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CHANGES IN DENSITY, AGE COMPOSITION, AND GROWTH RATE OF *PORTUNUS PELAGICUS* IN A LARGE EMBAYMENT IN WHICH FISHING PRESSURES AND ENVIRONMENTAL CONDITIONS HAVE BEEN ALTERED

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ABSTRACT

Commercial and recreational catches of the blue swimmer crab *Portunus pelagicus* in Cockburn Sound, a large marine embayment on the west coast of Australia, have risen markedly over the last 20–30 years. However, because commercial fishers changed from using tangle nets to traps to catch crabs during this period, the annual catch per unit effort data for the commercial fishery throughout this period are not directly comparable and cannot thus be used to elucidate whether the increased catches reflected an increase in crab density. Trawling was thus undertaken to estimate the densities of *P. pelagicus* in Cockburn Sound in the late 1990s to facilitate comparisons with those we estimated from trawl catch rates for this species in that embayment during the early 1970s. The comparisons demonstrate that, despite increases in commercial and recreational crab catches, the densities of *P. pelagicus* in Cockburn Sound have risen markedly between the above two periods. This change is probably related to a decline in the abundance of the large piscivorous predators of *P. pelagicus* as a result of heavy fishing pressure and possibly also to an increase in the abundance of the prey of this portunid. Size composition data demonstrate that appreciable numbers of crabs survived in Cockburn Sound until the end of their second year of life and even beyond during the early 1970s, whereas the vast majority of 1+ crabs were removed by heavy fishing pressure by the month (June) that they had reached 18 months in age in the late 1990s. The fact that, in the late 1990s, few legal-sized crabs still remained for fishing between July and December and the 0+ age class increased in number and size throughout the year accounts for the broad estimates of biomass becoming far greater in these months in the 1990s than in the corresponding months in the early 1970s. Growth during the first eleven months of life, i.e., in the period leading up to the age at which crabs reach the minimum legal size for retention, was significantly faster in the early 1970s than in the late 1990s when crab densities were much greater. The slower growth rate and the reduced longevity through heavy fishing pressure in the latter period would help account for females becoming mature at a smaller size and for ovigerous females being represented by one rather than two substantial size cohorts, respectively. The essentially single size cohort in the late 1990s and first cohort in the early 1970s correspond mainly to crabs in their first maturity instar, whereas the second cohort in the early 1970s predominantly represented crabs in their second maturity instar.

The declines in fish and crustacean stocks that occur as a result of increasing levels of exploitation are a major concern for fisheries managers (e.g., Christensen, 1998; Stevens *et al.*, 2000; Hutchins, 2001). However, there are examples of crustacean and fish stocks increasing in abundance when the productivity in their environment increases or the numbers of their predators decline (Bailey, 1982; Steckis *et al.*, 1995; Merrick, 1997; Stevens *et al.*, 2000). In some cases, increases in the density of crustaceans have been accompanied by a reduced growth rate and the attainment of maturity at a smaller size (Cobb, 1986; Polovina, 1989; Jernakoff *et al.*, 1994; Morrissy *et al.*, 1995; Pollock, 1995; McGarvey *et al.*, 1999).

The blue swimmer crab *Portunus pelagicus* (Linneaus, 1766), which is found in marine embayments and estuaries throughout the Indo-West Pacific (Stephenson, 1962), makes a substantial contribution to the commercial and/or recreational fisheries of many regions (Ingles and Braum, 1989; Sukumaran and Neelakantan, 1997; Food and Agriculture Organisation, 2000). The Catch and Effort Statistics (CAES) of the Department of Fisheries Western Australia show that the annual commercial catches of this portunid in Western Australia, which are now the greatest of any state in Australia, have risen markedly during recent years.

A preliminary investigation of CAES showed that in Cockburn Sound, the location of one of the two most important commercial fisheries for *P. pelagicus* in Western Australia, the commercial catches of this species have increased by about an order of magnitude since the early 1970s. It is thus relevant that, although there are no reliable commercial or appropriate long term recreational catch and effort statistics for finfish in Cockburn Sound, the commercial catch rates of species, such as pink snapper *Pagrus auratus* (Schneider, 1801), flathead *Platycephalus* spp., West Australian dhufish *Glaucosoma hebraicum* Richardson, 1845, whiting *Sillago* spp., silver bream *Rhabdosargus sarba* (Forsskål, 1775), and mulloway *Argyrosomus japonicus* (Temminck and Schlegel, 1844), which are predators of portunid crabs (Kailola *et al.*, 1993), have apparently declined markedly over the last 30 years (R. C. J. Lenanton, Fisheries Western Australia, personal communication). In the case of recreational fishing, such a conclusion is consistent with the great increase that has occurred in the number of people involved in this activity during those years (Sumner and Williamson, 1999). Furthermore, the environment in Cockburn Sound has changed between the early 1970s and late 1990s. For example, its seagrass beds have become approximately halved in area between those years because of the effects of the shading produced by the massive growths of epiphytic algae that developed as a result of the nutrient enrichment of this water body (Kendrick *et al.*, 2002). Although water quality has improved in Cockburn Sound during recent years, the substrate is rich in organic material, which helps account for the current presence of large numbers of polychaetes and other benthic macroinvertebrates that constitute the diet of *P. pelagicus* in eutrophic environments (de Lestang *et al.*, 2000; G. Kendrick, personal communication).

As commercial fishers in Cockburn Sound have changed from using tangle nets to traps to catch *P. pelagicus* during the 1990s, there are no directly comparable catch per unit effort data for the early 1970s and late 1990s that could be used to confirm that the marked increase in catches during the intervening years reflected an increase in the abundance of *P. pelagicus* in this water body. Thus, trawling was undertaken in Cockburn Sound during the late 1990s to obtain catch data that could be used to estimate the monthly densities of this species in this embayment during this period and thus facilitate direct comparisons with those we derived from catch rates recorded by the Department of Fisheries Western Australia for *P. pelagicus* in the same area during the early 1970s. Because these comparisons confirmed that the density of *P. pelagicus* in Cockburn Sound has increased markedly during the last 20–30 years (see Results), we then tested the hypothesis that this pronounced increase would have been accompanied by a reduction in both the growth rate and size at which *P. pelagicus* attains maturity. We have also hypothesised that the great increase in fishing pressure on *P. pelagicus* would have led to a reduction in the proportion of larger crabs and thus of females in their second maturity instar (for details see de Lestang *et al.*, 2003a, b).

Materials and Methods

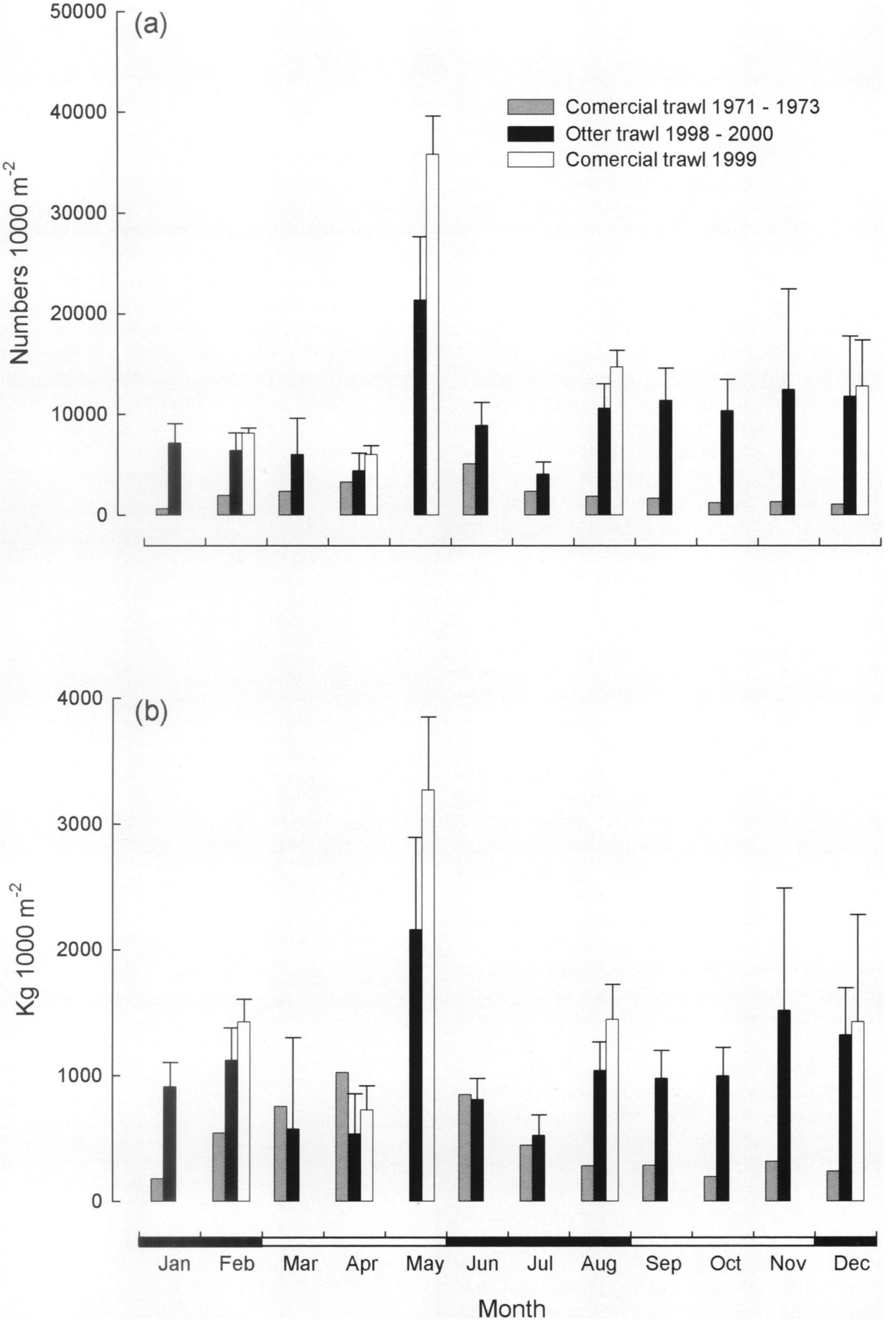
Sampling Regime

A commercial trawler sampled *Portunus pelagicus* in six randomly selected sites in the northern half of Cockburn Sound in each month between August 1971 and January 1973 except for May 1972 (Penn, 1977), and subsequently in February, April, May, August, and December 1999 (see Fig. 1 in de Lestang *et al.* (2003a) for locations and morphology of Cockburn Sound). The single trawl net used during the early 1970s possessed wings composed of 51-mm mesh and a cod end made of 45-mm mesh. A tickler chain was hung below the footrope. The effective fishing width (2/3 of the width of the head rope) and height of the net were about 12 and 1 m, respectively. On each sampling occasion, the net was towed for a period of about 30 min at a speed of about 6.5 km h^{-1} (Penn, 1977). During 1999, the trawler was equipped with two nets. As was the case with the single net used in the early 1970s, each of these nets consisted of 51- and 45-mm mesh in the wings and cod end, respectively, and had a height of 1 m and a tickler chain hung below the footrope. The effective fishing width was 8 m. The two nets were towed for about 20 min at a speed of about 4.6 km h^{-1} on each sampling occasion. The average areas covered during each trawl were 39,000 and 25,000 m^2 in 1971–1972 and 1999, respectively.

A small otter trawl net was also employed monthly between May 1998 and April 2000 (a period subsequently referred to as the late 1990s), to sample six randomly selected and comparable sites in the same area of Cockburn Sound as were sampled by the commercial trawler in both 1971–1973 and 1999. The net, which had an effective fishing width of 2.6 m, was 0.5 m high and 5 m long and consisted of 51-mm mesh in the wings and 25-mm mesh in the bunt. A tickler chain was hung below the footrope. The otter trawl net was towed at a speed of about 3.5 km h^{-1} for 150 to 500 m, the precise distance covered being dependent on the type of substrate and volume of detached macrophytes retained in the net.

Data Recorded

The carapace width (*CW*) of each crab, i.e., the distance between the tips of the two lateral spines of its carapace, was


(a)
Numbers 1000 m-2
50000
40000
30000
20000
10000
0
Comercial trawl 1971 - 1973
Otter trawl 1998 - 2000
Comercial trawl 1999
(b)
Kg 1000 m-2
4000
3000
2000
1000
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

measured to the nearest 10 mm in 1971–73 and to the nearest 1 mm in 1998–2000. A record was kept of which females were ovigerous.

The numbers of crabs caught at the six sampling sites in each calendar month between August 1971 and January 1973 were pooled and recorded in the Western Australian Department of Fisheries data files as a mean catch rate, i.e., mean number of crabs caught h^{-1}. The mean monthly catch rates, in conjunction with the area covered per hour of trawling, were used to calculate the mean density of crabs, i.e., number of crabs 1000 m^{-2}, in each calendar month during the early 1970s.

The number of crabs caught at each sampling site in the five months of sampling by the commercial trawl in 1999 and in each month by the small otter trawl between May 1998 and April 2000, in conjunction with the area covered during each trawl, were used to estimate the densities of crabs in the area trawled at each site on each sampling occasion. These values were then used to estimate the mean density, i.e., number of crabs 1000 m^{-2}, ± 1 SE (derived using both trawling methods) in each calendar month during the late 1990s.

The following series of calculations were used to obtain broad indices of the mean biomass (kg) of crabs 1000 m^{-2} in each month in the early 1970s and late 1990s. (i) The relationship between the body weight (W in g) and carapace width (CW in mm) of *P. pelagicus*, using data for crabs collected in the late 1990s and covering their full size range, was calculated. The resultant equation is $W = 0.00004 \times CW^{3.1281}$ ($R^2 = 0.962$, $n = 2478$). (ii) In the case of the data for the early 1970s, when the size of each crab was recorded only in terms of the 10-mm carapace width class to which it belonged, the above equation was used to calculate, for each sequential carapace width class, the weight of the crab whose carapace width was equivalent to the midpoint of that carapace width class. However, because the carapace width of each crab was recorded to the nearest 1 mm in the late 1990s, the above equation could be used to estimate the weight of each individual crab in each monthly sample at the 1-mm carapace width level of resolution. (iii) The monthly means and associated standard errors for the body weights of crabs in each period were then calculated using the following assumptions. The weight of each crab in each 10- and 1-mm carapace width class in each month in the early 1970s and late 1990s, respectively, was broadly equivalent to the weight of a crab with a size equal to the midpoint of its carapace width class. The number of crabs of each of those weights was considered to be equal to the number of crabs in its corresponding carapace width class. (iv) The mean weight of crabs in each month in the early 1970s was then multiplied by the density for each of the corresponding months to provide a broad estimate of the mean biomass (kg) 1000 m^{-2}. The same approach was adopted for the data for the late 1990s, but, in this case, the mean weight of crabs in each month was multiplied by the separate densities that were derived using the catches obtained from the commercial and otter trawls. Furthermore, because it had been possible to calculate standard errors for the mean monthly densities in the late 1990s, it was also possible to calculate a standard error for the biomass estimates derived from the catch data for both trawling methods in this period.

Analysis of Growth

Because previous work had shown that the growth rates of female and male *P. pelagicus* in Cockburn Sound were not significantly different, the CW data for females and males on each sampling occasion were pooled (de Lestang *et al.*, 2003a). Furthermore, chi-square tests employing Bonferroni corrections (data not shown) demonstrated that the CW distributions of *P. pelagicus* collected by the large and small otter trawls in the late 1990s were not significantly different in any of the five months in which both trawls were used for sampling ($P > 0.05$). Thus, the CWs of crabs caught by both trawls were pooled to produce the carapace width-frequency data for each calendar month in the late 1990s, and these were subsequently used to determine the growth rate of *P. pelagicus* in that period.

Because *P. pelagicus* spawned predominantly between October and December in Cockburn Sound during the late 1990s (de Lestang *et al.*, 2003b), this species was assigned a birth date of 1 December for determining the approximate age of the individuals in each cohort in each calendar month in that period. Furthermore, because Penn (1977) found that ovigerous females were most numerous in Cockburn Sound in the same months during the early 1970s, the crabs caught during this period were also assigned a birth date of 1 December.

The CW of each crab caught in each calendar month between August 1971 and January 1973 and between May 1998 and April 2000 was allocated to its appropriate 10-mm class interval. On the basis of previous studies of *P. pelagicus* in south-western Australia (Penn, 1977; Potter *et al.*, 1983; de Lestang *et al.*, 2003a), 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 CW distributions in each month. The chi-squared method of Schnute and Fournier (1980) was then used to determine which of these described the data best. Note that when two cohorts were present, the distributions of their CWs were assumed to have a common variance and that the curves were fitted to the overall size distribution without assuming that the mean sizes of the cohorts were related by a growth curve. This slight modification was necessary as Schnute and 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.

The location in any month of the CW distribution of a cohort within the overall frequency distribution, and its relationship to those in the previous and following months, were used to assign that cohort to either the 0+ or 1+ age class.

The following slightly modified version of the seasonal

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Fig. 1. (a) Mean monthly numbers and (b) broad biomass estimates for *Portunus pelagicus* 1000 m^{-2} in the northern region of Cockburn Sound in the early 1970s and late 1990s, as determined from catches obtained by a commercial trawler in the former period and by a commercial trawl and otter trawl in the second period. Standard errors are provided for the monthly means in the latter period, but could not be calculated for the densities or biomass in the earlier period. In this figure and Figs. 3 and 4, the black rectangles on the x-axis denote summer and winter months and the open rectangles autumn and spring months.

von Bertalanffy growth curve of Hanumara and Hoenig (1987, equation 7) was fitted to the means for the size distributions under the curves for either the single or two cohorts that were present in sequential months.

$$CW_t = \begin{cases} CW_\infty\left\{1 - \exp\left[-\left\{\frac{K(t-t_0')}{12} + \frac{CK}{2\pi}\sin 2\pi\frac{(3)}{12}\right\}\right]\right\} & \text{for } t < t_s + 3 \\ CW_\infty\left\{1 - \exp\left[-\left\{\frac{K(t-t_0')}{12} + \frac{CK}{2\pi}\sin 2\pi\frac{(t-t_s)}{12}\right\}\right]\right\} & \text{for } t \geq t_s + 3 \end{cases}$$

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 ($t_0 = t_0' + (6C/\pi)\sin(0.5\pi)$) 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 $0 \leq t_s \leq 12$) determines the phase of the seasonal oscillation with respect to t_0. Hanumara and Hoenig's equation was modified so that it assumed that the growth rate of young crabs, i.e., those less than about five months old, is at the maximum of this model. The value for t_0 approached zero far more closely using the modified seasonal growth curve than when employing the unmodified curve, and thus reflected far better the true growth during early life. Growth curves were fitted to the data from both periods using Solver in Microsoft Excel™.

The parameters for the growth curves of *P. pelagicus* in the early 1970s and late 1990s were compared using the likelihood-ratio test to ascertain whether they differed between these two periods (Cerrato, 1990).

Results

Changes in Density

The mean monthly densities of *P. pelagicus* in the early 1970s, derived from catch rates obtained by a commercial trawl between August 1971 and January 1973, ranged from a minimum of 632 crabs 1000 m^{-2} in January to a maximum of 5078 crabs 1000 m^{-2} in June (Fig. 1a). The mean monthly densities derived from the catches of a commercial trawler in five months during 1999 ranged from a minimum of 5998 crabs 1000 m^{-2} in April to a maximum of 35,842 crabs 1000 m^{-2} in May and, in each of the four months when comparisons could be made, were between 2 and 12 times greater than those estimated for the corresponding months of the year using the catch data obtained with the commercial trawl in the early 1970s (Fig. 1a).

In none of the five months when the commercial trawl and small otter trawl were both used during the late 1990s was there a significant difference ($P > 0.05$) between the mean monthly densities derived from the catches obtained using those two trawls (Fig. 1a). The mean density of crabs for each calendar month between January and April and between June and December in the late 1990s, derived from the catch data obtained by the small otter trawl, was always greater than that derived for the corresponding month using the commercial trawl catches in the early 1970s, and, in seven of those eleven months, they were greater by factors of between 3 and 11 (Fig. 1a). Note that comparisons could not be made between the two periods in May because no trawling was conducted in that month in the early 1970s.

The broad mean monthly estimates of biomass (kg) of crabs 1000 m^{-2} in eight months in the late 1990s, derived by extrapolation from data collected using the otter trawl, were greater than those in the corresponding months in the early 1970s, derived by extrapolation from data obtained using the commercial trawl (Fig. 1b). However, in two of the other three months for which there were data for both periods, the mean biomasses in the two periods were similar, and, in the third of those months, the mean biomass was greater in the early 1970s than the late 1990s. The biomass estimates derived from commercial trawl data in each of the five months of the late 1990s in which commercial trawling was conducted were not significantly different ($P > 0.05$) from those derived from otter trawl data in each of the corresponding months of that period (Fig. 1b).

Age Composition and Growth of *Portunus pelagicus* in Cockburn Sound

During the early 1970s, small 0+ recruits were first caught in March and April but only in small numbers (Fig. 2). However, substantial numbers of the 0+ age class were present by June, and the size distribution of this age class remained relatively distinct from that of the cohort of the larger and presumably mainly 1+ crabs until November (Fig. 2). In December, the size distribution of the cohort of smallest crabs, i.e., now early 1+ crabs, was merging with that of the cohort of largest crabs, i.e., now early 2+ (Fig. 2). From February onwards, the larger crabs, i.e., greater than 110-mm carapace width, comprised a single cohort. Although this cohort was represented in all subsequent months, its abundance tended to be lower in the second half of the year.

The trends exhibited by monthly size-frequency data for *P. pelagicus* in the late 1990s differed in the following two ways from those just described for the early 1970s (Fig. 2). Firstly, in the late 1990s, the 0+ age class was recorded earlier, i.e., January vs. March, and was relatively far more abundant in March and

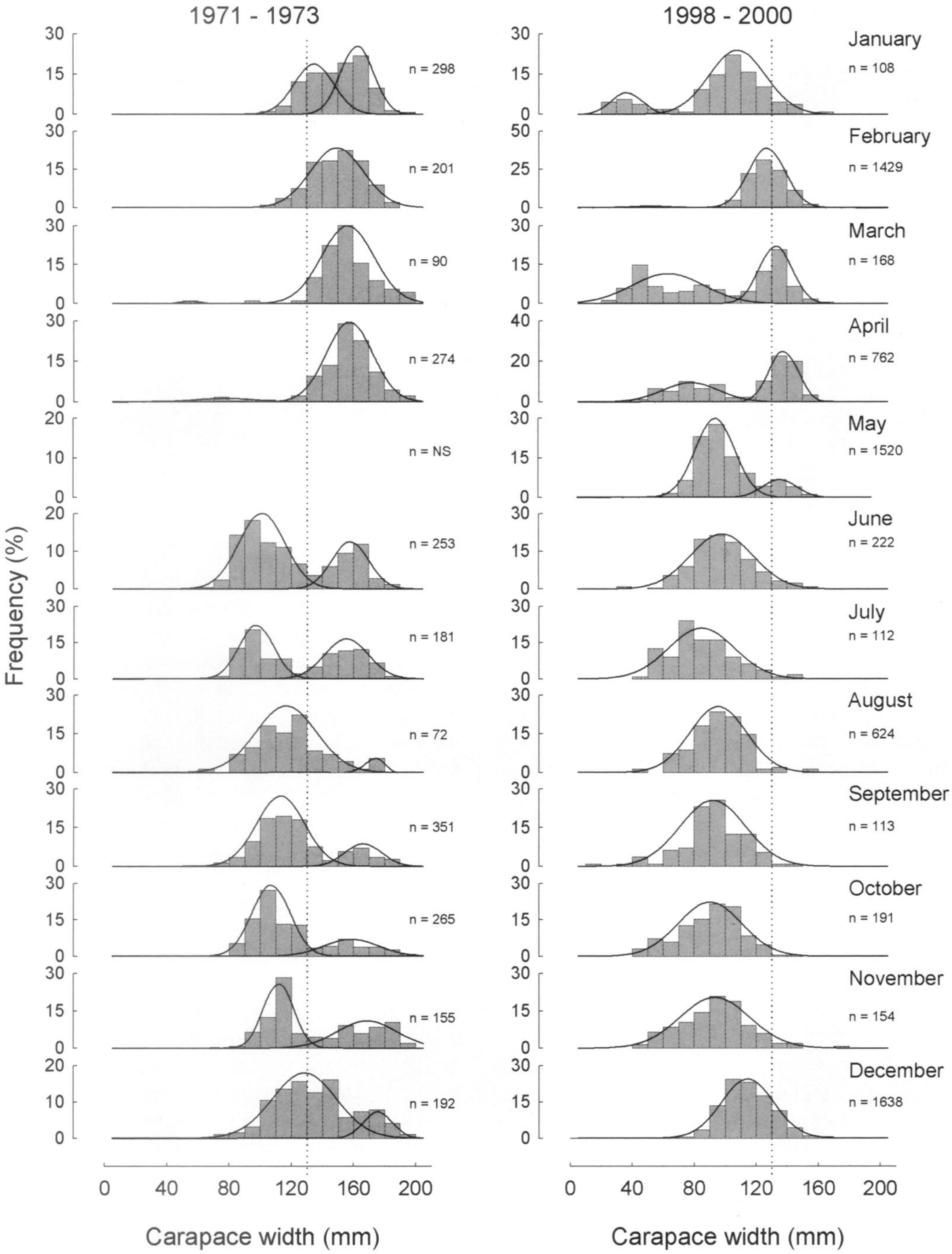

Fig. 2. Monthly carapace width-frequency histograms for female and male *Portunus pelagicus* in Cockburn Sound during the late 1970s and late 1990s. Normal distributions have been fitted to the carapace width frequency distributions of the one or two size cohorts present in each month in each period. The dotted line represents the minimum legal carapace width for retention. n = sample size. NS = no sample.

April. Secondly, 1+ crabs were scarcely caught after May in the late 1990s, whereas they were well represented in the ensuing months in the late 1970s (Fig. 2).

The very high coefficients of determination for the modified seasonal von Bertalanffy growth curves fitted to the mean *CW*s-at-age for *P. pelagicus* in the early 1970s and late

1990s, i.e., 0.977 and 0.964, respectively, showed that these curves provided a very good description for these size-at-age data for these two periods (Table 1).

The growth of *P. pelagicus* during early life was relatively rapid in Cockburn Sound in both the early 1970s and late 1990s, with the individuals in these two periods attaining, on average, *CW*s of 101 and 90 mm, respectively, by June when they were about six months old (Fig. 3). The size of *P. pelagicus* underwent essentially no change between seven and ten months of age, i.e., between early winter (June) and mid spring (October), but then increased progressively until the crabs were about 15 months old in March, by which month their *CW*s had reached, on average, 157 and 133 mm in the early 1970s and late 1990s, respectively (Fig. 3). Although the growth curves for *P. pelagicus* followed very similar seasonal trends in both periods, they were statistically different ($P < 0.05$), mainly because of a difference in their CW_∞s (Table 1).

Proportions of Legal-Sized *Portunus pelagicus*

The numbers of female and male *P. pelagicus* greater than the minimum legal size for retention (*MLS*), i.e., 130-mm *CW* for commercial fishers, relative to the total catches of the corresponding sex in each corresponding month of the year were greater during the early 1970s than the late 1990s (Fig. 4). However, during the late 1990s, the contributions of these large individuals rose progressively between January and April in females, but declined after February with males (Fig. 4).

Proportions and Size of Ovigerous *Portunus pelagicus*

The carapace widths of ovigerous females caught in Cockburn Sound in the early 1970s ranged widely from 90 mm to 209 mm, and their distribution was bimodal, with modal classes of 120–129 mm and 150–159 mm (Fig. 5). In contrast, in the late 1990s, the carapace widths of ovigerous females were more restricted in range, i.e., 77–170 mm, and their distribution was essentially unimodal, with a modal width class of 110–129 mm (Fig. 5). These differences between the early 1970s and late 1990s are reflected in significant differences ($P < 0.01$) in the mean carapace widths of ovigerous females ± 95% CI, i.e., 139 ± 3.3 mm and 114 ± 3.0 mm, respectively.

Table 1. Growth parameters and total sums 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 in the early 1970s and late 1990s. CW_∞ is the asymptotic carapace width, K is the curvature parameter, t_0 determines the theoretical age at which the estimated carapace width is zero, C is 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.

Sampling period	1971–1973	1998–2000
CW_∞	176.6	145.8
t_0	0.6	0.6
K	1.8	1.6
C	1.0	1.0
t_s	1.9	1.8
R^2	0.977	0.964
Total SS	670.2	678.1

Discussion

Increases in Density

The monthly catches obtained for *P. pelagicus* by the commercial trawl in each month in Cockburn Sound during the early 1970s were recorded by the Western Australian Department of Fisheries solely as the mean catch per hour for each month. Although these catch rates could thus be used to calculate the overall mean densities in each month during that period, they could not provide an estimate of the variation around each of those mean monthly densities. There were thus no replicated density values for each month in the 1970s that could be used to test statistically whether the densities of *P. pelagicus* in this period differed significantly from those in the late 1990s. However, it is highly relevant that the mean monthly densities of *P. pelagicus* in Cockburn Sound, derived from catches obtained by the commercial trawl in four months, exceeded by factors of between 2 and 12, those determined from commercial trawl catches in the corresponding months for which there were comparable data in the early 1970s. Furthermore, the mean densities of *P. pelagicus*, derived for each calendar month from the catches obtained by the small otter trawl over 24 months in the late 1990s, which were probably slightly more conservative than those derived from the large commercial trawl catches in that period, were also greater, and generally by a factor of between 3 and 11, than those determined for each calendar month using the commercial trawl catches in the early 1970s. There is thus overwhelming circumstantial evidence that the very marked rise that occurred

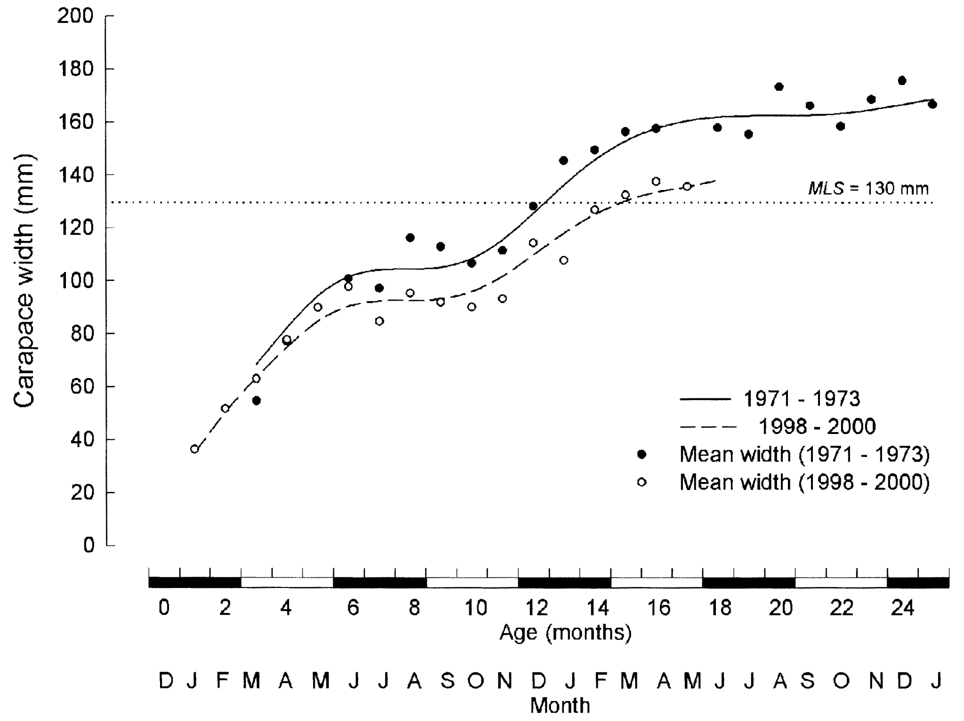

Fig. 3. Seasonal von Bertalanffy growth curves fitted to the monthly means for the carapace widths-at-age of *Portunus pelagicus* caught in the early 1970s and late 1990s in Cockburn Sound. The mean monthly carapace widths for the two periods, which are shown on the figure, were derived from the normal distributions fitted to the carapace width frequency histograms. *MLS* = minimum legal size for retention.

in the catches of *P. pelagicus* in Cockburn Sound between the early 1970s and late 1990s reflects a marked increase in the densities of this species.

Changes in Size Composition

Although few new 0+ recruits were caught in January to April in the early 1970s, considerable numbers of these small crabs were caught in January, March, and April, but not February, in the late 1990s. It is possible that, because 0+ crabs were in far greater densities in Cockburn Sound during the late 1990s than early 1970s, they exhibited a greater tendency to move out from their nearshore, nursery habitats into deeper waters in the latter period. However, a tendency to move offshore earlier in the late 1990s may also reflect the fact that the seagrass meadows in nearshore waters, which are often inhabited by small portunids (Etherington and Eggleston, 2000), had declined in area between the early 1970s and late 1990s (Kendrick *et al.*, 2002).

More importantly, the size-frequency distributions demonstrated that, while 1+ and subsequently 2+ crabs were obtained in substantial numbers between June and December in the early 1970s, they declined markedly in numbers in May and were rarely represented after this month in the late 1990s (Fig. 2). Indeed, the bimodal size-frequency distributions in November and December in the early 1970s, with the largest crabs having carapace widths of nearly 200 mm, strongly suggest that an appreciable number of crabs lived for at least two years in that period. In contrast, the size distributions in November and December in the late 1990s comprised a single size cohort whose maximum carapace width was less than 160 mm and represented crabs that were predominantly about one year old. Because the modal carapace width class of 1+ crabs increased between January and March in the late 1990s, with the result that it exceeded the *MLS* for the first time in the last of these months, it is assumed that the subsequent decline in the abundance of these crabs in this period is due to heavy fishing mortality.

The mean densities recorded for May in the late 1990s, on the basis of both commercial trawl and otter trawl data, were exceptionally high

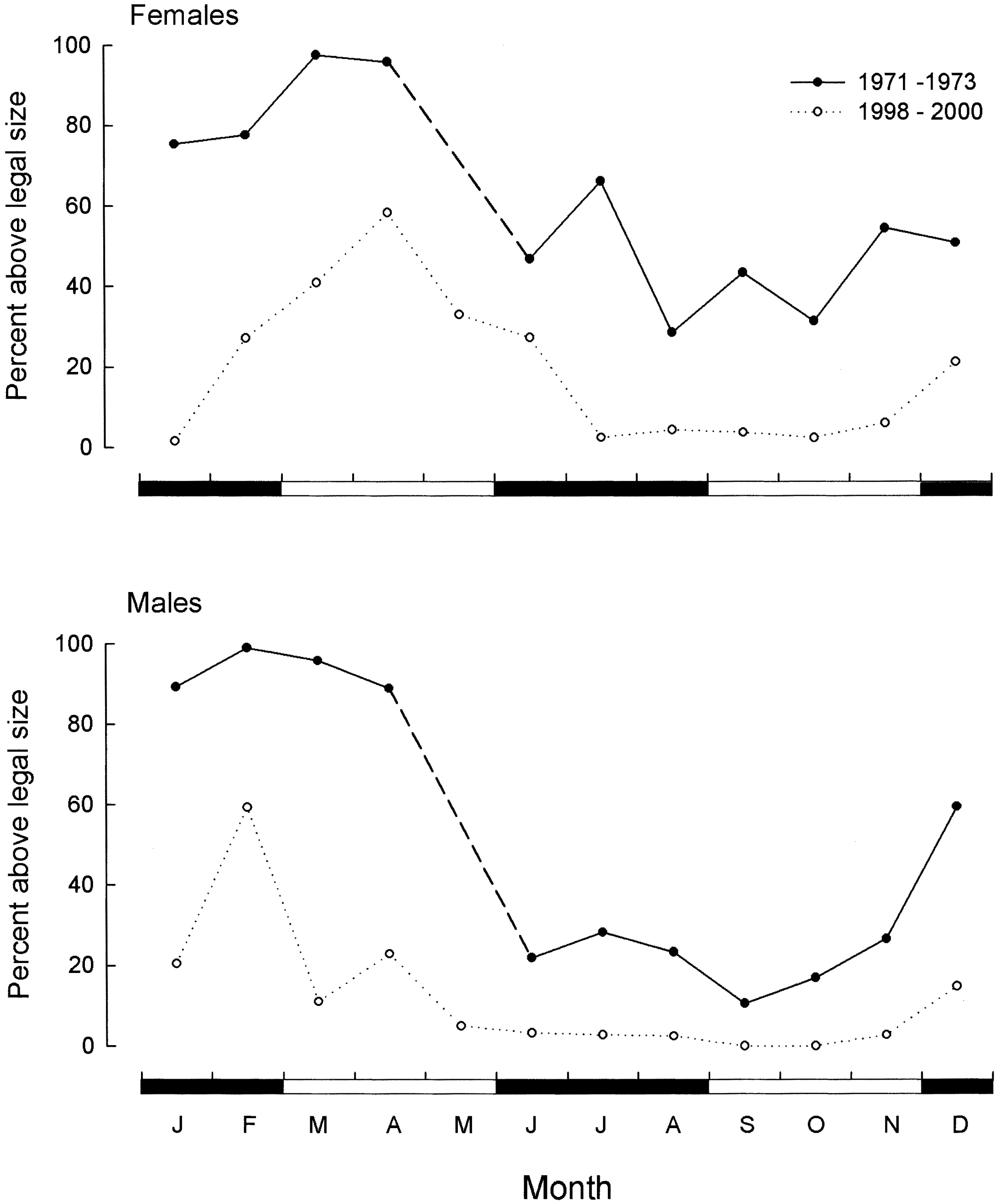

Fig. 4. Monthly percentages of legal-sized female and male *P. pelagicus* in the trawl catches in the early 1970s and late 1990s.

(Fig. 1a). It is proposed that the large catches in this month reflected a temporary immigration of crabs into this northern part of Cockburn Sound in late autumn and that this was probably related to an emigration of crabs from the Swan River Estuary just to the north of Cockburn Sound. Such a conclusion would be consistent with the fact that, in the following month, the numbers of crabs in the southern part of Cockburn Sound underwent a very pronounced increase (de Lestang, unpublished data).

The trends exhibited by the data shown in Fig. 1b illustrate clearly the differential effects of fishing mortality on our very broad estimates of the biomass of *P. pelagicus* in Cockburn Sound throughout the year in the early 1970s

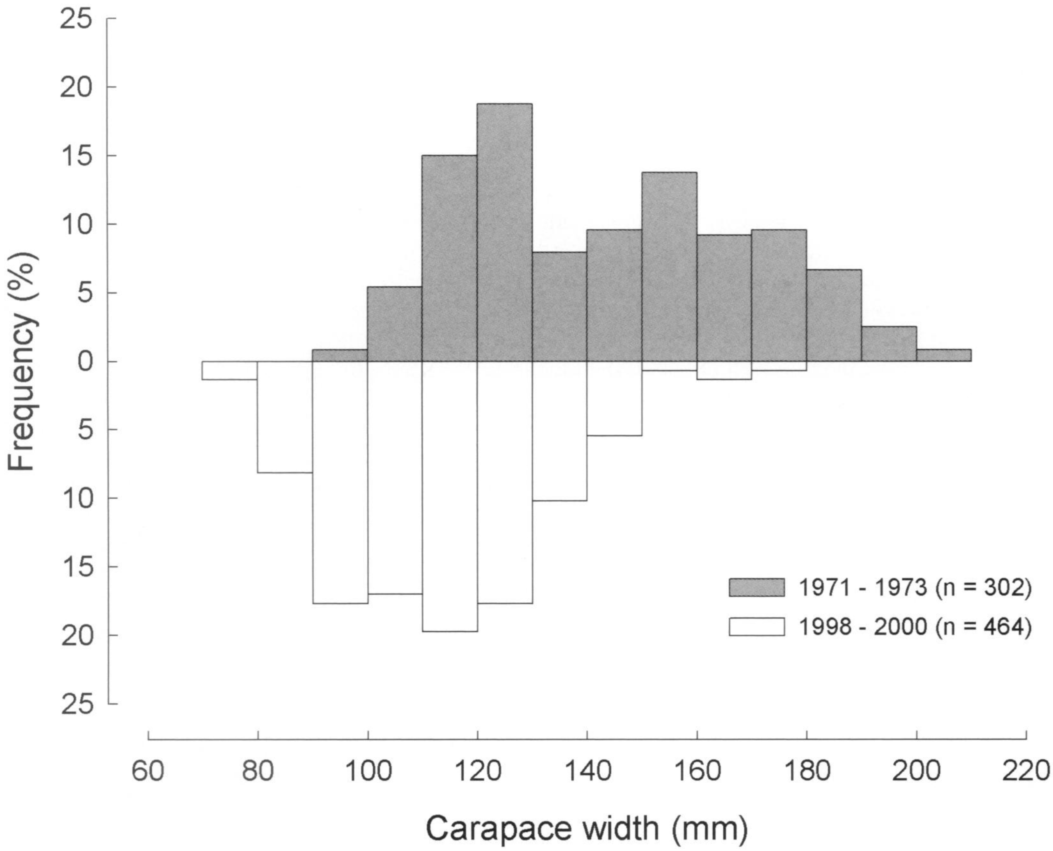

Fig. 5. Carapace width-frequency histograms of ovigerous females caught in Cockburn Sound during the early 1970s and late 1990s.

and late 1990s. For example, it was particularly relevant that the estimates of biomass 1000 m^{-2} in March, April, and June were greater in the early 1970s than the late 1990s, whereas the opposite situation became increasingly the case in the ensuing calendar months. The greater biomass in March to June than in the following seven months during the early 1970s can be attributed to the fact that a substantial number of crabs greater than the minimum legal size for capture were still present within Cockburn Sound during the latter months and were thus available for capture by fishers. In contrast, the increase in biomass that occurred in the months after July in the late 1990s was presumably related to the fact that, because of heavy fishing pressure in the early months of the year, few crabs were left above the *MLS* after July and the 0+ age class, which was not subjected to fishing pressure, was increasing in body size and thus biomass.

In the context of fishing pressure, it is highly relevant that, in the late 1990s, the percentage of female crabs above the *MLS* did not start decreasing until after April, whereas that of males above this size limit declined markedly after February. The later decline in the relative abundance of 1+ female crabs in the late 1990s can be attributed to the fact that many of these crabs are ovigerous during this period and fishers are thus obliged to return them to the water and that, for a period after their immediately ensuing moult, their flesh is undesirably soft.

Changes in Growth and Size at Sexual Maturity

Any comparisons between the seasonal von Bertalanffy growth curves for *P. pelagicus* in Cockburn Sound in the early 1970s and late 1990s must take into account the fact that, as a result of much heavier fishing pressure, a relatively far greater number of larger crabs will have been removed from the population in the latter than former period. Thus, to ascertain whether the very marked increase in density of *P. pelagicus* in this embayment over the last 20 to 30 years was accompanied by a reduction in the growth rate of this species, such comparisons should focus on the period before this species attains the *MLS*. As November was the last month when only a small number of 0+ crabs exceeded the *MLS*, comparisons were made between the sizes attained by this month, at which time the crabs would have been nearing the end of their first year of life. From the growth curves, *P. pelagicus* would have attained, on average, by November about 115-mm *CW* in the early 1970s, but only about 101-mm *CW* in the late 1990s, which represents a substantial difference of 14 mm.

Because *P. pelagicus* grew less during the first year of life in the late 1990s than early 1970s and spawning peaked at about the same time in both periods, *P. pelagicus* would be expected to attain maturity at a smaller size in the late 1990s than early 1970s. Although there are no data on the proportions of female crabs that underwent a pubertal moult in the early 1970s, and which could thus be used to determine the size at which these crabs attain maturity, the minimum *CW* of ovigerous females has been used as a proxy for the minimum size of female crabs at maturity (Jones and Simons, 1983). The minimum *CW* of ovigerous females in the late 1990s was 77 mm and thus appreciably less than that of such crabs in the early 1970s, when it lay at some point in the 90–99-mm carapace width class (Penn, 1977).

The percentage of ovigerous female crabs with a $CW > 150$ mm was far less in the late 1990s (2.6%) than early 1970s (42.0%). Furthermore, the distribution of the *CW*s of ovigerous female crabs was largely unimodal in the late 1990s (modal class = 110–129 mm) and essentially bimodal in the early 1970s (modal classes = 120–129 mm and 150–159 mm). The modal *CW*s of ovigerous females in the late 1990s thus encompasses the approximate mean *CW* of crabs during their first maturity instar, i.e., 111 mm (de Lestang *et al.*, 2003a). The fact that the first modal *CW* class for ovigerous females was greater in the early 1970s than late 1990s is presumably due to the faster rate of growth exhibited in that earlier period. It would then follow that the *CW* distribution that produced the second modal *CW* class for ovigerous females in the early 1970s corresponds to crabs that had entered their second maturity instar.

In summary, this study has shown that the density of *P. pelagicus* in Cockburn Sound has increased markedly over the last 20–30 years, even though the commercial catches of this portunid rose sharply during this period. It thus appears relevant that heavy fishing pressure on finfish stocks in Cockburn Sound during that period (Department of Fisheries, Western Australia) has apparently resulted in a pronounced decline in the abundance of species such as *Pagrus auratus*, *Platycephalus* spp., *Glaucosoma hebraicum*, *Sillago* spp., *Rhabdosargus sarba*, and *Argyrosomus japonicus*, which are major predators of *P. pelagicus* (Kailola *et al.*, 1993). Yet, the possibility that the increased densities of crabs may also reflect an increased abundance of food, such as polychaetes, cannot be ignored. Our data also imply that an increase in fishing pressure on *P. pelagicus* has led to a marked reduction in the relative abundance of the largest and, in the case of females, most fecund individuals. Finally, the increase in density of *P. pelagicus* has been accompanied by a reduction in growth rate and size at maturity.

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