Reproductive biology of the blue swimmer crab (*Portunus pelagicus*, Decapoda: Portunidae) in five bodies of water on the west coast of Australia

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Abstract—*Portunus pelagicus* was collected at regular intervals from two marine embayments and two estuaries on the lower west coast of Australia and from a large embayment located approximately 800 km farther north. The samples were used to obtain data on the reproductive biology of this species in three very different environments. Unlike females, the males show a loosening of the attachment of the abdominal flap to the cephalothorax at a prepubertal rather than a pubertal molt. Males become gonadally mature (spermatophores and seminal fluid present in the medial region of the vas deferentia) at a very similar carapace width (CW) to that at which they achieve morphometric maturity, as reflected by a change in the relative size of the largest cheliped. Logistic curves, derived from the prevalence of mature male *P. pelagicus*, generally had wider confidence limits with morphometric than with gonadal data. This presumably reflects the fact that the morphometric (allometric) method of classifying a male *P. pelagicus* as mature employs probabilities and is thus indirect, whereas gonadal structure allows a mature male to be readily identified. However, the very close correspondence between the CW_{50}'s derived for *P. pelagicus* by the two methods implies that either method can be used for management purposes. *Portunus pelagicus* attained maturity at a significantly greater size in the large embayment than in the four more southern bodies of water, where water temperatures were lower and the densities of crabs and fishing pressure were greater. As a result of the emigration of mature female *P. pelagicus* from estuaries, the CW_{50}'s derived by using the prevalence of mature females in estuaries represent overestimates for those populations as a whole. Estimates of the number of egg batches produced in a spawning season ranged from one in small crabs to three in large crabs. These data, together with the batch fecundities of different size crabs, indicate that the estimated number of eggs produced by *P. pelagicus* during the spawning season ranges from about 78,000 in small crabs (CW=80 mm) to about 1,000,000 in large crabs (CW=180 mm).

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Portunid crabs, such as *Portunus pelagicus*, *Scylla serrata,* and *Callinectes sapidus,* form the basis of important commercial and recreational fisheries. The blue swimmer crab (*P. pelagicus*) is found in sheltered nearshore marine waters and estuaries throughout the Indo-West Pacific (Stephenson, 1962; Kailola et al., 1993). In Australia, the commercial catches of this portunid have increased greatly during the last 20 years, and annual catches in 1998 reached 4377 metric tons (t) (Anonymous, 2000). The commercial fishery for *P. pelagicus* in Western Australia is the largest in Australia; the catch in the 1999–2000 financial year weighed 673 t and fetched a wholesale price of approximately $A3 million (CAES[1]).

Large numbers of portunids frequently enter estuaries as juveniles and remain there for an extended period (Hill, 1975; Potter et al., 1983; Perkins-Visser et al., 1996; Potter and de Lestang, 2000). Although female portunids sometimes become ovigerous in estuaries, such individuals emigrate into coastal marine waters, where they release their eggs (Van Engel, 1958; Metcalf et al., 1995; Potter and de Lestang, 2000). In contrast, the individuals of those assemblages of portunids that occupy marine embayments often do not leave these marine environments to spawn and, in cases where there is a salinity gradient, they spawn in the high salinity regions of those systems (e.g. Campbell, 1984; Sumpton et al., 1994; Prager, 1996; Potter and de Lestang, 2000).

The most common method for determining the size at which male crabs attain maturity is to estimate the size at which the pattern of growth of one of its appendages changes from that which characterizes juvenile crabs to that which characterizes adult crabs (e.g. Hartnoll, 1974; Somerton, 1980; Reeby et al., 1990; Muiño et al., 1999). However, this indirect approach is not precise and requires careful measurements of a considerable number of individuals covering a wide size range. Despite the fact that macroscopic characters can be used to distinguish sequential stages in the development of the vas deferentia of portunids (Ryan, 1967a; Meagher, 1971), few studies have attempted to use such staging to determine the body size at which the gonads of male crabs attain maturity (e.g. Reeby et al., 1990). Sumpton et al. (1994) considered that, as in female *P. pelagicus*, a marked loosening of the attachment of the abdominal flap to the cephalothorax signaled the attainment of maturity in male *P. pelagicus*. However, this criterion has yet to be shown to be valid for the males of this species. Although variations in the size at which crustaceans reach maturity among bodies of water and geographical regions may reflect,

[1] CAES (Department of Fisheries, Catch and Effort Statistics). 2002. Unpubl. data. Western Australian Department of Fisheries, Catch and Effort Statistics. Fisheries Western Australia, WA Marine Research Laboratories, West Coast Drive, Waterman, 6020, Perth, Australia.

in part, differences in such features as genetic composition and density, there is a strong overall tendency for the size at maturity of this crustacean to be inversely related to water temperature (Pillai and Nair, 1971; Jones and Simons, 1983; Polovina, 1989; Dugan et al., 1991; Miliou, 1996; Somerton and Donaldson, 1996; Fisher, 1999).

Estimates of the fecundity of crabs have typically been based on the number of eggs in a single batch of eggs (e.g. Potter et al., 1983; Melville-Smith, 1987; Ingles and Braum, 1989). However, such an approach does not take into account the fact that female crabs often produce more than one batch of eggs during a spawning season (Van Engel, 1958; Pillai and Nair, 1971; Campbell, 1984).

The aims of this study were as follows. 1) Compare the results of three methods directed at determining whether male *P. pelagicus* have attained maturity and elucidate whether each method produces reliable results. 2) Compare aspects of the reproductive biology of *P. pelagicus* in two estuaries and two marine embayments in temperate Australia with those of this species in a large marine embayment in a much warmer and more northern subtropical environment. Particular emphasis will be placed on comparing the size at maturity of both sexes and the periods during which ovigerous females are present, and on proposing reasons for the significance of any differences between the assemblages in these five bodies of water. 3) Use the data collected for one of the marine embayments to determine the age and time of year at which *P. pelagicus* becomes mature and develop a method for deriving the annual fecundity that takes into account the fact that the larger individuals of this species are believed to produce more than one batch of eggs in a spawning season.

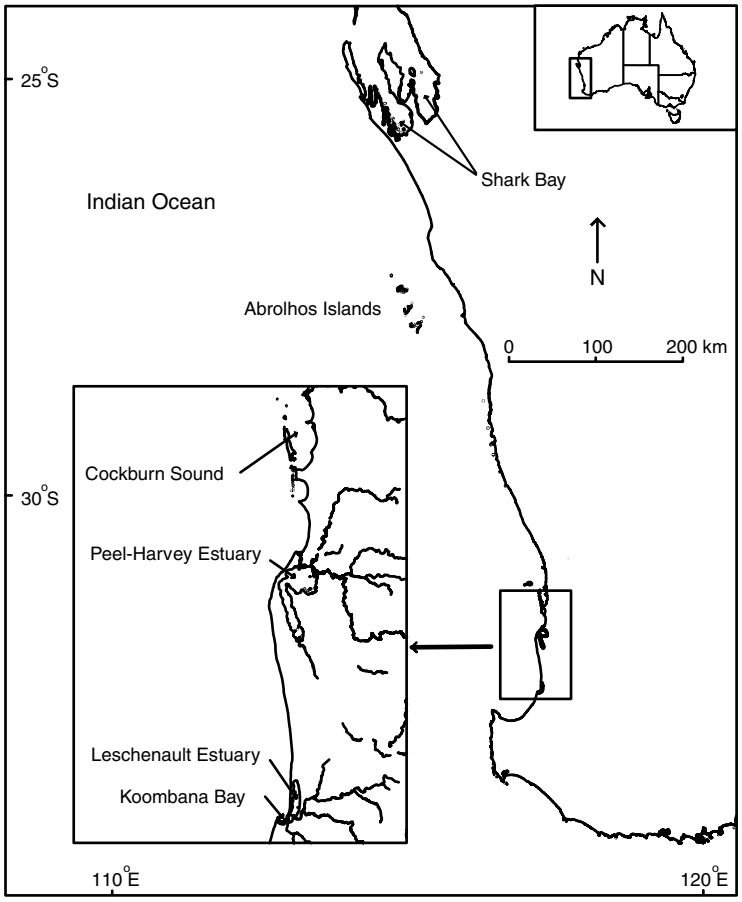

Figure 1

Map showing locations of the five bodies of water in which *Portunus pelagicus* was sampled on the west coast of Australia. The map of Australia (insert top right) shows the location (box) of the five bodies of water, and the map of the lower west of Australia (insert bottom left) shows the location of the four bodies of water sampled in this region.

Materials and methods

Sampling regimes

Up to 100 *Portunus pelagicus* were collected monthly for two years from the Leschenault Estuary (May 1997–April 1999), Koombana Bay, and Cockburn Sound (June 1998–May 2000), for three years from the Peel-Harvey Estuary (May 1995–April 1998), and bimonthly for two years from Shark Bay (July 1998–May 2000). The first four bodies of water are located on the lower west coast of Australia, approximately 800 km to the south of Shark Bay (Fig. 1). The nearshore, shallow waters in each of these bodies of water (water depth <1.5 m) were sampled for *P. pelagicus* by using a 21.5-m seine net with a bunt of 3-mm mesh; whereas offshore deeper waters were sampled by employing a small otter trawl net with a codend of 25-mm mesh and crab traps consisting of either 12- or 76-mm mesh (see Potter and de Lestang, 2000 for further details of the nets and traps). The mean water depths at the deeper offshore sites of the above five bodies of water were 3, 9, 19, 3, and 10 m, respectively. The water temperature at the bottom of the water column at each site was recorded on each sampling occasion.

Measurements and changes at puberty

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 length and height of the propodus of the largest cheliped, the length of the merus of the second walking leg, and the length of the primary pleopod of each male crab in Cockburn Sound and Shark Bay were measured to the nearest 0.1 mm. Because the relationship between the length of the dorsal propodus of the largest cheliped and the width of the carapace showed the greatest change over the size range of male crabs, that structure was chosen for allometric analysis to determine the size at which males become morphometrically mature.

Sex of small crabs, i.e. with a CW < about 30 mm, was determined with a dissecting microscope to ascertain whether their pleopods bore setae and thus the crabs were females. At CWs > about 30 mm, the female crabs could readily be distinguished from male crabs by their possession of a far wider abdominal flap (Van Engel, 1958; Warner 1977). During the pubertal molt of female portunids, the abdominal flap changes from a triangular to oval shape and from being tightly to loosely fixed to the cephalothorax (Ryan, 1967b; Fielder and Eales, 1972; Ingles and Braum, 1980; Fisher, 1999).

The size and time of occurrence of all ovigerous females were recorded. The ovary of each crab was assigned to one of four stages by using macroscopic characters similar to those described for the development of the ovaries of *P. pelagicus* and other portunids (Ryan, 1967b; Meagher, 1971; Krol et al., 1992; Kumar et al.[2]). The assignment of these stages was augmented by examining the characteristics of a subset of 200 of these ovaries in 6-μm histological sections that had been stained with Mallory's trichrome. For 5–10 ovaries of each macroscopic stage, the diameters of 30 randomly selected oocytes that had been sectioned through the nucleus were measured to the nearest 5 µm. Two measurements (the longest diameter and shortest diameter) for each oocyte were then averaged to provide an estimate of each oocyte diameter.

Male crabs were designated as either morphometrically immature or mature by using differences in the regression equations for the relationships between the natural logarithms of the length of the dorsal propodus of their largest cheliped and carapace width in what were clearly either juvenile (small and gonadally immature) or adult crabs (large and gonadally mature). For full description of the method see Somerton (1980).

On the basis of their macroscopic appearance, the vas deferentia of each male crab were assigned to one of three stages by using criteria derived from the description of gonadal development for *P. pelagicus* by Meagher (1971) and for *P. sanguinolentus* by Ryan (1967a). Aquarium studies by Meagher (1971) showed that male crabs with gonads at stages I and II did not copulate and are thus considered immature, whereas those with gonads at stage III copulated successfully with females and thus have mature gonads.

Ovaries and vas deferentia from a wide size range of at least 20 females and 20 males, respectively, from each sampling occasion in each of the five bodies of water were weighed to the nearest 0.01 g. The mean gonad weight at a constant carapace width for each sex in each month in each water body was determined by using analysis of covariance (ANCOVA) of the natural logarithm of the gonad weight as the dependent variable, month as a fixed factor, and the natural logarithm of the carapace width as a covariate. The common constant carapace width of crabs in all bodies of water was a default value calculated by the ANCOVA.

Size frequency and reproductive data for the corresponding months in the different years in each water body were pooled for describing intra-annual trends in these variables.

Size at maturity

The percentages of female crabs of different carapace widths which, in each water body, had undergone a pubertal molt, were subjected to logistic regression to determine the size at which 50% of the female crabs would have become mature *sensu* Hartnoll (1974). Data for each assemblage were randomly resampled and analyzed to create 1000 sets of bootstrap estimates of the parameters of the logistic regression and estimates of the probability of maturity within the range of recorded carapace widths. The 95% confidence intervals of the CW_{50}'s were derived by using this resampling technique, which produced slightly more conservative estimates than those obtained from the Hessian matrix of the logistic regression and thus reflected better the uncertainty of the parameter that was associated with the data. The 95% confidence intervals of the probability of maturity at each specified carapace width were taken as the 2.5 and 97.5 percentiles of the corresponding predicted values resulting from this resampling 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 percentages of mature male crabs at different carapace widths in each of the five bodies of water, with maturity being assigned by using firstly morphometric and then gonadal criteria (see earlier), were subjected to logistic regressions to determine the CW_{50}'s for these variables. The percentages of male crabs in Cockburn Sound and Shark Bay, which possessed an abdomen that was loosely fixed to the cephalothorax, were likewise subjected to logistic regression analysis. The logistic regressions relating maturity and carapace width for both the females and males in the different assemblages were compared by using a likelihood ratio test, as described by Cerrato (1990) and employing a Bonferroni correction.

Fecundity

The total wet weight of eggs in each batch of eggs of 40 early-stage ovigerous females, i.e. with yellow eggs, from Cockburn Sound and which covered a wide size range, was weighed to the nearest 0.001 g. The number of eggs in each of four replicate subsamples from each batch were recorded, after which each of those subsamples was weighed to the nearest 0.001 g. These data were then used to estimate the total number of eggs in each batch of eggs of each female. The relationship between batch fecundity (BF) and carapace width (CW) was described by using the equation $\ln BF_j = m \ln CW_j + b$.

The number of batches of eggs produced by a full size range of mature females during the spawning period was estimated by determining the spawning period (SP),

[2] Kumar, M., Y. Xiao, H. Williams, G. Ferguson, G. Hooper, and S. Venema. 1999. Blue crab fishery. South Australian Fisheries Assessment Series, 99/02, 64 p. South Australian Research Development Institute, Grenfell Centre Level 14, 25 Grenfell Street Adelaide 5000, Australia.

defined as the time (days) when > 5% of all mature females were ovigerous, and the proportions of ovigerous females among all mature females in sequential 10-mm CW intervals during the spawning period. The proportion of ovigerous females (O_j) in the jth size class during this period also represents the average time a mature female in this size class is ovigerous during that period and takes into account the fact that an ovigerous female spawns at least once during a spawning period and that the brood period (*BP*) of an ovigerous female is about 18 days at 20°C (Meagher, 1971). Thus, the mean number of batches (NB_j) produced by the mature female crabs in the jth size class during a spawning period (average water temperature 20.4°C) can be estimated with the equation $NB_j=O_jSP/BP$.

The relationship between number of broods and carapace width was described empirically by fitting a modified logistic curve, $NB=1+Nb_{max}/\{1+\exp[-\ln(19)(CW-a)/(b-a)\}$, ranging upwards from a minimum of one batch to a maximum of $1+NB_{max}$ batches, where a and b are parameters. The total fecundity of crabs at different carapace widths was calculated as the product of batch fecundity, BF, and the number of broods, NB, by using the relationships between BF and CW and NB and CW, as described above.

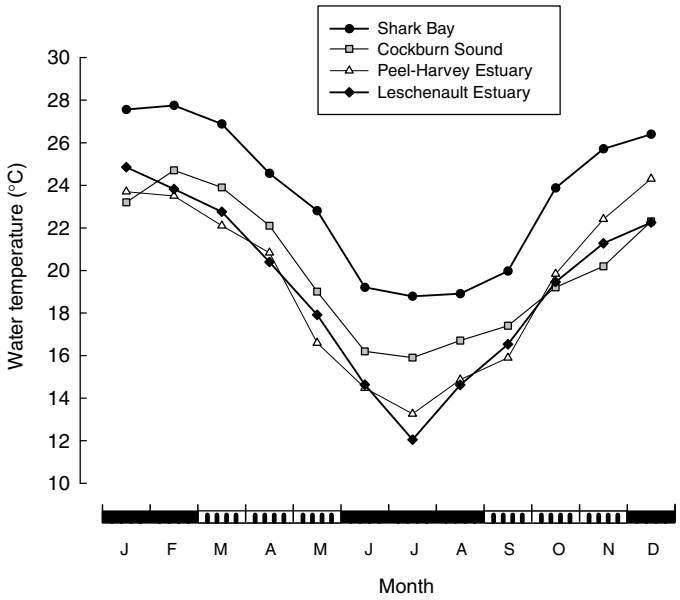

Figure 2

Mean monthly water temperatures for sampling sites in Shark Bay, Cockburn Sound, Peel-Harvey Estuary, and Leschenault Estuary (water temperatures in Koombana Bay were essentially the same as those in Leschenault Estuary). Mean monthly water temperatures in each water body were derived from data pooled for at least two years. The black rectangles on the x axis refer to summer and winter months and open rectangles to autumn and spring months.

Results

Water temperature

Mean monthly water temperatures at the bottom of the water column in the Leschenault Estuary, Peel-Harvey Estuary, Cockburn Sound, and Shark Bay followed the same trends, with values rising to a maximum in mid to late summer and declining to a minimum in mid-winter (Fig. 2). Water temperatures in Koombana Bay were essentially the same as those in Leschenault Estuary. Although the mean monthly water temperatures in the Leschenault and Peel-Harvey estuaries and Koombana Bay in corresponding months were similar, they were lower in these bodies of water than in Cockburn Sound in eight of the twelve months of the year (Fig. 2). However, the mean water temperatures in each month in Shark Bay were greater than those in the corresponding months in each of the above four more southern bodies of water. Thus, for example, although the maximum mean monthly water temperature was 28°C in Shark Bay, it never reached 25°C in any of the other bodies of water (Fig. 2). Likewise, the minimum monthly water temperature was greater in Shark Bay (19°C) than in either Cockburn Sound (16°C) or the Leschenault and Peel-Harvey estuaries (12–13°C).

Macroscopic and histological gonad staging

Macroscopic examination of the gonads of a large number of females and males of *P. pelagicus*, covering a wide size range, and, in the case of females, an histological examination of the ovaries of a subset of these crabs, showed that the ovaries and vas deferentia could be classified into four and three developmental stages, respectively (Tables 1 and 2).

Size at sexual maturity

The minimum carapace widths of female crabs that had undergone their pubertal molt ranged from 61 mm in both the Peel-Harvey Estuary and Shark Bay to 84 mm in the Leschenault Estuary. Although the CW_{50}'s derived for females at maturity in Cockburn Sound (86.4 mm) and Koombana Bay (86.9 mm) were not significantly different ($P>0.05$), both of these values were significantly less ($P<0.05$) than the 92.0 mm for females in Shark Bay (Fig. 3). The high CW_{50}'s for female crabs in the Peel-Harvey (97.5 mm) and Leschenault estuaries (98.0 mm) were not representative of females in their populations as a whole (see "Discussion" section).

The relationships between the dorsal length of the largest cheliped and carapace width of male *P. pelagicus* in each of the five bodies of water were described better by using two log-log lines (Fig. 4A) rather than a single log-log line. The CW_{50}'s of male crabs at morphometric maturity in the four bodies of water on the lower west coast, estimated with data obtained from an allometric approach and employing the above log-log regressions, ranged only from 86.2 mm in the Peel-Harvey Estuary and Cockburn

Table 1

Morphological characteristics of macroscopic stages in the development of the ovaries of *Portunus pelagicus* and the types of oocytes found in each of those stages. Mean diameters of oocytes at different stages in development are shown in parentheses.

Maturity stage		Macroscopic appearance of ovary	Types of oocytes
I	Immature	Relatively small, flattened and off white to ivory in color. Anterior region is small, and does not displace the hepatopancreas. The central "H" shaped region, located in the gastric region, is loosely joined to the dorsal surface of the spermathecae. The posterior section, located in the cardiac and intestinal regions, forms two parallel lobes.	Loosely packed oocytes, comprising oogonia (5 μm) and, to a lesser extent, chromatin nucleolar oocytes (10 μm) and perinucleolar oocytes (30 μm). These three types of oocytes are found in each of the next three ovarian stages.
II	Early development	Conspicuously larger than stage-I ovaries, 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, and the two lobes of the posterior region are starting to become convoluted.	Yolk-vesicle oocytes (90 μm) are present for the first time.
III	Late development	Large, yellow, and nodulated. Anterior region displaces the hepatopancreas, and 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, and some late yolk vesicle oocytes are present.
IV	Fully mature	Very large, deep yellow to orange, and highly nodulated. Hepatopancreas is now completely displaced from its former position by the enlargement of the anterior region of the ovary. The gastric, posterior, and intestinal cavities are completely filled with the enlarged 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).

Table 2

Morphological characteristics of stages in the development of the vas deferens of *Portunus pelagicus* and the location of spermatophores in those stages.

Maturity stage		External appearance of vas deferentia	Histological appearance of the vas deferentia
I	Immature I	Vas deferentia not detectable macroscopically.	NA
II	Immature II	Anterior vas deferentia (AVD) becoming enlarged, middle and posterior vas deferentia (MVD and PVD, respectively) straight and opaque.	Spermatophores present in AVD. MVD and PVD contain no spermatophores.
III	Mature I	AVD and MVD enlarged and white and PVD enlarged and convoluted but still opaque.	Spermatophores present in AVD and MVD. PVD contains no spermatophores.

Sound to 87.2 mm in the Leschenault Estuary (Fig. 4B). The CW_{50}'s for each of these bodies of water, which were not significantly different (P>0.05) from each other, were significantly less at $P < 0.05$ or 0.001 than the 96.0 mm determined for male crabs in Shark Bay.

The CW_{50}'s for males at gonadal maturity in each water body, derived from the prevalence of males with mature gonads, i.e. stage III (Fig. 4C), differed by only 0.3 to 2.2 mm from those derived for males in each corresponding water body by using the prevalence of morphometrically mature males (Fig. 4B). The CW_{50}'s derived for male crabs from gonadal data in the four southern bodies of water, which ranged only from 86.5 to 88.4 mm, did not differ significantly (P>0.05). However, on the basis of gonadal data, each of these CW_{50}'s differed significantly at P<0.05, 0.01, or 0.001 from the 97.0 mm estimated for male crabs in Shark Bay (Fig. 4C). These trends were parallel to those derived from morphometric data (Fig. 4B).

The logistic curves derived from gonadal data in each of the four southern bodies of water were significantly differ-

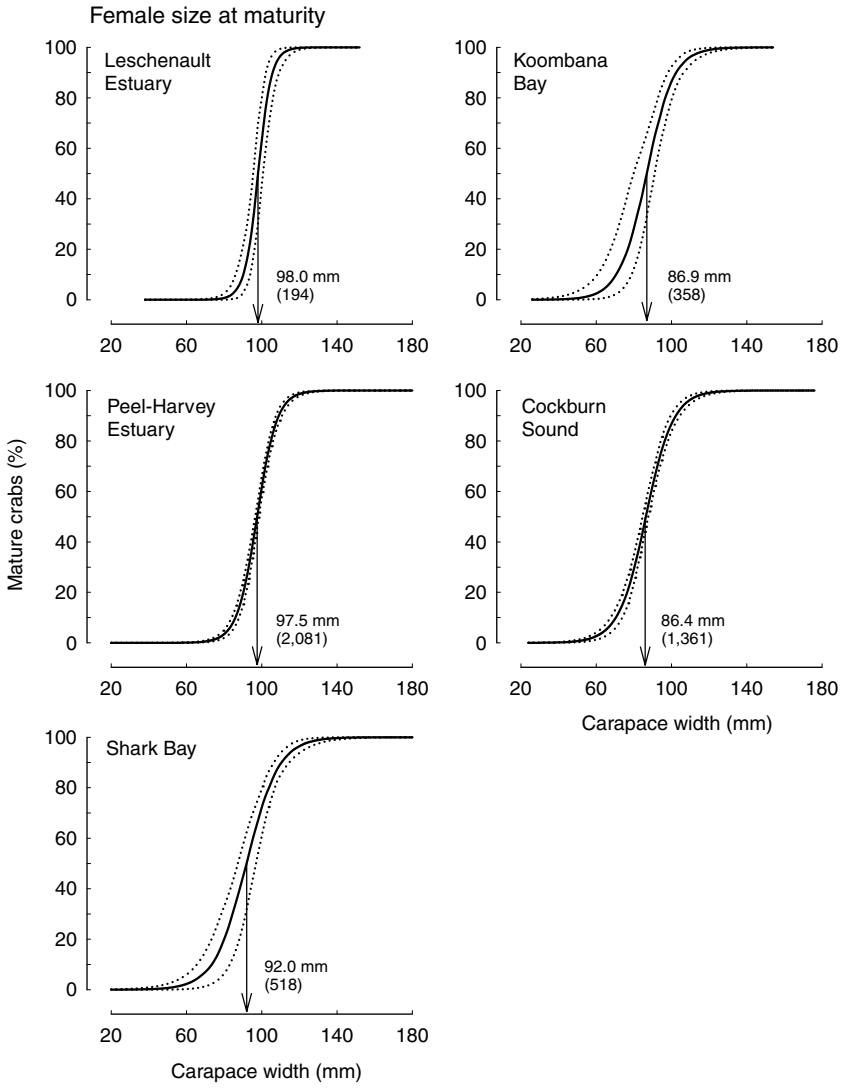

Figure 3

Logistic regressions and their 95% confidence limits fitted to percentage contributions of those adult females which, at each size, had undergone their pubertal molt in each of the five bodies of water sampled in Western Australia. Arrows and measurements denote CW_{50}'s and the numbers in parentheses refer to the number of crabs used to create the regressions.

ent (P>0.05) and had steeper slopes than those determined by using morphometric data (Fig. 4). The confidence limits for the logistic curves constructed from gonadal data were also usually tighter than those constructed from morphometric data.

The CW_{50} for male crabs with a loose abdominal flap in Cockburn Sound, i.e. 72.1 mm, differed significantly (P<0.05) from that in Shark Bay, i.e. 76.2 mm (data not shown). However, all of the male crabs in Cockburn Sound with carapace widths of 70 to 75 mm and loosely attached abdominal flaps contained gonads at stage I or II and were thus immature.

Trends exhibited by gonad weights and proportions of ovigerous females

The mean monthly gonad weight of mature female crabs with a standard carapace width (104 mm), as determined by ANCOVA (see "Material and methods" section), rose to a sharp peak of about 5 g in October in Koombana Bay and in September in Cockburn Sound (Fig. 5). In contrast, the mean monthly gonad weights of mature female crabs in the Leschenault and Peel-Harvey estuaries remained at <1.5 g and did not tend to peak sharply at any time of the year. The mean monthly gonad weights of mature female

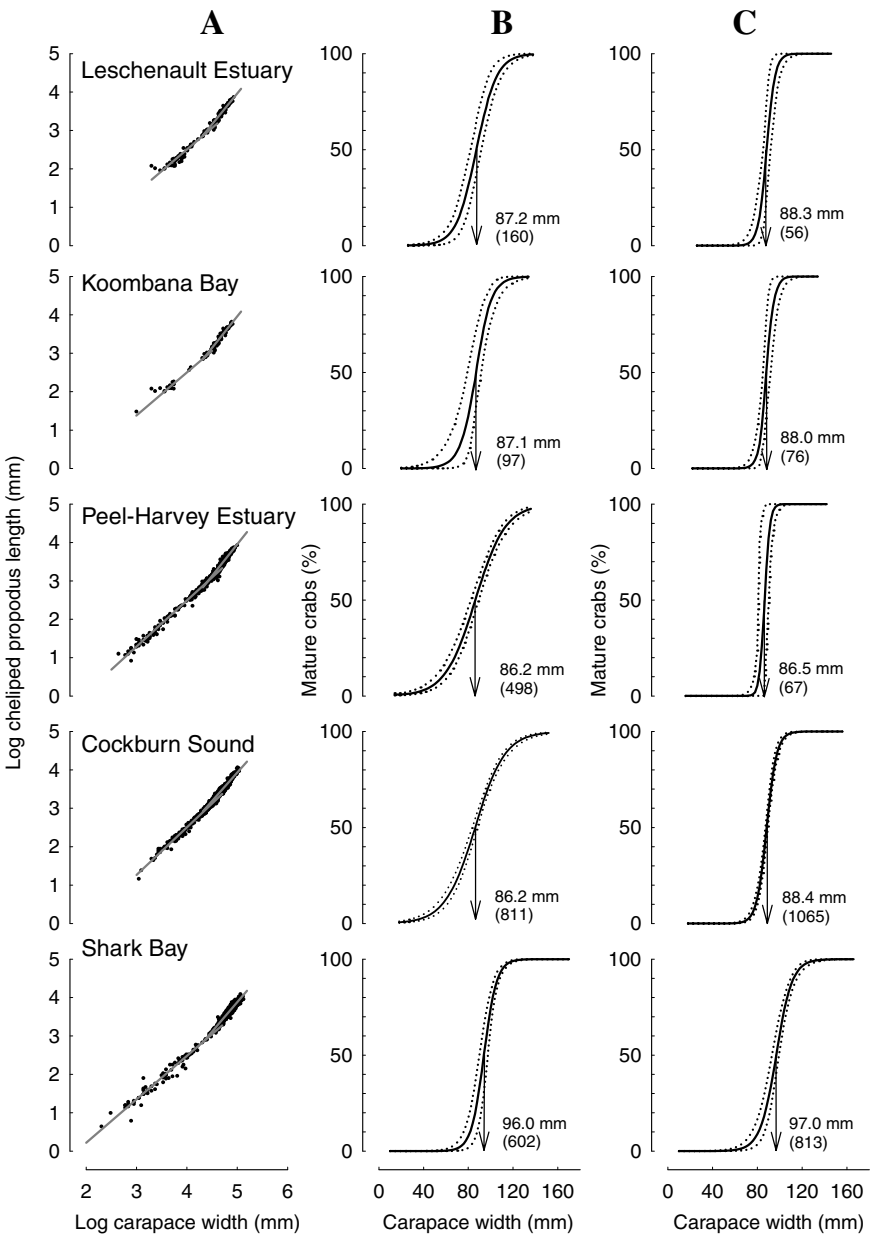

Figure 4

Maturity data for male *Portunus pelagicus* in the five bodies of water sampled in Western Australia. (**A**) Relationship between the natural log of length of the dorsal propodus of the largest cheliped and the natural log of carapace width. Logistic regressions and their 95% confidence limits were fitted to percentage contributions of those adult males, which, at each size, were (**B**) morphometrically mature and (**C**) possessed mature gonads. Arrows and measurements denote CW_{50}'s and the numbers in parentheses refer to the number of crabs used to create the regressions.

crabs in Shark Bay did not peak sharply at any time and were > 1 g in all but two of the ten months in which this embayment was sampled (Fig. 5).

The mean monthly gonad weights of male crabs with a standard carapace width of 118.4 mm, as determined by ANCOVA, varied little and never exceeded 1 g in any of the five bodies of water (data not shown). However, they did reach their maxima at a similar time of the year, i.e. late summer (February) or early autumn (March), in the four bodies of water on the lower west coast of Australia.

The monthly percentage contributions made by ovigerous female crabs from all mature female crabs in Koom-

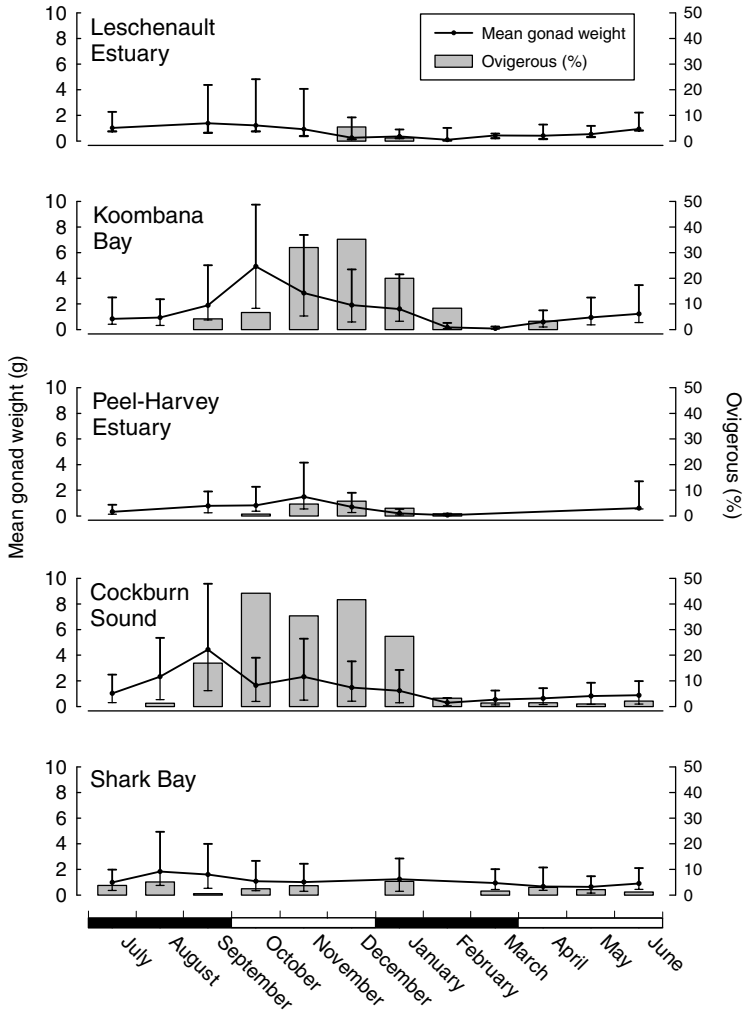

Figure 5

Mean monthly gonad weights ±95% confidence intervals for female *Portunus pelagicus* and the percentage of ovigerous females among all adult female *P. pelagicus* in the five bodies of water sampled. The black rectangles on the x axis refer to summer and winter months and open rectangles to autumn and spring months.

bana Bay and Cockburn Sound peaked at 32–36% in November and December in Koombana Bay and at 35–45% in October to December in Cockburn Sound. Although the corresponding percentage contributions of ovigerous female crabs were far lower in the Leschenault and Peel-Harvey estuaries than in the above two embayments, they still reached their maxima at the same time of the year (Fig. 5). Few or no ovigerous female crabs were caught in either of those estuaries or embayments between March and August. Ovigerous females were found in Shark Bay in each of the ten months in which that embayment was sampled and, unlike the situation in the two more southern marine embayments, their monthly contributions to the overall number of adult female crabs did not vary markedly throughout the year (Fig. 5).

Trends exhibited by oocyte development

The maximum diameter of the oocytes increased progressively from 95 µm in stage-I gonads to 315 µm in stage-IV gonads (data not shown). The modal oocyte diameter of the distinct and largest cohort of oocytes in stage IV (240–259 μm) was only slightly less than that of the fertilized yellow external eggs found under the abdominal flap of ovigerous females (300–319 μm). The most advanced oocytes in ovaries at stages III and IV were at the early and late yolk-granule stage, respectively. The presence of two distinct size cohorts of oocytes in the ovaries of large females with grey eggs under their abdomen (i.e. eggs that had been fertilized for several days) is consistent with the view that large female *P. pelagicus* are multiple spawners.

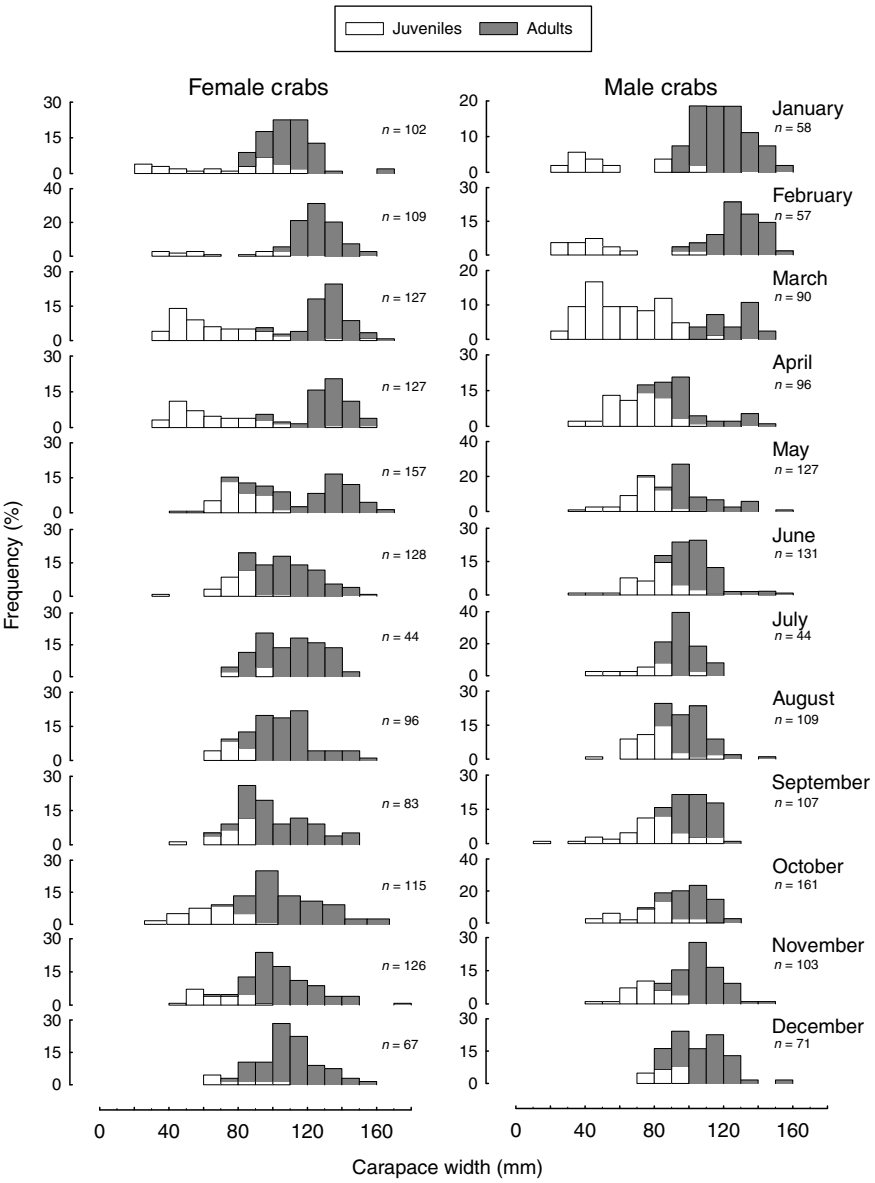

Figure 6

Frequency histograms for the carapace widths of juvenile and adult females and males of *Portunus pelagicus* in Cockburn Sound. *n* = number of crabs measured. Designation of males as mature was based on gonadal criteria described in the text.

Age and time of sexual maturation of *Portunus pelagicus*

The carapace-width frequency data for *P. pelagicus* in inshore and offshore waters in Cockburn Sound demonstrated that, in this marine embayment, males are represented by two main size cohorts in January and February (Fig. 6). The first size cohort represents the 0+ age class that resulted from the spawning period that commenced in the previous August–September, whereas the second cohort corresponds to 1+ crabs, which start to decline markedly in numbers after February and are rarely represented after June (Fig. 6). Although similar trends are exhibited by the data for females, the numbers of 1+ individuals of this sex remained higher for a longer period, i.e. until May. The above trends are entirely consistent with those reported in detailed studies of the age composition and growth of *P. pelagicus* in the Peel-Harvey Estuary (Potter et al., 1983) and Leschenault Estuary (Potter and de Lestang, 2000).

None or very few of the female and male 0+ crabs caught in Cockburn Sound in January, February, and March were mature. However, some of the larger 0+ crabs had become mature by May, i.e. when they would mostly have been

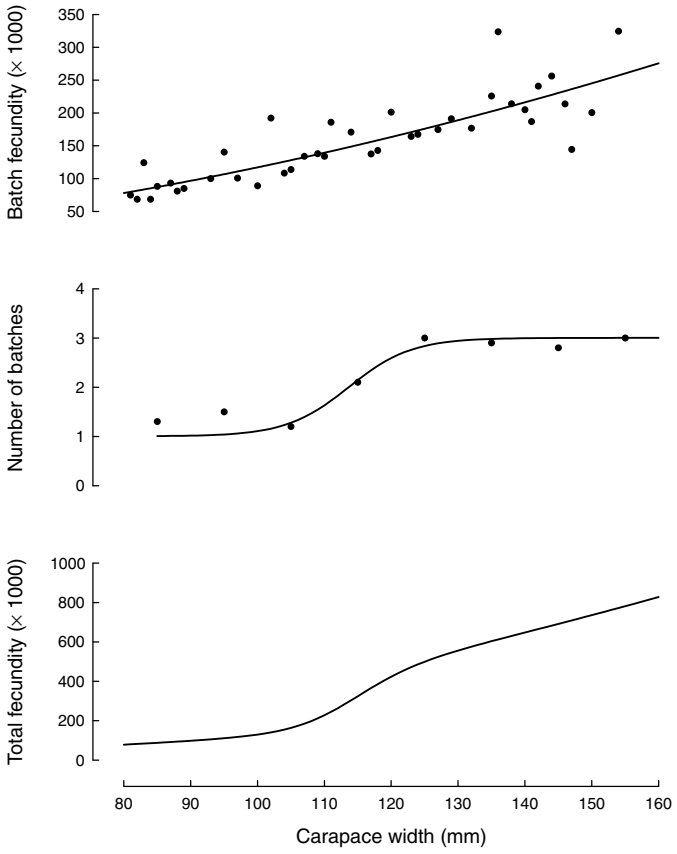

Figure 7

Batch fecundity, mean number of batches, and total fecundity of *Portunus pelagicus* in Cockburn Sound.

between four and eight months old (Fig. 6). The prevalence of mature crabs subsequently increased, with the result that the vast majority of crabs in the following January, i.e when they had just entered their second year of life, were mature (Fig. 6). Thus, all crabs have typically become mature when they are just over one year old.

Fecundity

In Cockburn Sound, the number of eggs recorded for a single batch of eggs under the abdomen of a female, ranged from 68,450 in a crab with a CW of 84 mm to 324,440 in a crab with a CW of 154 mm (Fig. 7). The relationship between batch fecundity (*BF*) and carapace width (*CW*) is described by the following equation: $\ln BF = 1.8208 \ln CW + 3.2862$.

The estimated mean number of egg batches, produced by female crabs in the different size classes over the spawning period, ranged from about one in crabs of 100–109 mm CW to about three in crabs of 150–159 mm CW (Fig. 7). A range of one to three batches per instar corresponds to that recorded by Campbell (1984) for *P. pelagicus* in aquaria experiments. The empirical relationship between the number of batches (NB) and carapace width (CW) is described by $NB_j = 1 + 2/\{1 + \exp[-\ln(19)(CW_j - 113.7)/13.8]\}$.

A combination of the equations for the relationships between batch fecundity and CW and the number of egg batches and CW was then used to determine the relationship shown between total fecundity (TF) and carapace width (CW) and which is shown in Figure 7.

Discussion

Designation of maturity in male crabs

Aquaria studies by Meagher (1971) demonstrated that male crabs with gonads at stage III, i.e. with spermatophores and seminal fluid in the medial vas deferentia, can copulate successfully with females. Because this parallels the situation recorded by Comeau and Conan (1992) for the snow crab (*Chionoecetes opilio*), we likewise regard such gonads as mature. Our study also showed that, because male *P. pelagicus* still possess immature gonads (stage II) when their abdominal flap becomes loosely attached to the cephalothorax, the latter change occurs at a prepubertal

molt and thus, unlike the supposition of Sumpton et al. (1994), does not coincide with the attainment of maturity. The situation in males thus contrasts with that in female *P. pelagicus*, in which the abdominal flap becomes loose as an outcome of the pubertal molt (Fielder and Eales, 1972; Campbell, 1984; Potter and de Lestang, 2000; Smith[3]).

The very close similarity between the corresponding CW_{50}'s derived for male *P. pelagicus* in each of the five bodies of water by using morphometric and gonadal data demonstrates that morphological and gonadal maturity are attained by this species at essentially the same carapace width. However, the question of whether a male crab of about the size of maturity has become morphometrically mature depends on determining whether the relative length of one of its appendages is closer to the regression line which relates the length of that appendage to the carapace width in either juvenile or adult crabs. Because the overall relationship between cheliped length and carapace width of *P. pelagicus* does not undergo a marked shift at around the attainment of maturity, the use of the allometric method never enabled us to determine with absolute certainty whether, in the region of size overlap, a male was morphometrically immature or mature. The lack of precision, when determining maturity with morphometric data, could account for the slopes of the logistic curves for the prevalence of "mature" individuals of *P. pelagicus* derived from these morphometric data in the four southern bodies of water being shallower than those obtained from gonadal data.

From the above, it follows that there would be an advantage in determining the CW_{50}'s for male *P. pelagicus* at maturity by using data on gonadal state obtained by the simple and direct procedure of examining the vas deferentia, rather than relying on data obtained by an allometric method that is indirect and relies on a careful measurement of the appendage lengths and carapace dimensions of a considerable number of individuals. However, the remarkable similarities between the CW_{50}'s derived by using morphometric and gonadal data show that, if it is desirable to avoid damaging the crabs, the data obtained from allometric analysis does yield a close approximation of this important measure for *P. pelagicus*. Thus, the CW_{50} derived from either gonadal or morphometric data for male *P. pelagicus* can be used for developing management plans for this species.

The very close correspondence between the size at which gonadal and morphometric maturity are attained by the males of *P. pelagicus* contrasts with the situation recorded by Comeau and Conan (1992) and Sainte-Marie et al. (1997) for the males of the snow crab *Chionoecetes opilio*. In this latter species, the males attain gonadal maturity at a smaller body size than that at which morphometric maturity is attained following the terminal molt. The males of *C. opilio* with large cheliped and large body size are at a competitive advantage over smaller males when courting (Comeau and Conan, 1992; Sainte-Marie et al., 1997). Because the aquaria studies of Campbell (1984) have shown that the large males of *P. pelagicus* also have a similar competitive advantage during courting, a male of this species with mature gonads and differentiated chelipeds may not be able to compete for females successfully if larger males are present.

Influence of migration on estimates of CW_{50} for female crabs

The mean monthly gonad weights recorded for post-pubertal individuals were less for females in estuaries than in marine embayments, strongly indicating that females often tend to emigrate from the estuaries to their spawning grounds before their gonads are fully developed (Van Engel, 1958; Potter and de Lestang, 2000). Such an emigration from estuaries by mature female *P. pelagicus* reduces the proportion of mature individuals within each carapace width interval, thereby increasing the proportion of immature females in these class intervals. This shifts the logistic curve to the right and consequently increases the CW_{50}, which accounts for the significantly greater CW_{50}'s derived for females in estuaries than in marine environments on the lower west coast of Australia. For this reason, subsequent comparisons of the CW_{50}'s for female crabs in the different bodies of water will focus on those derived for assemblages in the three marine embayments.

In contrast to the CW_{50}'s for females, the CW_{50}'s for males at maturity in the two estuaries and the two marine embayments on the lower west coast of Australia were not significantly different. This presumably reflects the fact that, unlike mature females, the large males of *P. pelagicus* tend to remain in estuaries during the spawning period (Potter and de Lestang, 2000).

Influence of temperature on reproductive biology

The CW_{50}'s derived for males at "maturity" in each of the five bodies of water never differed by more than 2.2 mm, irrespective of whether gonadal or morphometric data were used. However, the maximum CW_{50}'s determined for males in the two estuaries and two embayments by using gonadal and morphometric data, i.e. 88.4 mm for Cockburn Sound and 87.2 mm for the Leschenault Estuary, respectively, were 8.6 and 8.8 mm less than the corresponding CW_{50}'s determined for males in Shark Bay. Furthermore, the CW_{50}'s for female *P. pelagicus* in Koombana Bay and Cockburn Sound were 5.6 and 5.1 mm, respectively, less than that of females in Shark Bay.

The greater CW_{50}'s for *P. pelagicus* in Shark Bay than in the other four bodies of water, which are located approximately 800 km farther south, runs counter to the generalization that the CW_{50}'s for decapods tend to be inversely related to water temperature (e.g. Campbell and Robinson, 1983; Jones and Simons, 1983; Dugan et al., 1991). However, the opposite situation has sometimes been recorded and, in those cases, has been attributed to differences among populations of one or more of the following: density, predation pressure, and food availability (Hines, 1989; Polovina, 1989; Pollock, 1995; McGarvey et al., 1999). It thus appears relevant that the mean density of *P. pelagicus* was far lower

[3] Smith, H. 1982. Blue crabs in South Australia—their status, potential and biology. Report 6, p. 33–51. South Australian Fisheries Industry Council Grenfell Centre Level 14, 25 Grenfell Street Adelaide 5000, Adelaide, Australia.

in the sampling sites in Shark Bay, 0.6 crabs/100 m^2, than those in Cockburn Sound and Koombana Bay, 2.80 and 2.94 crabs/100 m^2, respectively. The mean density in Shark Bay was also far lower than those recorded in the Leschenault and Peel-Harvey estuaries between the middle of spring and middle of autumn, when *P. pelagicus* colonizes estuaries (Potter et al., 1983; Potter and de Lestang, 2000). Furthermore, commercial or recreational fishing pressure (or both), which leads to a reduction in CW_{50}'s at maturity in the spiny lobster (Polovina, 1989), is far greater for *P. pelagicus* in the southern bodies of water than in Shark Bay (Bellchambers[4]). Recent work with microsatellite DNA has also shown that the assemblages of *P. pelagicus* in Shark Bay are genetically distinct from those in more southern bodies of water, such as Cockburn Sound and the Peel-Harvey Estuary (Chaplin et al.[5]).

The marked differences between the CW_{50}'s at maturity for *P. pelagicus* in Shark Bay and bodies of water farther south emphasize the need for managers to take into account this type of variation when determining a minimum legal carapace width (MLCW) for capture. However, the current MLCW for *P. pelagicus* in Western Australia, 127 mm, is well above even the CW_{50} for this species at maturity in Shark Bay.

The prevalence of ovigerous females did not peak sharply at any time of the year in Shark Bay, whereas ovigerous females were found predominantly during spring and summer in Cockburn Sound and Koombana Bay. Moreover, the mean monthly gonad weights of a female *P. pelagicus* of standard carapace width lay within a relatively narrow range of 0.9 to 1.8 g in Shark Bay, whereas they rose to a sharp peak of about 5 g in spring and fell below 1 g in some months in Cockburn Sound and Koombana Bay. The trends exhibited by the reproductive variables of female *P. pelagicus* thus provided strong evidence that reproductive activity extends over much or all of the year in Shark Bay, whereas it occurs predominantly in spring and summer in the two southern embayments. The more protracted spawning period in Shark Bay presumably reflects the presence of higher water temperatures throughout the year and in particular during winter and early spring. Such a conclusion is consistent with the results of other studies, which have shown that water temperature influences ovulation and egg development in *P. pelagicus* and other decapods (Rahaman, 1980; Campbell, 1984; Pollock, 1995; Kumar et al.[2]).

Fecundity

The vast majority of previous estimates of the fecundity of crustaceans have been based on the number of eggs borne by females at a particular time which, in the case of multiple spawners, does not take into account the fact that larger crabs can produce two or more batches of eggs within a spawning period. The few previous attempts to obtain the total fecundity of crustaceans have involved tracking the number of batches of eggs borne by particular individuals at different times (e.g. Chubb et al.[6]). The advantage of the approach developed during the current study is that it uses a combination of batch fecundity and an estimate of the number of batches produced during the spawning period by female *P. pelagicus* of different carapace widths to determine the relationship between the total fecundity and body size of this species in a given population. Because the older crabs have a far longer intermolt period between copulation and egg extrusion than younger crabs, i.e. eight versus four months, they have a far greater amount of time to accumulate the energy reserves required to produce eggs. This difference accounts for the greater number of egg batches produced by larger than small crabs.

[4] Bellchambers, L. 2002. Personal commun. Fisheries Western Australia, WA Marine Research Laboratories, West Coast Drive, Waterman, 6020, Perth, Australia.

[5] Chaplin, J., E. S. Yap, E. Sezmis, and I. C. Potter. 2001. Genetic (microsatellite) determination of the stock structure of the blue swimmer crab in Australia. FRDC project 98/118, 84 p. Murdoch University, South Street, Murdoch, 6150, Perth, Australia.

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