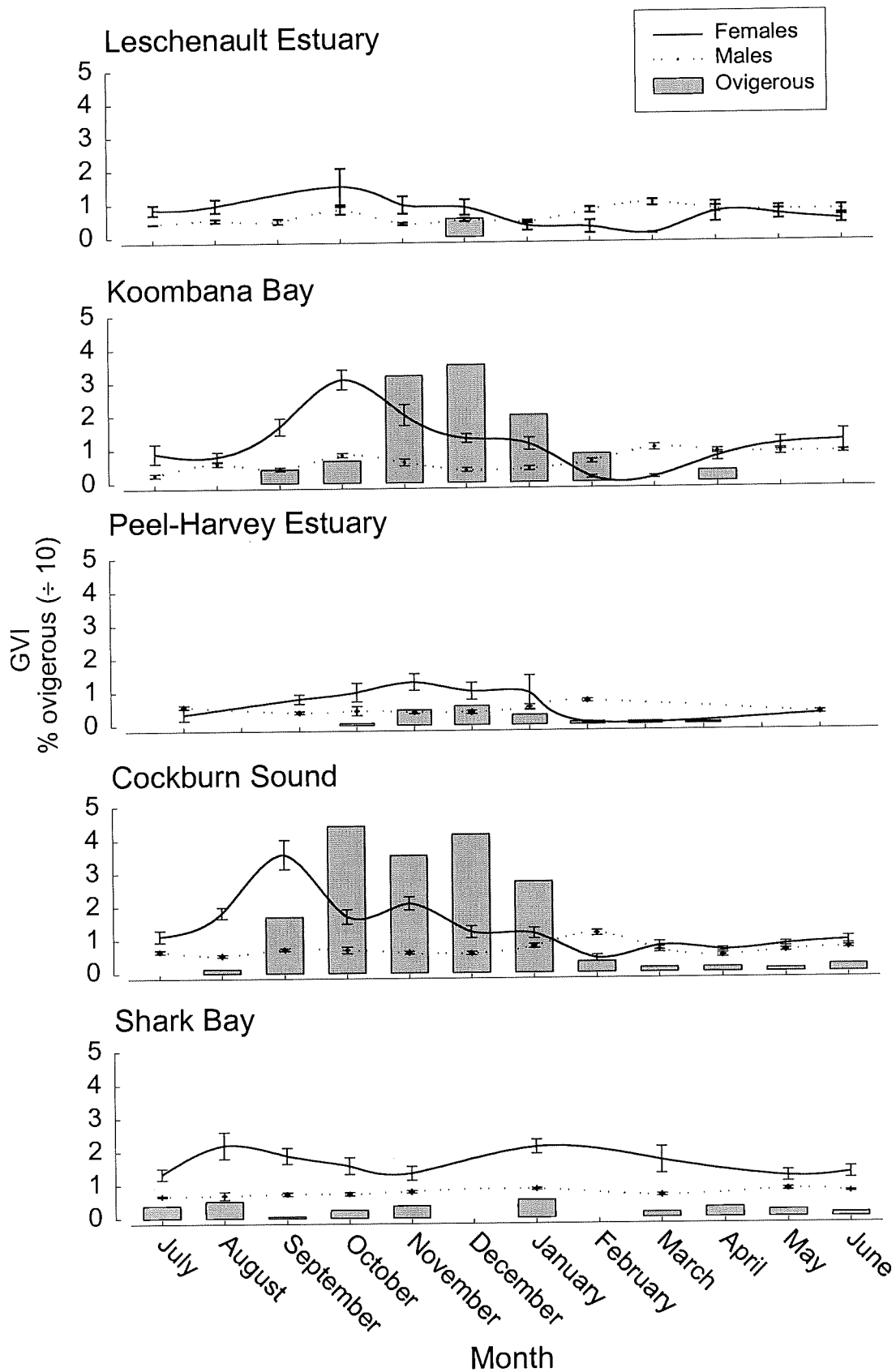
Figure 34. Mean monthly gonadovolumetric indices (GVI) ± 1 SE for female
and male *Portunus pelagicus* and the percentage of ovigerous
females among all adult female *P. pelagicus* in the five water
bodies in which sampling was conducted.
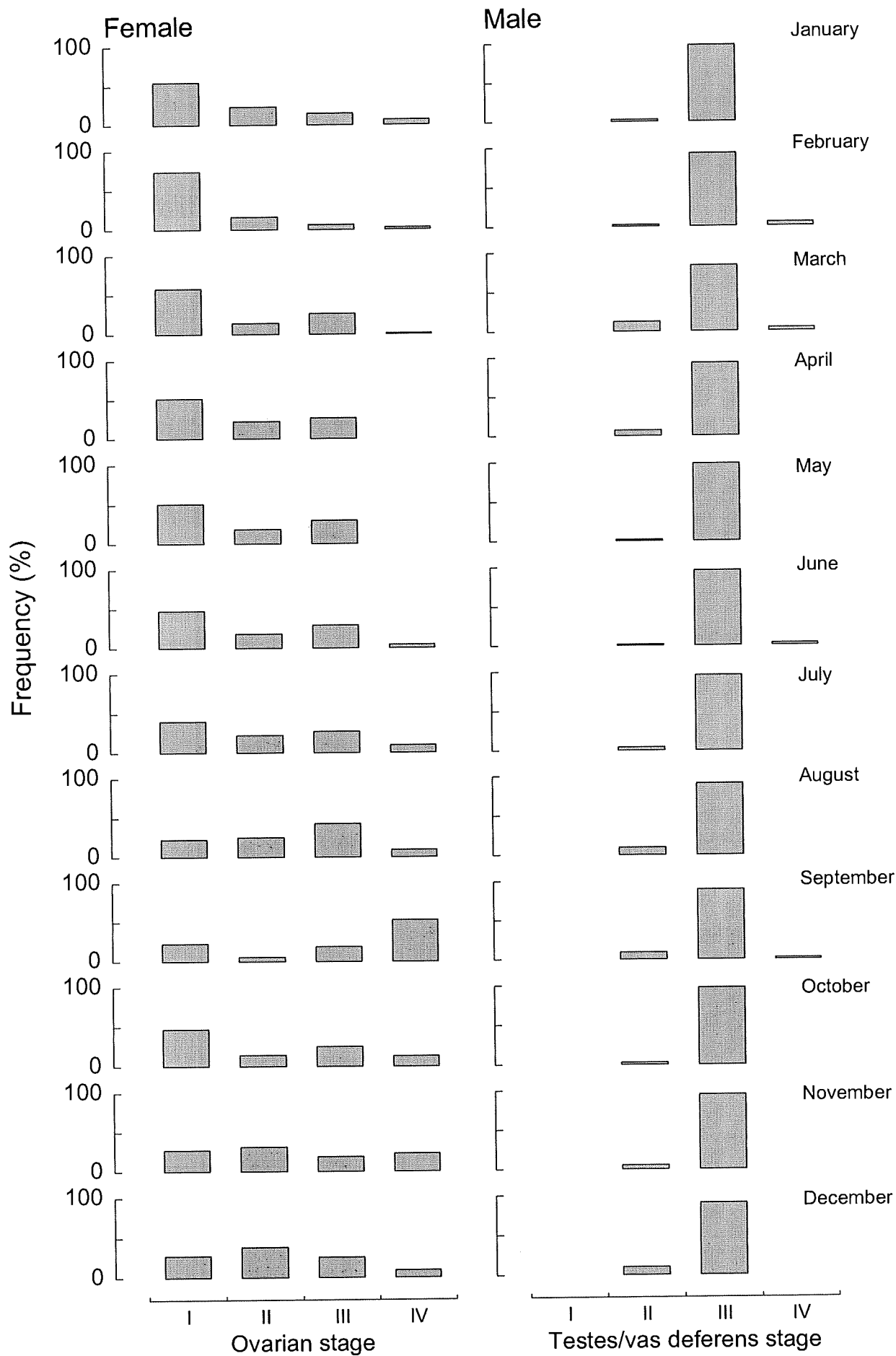
Figure 35. Percentage frequency of occurrence of ovaries and testes/vas deferens of adult *Portunus pelagicus* at different stages of development in sequential months in Cockburn Sound.
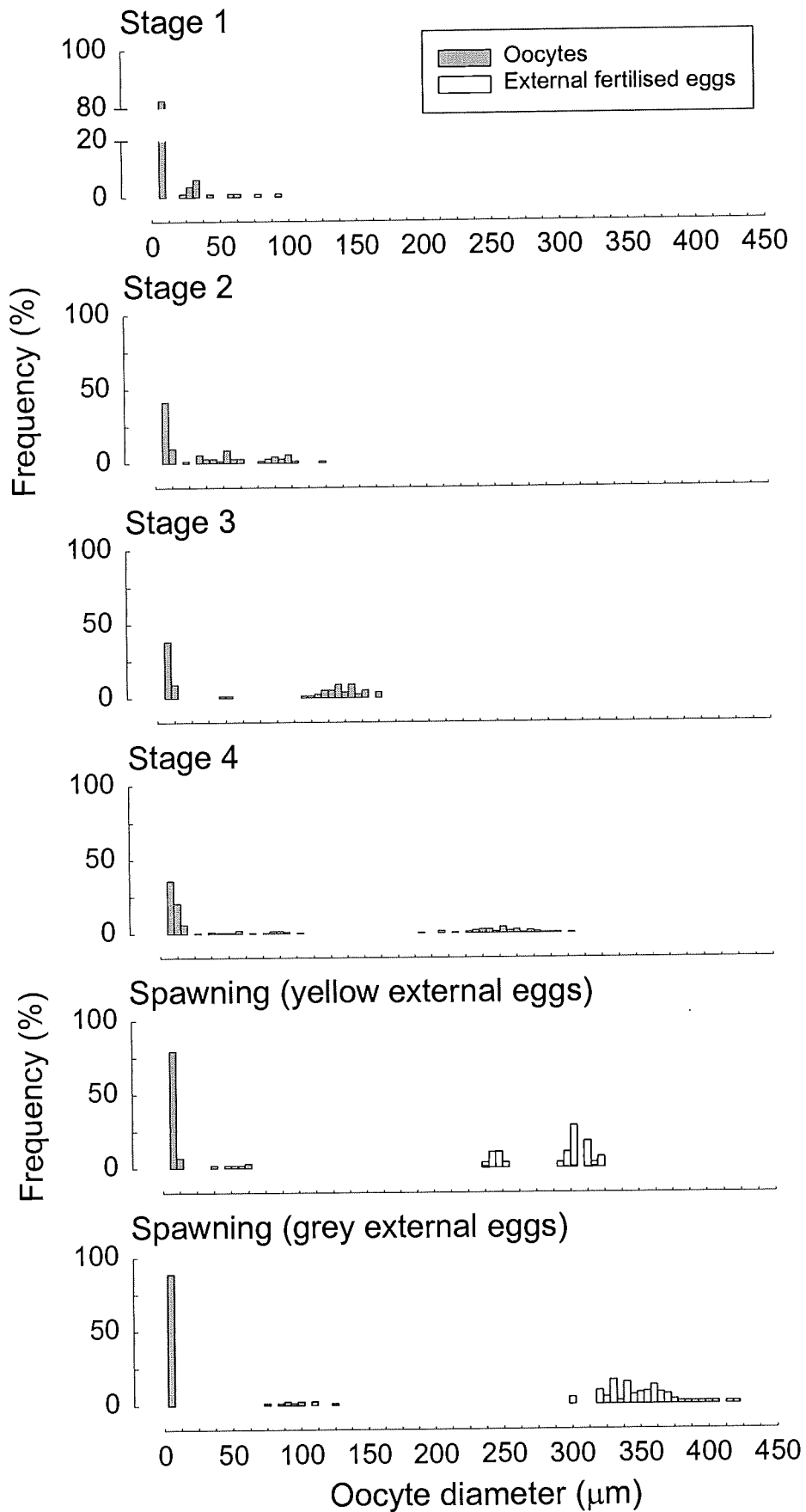
Figure 36. Frequency histograms for oocyte diameters in the four ovarian developmental stages of *Portunus pelagicus* in Cockburn Sound, and for the oocytes in both the ovary and for the fertilised eggs that lay under the abdominal flap of female crabs and which had either been recently extruded (yellow eggs) or had been extruded for some time (grey eggs).
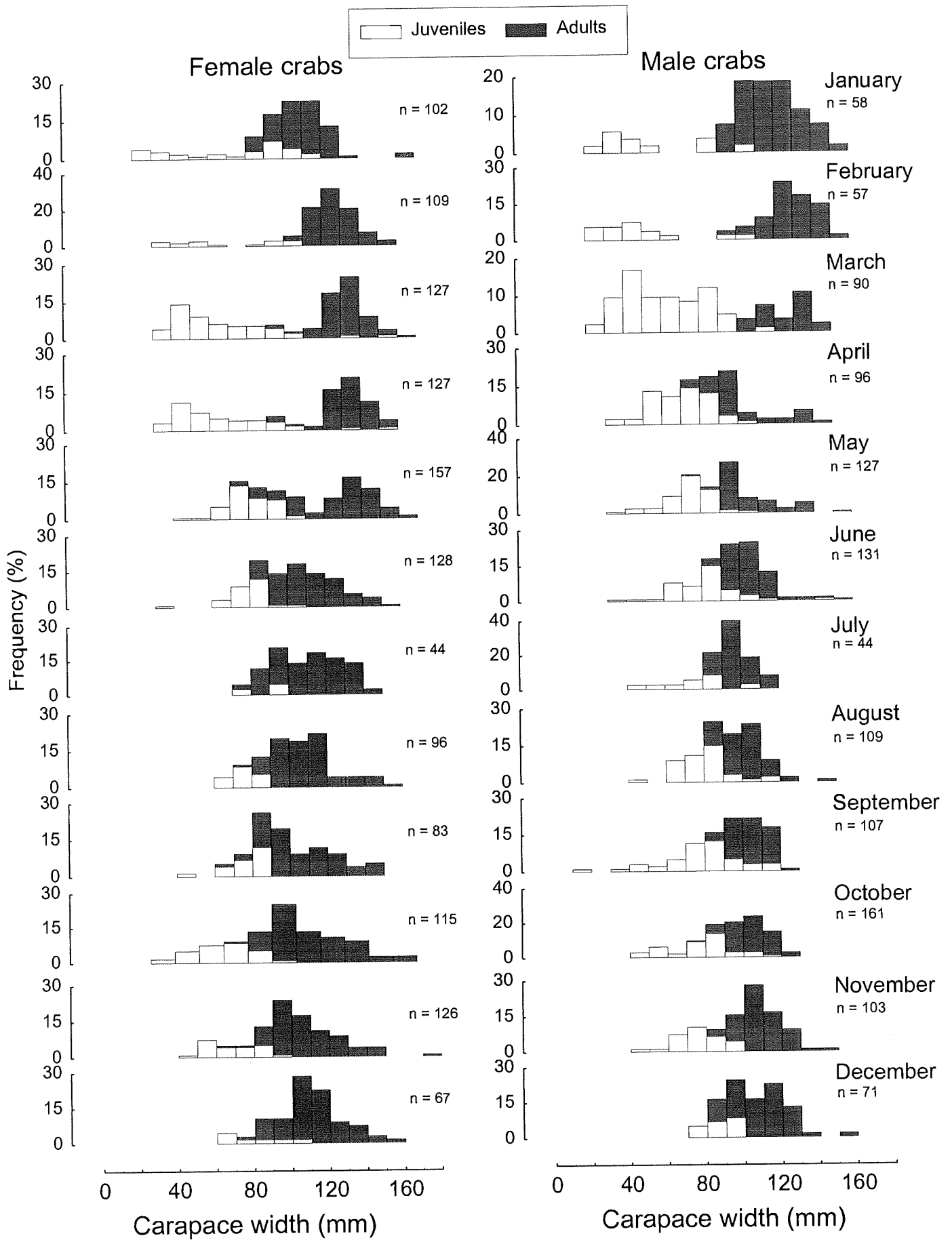
Figure 37. Frequency histograms for the carapace widths of immature and mature females and males of *Portunus pelagicus* in Cockburn Sound. n = number of crabs measured.
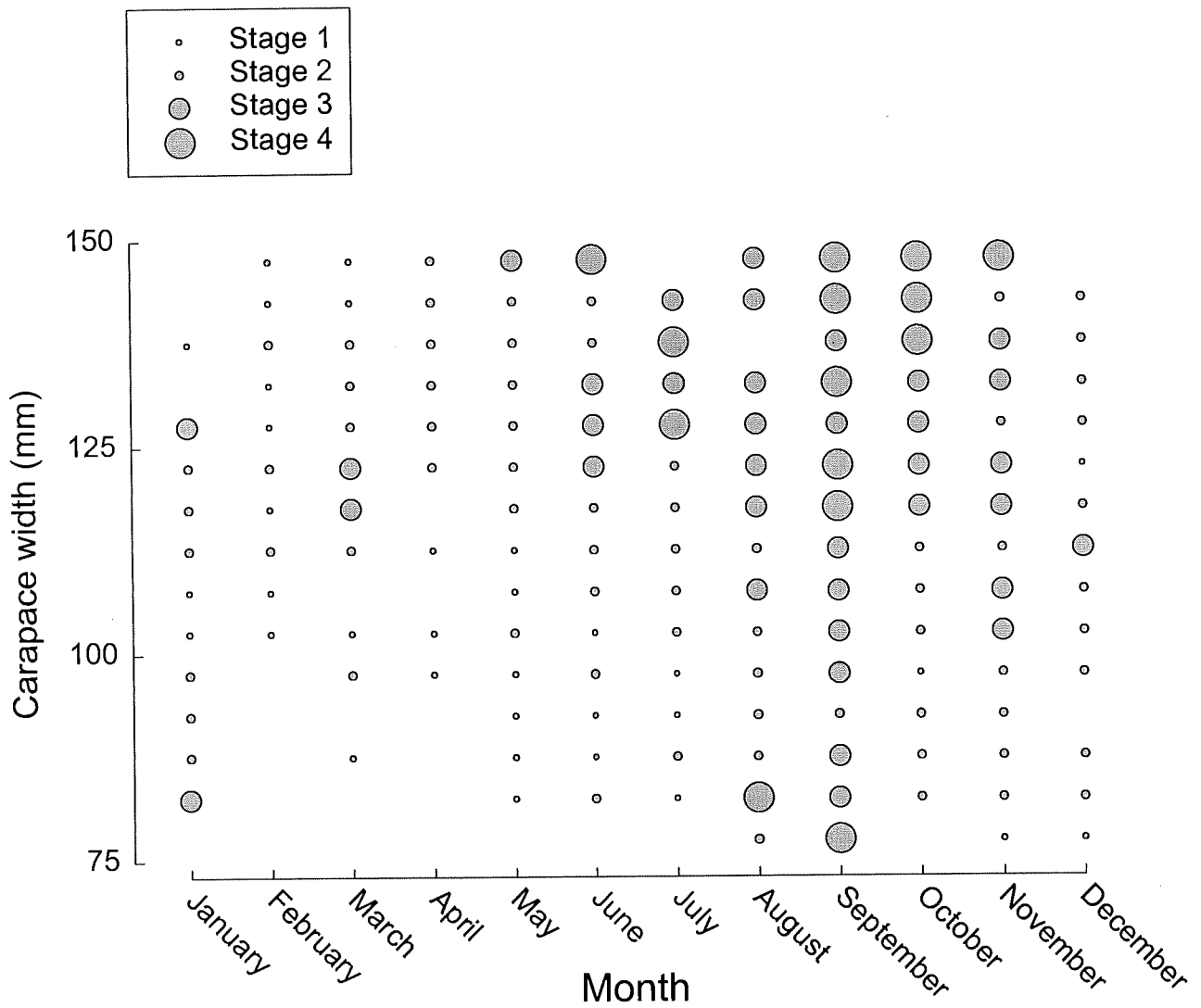
Figure 38. Modal stage of ovarian development in sequential 5 mm carapace width intervals of adult female *Portunus pelagicus* in Cockburn Sound.
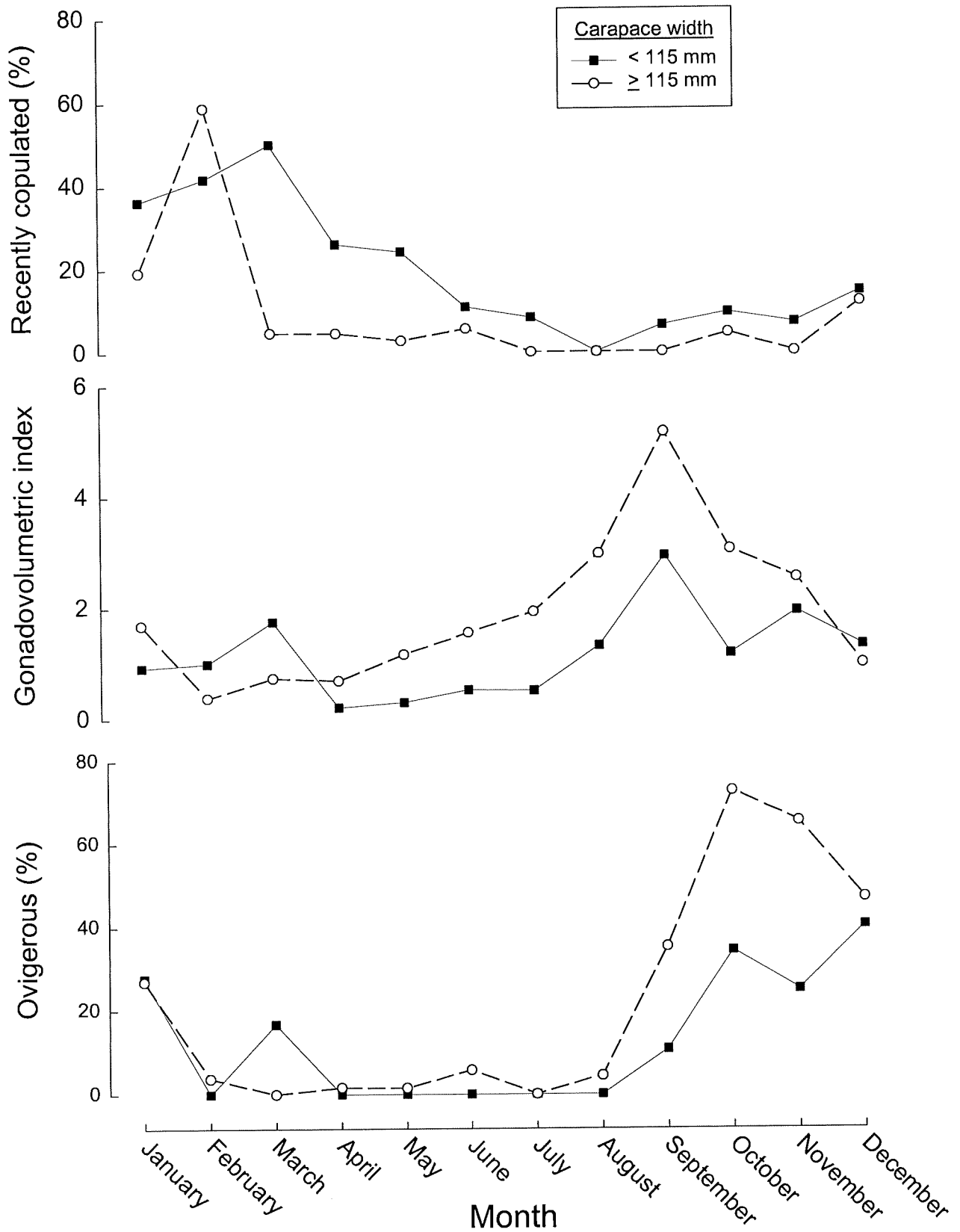
Figure 39. Mean monthly values for the gonadovolumetric index and percentage of recently-copulated and ovigerous adults of all adult female *Portunus pelagicus* in Cockburn Sound. Data have been separated into two size classes according to carapace width, *i.e.* < 115 mm and ≥ 115 mm.
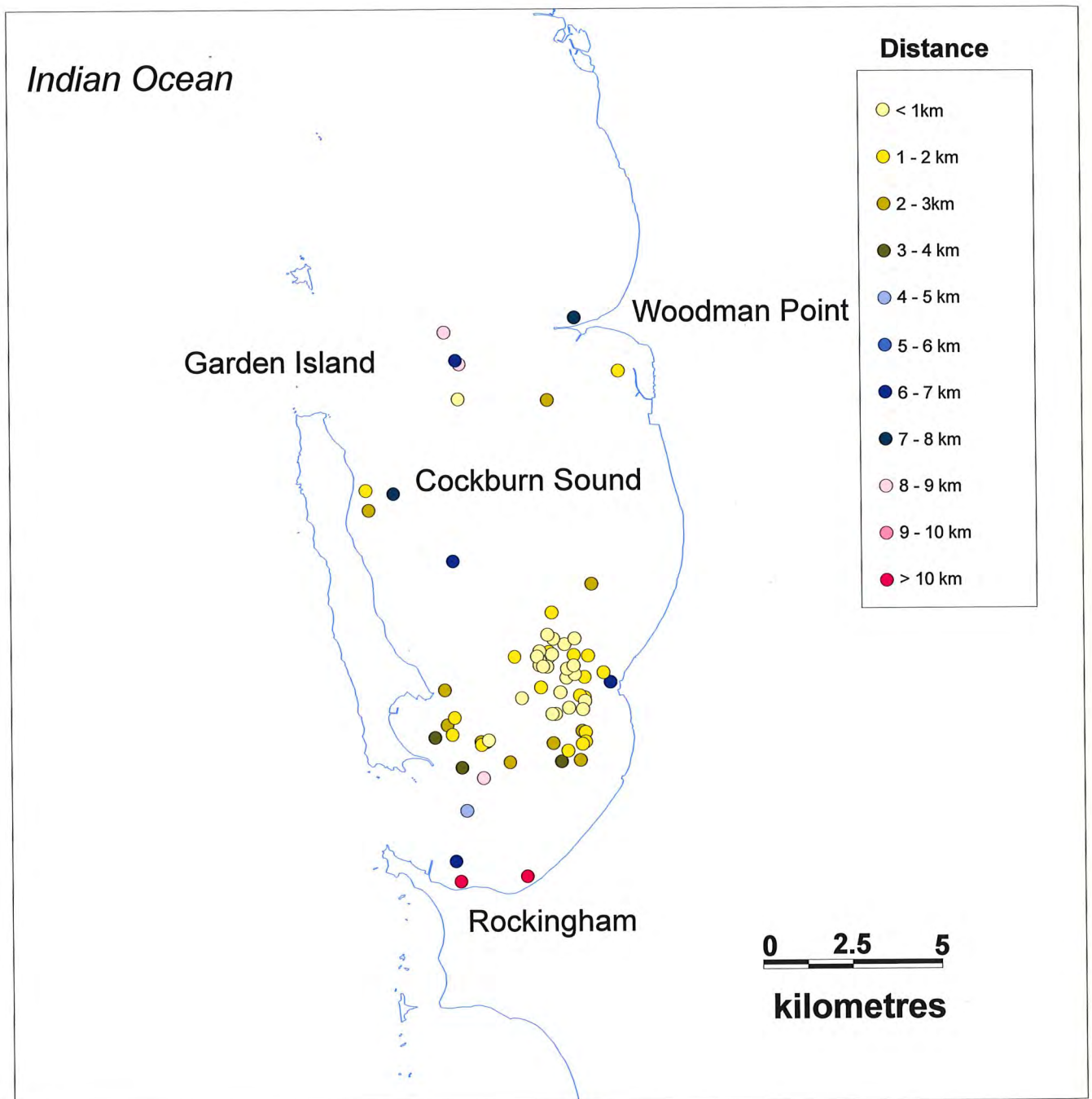
Figure 40. Distance between the points of release and recaptures of tagged blue swimmer crabs in Cockburn Sound.
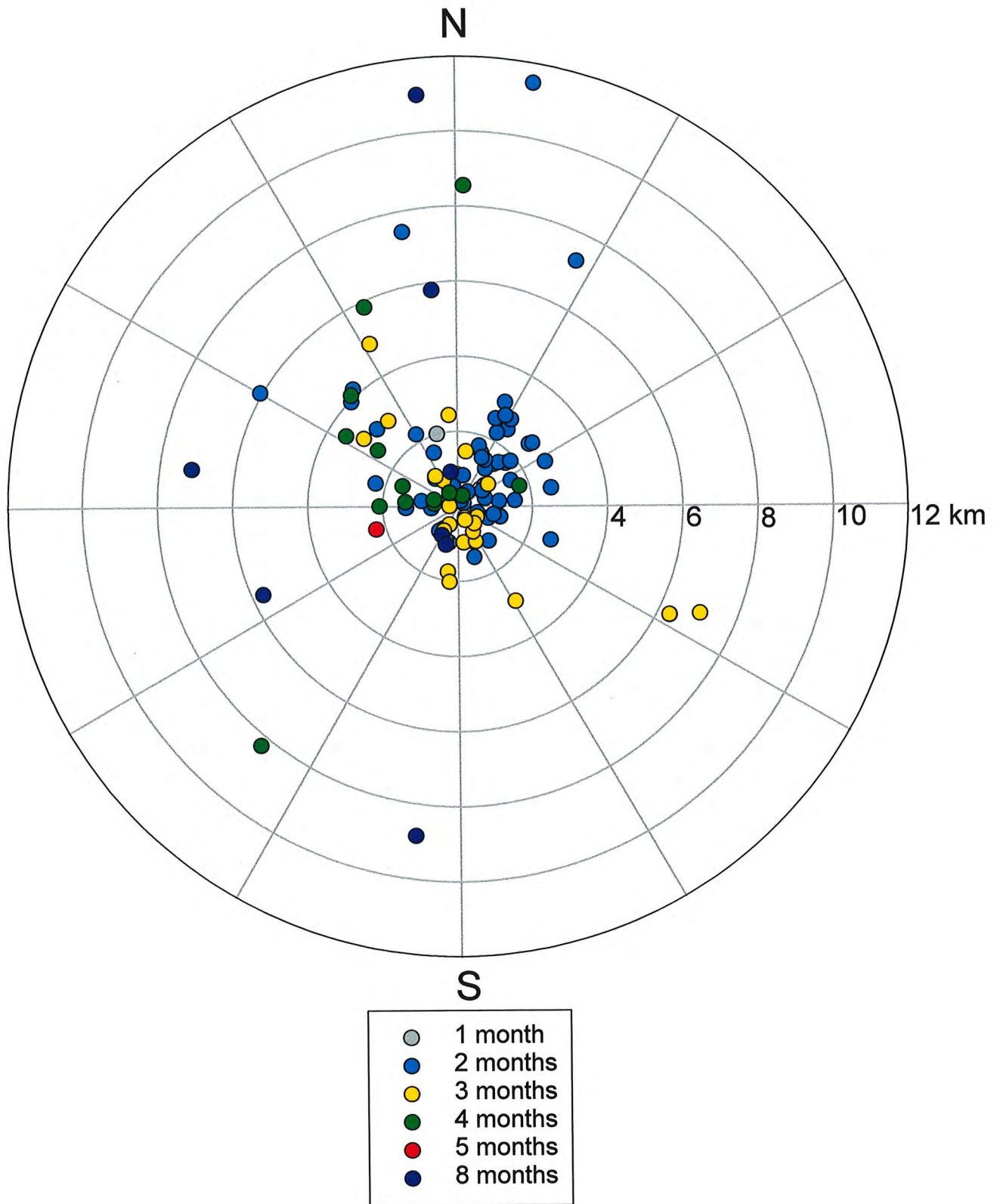
Figure 41. Distribution and time in the water of recaptured tagged *Portunus pelagicus* in Cockburn Sound.
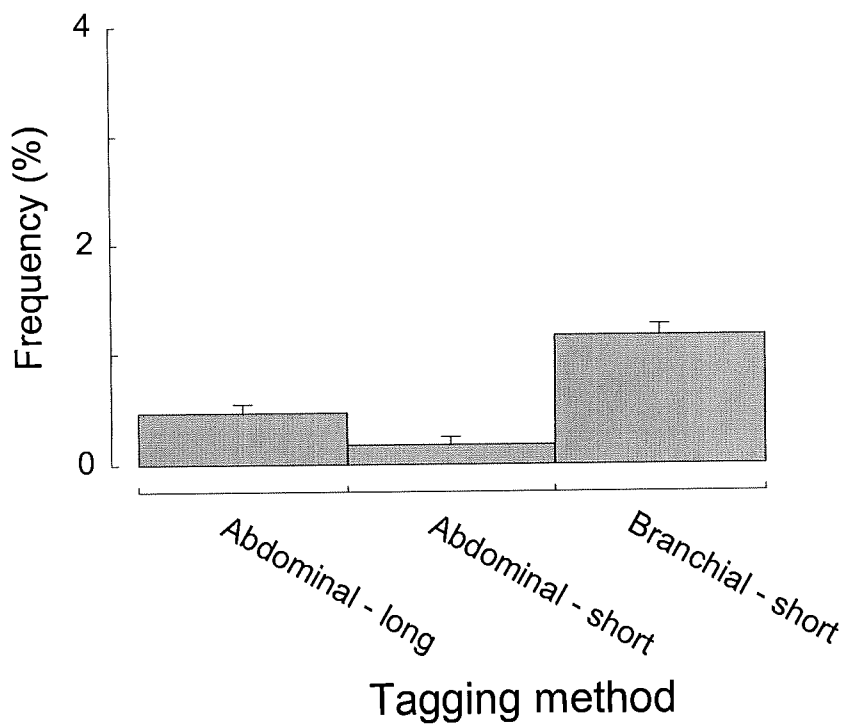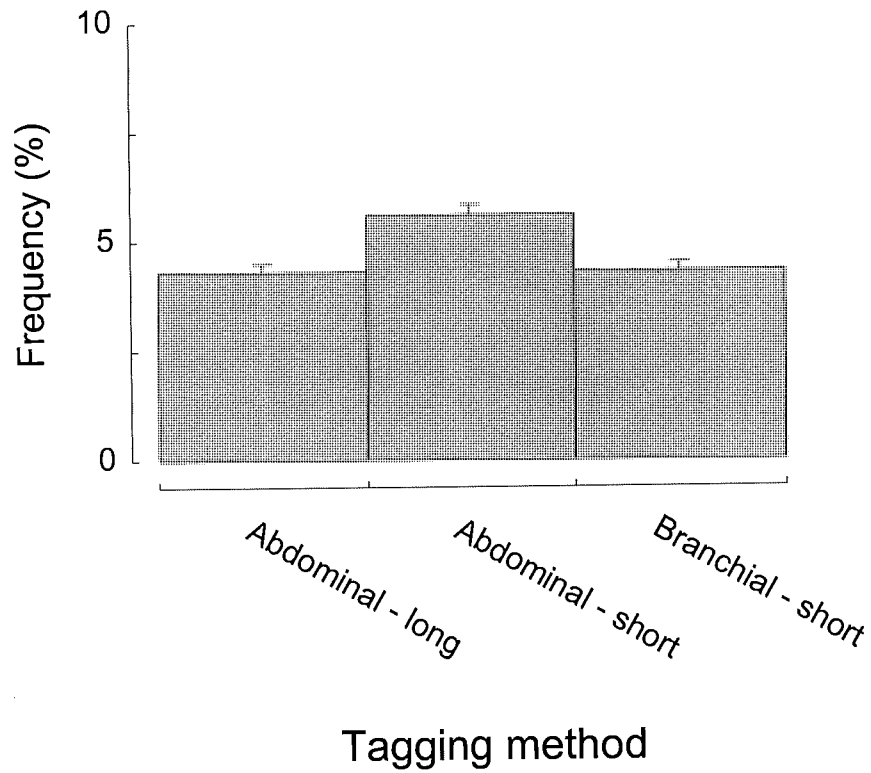
Figure 42. Frequency of occurence + 95% C.I. of recaptured tagged
Portunus pelagicus that had been tagged in three different ways
(above) and of those crabs in which the carapace width had
increased by 5 % (below).
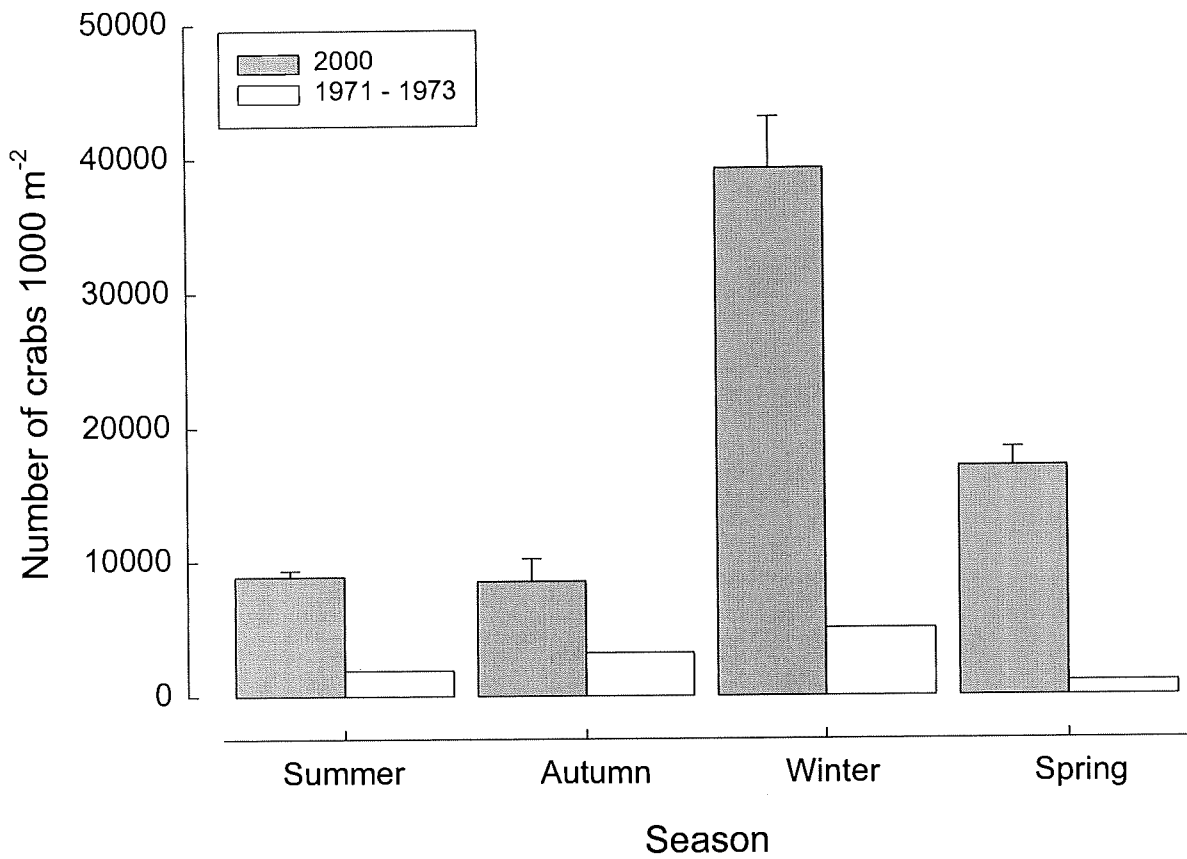
Figure 43. Mean seasonal densities +1 SE of *Portunus pelagicus* in Cockburn Sound derived from catches in samples obtained using a commercial trawler in each season between winter 1971 and summer 1972/1973 and between summer and spring 2000.
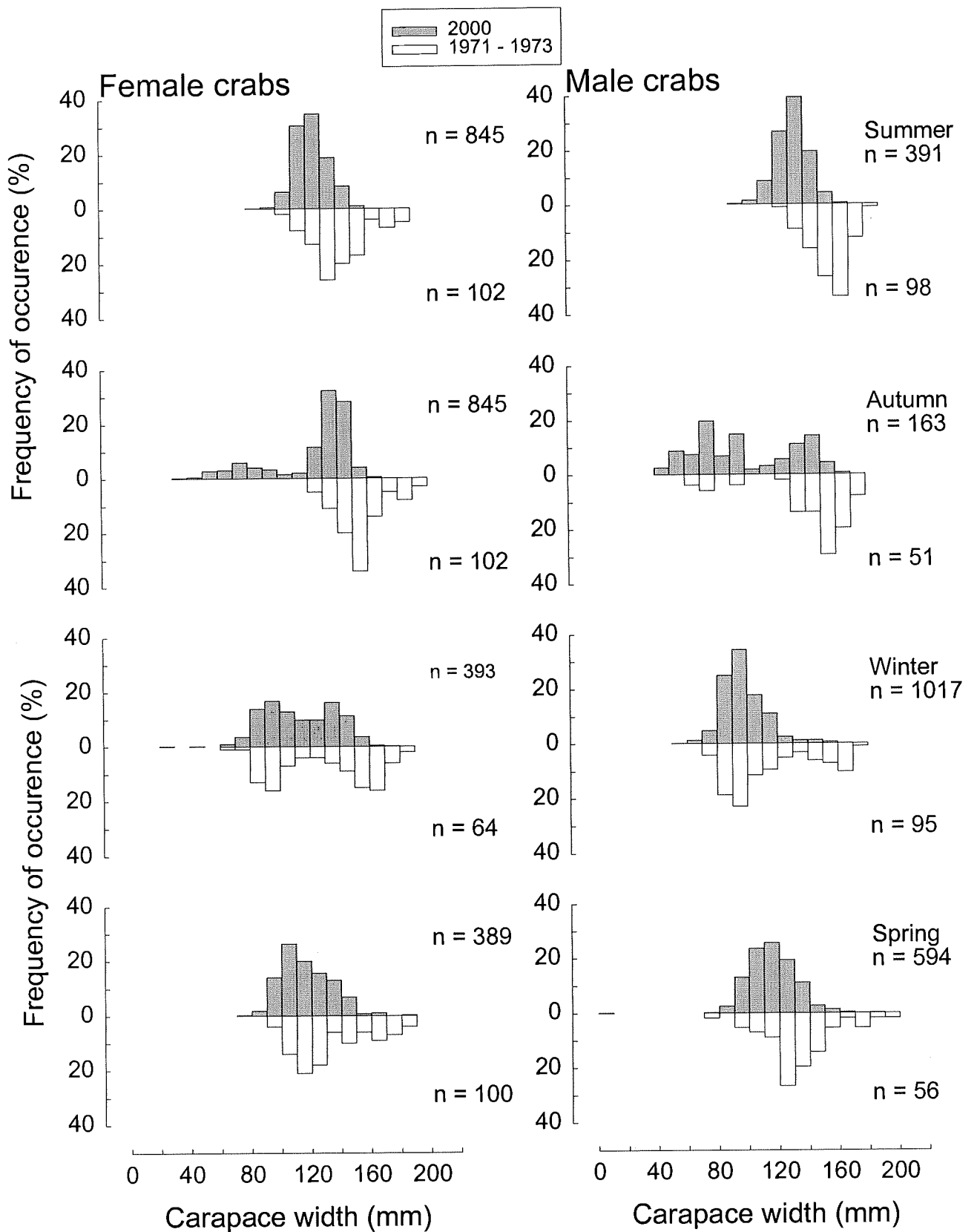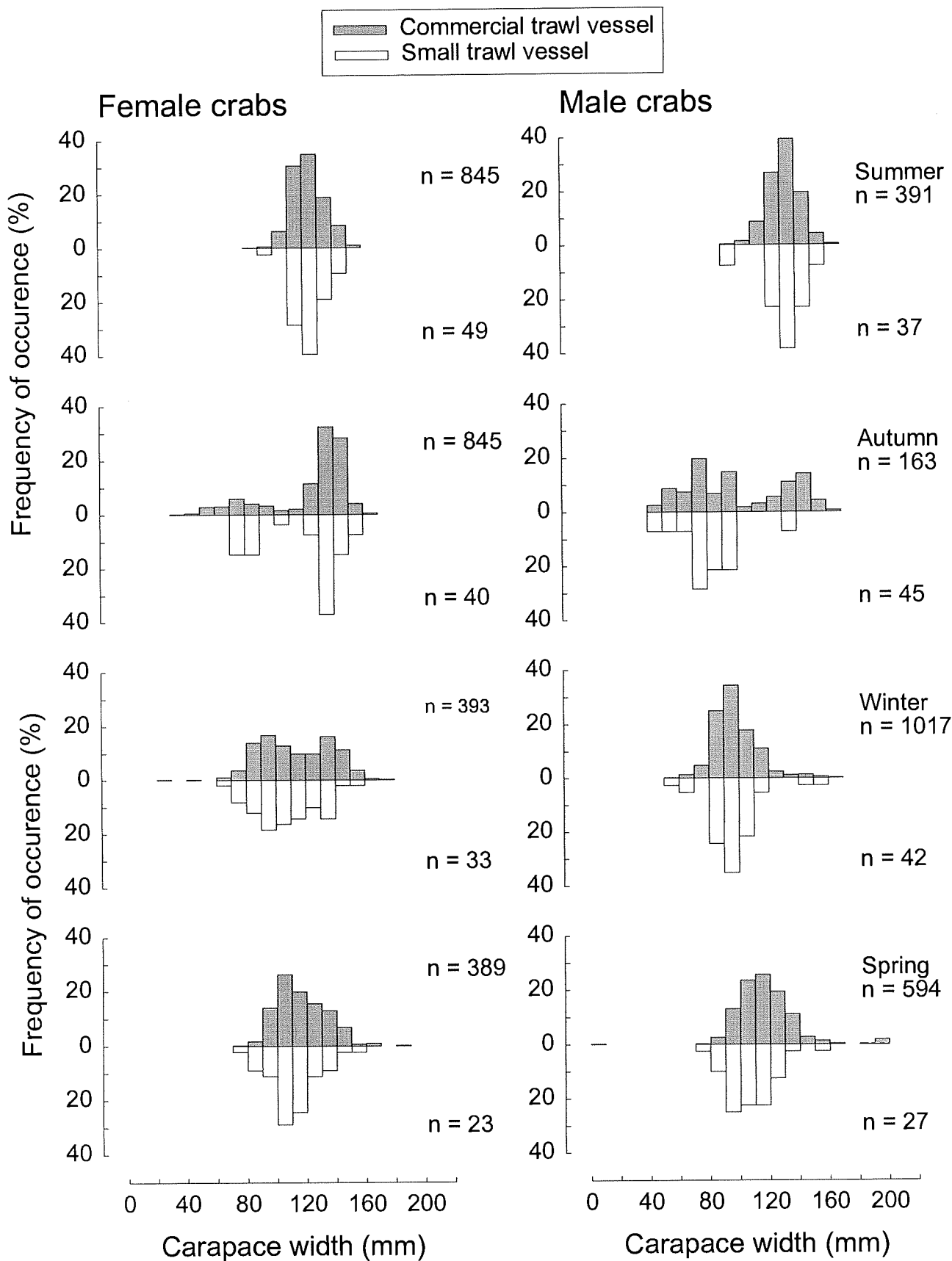
Figure 44. Seasonal size-frequency distributions of the carapace widths of *Portunus pelagicus* caught in Cockburn Sound using a commercial trawler between winter 1971 and summer 1972/73 and between summer and spring 2000. Note that since sampling with the commercial trawler was only undertaken in one month of each season in the 1990s, the corresponding month in each season in the 1970s was selected for making comparisons between corresponding seasons in the two decades.

Figure 45. Seasonal size-frequency distributions of the carapace widths of *Portunus pelagicus* caught in Cockburn Sound using a commercial trawler (summer to spring 2000) and a small trawl vessel (autumn 1998 to autumn 2000).
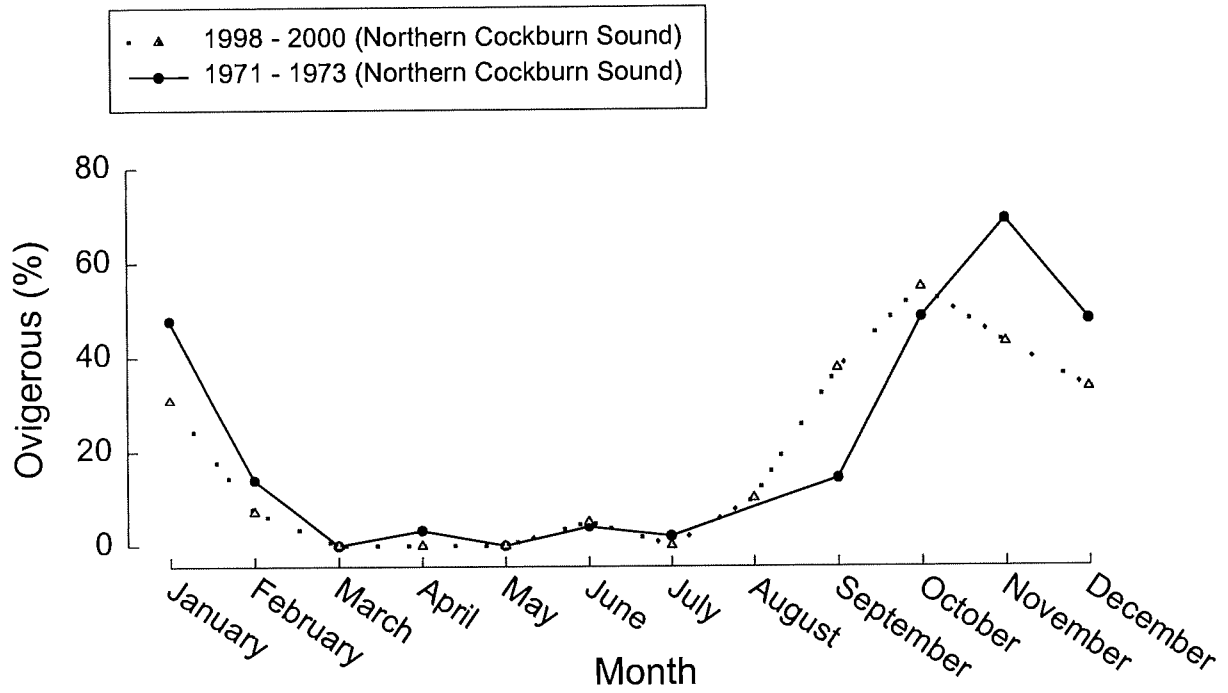
Figure 46. The percentage of ovigerous female crabs in samples collected by trawling between August 1971 and January 1973 and between May 1998 and April 2000. Data for the corresponding months of the year in each period have been pooled.
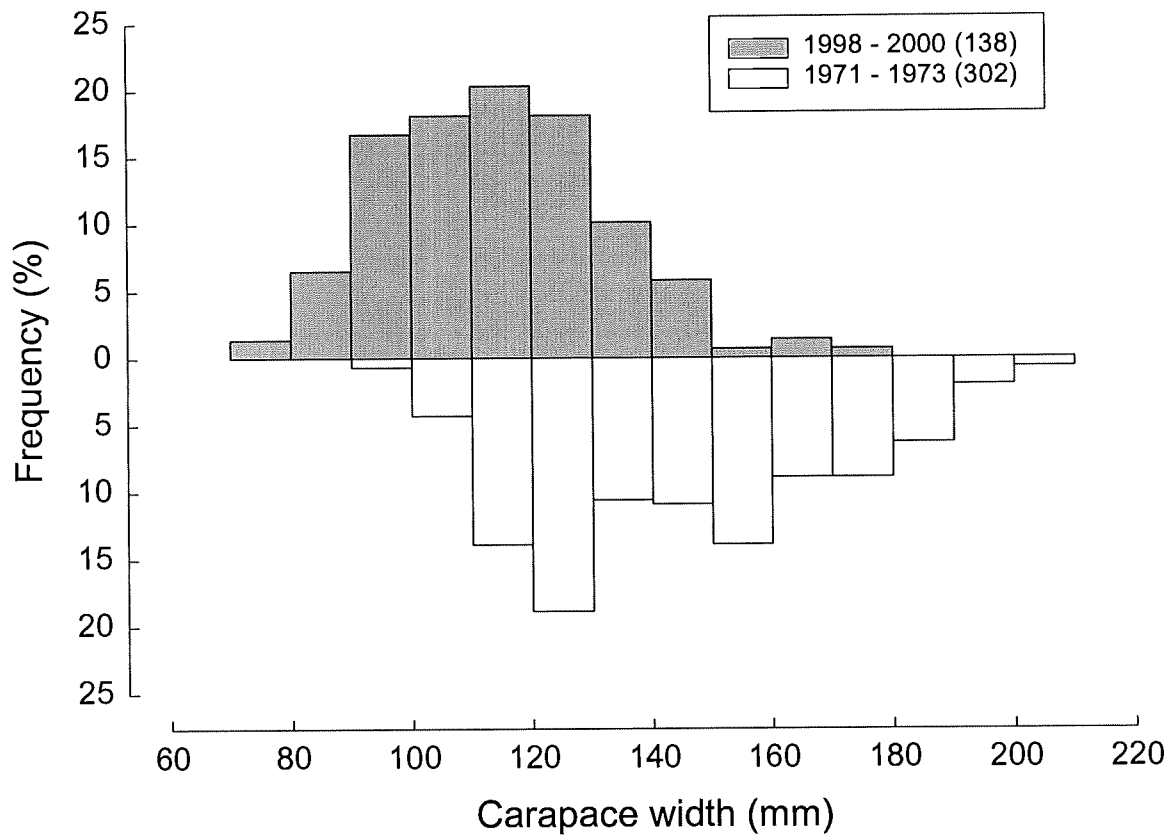
Figure 47. Carapace width histograms of ovigerous females collected by trawling between August 1971 and January 1973 and between May 1998 and April 2000.
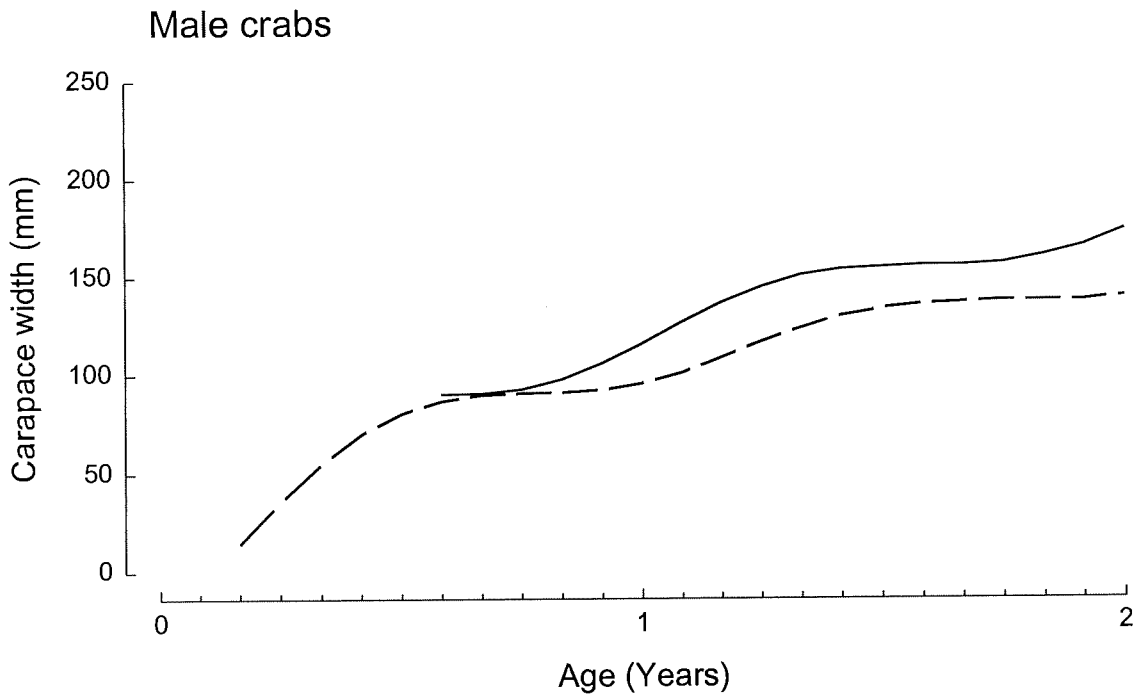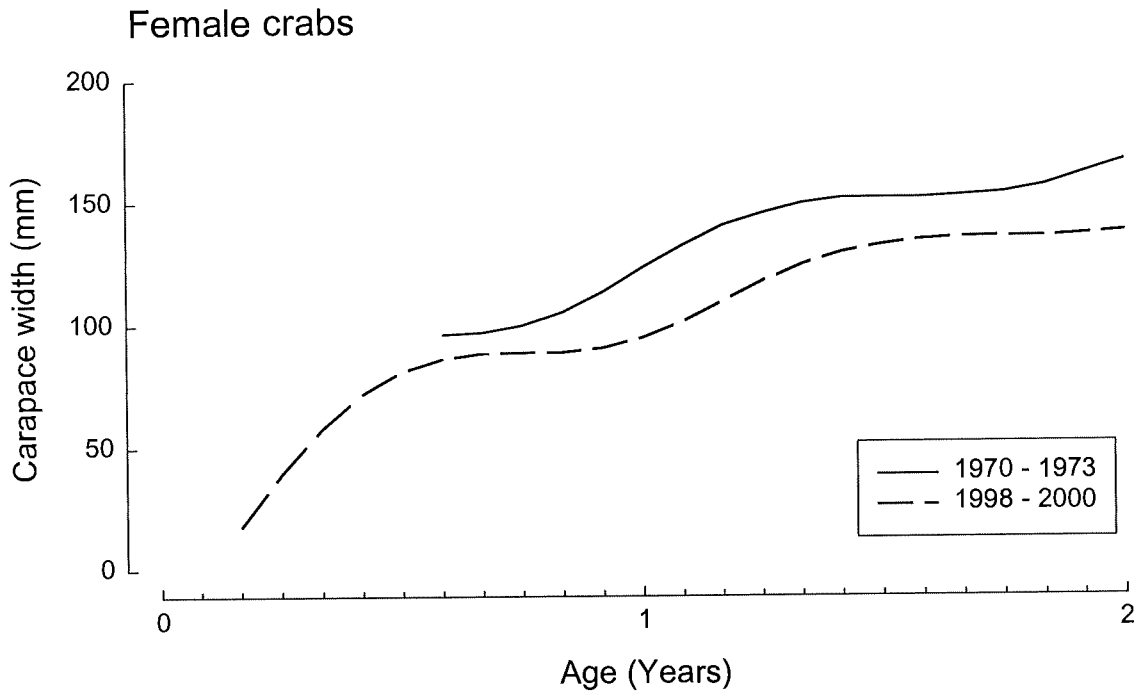
Figure 48. Estimated carapace width at age of female and male *Portunus pelagicus* caught in the early 1971 - 1973 and in 1998 - 2000 in Cockburn Sound, derived from analysis of the progression of modal carapace widths in sequential monthly samples.