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LIFE HISTORY AND REPRODUCTIVE BIOLOGY OF THE GILGIE, *CHERAX QUINQUECARINATUS*, A FRESHWATER CRAYFISH ENDEMIC TO SOUTHWESTERN AUSTRALIA

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A B S T R A C T

The gilgie, *Cherax quinquecarinatus*, a freshwater crayfish endemic to southwestern Western Australia, occupies a wide range of permanent and temporary aquatic environments. Reproductive and population biology parameters were determined in Bull Creek, southwestern Western Australia. Crayfish were collected monthly from May 2002 to April 2003. The seasonal von Bertalanffy growth curve, fitted for the first 14 months of life for female and male *C. quinquecarinatus*, had respective curvature parameters (K) and asymptotic orbital carapace lengths OCL_∞ (CL_∞) of 0.29 and 59.6 (71.2) mm for females and 0.25 and 73.8 (87.0) mm for males, respectively. This equates to OCLs (CLs) of females and males at age 12 months of 14.7 (19.2) and 14.1 (18.4) mm, respectively. *Cherax quinquecarinatus* was found to mature at a relatively small size, with the length at which 50% of individuals mature L_{50} for females and males being 18.8 and 24.5 mm OCL (24.1 and 30.9 mm CL), respectively. The majority of *C. quinquecarinatus* thus first spawned at the end of their second year of life. The potential (ovarian) and pleopodal fecundities of *C. quinquecarinatus* were relatively low compared to other freshwater crayfish species of similar size, being 81.7 (± 5.93 S.E.) and 77.1 (± 13.76 S.E.), respectively. *Cherax quinquecarinatus* underwent an extended spawning period, from late winter to late summer (i.e., August to February), with three spawning events facilitated by short brood and rapid gonadal recovery periods, traits consistent with other crayfish species able to exist in temporary environments. Estimates of total mortality (Z) were relatively high at 2.34 and 1.95/year based on age-converted catch curves for females and males, respectively, with a considerable proportion of this attributed to fishing mortality (exploitation rates of 0.76 and 0.75 for females and males, respectively). *Cherax quinquecarinatus* underwent a life-history strategy that showed characteristics of both a summer (r- strategist) and winter (K-strategist) brooder.

All native freshwater crayfish within Western Australia are endemic and are naturally restricted to the southwestern corner of the State. They encompass two genera: six species within the genus *Cherax*, the most widespread genus within Australia (Riek, 1967, 1969; Austin and Knott, 1996; Austin and Ryan, 2002); and all five (relatively small, burrowing) species of the genus *Engaewa* (Riek, 1967; Horwitz and Adams, 2000). This high (100%) endemism in southwestern Australia is likely to be the result of the long biogeographic separation of this coastal region of southwestern Western Australia (Crandall *et al*., 1999). Furthermore, *Cherax* species naturally occurring in Western Australian are monophyletic and clearly separated from the other *Cherax* species (Crandall *et al*., 1999). The extremely high rate of endemism (100%) of freshwater crayfish in this region, coupled with known processes threatening the aquatic systems (Crandall *et al*., 1999; Horwitz and Adams, 2000), ensures this biogeographic region being rated among the four most important for the conservation of Australian freshwater crayfish (Whiting *et al*., 2000).

Despite the conservation and ecological importance of the freshwater crayfish species of Western Australia (aside from that on the larger, recreationally and commercially important marron *C. cainii* (*sensu* Austin and Ryan, 2002) formerly known as *C. tenuimanus*), little is known about the biology of other wild populations (e.g., Morrissy, 1975; Beatty *et al*., 2003). This is surprising as these other endemic species are often locally abundant, growing to sizes that allow them to be targeted by recreational fishers. Furthermore, these endemic species are likely to be as ecologically important as other freshwater crayfishes (e.g., Momot, 1995; Rabeni *et al*., 1995).

Cherax cainii and the gilgie *Cherax quinquecarinatus* Gray, 1845, are the most naturally widespread species of freshwater crayfish in Western Australia. *Cherax quinquecarinatus* exhibits a large intraspecific genetic and morphological variation that has been shown to be as great as that exhibited between different freshwater crayfish species (Austin and Knott, 1996). Furthermore, *C. quinquecarinatus*, which has a propensity to burrow, occupies the widest range of habitats of any of its congeners in the region (Austin and Knott, 1996). These include permanent rivers, lakes, and streams, and naturally ephemeral habitats inundated for only 5–7 months of the year (Riek, 1967; Austin and Knott, 1996; Morgan *et al*., 1998, 2000). Although *C. quinquecarinatus* is relatively small compared with *C. cainii*, it is comparable in size with other crayfish consumed by humans, e.g., *Pacifastacus leniusculus* (Dana, 1852) (see Lewis, 2002) and *Procambarus clarkii* (Girard, 1852) (see Huner, 2002). Its relatively large size, wide distribution, and occurrence in a wide range of habitats (where it is often locally abundant) have resulted in it being targeted by recreational fishers and forming an important component of the traditional diet of local Aboriginals (Meagher, 1974). Currently, there is no closed season and no minimum size limits on this species. The only fishery regulation pertaining to this species is a mixed bag limit of 4L of any other species aside from *C. cainii*.

The study aims to describe the reproductive biology and life-history strategy of *C. quinquecarinatus* in a permanent

urban stream that anecdotal evidence suggests is subject to intense fishing pressure.

Materials and Methods

Sampling Regime

Bull Creek (32°02′57.4″S, 115°52′20.4″E), selected as the study site, is an urban drain containing relatively high numbers of *C. quinquecarinatus* that are recreationally fished. Samples of *C. quinquecarinatus* were collected over a 1 km stretch of Bull Creek each month between May 2002 and April 2003 using a variety of methods to capture a representative sample of the population. Sampling was carried out with a back-pack electrofisher (*Smith Root Model 12-A*), box-style freshwater crayfish traps (mesh width 10 mm set overnight for about 14 h), and an invertebrate sweep net with a mesh size of 500 μm. Upon capture, animals were placed in a plastic box, and a random sample of up to 93 individuals was made with a fine mesh scoop-net. The subsample was then placed immediately in ice slurry and transported back to the laboratory for dissection. The orbital carapace length (OCL) (i.e., the distance from the posterior margin of the orbital region to the posterior margin of the branchiostegite) of the remainder of captured individuals was measured to the nearest 1 mm, the animals were then released at their site of capture. The water temperature, conductivity, and pH at a depth of 20 cm were recorded at three locations in Bull Creek on each sampling occasion.

Morphological Relationships

In order to determine the relationship between the OCL and the carapace length (CL) of *C. quinquecarinatus*, 437 animals were measured to the nearest 1 mm OCL and CL. To determine the relationship between the OCL and wet weight, individuals retained for further dissection were patted dry and weighed to the nearest 0.01 g. Subsequently, a number of regression models were tested for both sexes for the relationship between both OCL and CL and OCL and wet weight using the SPSS statistical package (Saila *et al*., 1988). The growth function that produced the highest coefficient of determination was used to describe those relationships. In order to determine whether differences existed between the sexes for those relationships, likelihood ratio tests (Cerrato, 1990) were used. If no significant differences between sexes were revealed, sexes were pooled and the model was refitted.

Reproduction

Reproductive Cycle.—In order to describe the temporal trend in the reproductive biology of *C. quinquecarinatus*, monthly samples of up to 61 and 38 females and males, respectively, were weighed to the nearest 0.01 g, their gonads were then removed and also weighed to the nearest 0.01 g. The monthly gonadosomatic indices (GSI) of mature and immature female and male *C. quinquecarinatus* were determined using the equation:

$$\mathrm{GSI} = 100\left(\frac{W_1}{W_2}\right) \tag{1}$$

where W_1 is the wet weight of the gonad and W_2 is the wet somatic weight.

Gonads were initially assigned, on the basis of their macroscopic appearance using the verified staging of Beatty *et al*. (2003) for the congener *C. cainii*, to one of seven stages. The seven stages were: I, virgin (immature); II, maturing virgin/recovering; III, developing; IV, developed; V, mature (gravid); VI, ripe (spawning); and VII, spent. Subsequent histological verification of the macroscopically assigned stages immediately prior to and during the spawning period (June to February, see Results) was undertaken via fixing a subsample of up to 30 ovaries of each stage in Bouin's fixative for 24 h and dehydrating in 70% ethanol. All fixed gonads were then embedded in wax and sectioned transversely at 6 μm, stained with Mallory's trichrome solution, and examined for intracellular development (see Beatty *et al*., 2003). The oocytes were examined at 100× magnification under a compound microscope, diameters of oocytes in each ovarian stage were measured on a viewing screen, and size-frequencies for each stage were plotted.

Size at First Maturity.—In order to accurately determine the OCL at which 50% (L_{50}) and 95% (L_{95}) of *C. quinquecarinatus* matured in Bull Creek, only those individuals captured immediately prior to and during the major spawning period from June to February (see Results) were used. Logistic regression analysis, using bootstrapping of 1000 random samples, was undertaken on the percentage of mature females (ovarian stages III–VII) and males (testes stages III–V) in 2 mm OCL increments. The logistic equation is:

$$P_L = \frac{1}{\left[1 + \mathrm{e}^{-\ln 19(L-L_{50})/(L_{95}-L_{50})}\right]} \tag{2}$$

where P_L is the proportion of *C. quinquecarinatus* with mature gonads during the reproductive period at OCL interval L, and L_{50} and L_{95} are the OCLs at which 50% and 95% of the population mature.

Fecundity.—The relationships between the ovarian (*OF*) and pleopodal (*PF*) fecundity and OCL of female *C. quinquecarinatus* were determined via manual counts of oocytes in un-spawned gonads of ovarian stages IV–VI immediately prior to and during the spawning period from June to February (see Results) for OCL *versus OF*; and by manual counts of eggs, larvae, or hatchlings attached to the pleopods of ovigerous individuals (captured during the spawning period from August to February) for OCL *versus PF*. In order to count unreleased oocytes, ovaries were placed in Bouin's fixative for 24 h and then counted under a dissecting microscope at 6.4× magnification. The numbers of unspawned oocytes (for *OF*) or released eggs, larvae, and hatchlings (for *PF*) of each individual were then plotted against its OCL, and a number of regression equations were fitted for each relationship, with the one that maximised the coefficient of determination (r^2) selected. The length and width of a random subsample of 50 eggs from five ovigerous females were measured to the nearest 0.1 mm, and the mean diameter was determined.

Temporal Pattern in Hepatosomatic Indices

Up to 58 female and 46 male *C. quinquecarinatus* captured monthly from Bull Creek were weighed to the nearest 10 mg; their hepatopancreases were removed and weighed, placed in individual foil cups, dried at 80°C for 24 h, and reweighed. The dry hepatosomatic index and percentage of hepatopancreatic moisture were determined using the equations:

$$H_d = 100\left(\frac{W_{dh}}{W_s}\right) \tag{3}$$

$$H_m = 100\left(\frac{W_h - W_{dh}}{Ws}\right) \tag{4}$$

where H_d is the dry hepatosomatic index, H_m is the percentage of hepatosomatic moisture, W_h is the wet weight of the hepatopancreas (g), W_{dh} is the dry weight of the hepatopancreas (g), and W_s is the wet somatic weight of the crayfish (g).

Growth

The monthly length-frequencies (OCL) of female and male *C. quinquecarinatus* were plotted in 2 mm increments for the duration of the study period. Those juveniles that were unable to be confidently sexed (about less than 10 mm OCL) were randomly assigned to either the female or male length-frequency distributions. Upon examination, one or two normal distributions could be fitted in each month and a modified version of the chi-squared method of Schnute and Fournier (1980) (as described in de Lestang *et al*., 2003) was used to fit the most appropriate normal distributions to the data.

Spawning initially occurred from August, with the progeny of this event subsequently contributing to the greatest 0+ recruitment (see Results and Discussion). Therefore, allowing a short, about one month, incubation period (an estimate based on the short period between multiple spawning events, see Results section), the 1st of September was assigned as the birth date. Cohorts were assigned as 0+ and 1+ based on the size distribution within the month relative to previous and subsequent months.

A modification of the von Bertalanffy growth curve equation (Hanumara and Hoenig, 1987, equation 5) was applied to the mean OCL distributions of the curves of the cohorts fitted to monthly length-frequency distributions. The moult frequency of freshwater crayfish is greatest in the first few months of life (Reynolds, 2002); therefore, the modification of the equation was undertaken so that it assumed that the maximum growth rate occurred in young *C. quinquecarinatus*, i.e., less than about five 5 months (de Lestang *et al*., 2003):

$$OCL_t = \begin{cases} OCL_\infty\left\{1-\exp\left[-\left\{\frac{K(t-t_0')}{12}+\frac{CK}{2\pi}\sin 2\pi\frac{(3)}{12}\right\}\right]\right\} & \text{if } t < t_s+3 \\ OCL_\infty\left\{1-\exp\left[-\left\{\frac{K(t-t_0')}{12}+\frac{CK}{2\pi}\sin 2\pi\frac{(t-t_s)}{12}\right\}\right]\right\} & \text{if } t \geq t_s+3 \end{cases} \quad (5)$$

where OCL_t is the OCL estimate at age t months, OCL_∞ is the asymptotic OCL, K is the curvature parameter, t_0 is the theoretical age at which the estimated OCL is zero ($t_0 = t_0' - (6C/\pi)\sin(0.5\pi)$), C determines the relative amplitude of the seasonal oscillation in growth (where $0 \leq C \leq 1$), and t_s determines the phase of seasonal oscillation (i.e., start of the convex segment of the sinusoidal oscillation) relative to t_0. A likelihood-ratio test (Cerrato, 1990) was used to determine whether the growth functions of females and males were significantly different. Growth curves were fitted to the length-frequency data using Solver in Microsoft Excel™.

Mortality

The instantaneous mortality rate (Z) was determined for female and male *C. quinquecarinatus* in Bull Creek using a catch curve (the natural logarithms of numbers surviving over age) (Beverton and Holt, 1957; Ricker, 1975). However, as length-frequency data precluded accurately identifying frequency at age, an age-frequency distribution was created via the generation of a length-converted catch curve (Pauly, 1983; King, 1995):

$$\ln\left[\frac{N_i}{\Delta t}\right] = \alpha - Zt_i \quad (6)$$

where N_i is the number of individuals in each 2-mm size class, Δt is the time taken to grow through the size class i, t_i is the relative age of the size class i (ages determined using the inverse of the modified seasonal von Bertalanffy growth equation with $t_o = 0$ as only relative ages are required), α is a constant, and Z is the instantaneous total mortality rate (1/year). The regression lines were fitted ignoring the ascending data points, as they represent younger age groups that were not fully recruited to the population, and the eldest two data points on each curve as they had very low frequencies (i.e., fewer than 10) (King, 1995).

The instantaneous natural mortality rate (M) was estimated using the empirical equation of Pauly (1980), who examined 175 fish stocks of 84 species in a wide variety of marine and freshwater waters and found a highly reliable equation to predict M based on von Bertalanffy growth parameters and mean water surface temperature. The equation is:

$$\ln(M) = -0.0152 - 0.279\ln(OCL_\infty) + 0.6543\ln(K) + 0.463\ln(T) \quad (7)$$

where OCL_∞ and K are the growth parameters of the modified seasonal von Bertalanffy growth equation and T is the average mean annual water temperature of Bull Creek. Subsequently, the instantaneous rate of fishing mortality (F, 1/year) was determined using the equation of King (1995):

$$F = Z - M \quad (8)$$

The exploitation rate (E) was determined using the equation (Quinn and Deriso, 1999):

$$E = \frac{F}{Z} \quad (9)$$

Results

Environmental Variables

The water temperatures in Bull Creek fell from a maximum of 24.2°C in January to 17.8°C in September (Fig. 1). During the study period, conductivity of the stream did not exceed 661.3 μScm^{-1}, and pH ranged 6.6–7.4. Sudden increases in water levels were only experienced in Bull Creek during and immediately following (up to 24 h) rainfall events.

Morphological Relationships

The sex ratio of the 2316 *C. quinquecarinatus* captured from Bull Creek during the current study was 1 female : 1.43 males. There was a significant difference (likelihood-ratio test, $P < 0.05$) between sexes for the relationship between the OCL and wet weight. The relationships between the OCL and wet weight of female and male *C. quinquecarinatus* were: $W = 6 \times 10^{-4} OCL^{3.0282}$ and $W = 4 \times 10^{-4} OCL^{3.2000}$, respectively. There was, however, no significant difference between the sexes for the relationship between OCL and CL (likelihood-ratio test, $P < 0.05$). The relationship between the OCL and CL for *C. quinquecarinatus* was: $OCL = 0.6308 CL^{1.0663}$.

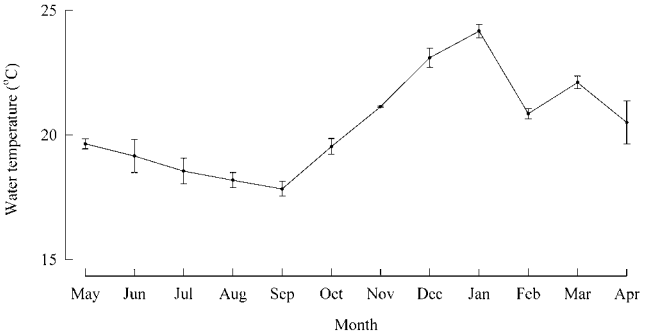

Fig. 1. The mean water temperature in Bull Creek during the sampling period.

Reproductive Biology

Macroscopic and Histological Description of Ovarian Development.—Histologically verified ovarian developmental stages closely corresponded to macroscopic stages based on intracellular development, in particular the presence of vitellin globules within the cytoplasm of oocytes of mature ovarian stages III–VI (Table 1, Fig. 2). Perinucleolar oocytes at the end of primary vitellogenesis (300–600 μm) were present in all mature stages of ovarian development including within ovigerous females (Figs. 2, 3).

Temporal Pattern in Reproductive Biology.—The mean GSI of mature female *C. quinquecarinatus* suggested that this species underwent a prolonged spawning period in Bull Creek between August and February and appeared to undergo three peaks in spawning during this period. In May, at the start of the study, the GSI of mature females was 0.48 (± 0.03 SE), increased slightly in July (0.66 ± 0.08) before increasing considerably to 1.95 (± 0.51) in August (Fig. 4). The mean GSI of mature females then declined to 1.20 (± 0.20) in September, again increased to 1.95 (± 0.33) in October, then declined to 1.27 (± 0.16) in November before increasing to 1.62 (± 0.3) in December (Fig. 4). In January, the GSI was 1.56 (± 0.27), which then declined to 0.44 (± 0.13) in February and then remained relatively constant. The mean GSI of males followed a similar pattern (Fig. 4).

Stage V ovaries (mature) were present in most months, i.e., June (2.9%), July (6.5%), August (42.9%), September (26.9%), October (17.9%), November (24.6%), December (15.4%), January (35.0%), and April (2.4%). However, stage VI (spawning) ovaries were first recorded in July (3.2% of females), which then increased to 7.1% in August and 11.5% in September (Fig. 5) with none recorded in subsequent months. The greatest proportion of ovigerous (stage VII) females was found in August (14.3%) before

Table 1. Macroscopic and histological descriptions of the oocytes of the different stages of ovarian development for female *Cherax quinquecarinatus*.

Ovarian stage	Macroscopic description	Maximum oocyte diameter (μm)	Histological description
I/II Immature/recovering	Ovaries very thin, string-like; some very pale orange oocytes discernable in an otherwise creamy ovarian matrix.	600	Oogonia, chromatin nucleolar and perinucleolar occytes dominate. Post-spent ovaries also contain atretic oocytes and post-ovulatory follicles.
III Developing (yolk vesicle)	Ovaries slightly thickened, with bright orange oocytes easily discernable.	1100	Perinucleolar oocytes that have undergone primary vitellogenesis dominate ovary. Oogonia oocytes still present.
IV Developed (late yolk vesicle)	Ovaries thickened with an obvious increase in size of oocytes, which are grey-green.	1800	Oocytes have distinct cytoplasmic yolk vesicle region and yolk granules present indicating secondary vitellogenesis. Perinucleolar oocytes present.
V Mature or gravid (yolk vesicle)	Ovaries slightly swollen, with oocytes becoming dark grey.	2200	Yolk granules dominate the cytoplasm indicating further vitellogenesis. Ovarian epithelium with follicle cells surround oocytes.
VI Ripe/spawning	Ovaries very swollen, containing very dark grey oocytes.	2500	Cytoplasm of oocytes dominated by yolk vesicles. Perinucleoar oocytes still present.
VII Spent	Ovaries thickened compared to virgins; orange oocytes of mixed sizes discernable in a predominantly creamy ovarian matrix.	1600	Post-ovulatory follicles present along with large unextruded ova and perinucleolar oocytes.

declining markedly in September (3.8%) and then increasing again in October (10.7%) and November (13.1%). While this suggests that some spawning had occurred between the July and August samples, the July sample was taken relatively late in the month, thus, it is most likely that spawning occurred from early August. Ovigerous females continued to be captured in December (7.7%), and a single ovigerous female was captured in February (Fig. 5). These data therefore suggest a protracted spawning period between August and February in Bull Creek.

The frequencies of testicular stages also indicated that the spawning period occurred from August to February and paralleled the trend of ovarian stage frequencies. For example, mature (stage V) testes occurred in 58.3% of males in August, declined to 2.6% of males in November before increasing to 14.4% in December and continued to be present in January and February, where they were present in 27.3 and 15.4% of males in those months, respectively (Fig. 5).

Size at Maturity.—The lengths at which 50% of females attained sexual maturity (L_{50}) was 18.8 mm OCL (24.1 CL, 95% confidence limits 17.9 and 19.7 mm OCL), and the male L_{50} was 24.5 mm OCL (30.9 mm CL, 95% confidence limits 23.3 and 25.6 mm OCL) (Fig. 6). The lengths at which 95% of females and males attained maturity (L_{95}) were 24.9 and 33.9 mm OCL (31.4 and 41.9 mm CL), respectively (Fig. 6). The smallest mature female and male captured measured 16 and 18 mm OCL (20.7 and 23.2 mm CL), respectively.

Fecundity.—The ovarian fecundity (*OF*) of 31 female *C. quinquecarinatus* (OCL 21–37 mm, CL 27–46 mm) in Bull Creek ranged from 39 to 149, with a mean of 81.7 (± 5.9). The relationship between the OCL and *OF* was: $OF = 0.3515OCL^2 - 13.469OCL + 172.1$, ($r^2 = 0.759$) (ANOVA $F = 43.79$, $P \leq 0.01$). The pleopodal fecundity (*PF*) of eight ovigerous females (OCL 24–33 mm, CL 30–41 mm) ranged from 40 to 147, with a mean of 77.1 (± 13.8). The relationship between the OCL and PF was: $PF = 0.0237OCL^3 - 0.8466OCL^2 + 208.9$, ($r^2 = 0.876$) (ANOVA $F = 17.66$, $P \leq 0.01$). Analysis of covariance (OCL as covariant) revealed that there was no significant difference between mean *OF* and *PF* ($F_{1,39} = 0.008$, $P = 0.929$). The mean diameter of 50 eggs attached to the pleopods of five female *C. quinquecarinatus* was 2.6 mm (± 0.01).

Temporal Pattern in Hepatosomatic Indices

The overall mean dry hepatosomatic indices of female and male *C. quinquecarinatus* were 2.5% (± 0.1) and 2.3% (± 0.1), respectively, which were significantly different (ANOVA, $F_{1,634} = 9.79$, $P < 0.01$). The mean dry hepatosomatic indices of both sexes were variable from May before reaching a minimum of 1.8% (± 0.1) and 1.5% (± 0.1) in October and August for females and males, respectively (Fig. 7). The mean dry hepatosomatic indices then rose progressively to reach a maximum in February, being 3.5% (± 0.2) and 3.3% (± 0.2) for females and males, respectively (Fig. 7). The mean dry hepatosomatic indices of both sexes generally then experienced a progressive decline (with the exception of a slight rise in June). The temporal trend in the percentage of hepatopancreatic moisture was effectively the inverse of the trend in the dry hepatosomatic indices for both females and males (Fig. 8).

Growth

Due to the considerable overlap of older length-frequency cohorts, the seasonal von Bertalanffy growth curves of female and male *C. quinquecarinatus* could be fitted confidently up to age 14 months (Figs. 9, 10), with the growth curves providing a good fit to these data given the high coefficients of determination ($r^2 = 0.99$) (Fig. 10, Table 2). The likelihood ratio test revealed that the growth curves for females and males were significantly different ($P < 0.01$). The seasonal von Bertalanffy growth curve revealed *K* for females and males of 0.29 and 0.25, respectively (Table 2). Considering that the von Bertalanffy growth curve could only be confidently fitted up to 14 months, the

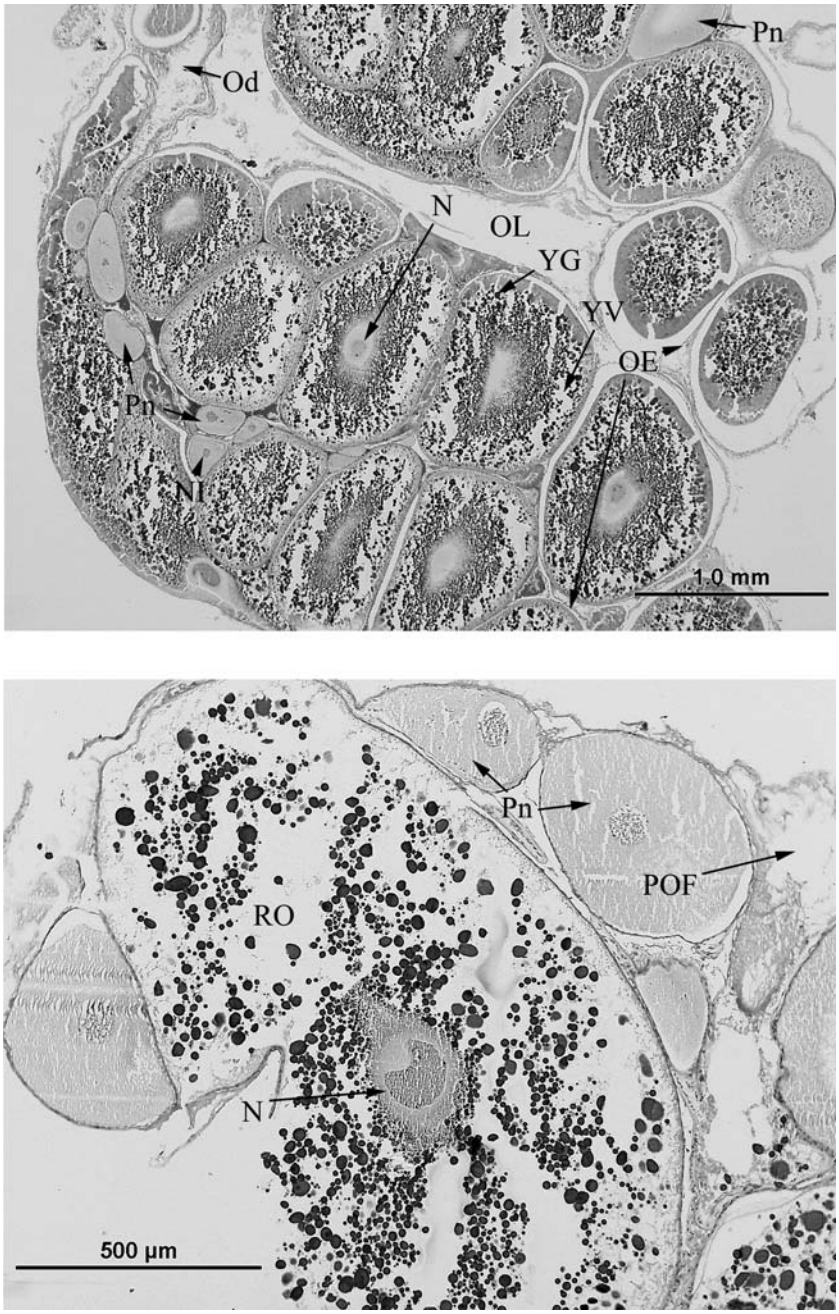

Fig. 2. Microscopic characteristics of the ovarian developmental stages IV and VII of *Cherax quinquecarinatus* from Bull Creek. Pn = perinucleolar oocyte; N = nucleus; NI = nucleoli; YG = yolk granule; YV = yolk vesicle; POF = post-ovulatory follicle; FC = Follicle cell; OE = Ovarian epithelium; OL = Ovarian lumen.

OCL_∞ values of 59.6 and 73.8 mm (CL_∞ of 71.2 and 87.0 mm) for females and males, respectively, were relatively close to the maximum observed in the field, with maximum sizes of 43 and 48 mm OCL (52 and 58 mm CL) for females and males, respectively.

Juvenile (0+) *C. quinquecarinatus* were first captured in Bull Creek in December with a size range of 2–6 mm OCL (mean of 4.6 mm OCL) (Fig. 9). The 0+ cohort then progressively increased in size in January and February, displaying a size range of between 2–12 and 2–14 mm OCL and a mean of 6.4 and 7.4 mm OCL in those months (Fig. 9). The seasonal von Bertalanffy growth curve revealed that the 0+ cohort of females and males reached 14.7 and 14.1 mm OCL in September at about one year of age, respectively (Fig. 10). By November, at 14 months of age, females and males had reached 15.5 and 15.3 mm OCL, respectively (Fig. 10).

Mortality

The *Z* values for females and males were 2.34 and 1.95/year (Fig. 11), whilst the empirical estimates of *M* for female and male *C. quinquecarinatus* were 0.55 and 0.48/year, re-

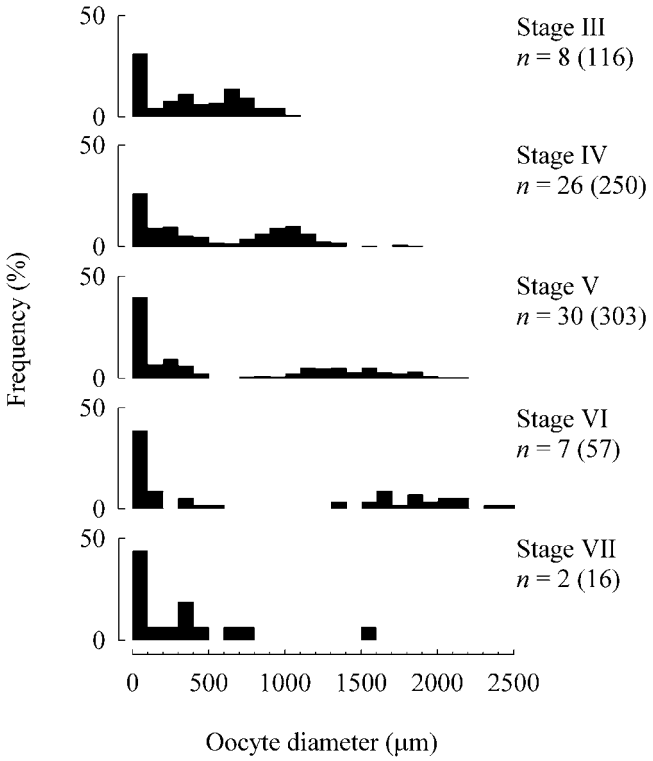

Fig. 3. Size-frequency distribution of oocytes in mature ovarian stages (III–VII) of female *Cherax quinquecarinatus* in Bull Creek.

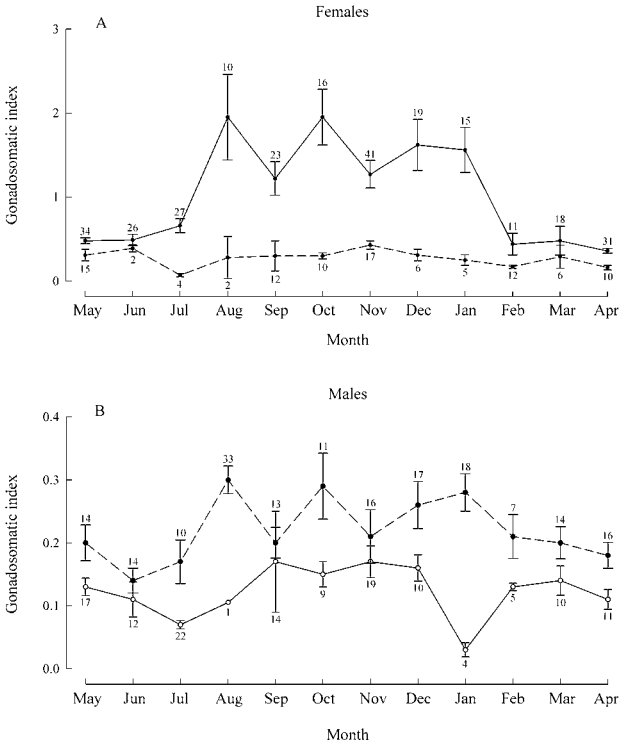

Fig. 4. Mean gonadosomatic indices (± 1 S.E.) for female (A) and male (B) *Cherax quinquecarinatus* in Bull Creek with immature (i.e., gonad stages I/II, lower line) and mature/maturing (i.e., gonad stages III–VI, upper line).

spectively (Table 2). The estimates of F and E for *C. quinquecarinatus* were 1.78/year and 0.76 for females and 1.47/year and 0.75 for males.

Discussion

Riek (1967) and Austin and Knott (1996) considered that *C. quinquecarinatus* (*sensu* Austin and Knott, 1996) had the widest natural distribution of all of the crayfishes endemic to the southwest of Western Australia. Furthermore, these authors reported that this species occurred in almost all types of aquatic systems that contained water for at least part of the year. Indeed, Austin and Knott (1996: 252) noted, "In comparison with the other species *C. quinquecarinatus* occurred at sites that have scores that span almost the full range of variation depicted on this first axis, which reflects that over its distribution this species can be found in habitats that range from semi-permanent swamps to deep rivers."

The utilisation of unpredictable, temporary environments or stable, permanent environments is associated with *r*- and K-selected species, respectively (MacArthur and Wilson, 1967; Pianka, 1970). Furthermore, summer-brooding crayfishes often display traits typical of *r*-strategists, whereas winter-brooding crayfishes display traits typical of K-strategists (Honan and Mitchell, 1995a). However, as mentioned, a species may display traits intermediate between these life-history strategies or display a mixture of traits typical of one group or the other. For example, the sympatric *Cherax cainii* occupies permanent aquatic systems (Austin and Knott, 1996), has a long, synchronised brooding period (Morrissy, 1970, 1975; Beatty *et al.*, 2003) and a large maximum size, weighing up to at least 2 kg (Coy, 1979), characteristics typical of a K-strategist and winter-brooding crayfish; however, it also broods in spring and summer and has a rapid growth rate, which are traits typical of a summer brooder (Morrissy, 1975; Beatty *et al.*, 2003).

The results of this study of one *C. quinquecarinatus* population further support the notion that a crayfish species may display characteristics that are typical of either life history or brooding groups or intermediate between them. This helps explain the success of this species within its natural range. That is, the combinations of *r*-selected and K-selected life-history strategies exhibited by this species are particularly well suited for life in the variable aquatic habitats found in southwestern Western Australia. However, it must be noted that many crayfish species show inter-population variation in many of their traits, and that Austin and Knott (1996) commented on the large degree of genetic and morphological variation exhibited by *C. quinquecarinatus*. It is therefore likely that the life-history characteristics described in this study, and summarised below, will also vary between populations, and in particular with those populations occurring within temporary habitats. Such plasticity would further increase this species' ability to successfully occupy a range of aquatic systems.

Reproductive Biology

Age at First Maturity.—The young age (and small size) at first maturity of *C. quinquecarinatus*, i.e., at the end of their second year of life (at 18.8 and 24.5 mm OCL for females and males, respectively), is considered to be advantageous

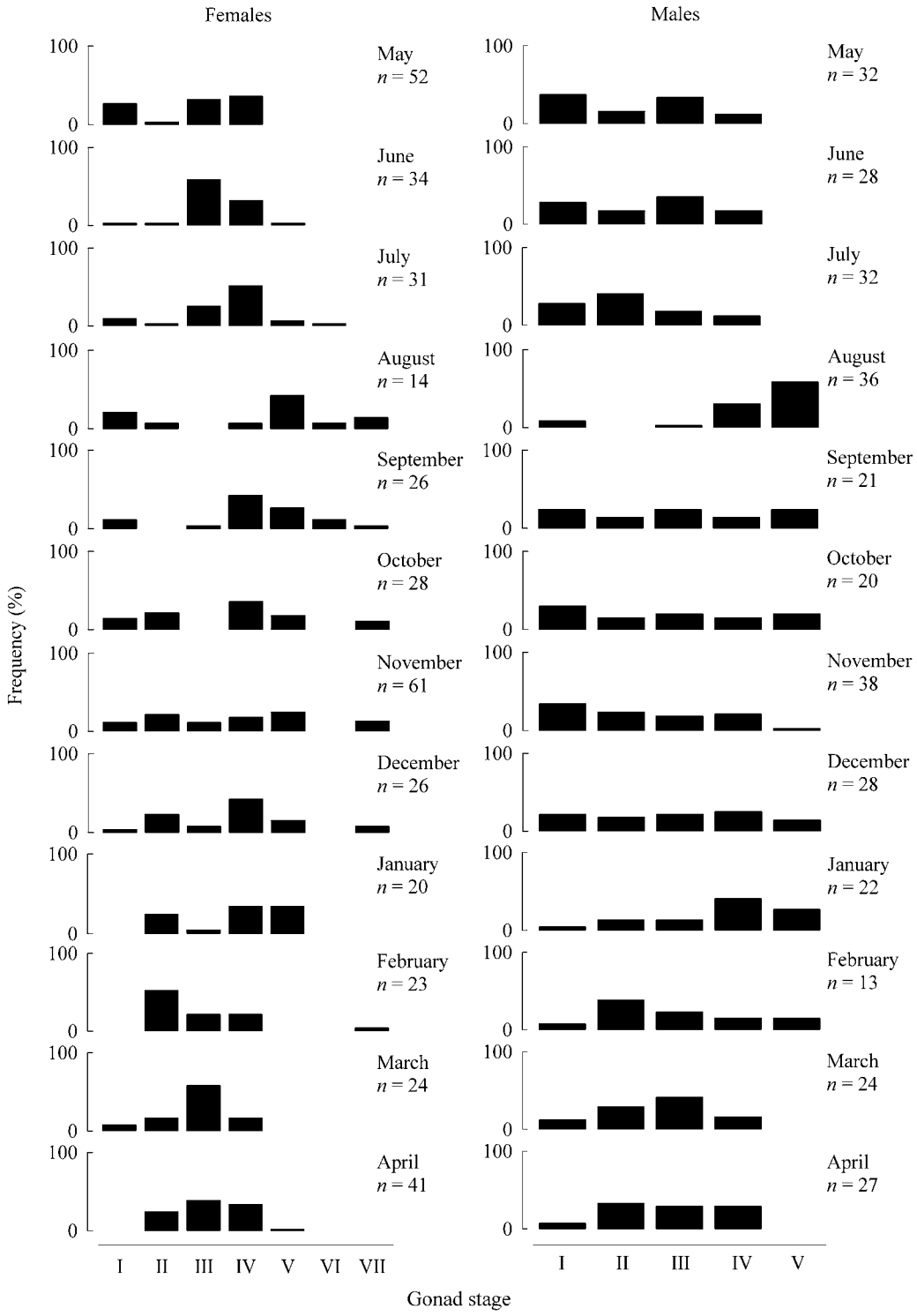

Fig. 5. Monthly frequency of different gonad developmental stages of female and male *Cherax quinquecarinatus* in Bull Creek.

in highly seasonal waterbodies that annually dry for extended periods. This is typical of summer-brooding crayfish species (Honan and Mitchell, 1995a) and *r*-strategists (Pianka, 1970). The relatively rapid attainment of maturity and the resultant short generation times enable *r*-strategists to increase rapidly in number and thereby take advantage of temporary habitats (Pianka, 1970). Whilst particularly suited for life in ephemeral systems, the *r*-strategy of multiple spawning ensures that this species can produce large numbers of offspring in permanent water bodies, many of which contain the larger, more fecund *C. cainii* (Beatty *et al*., 2003).

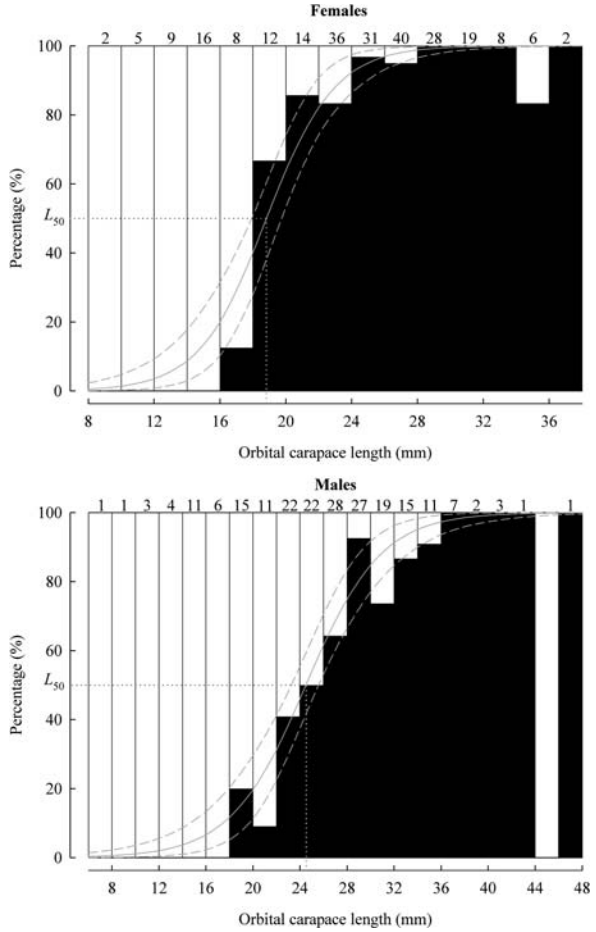

Fig. 6. Percentage contributions of immature (i.e., gonad stages I/II) and maturing/mature (i.e., stages III–VII) female and male *Cherax quinquecarinatus*, in sequential 2 mm OCL (L) intervals, immediately prior to and during the breeding season, i.e., June to February. N.B., the logistic curve and accompanying 95% confidence limits are shown, and the number of *C. quinquecarinatus* in each length interval is given at the top of each column.

Spawning Regime.—*Cherax quinquecarinatus* in Bull Creek had an extended spawning period (*r*-strategist) ranging from early August until the end of summer (February) with clear peaks occurring in August, October, and December/January. These peaks were indicative of multiple spawning events as evidenced by peaks in GSIs and histological staging that showed the perennial presence of oocytes at the end of primary vitellogenesis in mature females. A prolonged summer breeding period is typical of Australian summer-brooding species (Honan and Mitchell, 1995a) and would allow *C. quinquecarinatus* to successfully occupy the wide variety of aquatic habitats found throughout its range, including both those that undergo relatively short periods of inundation or are permanent.

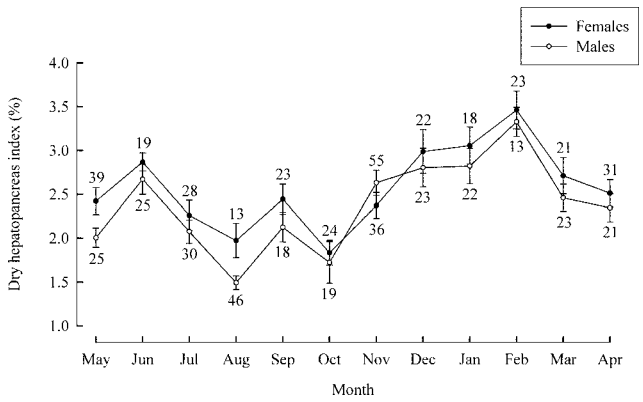

Fig. 7. Dry hepatosomatic indices of female and male *Cherax quinquecarinatus* in Bull Creek.

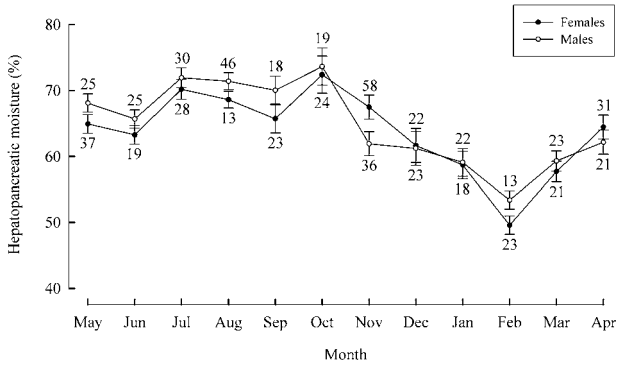

Fig. 8. Hepatosomatic moisture content (percent) of female and male *C. quinquecarinatus* in Bull Creek.

The relatively short length of time between multiple spawning events during the breeding period is comparable to that previously recorded for the summer-brooding congener *C. destructor* Clark, 1936 (about 60 days under laboratory conditions, Mitchell and Collins, 1989). In that study the short period between spawning events in *C. destructor* was facilitated by the perennial presence in mature gonads of oocytes that had undergone the relatively slow process of primary vitellogenesis that then underwent a rapid one–two week period of secondary vitellogenesis following moulting or the release of brood (McRae and Mitchell, 1995). Similarly, the constant presence of oocytes (about 300–600 μm) in mature (stage III–VII) *C. quinquecarinatus* that had undergone the relatively slow process of primary vitellogenesis would have allowed relatively rapid postspawning ovarian development, a reduced interspawning period, and multiple spawning in Bull Creek.

Fecundity.—Relative to body size, the mean pleopodal fecundity of *C. quinquecarinatus* recorded during the current study was relatively low (K-strategist) ranging 40–147 with a mean of 77 (female size range of 30–41 mm CL). This compares with the following: size adjusted (weight of 39.5 g) mean pleopodal fecundities of populations of *C. destructor* ranging 360–593 eggs (Austin, 1998); mean pleopodal fecundities ranging 110–190 for *Pacifastacus leniusculus* in various studies (summarised in Lewis, 2002); 55–575 pleopodal eggs on female *Orconectes rusticus* (Girard, 1852) with the maximum size of the species being 51 mm CL (Hamr, 2002); and 50–600 eggs on female *Procambarus clarkii* ranging from at 60–120 mm TL, respectively (Huner, 2002). The mean diameter of pleopodal eggs recorded here (2.6 mm) is moderately large (K-strategist) compared with similar sized species (cf a mean of 2.4 mm for *O. rusticus* (Corey, 1987) and a mean of 1.9 mm in *P. clarkii* (Noblitt *et al*., 1995). Lower fecundities and larger eggs are typically

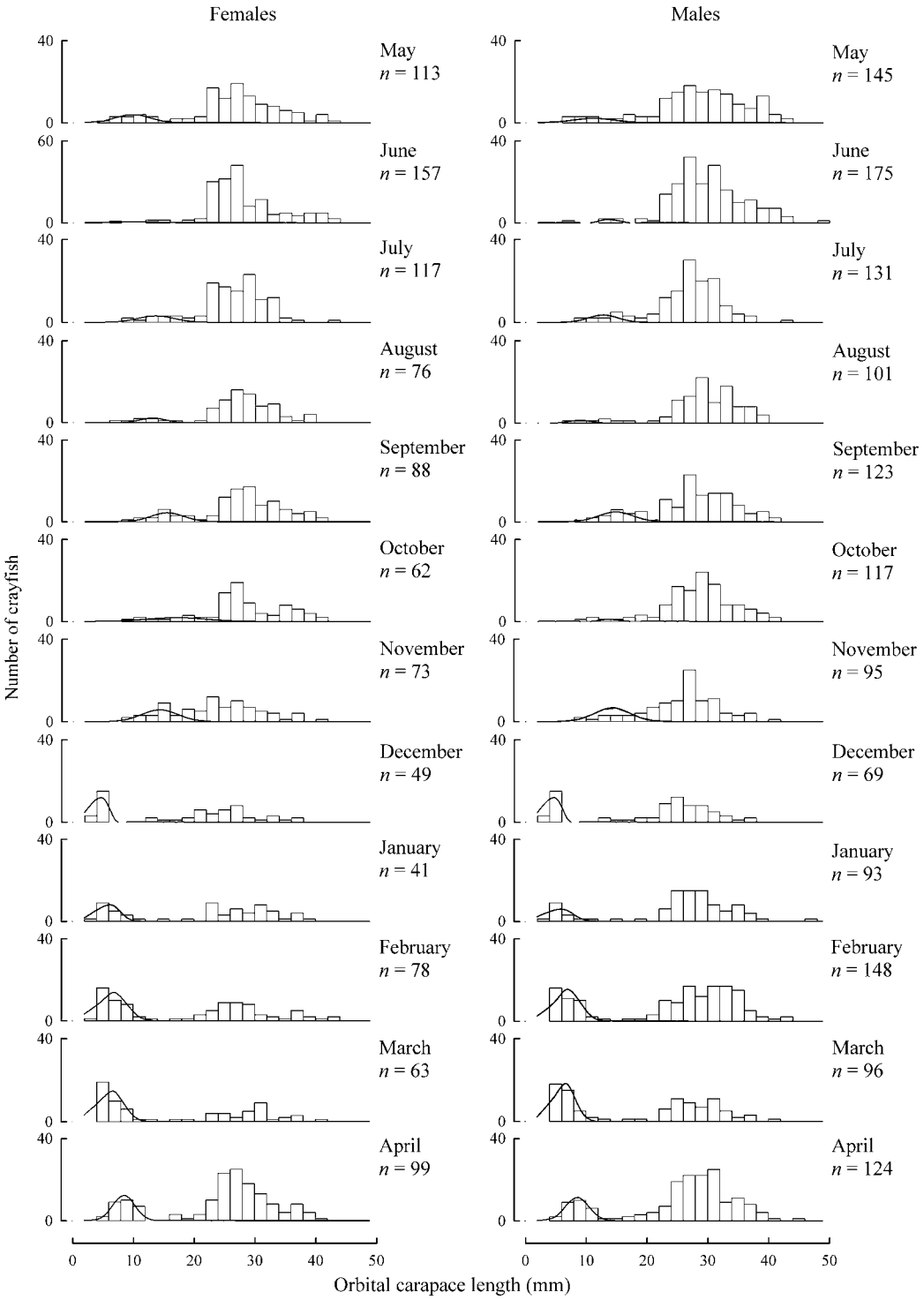

Fig. 9. Orbital carapace length-frequency histograms in each month for female and male *Cherax quinquecarinatus* in Bull Creek. Normal distributions have been fitted to the one or two size cohorts present in each month. N.B. n = sample size.

associated with freshwater crayfish species in cooler, more energetically demanding climates (Noblitt and Payne, 1995; Eversole *et al*., 2002), whereas summer brooders generally produce many small-sized eggs relative to their body size (Honan and Mitchell, 1995a). The freshwater ecosystems of southwestern Australia generally have low productivities compared to those in eastern Australia systems (Bunn and Davies, 1990). The low productivity of aquatic systems of the region may have resulted in the relatively low fecundity and moderate size of the eggs of *C. quinquecarinatus*, paralleling the situation in oligotrophic systems in Tasmania (Hamr and Richardson, 1994).

The strong positive correlation between size and fecundity for *C. quinquecarinatus* is consistent with other

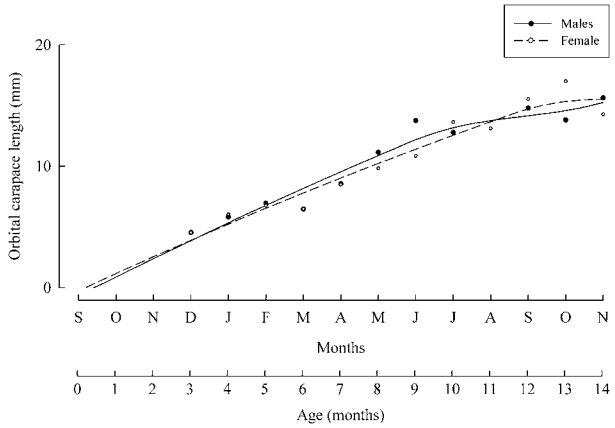

Fig. 10. Modified seasonal von Bertalanffy growth curves of *Cherax quinquecarinatus* in Bull Creek. Curves are fitted to the monthly length-frequency data for female and male *C. quinquecarinatus* in Bull Creek.

freshwater crayfish species and has been attributed to pleopodal attachment space and egg size (e.g., Austin, 1998; Taugbol *et al*., 1988; Gutiérrez-Yurrita and Montes, 1999; Eversole *et al*., 2002; Muck *et al*., 2002; Beatty *et al*., 2003). The minimum size of ovigerous female freshwater crayfish is close to the minimum estimated size at first maturity (Reynolds, 2002). During the current study, the smallest ovigerous *C. quinquecarinatus* captured was 23 mm OCL (29 mm CL), higher than the estimated L_{50} (18.8 mm OCL, 24.1 mm CL) and more closely approximating the L_{95} (24.9 mm OCL, 31.4 mm CL). However, relatively few ovigerous females were captured in the current study, which also presumably contributed to the skewed sex-ratio of 1 female : 1.43 males. The sex ratios of freshwater crayfish are generally 1:1 (Reynolds, 2002), a reflection of a simple sex determination mode based on sex chromosomes (Austin and Meewan, 1999). Reduced locomotor activity of ovigerous females, associated with lowered metabolism, may account for reduced catchability relative to nonincubating individuals that exhibit higher metabolic rates and greater foraging activity (see also Huner, 1988; Gutiérrez-Yurrita and Montes, 1999). It is also likely that the large numbers of burrows observed in Bull Creek were being utilised by relatively inactive ovigerous females, thereby reducing their chance of capture. Thus, the use of temporal patterns in the frequencies of female gonadal development stages, and not frequency of ovigerous females *per se*, is probably more appropriate in accurately describing the spawning frequency and timing, particularly for burrowing species.

Temporal Pattern in Hepatopancreatic Indices

The relative size and moisture content of the hepatopancreas have previously been used as condition indices to reflect the nutritional status of individuals and populations and aid in determining life-history strategies (e.g., Fotedar *et al*., 1999; Lindqvist *et al*., 1999). Species occupying temporary habitats (typically summer brooders) generally have a greater reliance on these energy reserves because of prolonged periods in burrows (Lindqvist *et al*., 1999). There was an obvious temporal trend in the dry hepatopancreas index of *C. quinquecarinatus* in Bull Creek. This results from the transfer of organic reserves from the hepatopancreas to the ovaries for the energetically costly process of secondary vitellogenesis, such as occurred in female *C. quinquecarinatus* during the peak spawning period in Bull Creek (see also Lindqvist *et al*., 1999). Given the intraspecific morphological and genetic variation and the wide range of habitats occupied by it, *C. quinquecarinatus* occupying temporary systems (Lindqvist *et al*., 1999) should exhibit even greater temporal variation in indices than those recorded in Bull Creek.

Table 2. Parameters for the seasonal von Bertalanffy growth curves and mortality of female and male of *Cherax quinquecarinatus* in Bull Creek, where OCL_∞ is the asymptotic orbital carapace length, K is the curvature parameter, t_0 is the theoretical age at which the estimated orbital carapace length is zero, C determines the relative amplitude of the seasonal oscillation (where $0 \leq C \leq 1$), t_s determines the phase of seasonal oscillation relative to t_0, r^2 is the coefficient of determination, Z is the instantaneous total mortality rate (1/year), M is the instantaneous natural mortality rate (1/year), F is the instantaneous rate of fishing mortality (1/year), and E is the exploitation rate.

Growth parameter	Female	Male
OCL_∞ (mm)	59.6 (71.2 mm CL)	73.8 (87.0 mm CL)
K	0.29	0.25
t_0 (month)	0.18	0.44
C	1	0.71
t_s	8.64	5.83
r^2	0.99	0.99
Z (1/yr)	2.34	1.95
M (1/yr)	0.55	0.48
F (1/yr)	1.78	1.47
E	0.76	0.75

Growth and Mortality

Growth.—The growth rates of female and male *C. quinquecarinatus* in Bull Creek were relatively low (more typical of a K-strategist and winter-brooding freshwater crayfish) with K for females and males being 0.29 and 0.25, respectively (cf Gutiérrez-Yurrita and Latournerie-Cervera, 1999; Gutiérrez-Yurrita and Montes, 1999). However, the OCL_∞ and the maximum size recorded were moderate (i.e., between the sizes typical of *r*- and K-strategists and summer and winter brooding species).

Faster growth by male relative to female freshwater crayfish has previously been attributed to higher energetic cost of female ovarian development and the lack of moulting of berried females (Sokal, 1988). The similar values of K for female and male *C. quinquecarinatus* in Bull Creek may be explained by the limited size-range/age to which the growth curves could be fitted, i.e., up to 14 months, at a time when maturity had not been attained. Consistent with the present study, female freshwater crayfish usually have a smaller maximum size due to the lack of moulting (and reduced feeding activity) when ovigerous (Reynolds, 2002) and a smaller moult increment due to greater energy required for ovarian development (e.g., Pursiainen *et al*., 1988).

Mortality.—Although the von Bertalanffy growth curve provided a good description of modal progression as indicated by a high coefficient of determination ($r^2 = 0.99$), it was only fitted to the modes of size-frequency cohorts of the first 14 months of life. Thus, some bias in the growth parameters, subsequently used in the length-converted catch curve to determine the relative ages of larger individuals, may exist.

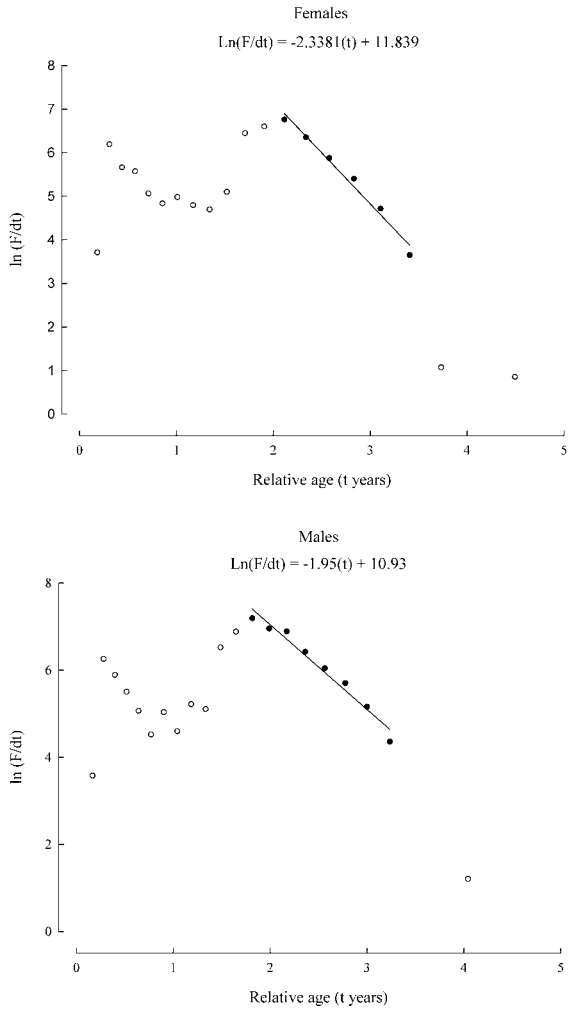

Fig. 11. Length-converted catch curve of female and male *Cherax quinquecarinatus* in Bull Creek. N.B. Slope of the regression line represents instantaneous mortality rate (*Z*) and data points with open circles were excluded as they represent mean ages that were not fully recruited (ascending data points) or those with small sample sizes (fewer than 10 individuals).

However, the data suggested that total mortality was relatively high in this population (females 2.34/year and males 1.95/year) (Table 2). As no teleost predators of *C. quinquecarinatus* were present in Bull Creek (Beatty, unpublished data) much of the mortality was presumably due to density-dependant intraspecific interactions such as competition and cannibalism or through fishing.

The capture of *C. quinquecarinatus* is not specifically governed by fisheries regulations. However, the level of recreational fishing activity observed during the study period results in the high exploitation rate (0.76 and 0.75 for females and males, respectively). Obviously, this species is heavily fished in the relatively small and easily accessible Bull Creek. Possibly, a proportion of the instantaneous fishing mortality was attributable to the removal of specimens during the current study. Despite the apparent heavy fishing pressure, the species was very abundant in Bulls Creek suggesting resilience to fishing.

Due to their life-history strategies, many winter-brooding freshwater crayfish species are not resilient to even low levels of fishing mortality (Honan and Mitchell, 1995a, b). Conversely, the replacement of natural mortality by fishing mortality in *Orconectes virilis*, a member of the summer-brooding group displaying many *r*-strategist traits, increased yields by reducing the density-dependant restriction by larger individuals on juvenile production (Morgan and Momot, 1988). The life-history parameters of *C. quinquecarinatus* allow it to inhabit a wide variety of habitats. Such parameters also provide its resilience to the considerable fishing exploitation in Bull Creek, and fishery regulations are not required in such permanent systems. However, further assessment of the life-history strategy of *C. quinquecarinatus* in temporary systems is required to determine its resilience throughout its wide habitat range, particularly so in light of the low fecundity and slow growth rate typical of a winter-brooding species, making it more vulnerable to exploitation in variable systems.

Conclusion

This study represents the first research on the population biology of *C. quinquecarinatus*. Traits that were described for *C. quinquecarinatus* in Bull Creek that are typically associated with summer brooders (and often *r*-strategists) included early maturation, an extended late winter-summer spawning period (with the likelihood of multiple annual spawning events), and high mortality rates. In contrast, the relatively slow growth rate, low fecundity, and moderately sized eggs are traits generally associated with winter-brooding species (often displaying K-selected life histories). The life-history strategy of *C. quinquecarinatus* described here would enable rapid population recovery in the event of a sudden decline. Although this species underwent considerable fishing exploitation in Bull Creek, its life-history parameters would enable this species to be resilient to that exploitation, at least in permanent aquatic systems.

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