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Do the age compositions and growth of the crab *Portunus pelagicus* in marine embayments and estuaries differ?

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Portunus pelagicus (Crustacea: Portunidae) was collected monthly for a minimum of two years from two marine embayments (Cockburn Sound and Koombana Bay) and two estuaries (Peel-Harvey and Leschenault) that are located between 32° and 33°S on the lower west coast of Australia. A birth date of 1 December, derived from estimates of the peak time of spawning, was used to determine the average age of crabs in the main size cohort(s) in carapace width–frequency histograms for each month in each water body. The resultant carapace width-at-age data for each sex in Cockburn Sound and the Peel-Harvey Estuary, in which recruitment occurs at an early age, were then described using a seasonal von Bertalanffy growth curve. The results demonstrated that the growth rates of *P. pelagicus* differed significantly neither between females and males nor between crabs in the two water bodies and that growth was highly seasonal, with little or no increase in size occurring during the cold winter and early spring months. They also showed that relatively few *P. pelagicus* live beyond 18 months and indicate that, as a result of legal restrictions against retaining ovigerous crabs and the poor quality of recently-moulted females, fishing mortality is far lower amongst female than male crabs. The fact that the carapace widths attained by *P. pelagicus* at the end of its first year of life in Cockburn Sound (105 mm) and the Peel-Harvey Estuary (109 mm) were very similar to those in the Leschenault Estuary (105 mm) and Koombana Bay (107 mm) into which that estuary discharges emphasizes that the growth of *P. pelagicus* in each of these systems was similar. Data are also presented which strongly indicate that the second moult undergone by mature females is accompanied by an increase in the relative size of the abdominal flap.

INTRODUCTION

The Portunidae is one of the most economically important families of the Brachyura or true crabs, containing species such as *Portunus pelagicus*, *Portunus sanguinolentus*, *Scylla serrata*, *Callinectes sapidus* and *Necora puber*, which collectively contribute to commercial and recreational fisheries in Australia, south-east Asia, South Africa, North America and Europe (Stephenson, 1962; Debelius, 1999; Anon., 2000). Some idea of the economic importance of the blue swimmer crab *P. pelagicus* (L. 1766), which is widely distributed throughout the Indo-west Pacific (Stephenson, 1962; Kailola et al., 1993), can be gauged from the fact that the total annual commercial landings of this species worldwide in 1998, i.e. 109,000 tn, represented nearly 10% of the total commercial landings of all brachyuran crabs in that year (Anon., 2000). Although this marine species is often represented by resident populations in protected marine embayments (e.g. Penn, 1977; Sumpton et al., 1994; Sukumaran & Neelakantan, 1997), it frequently enters estuaries early in life and remains there for several months, during which period it undergoes considerable growth (e.g. Potter et al., 1983a).

Most of the attempts to age and describe the growth of *P. pelagicus* and other portunids have employed largely subjective examinations of the progression of modes in size–frequency data for sequential months in the year (e.g. Paul, 1982; Potter et al., 1983a; Sumpton et al., 1994; Sukumaran & Neelakantan, 1997). However, this approach to determining growth has occasionally been supplemented by the use of data obtained from tagged individuals, as in the case of *Scylla serrata* (e.g. Hill, 1975) or from aquaria studies, as with *P. pelagicus* (e.g. Meagher, 1971; Campbell, 1984). Although several attempts have been made to tag *P. pelagicus* to obtain data on the growth of this species, this approach, unlike that conducted with *S. serrata*, has proved unsuccessful due to moulting inhibition, tag shedding and mortality (Potter et al., 1991, 2001).

MULTIFAN (Fournier & Silbert, 1990) and ELEFAN (Pauly & David, 1981) were employed by Sumpton et al. (1994) and Sukumaran & Neelakantan (1997), respectively, for analysing size–frequency distributions of *P. pelagicus*. However, the von Bertalanffy growth curves they derived for female and male crabs from their analyses did not contain a term in their growth equations that would take into account any seasonal variations in the rate of growth of a species that appears typically to live for $1\frac{1}{2}$ to $2\frac{1}{2}$ years (Smith, 1982; Campbell, 1984; Sumpton et al., 1994; Sukumaran & Neelakantan, 1997). Furthermore, there have apparently been no attempts either to compare the rates of growth of female and male *P. pelagicus* statistically

or to compare growth rates in different environments, i.e. marine embayments and estuaries, in the same geographical region.

In *P. pelagicus*, the pubertal moult, and thus the attainment of maturity, occurs during the first year of life and usually at carapace widths of 80 to 100 mm (Smith, 1982; Campbell, 1984; Sumpton et al., 1994; Sukumaran & Neelakantan, 1996; de Lestang et al., in press). Laboratory studies have demonstrated that the females of *P. pelagicus* undergo a subsequent moult to produce a second maturity instar and thus increase in body size (Meagher, 1971; Campbell & Fielder, 1986). Meagher (1971) proposed that, following moulting, the shape of the abdomen of mature female *P. pelagicus* becomes relatively larger and more rounded. However, no attempt has been made to determine quantitatively whether the abdomens of female *P. pelagicus* in their first and second maturity instars are morphologically different.

This study has identified statistically the main size cohorts of female and male *P. pelagicus* in two coastal marine embayments and two estuaries on the lower west coast of Australia during each month of the year. These data were then used to ascertain the age compositions of this species in each water body and how they changed during the year. The trends exhibited by the means of the distributions fitted to the main cohort(s) in the carapace width distributions were then described using a modified von Bertalanffy growth equation, which had a seasonal component that would take into account any differences between the growth rates exhibited during the warmer and colder periods of the year. The resultant growth curves were used to ascertain whether female and male crabs grow at different rates and whether *P. pelagicus* grows faster in the two estuaries, which are very productive (McComb et al., 1981; Rose, 1994; Semeniuk et al., 2000), than in the two marine embayments. Finally, we show that the mature females of *P. pelagicus* are represented by two groups that could be distinguished on the basis of differences in the relative sizes of their abdomens, and which when considered in conjunction with the growth curve, are found to represent individuals at maturity instars I and II.

MATERIALS AND METHODS

Sampling regimes

Portunus pelagicus was collected at monthly intervals by seine netting and otter trawling for two years in the Leschenault Estuary, Koombana Bay and Cockburn Sound and for three years in the Peel-Harvey Estuary (Figure 1). All sampling was conducted between 1995 and 2000.

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 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 $\sim 116\,m^2$. The net was

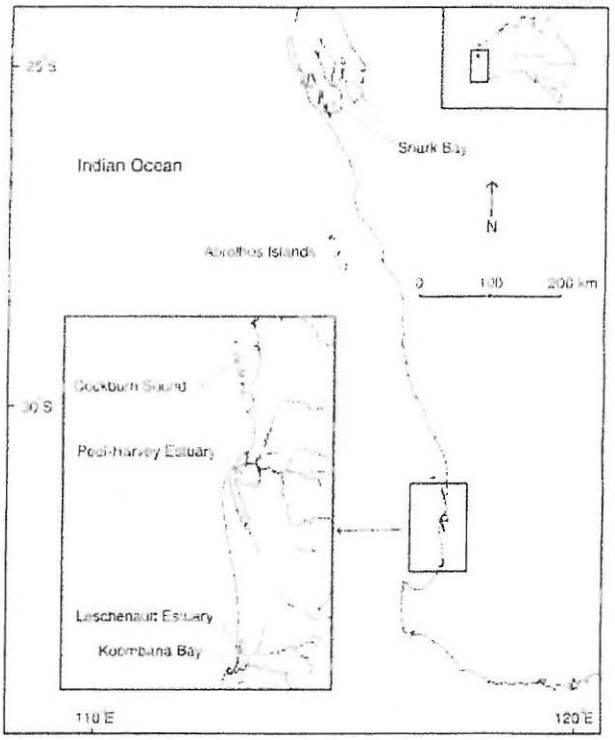

Figure 1. Map showing the location of the two marine embayments and two estuaries on the lower west coast of Australia and of Shark Bay to the north that were each sampled for *Portunus pelagicus*.

carried out from the beach for ~10 m and then extended parallel to the shoreline, after which it was dragged shorewards and on to the beach.

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×4. The otter trawl net was towed at $\sim 3.5\,km\,h^{-1}$ for between 150 and 500 m.

The carapace width of each female and male crab, i.e. the distance between the tips of the two lateral spines of their carapace, was recorded to the nearest 1 mm. The maximum widths of the abdomen of 146 mature female crabs from the Peel-Harvey Estuary, which were selected to cover a wide size range of mature individuals, were also recorded to the nearest 0.1 mm. Note that a mature female *P. pelagicus* could readily be identified by the shape and colour of its abdominal flap (Fielder & Eales, 1972).

Analysis of age and growth

The carapace width of each female and male crab caught in each calendar month was allocated to the appropriate 5 mm class interval. On the basis of previous studies of *P. pelagicus* in south-western Australia (Penn, 1977; Potter et al., 1983a; Potter & de Lestang, 2000), it was assumed that only one or two main size cohorts would be present in each month. A single normal distribution and a mixture of two normal distributions were fitted separately to the carapace width distributions for each sex in each

month, after which the chi-squared method of Schnute & Fournier (1980) was used to determine which of these described the data best. Note that, when two cohorts were present, the distributions of their carapace widths were assumed to have a common variance and curves were fitted to the overall size distribution, but without assuming that the mean sizes of the cohorts were related by a growth curve. This slight modification was necessary as Schnute & Fournier's technique of simultaneously fitting a growth curve and a mixture of normal components to the size–frequency distributions required the presence of more than two components. For those few data sets in which outliers appeared to be present in the monthly carapace width–frequency distributions, the outliers were assigned a normal component with a very tight standard deviation to eliminate their influence on the component distribution(s) fitted to the remainder of the carapace width–frequency data.

Since November and December are the main months when *P. pelagicus* spawns in south-western Australia (de Lestang et al., in press), this species was assigned a birth date of 1 December for determining the approximate age of the individuals of each sex in each cohort in each month. The location in any month of the carapace width distribution of a cohort within the overall frequency distribution, and its relationship to those in the previous and following months, was used to assign that cohort to either the 0+ or 1+ age-class.

The following slightly modified version of the seasonal von Bertalanffy growth curve of Hanumara & Hoenig (1987, eqn 7) was fitted to the means for the curves for the size distributions of either the single or two cohorts of each sex that were present in sequential months:

$$CW_t = \begin{cases} CW_\infty \left\{ 1 - \exp\left[-\left\{ \dfrac{K(t-t_0)}{12} + \dfrac{CK}{2\pi} \sin 2\pi \dfrac{(3)}{12} \right\} \right] \right\} & \text{for } t < t_s + 3 \\ CW_\infty \left\{ 1 - \exp\left[-\left\{ \dfrac{K(t-t_0)}{12} + \dfrac{CK}{2\pi} \sin 2\pi \dfrac{(t-t_s)}{12} \right\} \right] \right\} & \text{for } t \geqslant t_s + 3 \end{cases} \quad (1)$$

where CW_t is the estimated carapace width at age t months, 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 $0 \leqslant C \leqslant 1$) determines the relative amplitude of the seasonal oscillation and t_s (where $0 \leqslant t_s \leqslant 12$) determines the phase of the seasonal oscillation with respect to t_0. Hanumara & Hoenig's equation was modified so that it assumed that the growth rate of young crabs, i.e. those $< \sim 5$ months old, is at the maximum of this model. When our carapace widths at age were inserted into our modified seasonal growth curve, the value for t_0 approached zero far more closely than was the case when using the unmodified curve, and thus reflected far better the true growth during early life. Growth curves were fitted, using Solver in Microsoft™ Excel, to the data from Cockburn Sound and the Peel-Harvey Estuary. However, inadequate data existed for younger crabs from the Leschenault Estuary and Koombana Bay due to the delayed recruitment of crabs into these two water bodies (see Results).

The parameters for the modified seasonal von Bertalanffy growth curves for *P. pelagicus* in Cockburn Sound and the Peel-Harvey Estuary were compared, using a likelihood-ratio test (Cerrato, 1990). Since these parameters did not differ significantly between the two sexes in any of these water bodies (see Results), a common growth curve was constructed for both sexes in each water body. The parameters for these common curves were then compared by the likelihood-ratio test to ascertain whether they differed between the assemblages in the two different water bodies. The test statistic used for the above comparisons with sample sizes n_1 and n_2 and standard deviations σ_1 and σ_2 of residuals are given by $-2\ln(\Lambda)$, where

$$\Lambda = \left(\frac{\hat{\sigma}^2_{1\omega}}{\hat{\sigma}^2_{1\Omega}} \right)^{-n_1/2} \left(\frac{\hat{\sigma}^2_{2\omega}}{\hat{\sigma}^2_{2\Omega}} \right)^{-n_2/2} \quad \text{(Cerrato, 1990)}, \quad (2)$$

and the null hypothesis is rejected at the α level of significance when $-2\log(\Lambda) > \chi^2(q)$, where q is the number of linear constraints, i.e. parameters that are assumed to be equal in model ω, and where Ω represents the model in which all parameters are assumed to be distinct.

Morphological distinction between maturity instars I and II

Differences among the abdomen widths of mature female *P. pelagicus* in different months in the Peel-Harvey Estuary were examined using univariate ANOVAs, treating carapace width as a covariate. Data were subsequently pooled for those months in which no significant differences were detected. Linear regressions were then fitted to describe the relationship between the abdomen and carapace widths for the resultant groups.

RESULTS

Size and age compositions of Portunus pelagicus

Small female and male *Portunus pelagicus* were first caught in Cockburn Sound in January, but only in small numbers (Figure 2). This cohort of recently-recruited 0+ crabs, which was the product of spawning in the previous two to three months (de Lestang et al., in press), was quite distinct from the cohort of larger and presumably, at least mainly, 1+ crabs. The modal carapace widths of the females and males of this second cohort in January were 100–119 and 120–129 mm, respectively (Figure 2). The size distributions of the two cohorts in the size–frequency distributions for females remained relatively discrete until May, after which the numbers of the cohort of larger individuals declined in abundance. Although the same trends were observed with males, the number of individuals representing the cohort of larger crabs declined earlier, i.e. between March and April (Figure 2).

Figure 2 strongly demonstrates that the normal curves fitted to the underlying size distributions for the two size cohorts of both female and male *P. pelagicus* in the different months were accurate and appropriate. The means of the normal curves for female crabs followed a highly consistent trend, with values increasing from 40.5 mm in

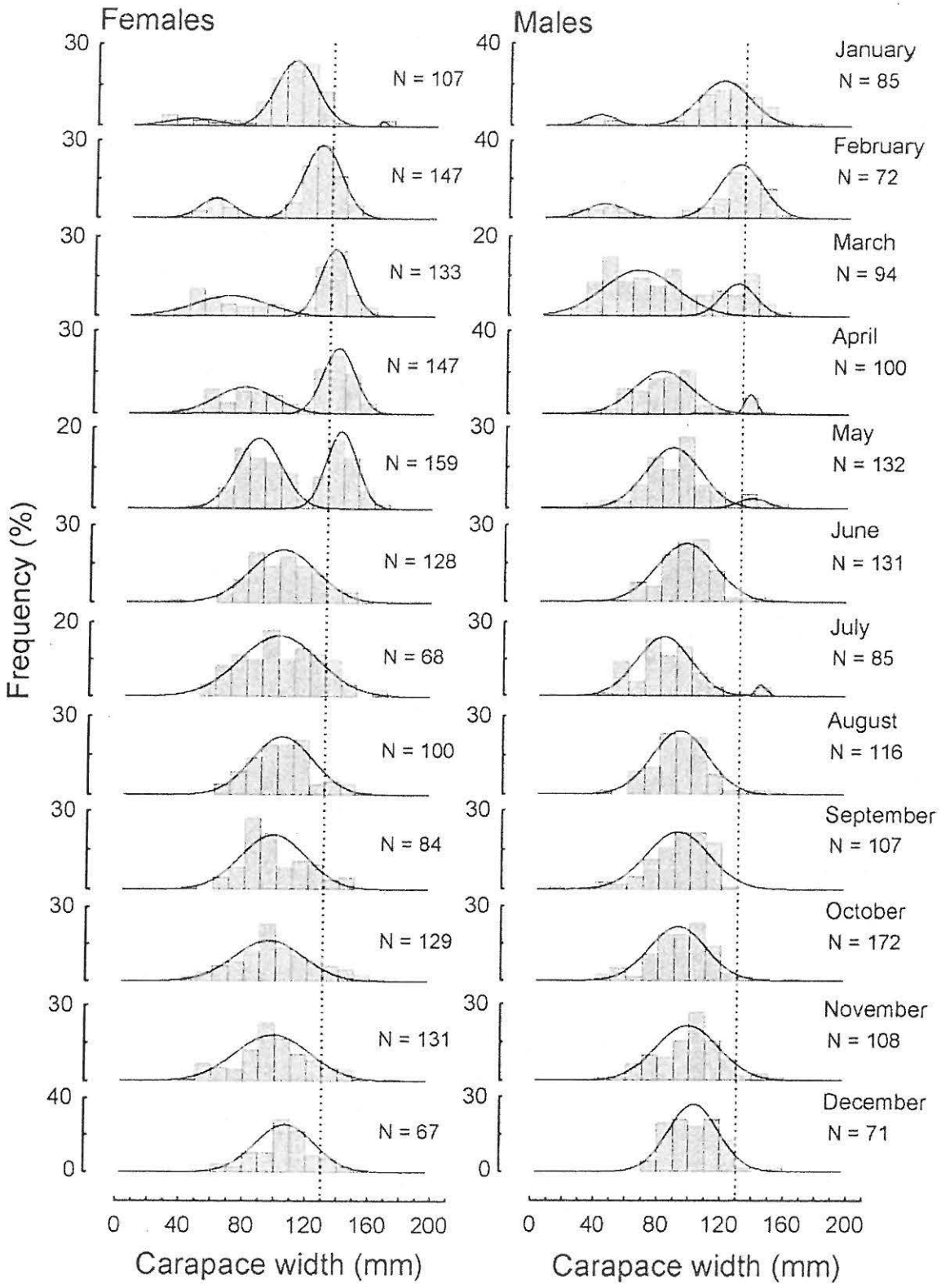

Figure 2. Carapace width–frequency distributions for *Portunus pelagicus* caught by seine netting and otter trawling in Cockburn Sound between 1998 and 2000. Data for corresponding months in the different years have been pooled. The dotted line represents the minimum legal carapace width for retention of *P. pelagicus* by fishers in Cockburn Sound. N, number of crabs caught and measured.

January to 88.0 mm in May and 107.2 mm in December, at which time the crabs were, on average, approximately 12–13 months old (Figure 2). The subsequent progression of the monthly means for the normal curves for the females during the first five to six months of their second year of life continued to follow a highly consistent pattern, with the values increasing from 107.0 mm in January to 138.4 mm in May. A very similar trend was exhibited by

the means for the carapace widths of male crabs during the first 15–16 months of life (Figure 2).

The monthly size–frequency distributions for the main cohort(s) of the females and males of *P. pelagicus* in the Peel-Harvey Estuary (data not shown) were very similar to those just described for the two sexes of this species in Cockburn Sound. Although an additional group of small crabs, i.e. with carapace widths <40 mm, was found in the Peel-Harvey Estuary, it persisted for only a short period and was not represented by a corresponding group during an earlier study of *P. pelagicus* in that estuary (Potter et al., 1983a). Thus, our subsequent analysis of the growth of *P. pelagicus* in the Peel-Harvey Estuary was based on the trends displayed by the means for the normal curves fitted to the size–frequency distributions for the main and persistent cohorts.

The timing of recruitment of the 0+ age-class of *P. pelagicus* in Leschenault Estuary and Koombana Bay differed markedly from those in Cockburn Sound and Peel-Harvey Estuary. Thus, in contrast to the situation in those latter two water bodies, very few 0+ *P. pelagicus* are recruited into Koombana Bay and Leschenault Estuary until August, i.e. until they are about eight months old (Potter & de Lestang, 2000).

Growth of Portunus pelagicus *in different water bodies*

The likelihood ratio test showed that the parameters for our modified seasonal von Bertalanffy growth curves for females and males were not significantly different in either Cockburn Sound or the Peel-Harvey Estuary, and that it was thus legitimate to fit growth curves to the combined carapace width-at-age data for the two sexes in each of these systems. The lack of a significant difference between the growth curves for the females and males in both of these water bodies is consistent with the fact that the mean carapace widths-at-age of neither sex showed any overall tendency to be greater than that of the other sex throughout life (Figure 3).

The plots shown in Figure 3 demonstrate that our modified seasonal von Bertalanffy growth curve provided a good fit to the mean carapace widths-at-age for *P. pelagicus* in both Cockburn Sound and the Peel-Harvey Estuary. This conclusion is further substantiated by the fact that the coefficients of determination (R^2) for these two assemblages were as high as 0.971 and 0.949, respectively (Table 1).

The growth of *P. pelagicus* during the first five months of life was relatively rapid in Cockburn Sound and the Peel-Harvey Estuary, with the individuals in these two systems attaining, on average, carapace widths of 86.4 and 93.5 mm, respectively, by the end of this period, i.e. May (Figure 3). The size of *P. pelagicus* in these two water bodies underwent essentially no change between five and ten months of age, i.e. between late autumn (May) and mid spring (October), but then increased progressively until the crabs were 15 months old in March, by which time their carapace widths had reached, on average, ~133 and 124 mm respectively (Figure 3). Despite the fact that the growth curves for *P. pelagicus* followed very similar trends in both systems, they were statistically different at $P<0.05$, mainly due to a difference in the CW_∞s. The latter difference may have been due either to

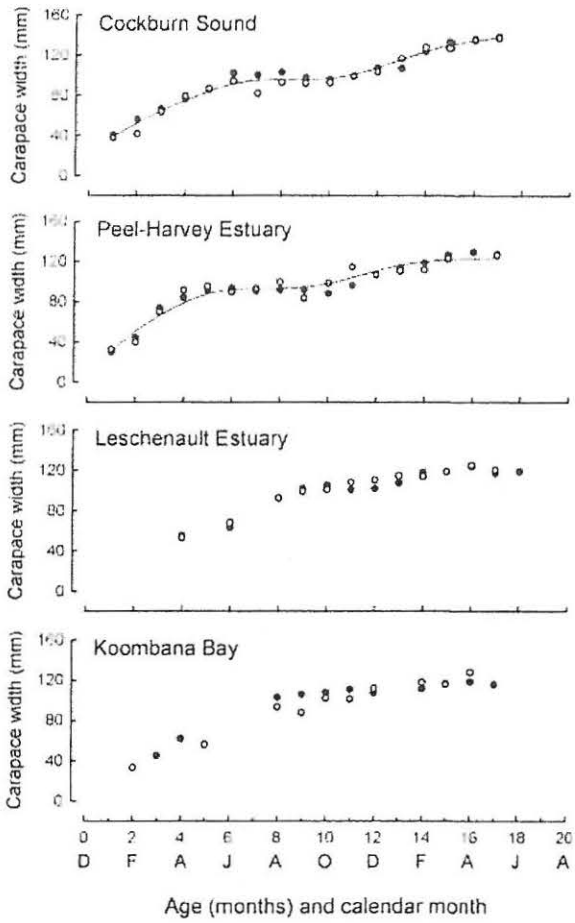

Figure 3. Seasonal von Bertalanffy growth curves for mean carapace widths-at-age of individuals of *Portunus pelagicus* in Cockburn Sound and the Peel-Harvey Estuary. Note that while each curve is derived from combined data for both sexes, the points for the mean carapace widths-at-age of females (•) and males (○) in each month are shown to illustrate the similarity in these values for the two sexes. Furthermore, only mean values for females and males are given for the Leschenault Estuary and Koombana Bay because there were insufficient data for the smaller crabs to derive reliable growth curves.

the emigration of larger individuals from the Peel-Harvey Estuary and/or to the particularly heavy exploitation of crabs >127 mm, i.e. the legal minimum carapace width for retention by fishers. Thus, a further comparison was made between the growth curves for crabs in the two systems, but this time using curves fitted only to the size-at-age data for crabs caught during the first 12 months of life, and thus restricted to the period of growth that occurs before a substantial proportion of the crabs reach the legal minimum size for retention. The growth curves for this period were not significantly different ($P>0.05$). The similarities between the growth curves during the first year of life are emphasized by the fact that, by the end of this period, the mean carapace width of *P. pelagicus* in Cockburn Sound (104.8 mm) differed by only ~4 mm from that in the Peel-Harvey Estuary (109.0 mm).

The virtual absence of crabs with carapace widths <70 mm in both the Leschenault Estuary and Koombana Bay meant that it was inappropriate to fit growth curves to the size-at-age data for *P. pelagicus* in these two systems.

Table 1. *Growth parameters and total sum of squares for the seasonal von Bertalanffy growth curves, that were derived from the mean carapace widths-at-age of individuals of* Portunus pelagicus *in Cockburn Sound and the Peel-Harvey Estuary.* 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 *determines the relative amplitude of the seasonal oscillation,* t_s *determines the phase of the seasonal oscillation with respect to* t_0 *and* R^2 *is the coefficient of determination.*

Water body Sampling period	Cockburn Sound 1998–2000	Peel-Harvey Estuary 1995–1998
CW_∞	152.7	125.9
t_0	0.57	1.7
K	1.5	2.82
C	1.0	1.0
t_s	2.4	1.5
R^2	0.971	0.949
Total SS	730.2	1143.4

Thus, the mean values for the size-at-age of those ages of females and males that were well represented in the Leschenault Estuary and Koombana Bay are shown just as points in Figure 3. A *t*-test demonstrated that, in both of these systems, the mean carapace widths of females and males at 12 months of age were not significantly different ($P > 0.05$) (Figure 3) and thus the carapace width data for both sexes in each of these systems have been pooled. A one-way analysis of variance (ANOVA) showed that the mean carapace widths of *P. pelagicus* at 12 months of age did not differ significantly among the four water bodies ($P > 0.05$).

Morphological distinction between maturity instars I and II

Univariate ANOVA showed that the abdomen widths of mature female *P. pelagicus* caught in May in the Peel-Harvey Estuary differed significantly ($P < 0.001$) from those caught in July, September and October. However, univariate ANOVA showed that there were no such differences among July, September and October ($P > 0.05$). Regression lines were then fitted to those crabs caught in May and those caught in the other three months (Figure 4). These two regression lines ($CW_1 = 0.34\,AW_1 - 8.45$ and $CW_2 = 0.40\,AW_2 - 8.45$, $R^2 = 0.951$) provided a far better description of the relationship between the abdomen width and carapace width than that obtained using a single regression line (likelihood-ratio test, $P < 0.001$). The mean carapace width of these mature female crabs caught in May was 120.8 mm while that of the above crabs caught in July, August and October was 109.1 mm.

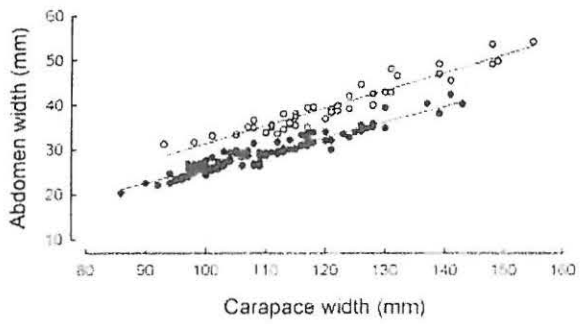

Figure 4. Relationship between abdomen and carapace widths of mature female *Portunus pelagicus* caught in the Peel-Harvey Estuary in July, September and October (•) and in May (○).

DISCUSSION

The present study demonstrates that the new 0+ juveniles of *Portunus pelagicus* become recruited into the nearshore, shallow waters of Cockburn Sound and the Peel-Harvey Estuary at the same time of the year. The use of the chi-squared method of Schnute & Fournier (1980) proved invaluable in determining whether one or two main cohorts were present in each month. The resulting normal distributions showed that, in corresponding months of the year, the size compositions of this portunid in the above two water bodies were also similar. Moreover, the fitting of a curve to the mean monthly values for the normal distributions for the carapace widths of the cohort(s) in the carapace width–frequency data showed that the pattern of growth of *P. pelagicus* in Cockburn Sound and the Peel-Harvey Estuary followed the same very consistent trends during the year. In this context, it was noteworthy that the contrast between the growth that takes place during summer and the cessation of growth during winter could be taken into account by the use of a seasonal von Bertalanffy growth curve, that was modified to allow for the very rapid growth that occurs early in life. Our data also demonstrated that, despite the ability of the likelihood-ratio test to detect small differences between growth curves, that test did not detect a significant difference between the growth curves of females and males of *P. pelagicus* in either Cockburn Sound or the Peel-Harvey Estuary. Thus, it was appropriate to combine the carapace widths-at-age of females and males to produce a common growth curve for both sexes of *P. pelagicus* in each system.

It was thus noteworthy that concurrent sampling in Shark Bay, which is located nearly 1000 km to the north of the study region (Figure 1), yielded small crabs, i.e. with carapace widths <30 mm, throughout the year. This finding is consistent with the fact that reproductive studies had demonstrated that, unlike the situation in water bodies on the lower west coast of Australia, *P. pelagicus* spawns throughout the year in this sub-tropical region of Shark Bay (de Lestang et al., in press). This continual spawning accounts for the absence of discrete and persistent cohorts that could be traced through the sequential monthly carapace width–frequency histograms. Consequently it was not possible to use modal progressions in size–frequency data to construct growth curves for *P. pelagicus* in Shark Bay.

Recruitment, growth and duration of life

An examination of a combination of the trends exhibited by the main cohorts in sequential monthly carapace width–frequency distributions and by those followed by the von Bertalanffy growth curves allows the following generalization to be made regarding the assemblages of

P. pelagicus in Cockburn Sound and the Peel-Harvey Estuary. The members of this species start to become recruited into both systems in January, i.e. mid summer, and have attained, on average, a carapace width of ~95 mm by the following November, i.e. late spring, when they are about ten months old. During subsequent months, *P. pelagicus* continues to increase in size, with their carapace widths reaching, on average, ~130 mm in March, i.e. early autumn, and then undergoes a marked reduction in numbers during either the immediately ensuing months as with males or after May as with females. The above data imply that relatively few *P. pelagicus* survive beyond 18 months. This parallels the conclusion drawn for *P. pelagicus* in the Peel-Harvey Estuary on the basis of a subjective assessment of modal progressions in sequential monthly carapace width–frequency distributions for 1979 to 1981 (Potter et al., 1983a), i.e. prior to the time when this estuary was greatly modified through the construction of a large and additional entrance channel (Bradby, 1997). It also parallels the conclusions drawn by Smith (1982), Sumpton et al. (1994) and Sukumaran & Neelakantan (1996) on the basis of subjective assessments of the trends in size–frequency data for populations in South Australia, Queensland and India. This is a far shorter life span than the three years estimated for other commercially and recreationally important portunids such as the blue crab *Callinectes sapidus* and the mud crab *Scylla serrata* (Van Engel, 1958; Hill, 1975).

The growth curves show that, in both Cockburn Sound and the Peel-Harvey Estuary, the growth of 0+ *P. pelagicus* is rapid during summer and most of autumn, and starts to slow down in late autumn before becoming negligible during the ensuing months until the middle of spring. The cessation of growth by this poikilotherm during winter and early spring is presumably related, at least in part, to the decline in water temperature that occurs in south-western Australian marine and estuarine waters during this period (Potter et al., 1983a). However, it is also relevant that the majority of 0+ female *P. pelagicus* attain maturity and copulate in late autumn and retain sperm until the following spring when the eggs are fertilized. The retention of sperm is thus facilitated by the absence of moulting during the late autumn to mid-spring period, as such a moult would lead to the sloughing of the spermathecal lining in which the sperm is stored.

Declines in abundance of 1+ crabs

The monthly carapace width–frequency histograms for *P. pelagicus* showed that, in Cockburn Sound, the abundance of female 1+ crabs remained relatively high until May, whereas that of 1+ males declined progressively after January, with the change being particularly abrupt after March. The maintenance of high numbers of 1+ female crabs in January can largely be attributed to the effects of legislation, which oblige fishers to return ovigerous crabs to the water. The 1+ females were maintained at a relatively high level during February and March by the fact that, unlike 1+ males, they undergo a highly synchronized post-spawning moult at this time (de Lestang et al., in press) and thus, because they have a soft shell and poor quality flesh, are returned to the water. Since substantial numbers of *P. pelagicus* start to attain the minimum legal carapace width in January, the main fishing pressure during the prime fishing period of December to April falls on the males.

Although the 1+ males also declined in abundance more rapidly than the 1+ females in the Peel-Harvey Estuary, the difference in the rate of decline was not as great in this system. This can be attributed to the fact that, unlike the situation in Cockburn Sound where there is a resident population of *P. pelagicus*, the mature females tend to leave the estuary prior to extruding their eggs (de Lestang et al., in press). They do however sometimes return to the estuary.

Comparisons between growth in marine embayments and estuaries

The presence of large numbers of *P. pelagicus* in the two marine embayments (Cockburn Sound and Koombana Bay) and the two estuaries (Peel-Harvey and Leschenault) in which the current study was carried out emphasizes that these protected water bodies contain ideal habitats for this portunid. However, the characteristics of the embayments and estuaries differ markedly in certain respects, such as salinity regimes and water depth. For example, salinities in the two embayments typically remain close to 35 psu throughout the year, whereas those in parts of both estuaries decline to <10 psu in winter and exceed that of full-strength seawater (35 psu) during late summer and early autumn (Potter et al., 1983b; Potter & de Lestang, 2000). It was thus surprising to discover that, despite these and other differences, the pattern and rate of growth in Cockburn Sound and the Peel-Harvey Estuary were so similar, a point emphasized by the fact that the mean carapace widths of *P. pelagicus* at the end of their first year of life in these two systems were virtually identical.

Since *P. pelagicus* does not become recruited in large numbers into either Koombana Bay or the Leschenault Estuary until it is about nine months old, it was not possible to determine the early growth of this species in these two water bodies. However, the substantial numbers of 12-month-old *P. pelagicus* that are present in Koombana Bay and the Leschenault Estuary, meant that a reliable estimate of the mean carapace widths for these individuals could be determined at this age. These mean carapace widths, i.e. 107.4 mm and 105.1 mm, respectively, were very similar to each other and also to those in Cockburn Sound and the Peel-Harvey Estuary. These results suggest that, in a given geographical region, the rate of growth of *P. pelagicus* is, to a large extent, genetically determined and that it would vary markedly only if there were, in particular, large differences in the availability or quality of food.

Identification of maturity instar II

The relationship between the abdomen and carapace widths of mature female crabs caught in July, September and October differed significantly from that of those crabs caught in May. From the growth curve for *P. pelagicus* in the Peel-Harvey Estuary, it follows that the former data represent crabs of ages between seven and ten months old, and thus in their first maturity instar (MI), while the latter data represent crabs that are ~17 months old and in their second maturity instar (MII).

Furthermore, the mean carapace width of the older group (MII) is very similar to the mean carapace widths of crabs in their second year of life. However, the mean carapace width of the younger group (MI) was slightly greater than that of those crabs in mid winter to late spring. This difference can be attributed to the inclusion of immature crabs in the width-at-age data used for analysis of growth. Thus, the relationship between abdomen and carapace widths can be used to distinguish between maturity instars of female *P. pelagicus*.

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